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The shape of success in a turbulent world: wave exposure filtering of coral reef herbivory

Sonia Bejarano*,[1], Jean-Baptiste Jouffray[2,3], Iliana Chollett[4], Robert Allen[5], George Roff[6], Alyssa Marshell[6,7], Robert Steneck[8], Sebastian C. A. Ferse†,[1,9] and Peter J. Mumby†,[6]

[1]*Department of Ecology, Leibniz Centre for Tropical Marine Research (ZMT), Fahrenheitstraße 6, 28359 Bremen, Germany;* [2]*Global Economic Dynamics and the Biosphere Academy Programme, Royal Swedish Academy of Sciences, PO Box 50005, Stockholm 104 05, Sweden;* [3]*Stockholm Resilience Centre, Stockholm University, Stockholm 106 91, Sweden;* [4]*Smithsonian Marine Station, Smithsonian Institution, Fort Pierce, FL 34949, USA;* [5]*Department of Life Sciences Silwood Park, Imperial College London, Ascot, UK;* [6]*Marine Spatial Ecology Lab, School of Biological Sciences & ARC Centre of Excellence for Coral Reef Studies, The University of Queensland, St. Lucia, Qld 4072, Australia;* [7]*Department of Marine Science and Fisheries, College of Agricultural and Marine Sciences, Sultan Qaboos University, PO Box 34, Al Khoud 123, Muscat, Oman;* [8]*School of Marine Sciences, University of Maine, Darling Marine Center, Walpole, ME 04573, USA; and* [9]*Department of Geography, University of Hawaii Mānoa, 2424 Maile Way, Honolulu, HI 96822, USA*

Summary

1. While environmental filters are well-known factors influencing community assembly, the extent to which these modify species functions, and entire ecosystem processes, is poorly understood.

2. Focusing on a high-diversity system, we ask whether environmental filtering has ecosystem-wide effects beyond community assembly. We characterise a coral reef herbivorous fish community for swimming performance based on ten functional traits derived from fish morphology. We then investigate whether wave exposure modifies the functional make-up of herbivory, and the absolute and relative feeding frequency of distinct feeding functional groups.

3. Herbivorous fish species conformed to either *laterally compressed* or *fusiform* body plans, which differ in their morphological design to minimise drag. High wave exposure selectively limited the feeding function of the deepest body shapes with highest caudal thrust efficiency, and favoured fusiform bodies irrespective of pectoral fin shape.

4. Traditionally recognised herbivore feeding functional groups (i.e. grazers–detritivores and scrapers–small excavators) differed in swimming performance, and in their capacity to feed consistently across levels of wave exposure. We therefore emphasise the distinctness of their ecological niche and functional complementarity.

5. Species within the same feeding functional group also had contrasting responses to wave exposure. We thereby reveal a further ecological dimension of niche partitioning, and reiterate the risk of assuming functional redundancy among species with a common feeding mode.

6. Contrasting responses of species within feeding functional roles (i.e. response diversity) allowed the preservation of critical trophic functions throughout the gradient (e.g. macroalgal browsing), and likely explained why overall levels of herbivory were robust to filtering. Whether ecosystem functioning will remain robust under the additive effects of environmental stress and human-induced disturbances remains to be tested.

Key-words: environmental filtering, feeding frequency, functional traits, herbivorous fish species niches, swimming performance

Introduction

Herbivory is a fundamental regulatory process in most ecosystems on Earth. Not only is it implicated in the structuring of ecosystems (Olff & Ritchie 1998; Grimme 2002), but it can also play a crucial role in their stability, and resilience to disturbances (Van Langevelde *et al.* 2003; Ledlie *et al.* 2007; Huntley 2009). Quantifying the spatial heterogeneity of herbivory is therefore an urgent step towards predicting whether ecosystem integrity and services can be maintained in case of environmental change. In this context, the relationship between herbivore diversity and function in response to physical gradients has been the focus of extensive interest (McNaughton 1994; Steneck & Dethier 1994; Hooper & Vitousek 1997; Duffy 2002; Burkepile & Hay 2008; Halpern & Floeter 2008; Poore *et al.* 2012). In particular, quantifying the extent to which herbivore diversity and functional redundancy (i.e. the capacity of certain species to functionally compensate for the loss of others) vary spatially is an important concern in community ecology and conservation (Sadovy 2005; Nyström 2006; Sasaki *et al.* 2009; Cadotte, Carscadden & Mirotchnick 2011).

High herbivore diversity may not necessarily herald high functional redundancy (Bellwood, Hoey & Howard Choat 2003; Micheli & Halpern 2005), especially when the latter is interpreted in light of the inherent multidimensionality of species' trophic niches (Rosenfeld 2002). To facilitate the mechanistic understanding of their function, herbivores are usually compartmentalised in functional groups with fundamental differences in their feeding modes (Steneck & Watling 1982; Green & Bellwood 2009; Davidson *et al.* 2010). Taxonomically distinct species within these coarse groups are often considered ecologically redundant (Micheli & Halpern 2005). However, substantial empirical evidence demonstrates subtle, yet important interspecific differences in resource use within these functional groups (Hoey & Bellwood 2009; Johansson *et al.* 2013; Brandl & Bellwood 2014; Brandl *et al.* 2015; Kartzinel *et al.* 2015). Further, coexisting theory predicts that species occupying similar dietary niches, will differ in niche occupation along environmental axes (MacArthur & Levins 1967). The prevalent assumption that consumers performing similar ecological functions will buffer the loss of others within coarse functional groups is therefore risky, as it is to assume that such interchangeability will prevail throughout environmental gradients.

Environmental factors determine spatial patterns of species occurrence based on species traits, through a community assembly process known as filtering (Keddy 1992; Mason *et al.* 2007; Lebrija-Trejos *et al.* 2010). The extent to which extreme conditions modify the behaviour of unfiltered species, thus altering their functional role, is known only for a limited number of species (Stoll, Hofmann & Fischer 2010; Noble *et al.* 2014). While trophic functional traits are important determinants of species ecosystem roles, morphological traits related to species performance can strongly influence the breadth of niches they can

exploit (Mason *et al.* 2007; Villéger, Novack-Gottshall & Mouillot 2011), and are likely to also play an important role in determining ecosystem functioning. If species lack the performance traits required to maintain their usual behaviours under challenging conditions, their particular functional role could be suppressed. In the case of herbivores, harsh physical conditions found at the extremes of strong gradients may alter feeding consistency. Feeding functional groups could be affected differently, thus leading to shifts in relative and absolute levels of herbivory. If several species within a feeding functional group are suppressed, functional redundancy will be disproportionally lower than generally assumed based on trophic similarity.

