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Trophic distribution of nutrient production in coral reef fisheries

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Abstract

Coral reef fisheries supply nutritious catch to tropical coastal communities, where the quality of reef seafood is determined by both the rate of biomass production and nutritional value of reef fishes. Yet our understanding of reef fisheries has largely used fish biomass, rather than individual growth (i.e. biomass production) and nutrient concentration (i.e. nutritional value), limiting the ability of management to protect fisheries productivity and nutritious catches. Here, we use modelled growth coefficients and nutrient concentrations to understand the nutrient productivity of coral reef fishes, and combine these predictions with surveys from four tropical countries to examine the distribution of fishery services among trophic groups. Species' growth coefficients were associated with size-linked nutrients (calcium, iron, selenium, zinc), but not total nutrient density, showing that both slow- and fast-growing species can be nutritious for people. We integrated these values with fish abundance data to show that herbivorous species dominated standing biomass, biomass turnover, and nutrient production on most reefs. Such bottom-heavy trophic distributions of nutrients were observed across fishing and benthic composition gradients. Management restrictions that promote sustainability of low-trophic-level species, including time, gear, and area restrictions, can help to protect biomass and nutrient production from reef fisheries.

Introduction

Measuring the structure and composition of ecological communities provides insights into how energy and nutrients flow through food webs [1,2], and reveals impacts of anthropogenic stressors on ecosystem services [3,4]. Many aquatic ecosystems provide services through fisheries [5], particularly in the tropics where coastal habitats such as coral reefs contribute to local food systems [6]. Much of our understanding of how coral reef fishes contribute to fisheries is based on studies measuring fish biomass at one point in time in multiple places, such as regional analyses that reveal how fish assemblage composition changes along

gradients in fishing pressure [7,8] and abiotic processes, such as temperature [9]. However, fish biomass is a static snapshot of a coral reef assemblage that fails to capture the growth of targeted populations [10,11], which determines the rate of biomass production, and turnover over time [12]. Analyses of fish biomass also overlook social aspects of reef fisheries, such as the nutritional quality of fisheries catches [13], limiting the usefulness of biomass in quantifying fisheries contributions to food and nutrition security. Considering associations between production of biomass and nutrients, and how these processes vary between fish species, will more accurately capture potential fisheries service contributions in tropical food systems.

In practice, both growth rate and nutrient concentration determine the quantity and quality of food production from coral reefs, but associations between species-level productivity and nutrient concentration remain unclear. Recently, empirical models have been developed to predict growth rates [14] and nutrient concentrations of diverse reef fish species [5,13], providing insights into production of nutritious food on coral reefs. For example, population turnover in smaller, targeted species can increase at moderate fishing levels, buffering biomass depletion [15], while growth in herbivore populations rich in iron and zinc can maintain the nutritional value of reef catch following climate disturbances [13]. Reef fish productivity captures the rate at which biomass is produced by an individual fish (i.e. somatic growth), is predictable for any reef fish species, and can be combined with abundance and size survey data to estimate assemblage-level biomass production [10,14]. Similarly, nutrient models use ecological and environmental trait information to predict the concentration of essential dietary nutrients contained in fish muscle tissue, and can be combined with species' biomass (or catch) data to estimate the nutrient availability (or yield) for fisheries, providing information on the nutritional quality of reef seafood [13]. Growth rates have been combined with elemental stoichiometry to model carbon and nitrogen flux in reef fish [16], suggesting that productivity and nutrient models could be similarly combined to estimate nutrient production rates in reef fishes. Strong effects of size, diet and feeding categories on growth rate [14] and nutrient concentration [5] suggests that nutrient productivity on coral reefs is likely governed by trophic structure. As such, analysis of nutrient productivity among reefs that vary in benthic composition and fishing pressure should help improve understanding of how changes in the reef food web might impact the availability of nutritious catch for fisheries.