Coral reefs are model ecosystems to investigate the connections between biodiversity and function because of their high species diversity (Connolly *et al.* 2005; Mora *et al.* 2011). Herbivory is sustained by a multifaceted array of species responsible for grazing algal turfs (Marshell & Mumby 2012), scraping and excavating the reef substratum (Hoey & Bellwood 2009), removing macroalgae (Bellwood, Hughes & Hoey 2006; Mantyka & Bellwood 2007) and consuming detritus (Goatley & Bellwood 2010; Marshell & Mumby 2012). Reflecting these different functional roles, four feeding functional groups of herbivorous fish are widely recognised (i.e. grazers–detritivores, scrapers–small excavators, macroalgal browsers and bioeroders *sensu* Green & Bellwood 2009). Coral reefs also offer a wealth of physical gradients ideal to explore the effects of environmental filtering (Fabricius 2005; Golbuu *et al.* 2011; Goatley & Bellwood 2012; Madin, Hoogenboom & Connolly 2012). Wave exposure, for instance, has profound implications for herbivorous fish diversity because it tends to exclude slow-swimming species from turbulent habitats (Fulton, Bellwood & Wainwright 2005). However, the extent to which wave exposure structures herbivory by selectively limiting the capacity of certain species to feed remains largely unexplored. While wave exposure enhances primary productivity (Leigh *et al.* 1987; Renken *et al.* 2010; Williams *et al.* 2013; Roff *et al.* 2015a) and could lead to increased levels of herbivory, feeding effectively under turbulent conditions may prove costly for species that are poorly equipped to cope with swell (Bellwood & Wainwright 2001). Herbivorous fish rely largely on their pectoral fins for propulsion (Fulton 2007), and are therefore regarded as optimally suited to exploit benthic resources and manoeuvre closely around complex reef structures (Blake 2004). Swimming performance is however more comprehensively described by multiple morphological traits (Villéger *et al.* 2010), which could reveal interspecific differences in niche breadth and herbivory. If wave exposure filtering constrains the realised trophic niches of certain species, and filtering is strong enough to narrow the portfolio of species within different feeding functional groups, important limits to overall herbivory may be revealed. In turn, insufficient levels of herbivory could affect the capacity of reefs to recover following disturbance (Nyström *et al.* 2012; Cheal *et al.* 2013), and

functional redundancy within broad feeding functional groups would be lower, and less spatially homogeneous than generally assumed.

In this study, we investigate whether a wave exposure gradient in the Palau archipelago modifies the herbivory function, thus having ecosystem-wide effects beyond community assembly. First, we characterise a speciose herbivorous fish community ($n = 37$ species) for swimming performance based on ten functional traits derived from 14 morphometric parameters. We then use a trait-based multidimensional functional space approach (Violle *et al.* 2007; Laliberté & Legendre 2010; Maire *et al.* 2015) to test how differences in wave exposure affect the functional make-up of herbivory, based on the species' swimming performance. Lastly, we examine the implications of filtering for the absolute and relative feeding frequencies of different feeding functional groups. In addressing these questions, we provide new insights into the interaction between environmental filtering and the multidimensionality of species niche, and challenge the notion of functional redundancy within broad herbivore feeding functional groups.

Materials and methods

THE WAVE EXPOSURE GRADIENT

This study was conducted on the eastern barrier reef of the Palau Archipelago because prevailing wind direction in the region causes it to be exposed to relatively high levels of wave exposure for most of the year (November–June). All field surveys were conducted during February and March 2012 and focused on shallow forereefs (6.8 ± 0.3 m) over a 20-km section of the barrier situated c. 10 km off the most populated island of Koror. Wave exposure was quantified using a wave-theory GIS approach (Chollett & Mumby 2012) that integrates information on the configuration of the coastline and reef crests (Battista, Costa & Anderson 2007), and the wind patterns of the area during the study period. Twelve survey sites, separated by at least 2 km from each other, were stratified across three levels of wave exposure: *low* ranging from 0.9–23.6 J m^{-3} ($n = 4$), *moderate* varying from 46.7–72 J m^{-3} ($n = 5$), and *high* at $\sim$220 J m^{-3} ($n = 3$) (Fig. 1). Primary productivity, determined as the rate of linear growth of algal turfs in the absence of herbivory, was significantly higher on highly and moderately exposed reefs compared to low exposure reefs ($P = 0.01$, Fig. S1a in Supporting Information). Percent cover of substrata available for feeding (i.e. algal turfs, macroalgae, crustose, non-crustose and articulated coralline algae) was marginally higher on exposed reefs compared to low and moderately exposed reefs ($P = 0.06$, Fig. S1b).

QUANTIFYING FEEDING FREQUENCY AS A PROXY FOR HERBIVORY

Herbivory is a function of the abundance and feeding behaviour of herbivorous species. However, as the abundance of herbivorous fishes does not necessarily equate to their function (Fox & Bellwood 2008), herbivory is most effectively quantified through direct observations of their feeding frequency (Bellwood, Hughes & Hoey 2006; Fox & Bellwood 2007, 2008). Therefore, although the entire herbivorous fish community ($n = 37$ species) was surveyed using both fish censuses along 30 × 4 m transects (Mumby
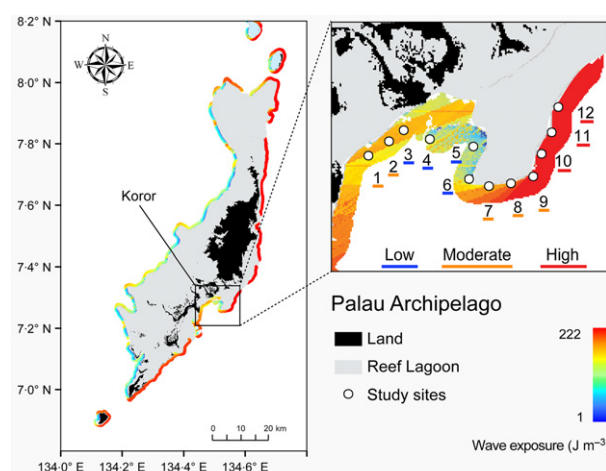

Fig. 1. Map of the Palau Archipelago indicating the location of 12 study sites distributed across eastern forereefs. A wave-theory GIS approach was used to quantify wave exposure over the study period. Sites were separated into low (0.9–23.6 J m^{-3}, sites 3–6), moderate (46.7–72 J m^{-3}, sites 1–2, 7–9) and high (c. 220 J m^{-3}, sites 10–12) wave exposure.

unpubl. data) and video cameras, we focused only on the assemblages video-recorded feeding ($n = 26$ species), in order to quantify feeding frequency as a proxy for herbivory.

Feeding frequency surveys were conducted using five unmanned stationary high-definition video cameras per site. Video surveys were performed in the afternoons at all sites to avoid bias due to diel variability in fish bite rates (Zemke-White, Choat & Clements 2002), and continuous recordings were obtained for one hour in the absence of divers to avoid interference with normal fish behaviour. Each camera filmed one replicate benthic patch of 1 m^2, which was also photographed from above in order to quantify the area available for herbivory (i.e. percent cover of algal turfs, macroalgae, crustose, non-crustose, and articulated coralline algae).

Feeding frequency, defined here as the total number of bites per hour and square metre of substratum available for herbivory (bites h^{-1} m^{-2}), was quantified for all parrotfishes (Labridae of the subfamily Scarinae), surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae) >5 cm in total length. We concentrated on these families because they are consistently abundant on Micronesian reefs (Mumby *et al.* 2013), and primarily responsible for herbivory on Pacific coral reefs (Green & Bellwood 2009). Less common macroalgal consumers such as chubs (Kyphosidae) and batfishes (Ephippidae) were not included in our surveys. Mean feeding frequency per species per site was computed by averaging the totals of the corresponding benthic patches ($n = 5$), and site means were averaged to obtain wave exposure level means ($n_{low} = 4$, $n_{moderate} = 5$, $n_{high} = 3$).

CHARACTERISING THE HERBIVOROUS FISH COMMUNITY FOR SWIMMING PERFORMANCE

The entire herbivore community (i.e. species captured by either visual censuses or video cameras, $n = 37$) was characterised in terms of its swimming performance using ten functional traits known to be strongly related to swimming mode, speed and manoeuvrability (Table S1). All ten functional traits were continuous and were computed from 14 morphometric parameters measured on three photographs per species of pinned specimens of known size (Fig. S2). To account for allometry, functional trait values were regressed

against individual standard length (SL), and replaced by residuals if the relationship was significant (Bellwood *et al.* 2014). Mean values of all functional traits were then calculated per species, standardised (mean = 0 and standard deviation = 1), and used to compute a Principal Coordinate Analysis (PCoA) based on the matrix of Euclidean distance between all pairs of species (i.e. swimming performance morphospace). In addition, Ward's hierarchical clustering with squared Euclidean distances (Murtagh & Legendre 2012) was performed to identify species groups, whose distribution within the morphospace was considered informative of their swimming performance (Villéger *et al.* 2010; Bellwood *et al.* 2014). The appropriate number of clusters was determined by assessing 30 statistical indices using the *NbClust* package to select the best clustering scheme (Charrad *et al.* 2014). Lastly, to compare the distribution of feeding functional groups (i.e. bioeroders, scrapers–small excavators, grazers–detritivores and macroalgal browsers) over the swimming performance morphospace, we computed the volume inside the different convex hulls enclosing the corresponding species. Volumes, as well as percentages of overlap among feeding functional groups, were calculated in a four-dimensional space (capturing 85% of the variance).

EFFECTS OF WAVE EXPOSURE ON HERBIVORY

To investigate potential impacts of wave exposure on herbivory, we focused on the species recorded feeding ($n = 26$) and took two steps. First, we used the multidimensional functional space constructed above to investigate whether wave exposure acts as an environmental filter of herbivory based on the species' swimming performance. Second, we quantified the differences in overall herbivory, as well as in the relative levels exerted by distinct feeding functional groups under different wave exposures (Fig. 2).

Testing for environmental filtering of herbivory using a swimming performance morphospace

Two complementary functional diversity indices were calculated per wave exposure level to describe the amount of morphospace filled by the assemblages recorded feeding, and the distribution of the feeding frequency within this functional space (Villéger, Mason & Mouillot 2008). Functional richness (in terms of swimming performance) (FRic) of a given assemblage was measured as

Fig. 2. Diagram explaining the analytical approach used to assess herbivore swimming performance from a set of relevant functional traits and determine the effects of wave exposure on coral reef fish-based herbivory.

the volume inside the convex hull enclosing all its species (Villéger *et al.* 2008), and expressed as the percentage of the volume of the global convex hull enclosing all species observed in the study (n = 37). A contraction of the convex hull with increasing wave exposure would therefore indicate that herbivory on exposed reefs is sustained by assemblages that occupy a narrower swimming performance niche space compared to those feeding on sheltered forereefs (Villéger, Mason & Mouillot 2008), and that high wave exposure suppresses the functional contribution of certain species to herbivory due to their swimming performance traits. Although FRic is useful for reflecting the range of traits within an assemblage, it does not account for the species dispersion across this range, nor their feeding frequencies (Laliberté & Legendre 2010). Functional dispersion (FDis) was therefore computed using a matrix of mean feeding frequency (bites h^{-1} m^{-2}) per species and exposure level, to reflect the weighted average distance of individual species to the weighted centroid of the assemblage (Laliberté & Legendre 2010). Values of FDis that are significantly lower than those expected at random imply that environmental filtering plays a strong role in distributing overall feeding frequency among species that are highly similar in manoeuvrability (Ricotta & Moretti 2011). A significant decrease in FDis with increasing wave exposure will therefore reflect that herbivory is disproportionally sustained by species that are more similar to each other in terms of swimming performance (Gerisch *et al.* 2012).

FRic and FDis were also calculated for scrapers and grazers–detritivores across levels of wave exposure, with FRic consistently expressed as a percentage relative to the volume of the global convex hull enclosing the entire community. Large excavating-bioeroding herbivores were only recorded feeding in one site, and rarely were more than two browsing species recorded feeding at the same site or exposure level. Therefore, the indices for those feeding functional groups could not be computed.

A null model approach (see Appendix S1) was designed to account for the uneven replication within levels of wave exposure, and to assess whether FRic and FDis at different levels of wave exposure were (i) significantly different from those expected due to random processes, or to differences in the number of species and bites per exposure level, and (ii) significantly different from each other. This null model randomly sampled bites from the total observed across all camera recordings and distributed them across wave exposure levels while preserving the respective species identity, the number of bites per species and exposure level, and the total number of species feeding in the study area and per exposure level (Appendix S1).

In order to assess how representative of the entire community were the assemblages recorded feeding, the percent of functional space filled by the assemblages recorded by video cameras at each wave exposure level, relative to that occupied by the entire herbivore community was also computed.