Here, we combine size-based growth models with trait-based nutrient models to estimate the nutrient productivity of coral reef fishes from standard biomass surveys. We use established predictive frameworks to estimate growth coefficients (K_{max} , rate at which each species approaches its theoretical maximum size [14]) and concentrations of six nutrients (calcium, iron, selenium, zinc, vitamin A, omega-3 fatty acids) for 541 fish species observed in Belize, Fiji, Madagascar, and Solomon Islands. Our new metric combines ecological and fisheries theory with aspects of food systems and human health to understand supply of nutritious seafood from coral reef-associated fisheries. Using underwater visual census data from 333 reef surveys, we assess fishing and benthic drivers of three fishery services: standing biomass, biomass turnover, and nutrient production. Surveys were conducted on reefs

spanning 19 kg ha⁻¹ to over 5,000 kg ha⁻¹ of fishable biomass, including no-take areas and areas under fisheries restrictions, that varied substantially in benthic composition (hard coral, turf algae, macroalgae, rubble). We used Bayesian multivariate models to quantify fishing and benthic drivers of the trophic distribution of three key fishery services, and use these models to provide management recommendations and insights into fisheries supported by future reef habitats.

Methods

Underwater surveys

Coral reefs were surveyed at 320 sites between 2016 and 2020 in four countries spanning three marine ecoregions (Tropical Atlantic: Belize; Western Indian Ocean: Madagascar; Southwest Pacific: Fiji, Solomon Islands). Reefs included areas without fisheries regulations (open-access in Madagascar) and, in all four countries, those with partial fisheries management (e.g. time and area closures, gear restrictions) and no-take zones. 22 sites were surveyed in Belize (2019, 2020), 168 sites in Fiji (2016-2019), 75 sites in Madagascar (2015, 2016, 2020) and 59 sites in the Solomon Islands (2016, 2018, 2019). Fish were surveyed using belt transects (5 x 50 m in 79% of surveys, 10 x 50 m in 14% of surveys, 2 x 30 m in 7% of surveys), for 1-8 transects at each site (median replicates = 3). Fish were sized to the nearest cm, identified to species-level, and enumerated. We converted fish lengths to mass using published length-weight relationships [17], and estimated the biomass (kg ha⁻¹) of each observed fish. We excluded fish less than 5 cm in length, damselfish species that are not targeted in fisheries, and highly mobile elasmobranch species that are difficult to survey accurately [18]. Benthic surveys were conducted during fish surveys using point intercept transects, with benthic taxa identified at every 50 cm point along a 50 m transect line. All data were extracted from MERMAID (<https://datamermaid.org/>).

Nutrient concentrations of fish tissue

Nutrient content in fishes is predicted by phylogeny and multiple ecological traits, including body size, feeding pathway, trophic level, and habitat use [5,13]. We predicted the concentration (100 g⁻¹) of calcium, iron, selenium, zinc, vitamin A, and omega-3 fatty acids in the raw muscle tissue of each reef fish species, using a hierarchical Bayesian model, available on Fishbase [5,17]. We then used information on recommended nutrient intakes [19] to estimate the nutrient density of each species [20,21], defined as the contribution of one fillet 100 g portion to recommended daily intakes of all six nutrients for adult women (18-65 years old) (contributions capped at 100%).

Fish biomass production

We estimated the daily productivity of each individual reef fish following [10], using standardised species' growth coefficients (Kmax) derived from a meta-analysis of reef fish growth curves [10,14]. Kmax is the growth coefficient of the von Bertalanffy growth

equation, representing the potential growth trajectory of an individual fish towards its species' maximum size, that can range between 0.011 and 16.43 [14]. Using data and model structure in [14], we predicted K_{\max} using species' maximum lengths (L_{\max}) and trophic groups for each of the 541 species observed in underwater surveys. 371 species (66% of total species) were out-of-sample predictions using published sources for L_{\max} [17] and diet group [22]. We then estimated the daily somatic growth (cm) of each individual fish surveyed, according to its observed size (body length) and species-level K_{\max} . Daily somatic growth in length was converted to daily growth in mass using published length-weight coefficients [17]. This procedure thus estimated the daily biomass production potential of each fish observation, which we use as the basis for estimating potential nutrient productivity. Our analysis thus focuses on a snapshot of the maximum (potential) daily productivity of reef fishes, excluding effects of natural mortality and fisheries exploitation.