Effect of wave exposure on the herbivory exerted on the substratum

Although wave exposure may selectively affect the capacity of certain species to feed, overall herbivore feeding frequency is likely to increase with wave exposure as a result of increased primary productivity (Russ 2003). Importantly, if species within certain feeding functional groups are more strongly affected by wave exposure compared to others, the relative feeding frequency of these groups may also change with wave exposure. In order to test these hypotheses, we compared mean herbivore feeding frequency (overall and per feeding group) across wave exposure levels. Comparisons were conducted using one-way ANOVAs with a variance structure of *VarIdent* class allowing for a different spread of overall feeding frequency per exposure level, which produces no heteroscedastic pattern in the normalised residuals (Fig. S3) (Zuur,

Ieno & Elphick 2010). No variance structure was required when comparing feeding frequencies of the different feeding functional groups among wave exposure levels. ANOVAs were followed by pairwise comparisons using closed Tukey tests, and Westfall *P*-value adjustment procedures (Bretz, Hothorn & Westfall 2011).

All statistical analyses were implemented in the software R v. 3.2.3 (R Development Core Team 2016). Functional indices were computed using the *MultidimFD* function (Villéger, Mason & Mouillot 2008; Mouillot *et al.* 2013; Maire *et al.* 2015).

Results

HERBIVORE SWIMMING PERFORMANCE

Based on the functional traits, we classify coral reef herbivores in the *laterally compressed* (LCBP) and *fusiform* (FBP) body plans, which likely differ in their morphological design to minimise drag (Figs 3 and S4). LCBP encompassed 17 species including surgeonfishes (Acanthuridae) and rabbitfishes (Siganidae), and was primarily defined along PC1 (47·8% explained variance) by the highest values of (i) body aspect ratio, (ii) caudal peduncle throttling and (iii) caudal fin aspect ratio (Fig. 3a,b). Based on these traits, surgeonfishes and rabbitfishes have relatively deep and highly manoeuvrable bodies that may derive relatively higher thrust efficiency from their caudal fin compared to parrotfishes (Fig. 3a,b; Table S1). LCBP were widely spread along PC2, which explained a modest 15% of the variance while marking a continuum between low and high pectoral fin aspect ratio. Collectively, surgeonfishes and rabbitfishes were therefore heterogeneous in their swimming mode, with certain species displaying elongated fins for fast flapping or lift-based swimming and others having rounded rowing fins for enhanced manoeuvrability at slower speeds (Fig. 3a,b; Table S1). The FBP comprised a more compact cluster of 19 parrotfishes (Labridae of the subfamily Scarinae) characterised by the maximum values of (i) pectoral fin position, (ii) head depth, (iii) narrowest point of the caudal peduncle, (iv) length of the medial caudal fin ray and (v) head length. These characteristics suggest that parrotfishes may obtain relatively less thrust from their caudal fin compared to surgeonfishes and rabbitfishes, but may instead minimise drag via their fusiform morphology, while relying heavily on their pectoral fins for propulsion. Based on their deep heads, parrotfishes may have relatively superior manoeuvrability in highly complex habitats (Fig. 3a,b; Table S1).

Two feeding functional groups (i.e. grazers–detritivores and scrapers–small excavators) also differed in the swimming performance predicted by their functional traits (Fig. 3c). Grazers–detritivores were associated with LCBP, whereas scrapers–small excavators occupied the full extent of FBP, with no overlap in the morphospace. On the other hand, while the two large excavating species were concentrated within FBP, the swimming performance space of macroalgal browsers overlapped with both LCBP and FBP and seemed dictated by the morphology of the corresponding family.
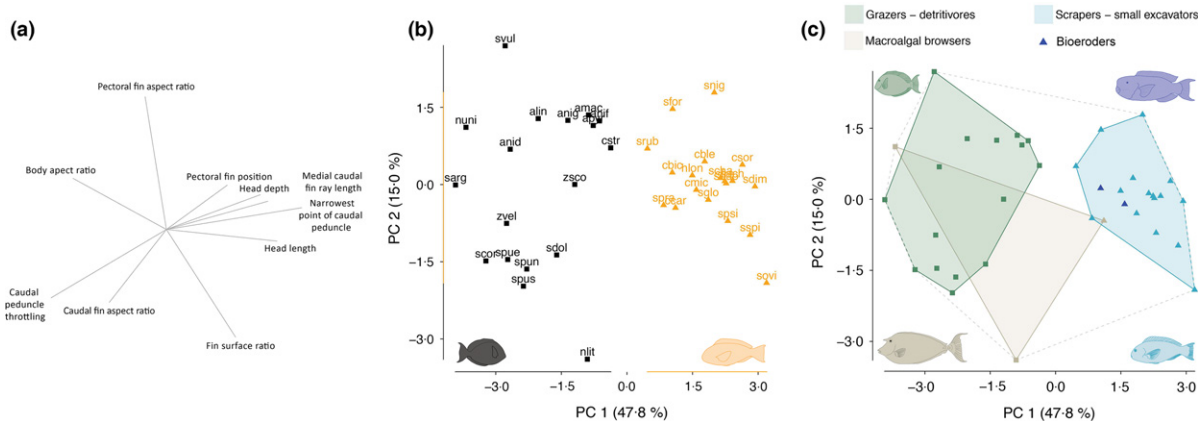
Fig. 3. (a) Functional traits as vectors associated to the principal coordinate analysis (PCoA), (b) PCoA displaying the distribution of species and two distinct body plans obtained through Ward's hierarchical clustering: *Laterally compressed* as black squares, and *fusiform* as yellow triangles. Ranges of the clusters are reported on the axes (c) amount of swimming performance morphospace occupied by different feeding functional groups. For visual convenience, only the two first principal components are displayed (62·8% explained variance). Species names are abbreviated as follows: alin: *Acanthurus lineatus*, amac: *A. maculiceps*, anig: *A. nigricans*, anid: *A. nigricauda*, anif: *A. nigrofuscus*, apyr: *A. pyroferus*, ccar: *Calotomus carolinus*, cbic: *Cetoscarus bicolor*, cble: *Chlorurus bleekeri*, csor: *C. sordidus*, cstr: *Ctenochaetus striatus*, hlon: *Hipposcarus longiceps*, nlit: *Naso lituratus*, nuni: *N. unicornis*, scha: *Scarus chameleon*, sdim: *S. dimidiatus*, sfor: *S. forsteni*, sglo: *S. globiceps*, snig: *S. niger*, sovi: *S. oviceps*, spra: *S. prasiognathos*, spsi: *S. psittacus*, squo: *S. quoyi*, srub: *S. rubroviolaceus*, ssch: *S. schlegeli*, sspi: *S. spinus*, sarg: *S. argenteus*, scor: *S. corallinus*, sdol: *S. doliatus*, spue: *S. puellus*, spus: *S. punctatisimus*, spun: *S. punctatus*, svul: *S. vulpinus*.

EFFECTS OF WAVE EXPOSURE ON HERBIVORY

Wave exposure and swimming performance of herbivore assemblages

From a swimming performance perspective, overall herbivore functional richness decreased with increasing wave exposure. In other words, assemblages recorded feeding at high and moderate wave exposures filled smaller portions of the swimming performance morphospace (FRic = 13·1 and 26·0%, respectively) compared to those feeding at low exposures (FRic = 64·7%). Overall functional dispersion was also significantly reduced by wave exposure with differences among all exposure levels being significant (Figs 4 and S5g,h).

Wave exposure acted as a strong environmental filter for grazers–detritivores but not for scrapers–small excavators. At high wave exposure, herbivory of grazer–detritivores was sustained by a significantly more similar group of species than expected at random, and compared to low and moderate wave exposures (Figs 4 and S5d,j). Grazers–detritivores recorded feeding at low and moderate wave exposures were in turn significantly more dissimilar than expected by chance (Figs 4 and S5d). In contrast, functional dispersion of scrapers–small excavators under moderate and high wave exposures was no different from those expected by chance, but significantly higher than values observed at low wave exposure. Herbivory of scrapers–small excavators at moderate and high wave exposures was therefore disproportionally sustained by species that were more similar in terms of swimming performance, compared to low wave exposure (Figs 4 and S5f,i).

Effect of wave exposure on the herbivory exerted on the substratum

Herbivory was significantly influenced by wave exposure. Assemblages recorded feeding occupied 71, 67 and 33% of the morphospace volume filled by the communities occurring at low, moderate and high levels of wave exposure, respectively (Fig. S6). High and moderate levels of wave exposure filtered the feeding function (i.e. precluded the fish from feeding) of 22% of species recorded feeding under calmer conditions (Fig. 5b). Feeding functional groups, and species within them differed in their capacity to feed consistently across levels of wave exposure (Figs 5 and S7). Representatives of grazer–detritivores, scrapers–small excavators and macroalgal browsers were recorded feeding across all levels of wave exposure, whereas the single bioeroding species encountered in the study area fed only at low wave exposure. Respectively, 78, 43 and 50% of the scrapers–small excavators, grazers–detritivores and macroalgal browsers recorded feeding at low wave exposure fed also in more exposed conditions (Fig. 5c). Only in the former two feeding functional groups, species that were precluded from feeding at moderate and high wave exposures, were compensated by counterparts of the same feeding functional group (Fig. 5d).

Among the species consistently recorded feeding at all levels of wave exposure (Fig. 5c), a macroalgal browser (*Naso lituratus*) and a grazer–detritivore (*Zebrasoma scopas*) fed less frequently at high wave exposure (Fig. S7a,c), whereas a scraper (*Chlorurus sordidus*) and a grazer (*Ctenochaetus striatus*) attained maximum feeding frequencies under high wave exposure (Fig. S7a,b).
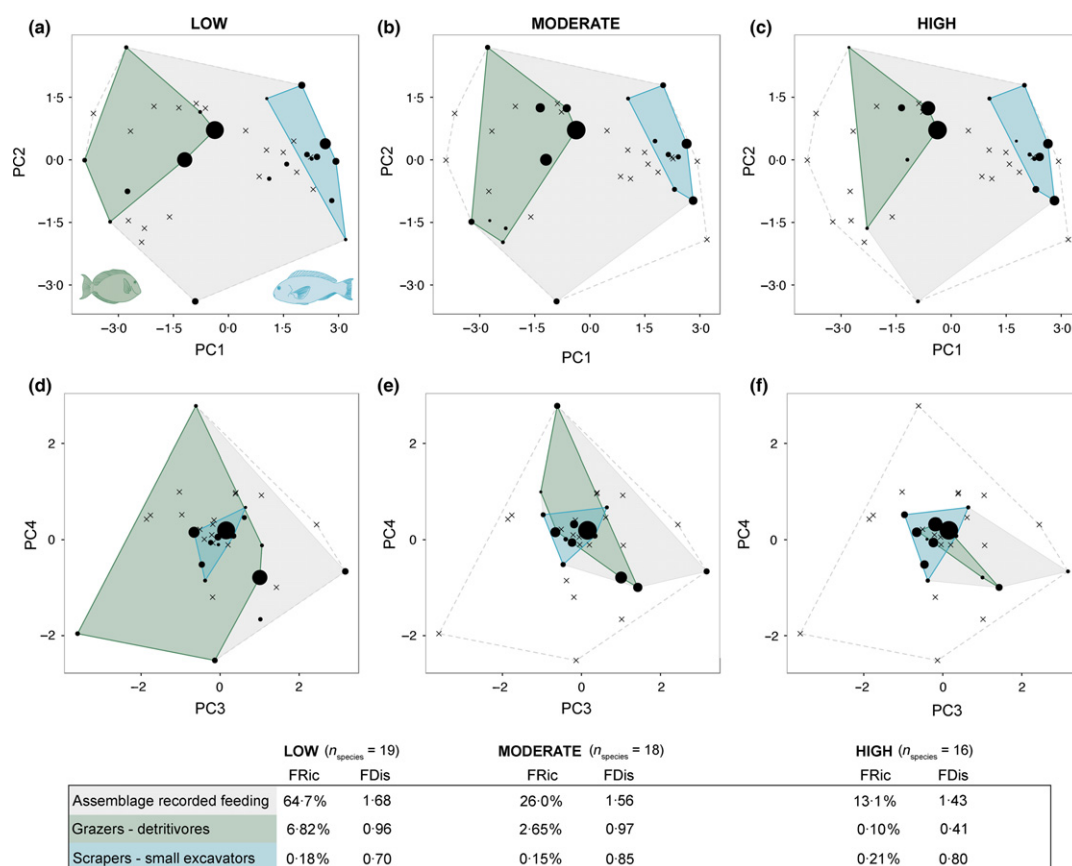
Fig. 4. Principal coordinate analyses (PCoA) indicating in grey the volume of swimming performance morphospace occupied by herbivore assemblages recorded feeding on reefs subject to low, moderate and high wave exposure. PC1 and PC2 (a–c) and PC3 and PC4 (d–f) are the first four principal components which collectively account for >85% of the total variability. Volumes of morphospace occupied by grazer–detritivores and scrapers–small excavators (expressed as a percentage of the global convex hull) are displayed in green and light blue, respectively. Dashed lines reference the global convex hull encompassing all species occurring throughout the whole study area (n = 37). Dots represent species and their size is proportional to feeding frequency (bites h^{-1} m^{-2}). The × symbols indicate species not recorded feeding at a given exposure level. Mean functional richness (FRic, expressed as a percentage of the global convex hull) and functional dispersion (FDis) are summarised per exposure level.

Overall herbivore feeding frequency almost doubled under high wave exposure, compared to low and moderately exposed reefs (P = 0·009, Fig. 6). Respectively, grazers–detritivores and scrapers–small excavators contributed a consistent 72–77 and 20–28% at all levels of wave exposure (Fig. 6). In contrast, the scarce contributions of browsers (3%) and bioeroders (1·4%) became negligible to null under high levels of wave exposure (Fig. 6).

Discussion

Physical constraints on ecosystem functioning may drive much of the spatial heterogeneity in the ecosystem services available for humanity. Studying the interaction among environmental filters, species niches and ecological processes can help determine what erodes ecosystem stability. Focusing on coral reef fish herbivory over a wave exposure gradient, we find that environmental filtering can change species feeding behaviours, narrow their realised ecological niches and modify ecosystem processes. Traditionally recognised herbivore feeding functional groups differed in

the swimming performance predicted by their functional traits and had opposite responses to wave exposure. This finding emphasises the distinctness of their ecological niche, and therefore adds a further layer to their functional complementarity. However, species within feeding functional groups also differed in their responses to wave exposure. While the feeding capacity of certain species was limited under turbulent conditions, others were either unaffected or increased their feeding frequencies under high wave exposure. These findings supplement emerging evidence demonstrating that species partition their niches much more finely than can be captured by a single category (Fox & Bellwood 2013; Plass-Johnson, McQuaid & Hill 2013; Brandl & Bellwood 2014; Adam *et al.* 2015), and caution against assuming high functional redundancy within speciose feeding functional groups. In certain cases, the diversity of species responses to wave exposure allowed the preservation of critical ecosystem functions (e.g. macroalgal browsing) throughout the gradient, and likely explained why overall levels of herbivory were robust to filtering. Although herbivore biomass is often used or
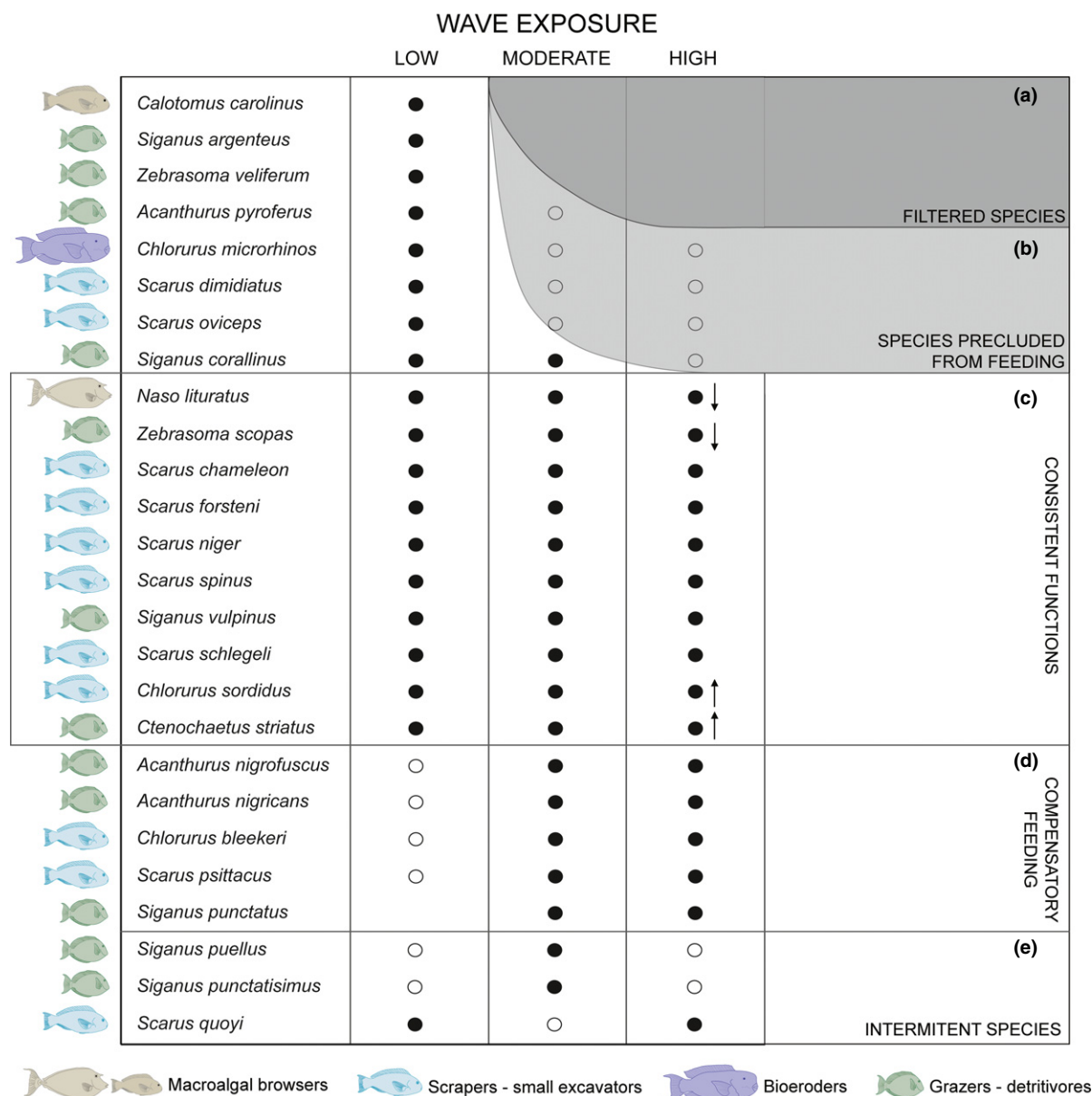
Fig. 5. Diagram representing the effects of wave exposure filtering on herbivorous fish communities in the Palau archipelago. Names of all species recorded feeding at low, moderate and high wave exposures are listed in the left, fish diagrams are colour-coded according to feeding functional group. The ○ symbol marks that the species was present at the corresponding wave exposure level (i.e. captured by either visual censuses or video cameras), and ● indicates that it was present and recorded feeding. Filtering precluded 22% of species from engaging in feeding on moderate and high exposure reefs (i.e. filtering at the feeding functional level).
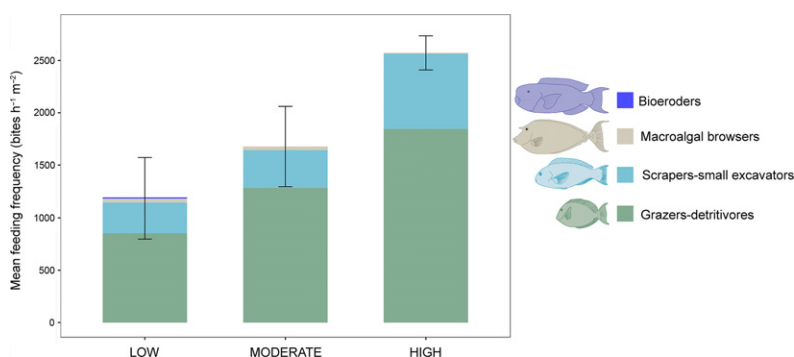

Fig. 6. Mean overall herbivore feeding frequency (±SE) at low moderate and high levels of wave exposure, indicating the portion accounted for by different feeding functional groups. Feeding frequency was significantly higher at high compared to low and moderate wave exposures ($P = 0.009$).

advocated as a suitable proxy for herbivory (Heenan & Williams 2013; Graham *et al.* 2015; Jouffray *et al.* 2015), our results suggest that may not be the case at the ends of environmental gradients.

Coral reef herbivore morphologies are considered ideal to exploit exposed and highly productive coral reef habitats (Bellwood *et al.* 2014). A detailed interspecific comparison of swimming performance based on multiple traits (other than pectoral fin ratio) was however lacking. Species distribution in our multidimensional swimming performance morphospace indicated that herbivorous fishes could not be ranked in a simple continuum of low-to-high swimming performance. Rather, species conformed to either the *laterally compressed* (LCBP) or *fusiform* (FBP) body plans, which likely utilise contrasting strategies to minimise drag during movement. Further investigation is required to determine whether swimming performance predicted by the functional traits assessed here covaries with *in situ* metrics of swimming performance. If this is the case, herbivore ecomorphs differing in their capacity to perform their function along wave exposure gradients may be revealed.

Herbivores conforming to the *fusiform* body plan comprise the subfamily Scarinae, whereas those clustered as *laterally compressed* include two families of the monophyletic group of acanthuroid fishes (i.e. Acanthuridae and Siganidae, Wainwright & Bellwood 2002). Importantly, similarity among the closely related taxa clustered into these body plans could have emerged from the conservative evolution of functional traits (Webb *et al.* 2002). Phylogenetic niche conservatism may occur due to a reduction in the potential range of evolution of ecological traits caused by the fixation of ancestral traits (Westoby, Leishman & Lord 1995). Procedures to disentangle the percent of trait variation that can be attributed to phylogeny and ecology (Westoby, Leishman & Lord 1995; Lovette & Hochachka 2006) remain a subject worthy of further investigation. Phylogeny must, for instance, account for much of the intrinsic heterogeneity of *laterally compressed* families which encompass five genera. On the other hand, phylogenetically distinct species can share common functional traits related to social behaviours and resource use (Brandl & Bellwood 2013). It seems therefore reasonable to suggest that surgeonfishes and rabbitfishes may share certain functional traits related to resource exploitation across wave exposure gradients. The large spread of *laterally compressed* species over PC2 (Fig. 3) mostly reflects that surgeonfishes and rabbitfishes spanned a wider range of pectoral fin aspect ratio (PAR) (0·78–5·13) compared to parrotfishes (1·76–3·58). Tapered fins (high PAR) maintain high sustained speeds, whereas rounded fins (low PAR) are most effective for low-speed manoeuvrability (Vogel 1994; Webb 1994; Wainwright, Bellwood & Westneat 2002). Diversification of pectoral fin shape among *laterally compressed* herbivores seems necessary to accommodate their wide diversity of feeding behaviours, and the marked interspecific differences in microhabitat utilisation and foraging

distance (Meyer & Holland 2005; Fox *et al.* 2009; Fox & Bellwood 2013; Brandl & Bellwood 2014). Interestingly, a small-bodied surgeonfish (i.e. *Zebrasoma veliferum*) occurred closer to rabbitfishes than to other surgeonfishes in the swimming performance morphospace. This proximity had also been captured when examining the cranial morphology in relation to the exploitation of cryptic microhabitats (Brandl & Bellwood 2013). For these long-snouted species, lateral compression might thus confer a further common trait to facilitate the exploitation of cryptic microhabitats.

Abiotic factors have long been recognised as filters preventing the access of species to certain habitats based on their traits (Floeter *et al.* 2005; Fulton, Bellwood & Wainwright 2005; Hopcraft, Olff & Sinclair 2010). Here, we demonstrate that environmental stress can also limit the feeding behaviour of occurring species, based on functional traits linked to performance, thus narrowing their ecological niches. Streamlined body shapes with high caudal fin aspect ratio are predicted to be particularly favoured in high flow environments (Langerhans & Reznick 2010). Feeding under high swell may however select for traits that facilitate the location and acquisition of food while holding a stable position at minimal energy cost. With species conforming the FBP being most streamlined, and those of LCBP attaining the highest caudal and pectoral fin aspect ratio, either body plan could fit the shape of success across all levels of wave exposure.

Wave exposure acted as a strong environmental filter for scrapers–small excavators (which conformed to the LCBP) but not for the grazers–detritivores (which fitted the FBP). High wave exposure selectively limited the feeding function of the deepest body shapes with highest caudal thrust efficiency, and favoured fusiform bodies irrespective of pectoral fin shape. A larger number of FBP than LCBP species fed consistently at all levels of wave exposure ($n = 7, 3$, respectively, Fig. 5). Moreover, FDis increased steadily with wave exposure for FBP, whereas it decreased for LCBP. Perhaps a fusiform shape facilitates holding a stable position at a lower energetic cost than maintaining it via fin propulsion. Both *fusiform* and *laterally compressed* species that fed consistently throughout the gradient spanned a wide range of pectoral aspect ratio values observed for the respective body plan. Irrespective of the pectoral fin shape, specific feeding frequencies of *fusiform* species were unaffected by wave exposure. In contrast, feeding frequencies of *laterally compressed* species with the most tapered fins were either unaffected (*Siganus vulpinus*) or increased (*C. striatus*) by wave exposure, and species with the most rounded pectoral fins (e.g. *Z. scopas* and *N. lituratus*) experienced a four-fold decrease in feeding frequency at high wave exposure (Figs 5 and S7).

The contrasting responses of groups with *laterally compressed* and *fusiform* body plans to wave exposure imply that two distinct herbivore feeding functional groups (i.e. grazers–detritivores and scrapers–small excavators) differed in their capacity to exert their functional role across

levels of wave exposure. Moreover, species within these functional groups responded differently to wave exposure. We elaborate here on the major implications of these findings. First, we emphasise the distinctness of the ecological niches of grazers–detritivores and scrapers–small excavators, and therefore their functional complementarity. Second, herbivores categorised within the same feeding functional group are often presumed functionally redundant. However, a more comprehensive view of species niches recognises that a range of biotic and abiotic factors can pose limits to the realised range of resources that a species can use (Brandl & Bellwood 2013).

Spatio-temporal segregation of resource use can also contribute to the partition of food resources among herbivores (Kartzinel *et al.* 2015). We demonstrate that wave exposure filtering introduces a further level of niche partitioning within traditional coral reef feeding functional groups. In cases where wave exposure regimes change seasonally or as a result of climatic perturbations, it could also drive the temporal segregation of resource use (e.g. Kench & Brander 2006; Madin & Connolly 2006; Fabricius *et al.* 2008). Demonstrating that the environment may pose more profound and complex spatial boundaries for herbivory than previously thought, we highlight the issues that arise from assuming functional redundancy within coarse functional categorical groupings. The effect of environmental conditions on the extent of functional redundancy has also been demonstrated for microbial communities, where species found to be functionally redundant in one environment became pivotal in another due to shifting roles and interactions (Fetzer *et al.* 2015).

A high degree of functional complementarity and redundancy can be interpreted as desirable attributes of ecosystems (Nyström 2006; Burkepile & Hay 2008), when these correspond respectively to the presence of complementary feeding functional groups, and a high number of species per feeding functional group. In our case, high wave exposure did not exclude grazers–detritivores or scrapers–small excavators, but it had opposing effects on their feeding rates. Consequently, we conclude that co-occurrence of different feeding functional groups throughout an environmental gradient may not always herald that these are exerting strong levels of their respective trophic function. We therefore caution against interpreting complementarity and redundancy of ecosystems based on species co-occurrence, especially at the ends of environmental gradients.

Although high wave exposures hindered the feeding consistency of certain herbivorous species, overall herbivory remained robust to this intrinsic reorganisation. We argue that such robustness emerged in two ways. First, species of the same broad feeding functional group increased their feeding frequency in response to wave-exposure stress. If environmental conditions other than wave exposure remained equal across the study area, turbulence could reduce herbivory due to the challenges faced by fish to feed and manoeuvre. Contrary to this expectation, we observed a two-fold increase in overall herbivory on highly exposed reefs. This pattern could be reflecting the strong role played by the productivity of the food resource (Fig. S1). Wave exposure may have increased the productivity potential of the environment which is driven in marine systems by light and water motion (Steneck & Dethier 1994). Specifically, this may have increased the capacity of plants to acquire nutrients and utilise sunlight (Leigh *et al.* 1987; Hurd, Harrison & Druehl 1996), thus increasing the productivity of coral reef benthic algae (Marsh 1970; Renken *et al.* 2010), and attracting aggregations of grazers (Russ 2003). At our study sites in particular, wave exposure significantly enhanced the vertical growth rate of algal turfs (Fig. S1a). Maximum levels of herbivory observed under high wave exposure may have also been facilitated by the selective limitation of certain species' functions. Likely released from competition-related interference, remaining species may have achieved higher feeding rates thus elevating the overall process rates. Corroboration of this mechanism deserves further investigation. If filtering did effectively reduce interference, our results deviate from an important theoretical hypothesis according to which species diversity and process rates should be positively correlated (MacArthur 1955). Instead, our findings suggest that environmental filtering might be one of the mechanisms for the emergence of inverse relationships between species diversity and process rates.

Absolute levels of herbivory are ultimately a function of the intrinsic characteristics of the species sustaining it, and of species responses to prevailing environmental conditions. While relative levels of herbivory are bounded by species skull morphology and body size (Bellwood & Choat 1990; Van Soest 1996; Perez-Barberia & Gordon 1999; Papachristou, Dziba & Provenza 2005; Lokrantz *et al.* 2008), spatial limits to these levels can be imposed by top-down mechanisms or bottom-up constraints (Hopcraft, Olff & Sinclair 2010). Although the most logical spatial boundaries to species trophic niches are those dictated by the availability of their food resource (White 1984; Rand 2002), we demonstrate that herbivore trophic niches can also be constrained by physical factors affecting the consistency with which they can engage in feeding. Maintaining high levels of herbivory is especially desirable in high primary productivity areas such as turbulent reefs, because those are particularly prone to negative post-disturbance trajectories (e.g. algal blooms) (Roff *et al.* 2015a,b).

Harvesting of herbivorous fishes is not only a vastly spread practice across the Tropical Pacific, but is also deeply embedded in the cultural customs of numerous societies (Dalzell 1993; Aswani & Hamilton 2004). Indiscriminate targeting behaviours often lead to large catch volumes spanning a large number of species (Rhodes & Tupper 2007). Our results contribute a cautionary note concerning the complex issues surrounding the management and protection of herbivorous fishes. Fish communities comprised by larger numbers of species of the same broad functional group could be erroneously regarded as

robust to overexploitation because species are assumed to be functionally redundant. Hence, we highlight the risk involved in this perception, and caution against decisions based on this unidimensional definition of species' niche. While it might be argued that more speciose groups could have a greater scope for functional redundancy based on the species similarities in feeding mode, this scope is not an accurate reflection of the realised level of functional redundancy (i.e. the actual capacity of one species to compensate the absence of another) within communities. Consequently, the extent to which processes will remain robust in the presence of compound disturbances is uncertain, and must not be taken for granted. Our results highlight that ecosystem function rates as well as levels of functional complementarity and redundancy are more spatially heterogeneous than assumed based simply on species' occurrence and trophic roles. At the ends of environmental gradients for instance, functions will tend to be supported by fewer species. Retention of important ecosystem functions along environmental gradients will therefore be contingent upon conserving a broad range of species with high response diversity.

Authors' contributions

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Data accessibility

Data available from the Dryad Digital Repository http://dx.doi.org/10.5061/dryad.fs47h (Bejarano *et al.* 2017).

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Supporting Information

Details of electronic Supporting Information are provided below.

Fig. S1. Benthic features across levels of wave exposure.

Fig. S2. Morphometric parameters.

Fig. S3. Residual plots of feeding frequency model.

Fig. S4. Dendrogram of species conforming the swimming performance body plans.

Fig. S5. Results of the null model.

Fig. S6. Representativeness of the morphospace of species recorded feeding.

Fig. S7. Feeding frequency per species under different levels of wave exposure.

Table S1. Functional traits related to fish swimming performance.

Appendix S1. Null model approach.