Fishery services

We combined daily productivity estimates with nutrient concentrations to estimate the daily nutrient production of the reef fish assemblage at each site. Specifically, nutrient productivity was the daily productivity of each observed fish multiplied by its edible portion (average value for finfish 87%, [23]) and nutrient concentration, thus representing the maximum daily potential production of nutrients contained in edible, muscle tissue of reef fish, estimated for each of the six nutrients. At each transect, for each trophic group, we estimated the standing biomass (kg ha^{-1}), biomass production ($\text{g day}^{-1} \text{ ha}^{-1}$), biomass turnover (biomass production divided by standing biomass, %), and nutrient production (calcium, iron, zinc: $\text{mg day}^{-1} \text{ ha}^{-1}$, selenium, vitamin A: $\mu\text{g day}^{-1} \text{ ha}^{-1}$, omega-3 fatty acids: $\text{g day}^{-1} \text{ ha}^{-1}$). Trophic groups were defined according to published schemes and expert knowledge, representing herbivores (scraping detritivores), herbivores (browsing macroalgal feeders), planktivores, omnivores (mixed-diets), sessile invertivores, mobile invertivores, and piscivores. We excluded sessile invertivores from all analyses as these species contributed an average 2% of nutrient production and were not targeted in fisheries. Transect-level estimates were averaged to give site-level estimates of standing biomass, biomass turnover, and nutrient production of each trophic group. These metrics describe three fisheries services, representing catch available to fishers (e.g. fishable biomass), long-term catch turnover (e.g. biomass production and turnover), and the potential contribution of reef fish to diets through fisheries (e.g. nutrient production). We then converted these estimates into relative contributions of each trophic group to each fishery service (%), which we use as a representation of fish assemblage trophic structure.

Drivers of fishery services

We developed statistical models to assess the drivers of fishery service trophic structure: the relative contributions of three functional fish groups targeted by fishers (herbivores, mobile invertivores, piscivores) to biomass, biomass turnover, and nutrient productivity. As such, we recalculated contributions for each group, combining browsing and detritivorous herbivores into one group, for each reef site ($n = 333$). We also estimated the mean percent cover of five

major benthic groups at each site (hard coral, turf algae, macroalgae, rubble, bare substrate). These estimates were fitted to Bayesian models with Dirichlet distributions, using fixed covariates of total fishable biomass (kg ha^{-1}), benthic cover (hard coral, turf algae, macroalgae, rubble, bare substrate), and depth (m). To capture potential for different fishing (e.g. selectivity, gear, effort) and environmental effects (e.g. upwelling, primary productivity) in each country, we fitted country-level biomass effects (i.e. varying slopes). Management regime was included as a group-level intercept nested with country, and fishable biomass effects varied between countries (i.e. varying slopes).

All continuous variables were centred with a mean of 0 and scaled by dividing each variable by its standard deviation. Models were implemented in brms [24] and sampled in Stan, using R v4.2.0 [25]. We sampled four chains with 3,000 iterations each, and ensured model convergence by inspecting divergent transitions and ensuring that was < 1.01 . For each fishery service, model posteriors were sampled to estimate the median posterior trophic structure at each reef (proportion of herbivore, mobile invertivore, piscivore). We used these estimates to quantify reef trophic pyramid structure, where reefs with $>50\%$ contributions from herbivores were bottom-heavy and reefs with $<50\%$ contributions from herbivores were top-heavy. For nutrient productivity, we also generated out-of-sample predictions of trophic contributions from herbivores, mobile invertivores and piscivores along fishable biomass gradients in each country.

Results

Associations between growth rate and nutrient concentration

Most reef fishes had nutrient concentrations that met recommended intakes of 2-3 nutrients in a 100 g portion (nutrient densities between 90-250%), including species with ‘slow’ or ‘fast’ growth coefficients (K_{max} between 0.06-2.8). Species with the highest nutrient densities ($>300\%$, met recommended intakes for more than three nutrients) were mostly piscivores and mobile invertivores, including slow-growing species such as snappers (Lutjanidae) and groupers (Epinephelidae) with lower K_{max} values of 0.3 (Fig. 1a). The fastest growing species ($K_{\text{max}} > 1$) were dominated by planktivores and sessile invertivores, most of which had nutrient densities below 200%, and only a few mobile invertivores were both highly nutritious and fast growing (Fig. 1a). Nutrient density and K_{max} were weakly associated ($r = -0.1$), but nutrient density obscured associations between K_{max} and concentrations of specific nutrients. For example, size-linked nutrients [5] (Fig. S1) were more strongly correlated with K_{max} , with growth ~ nutrient relationships that were positive for calcium, iron, and zinc, and negative for selenium (Fig. 1b). In contrast, omega-3 fatty acid and vitamin A concentrations were not associated with K_{max} .

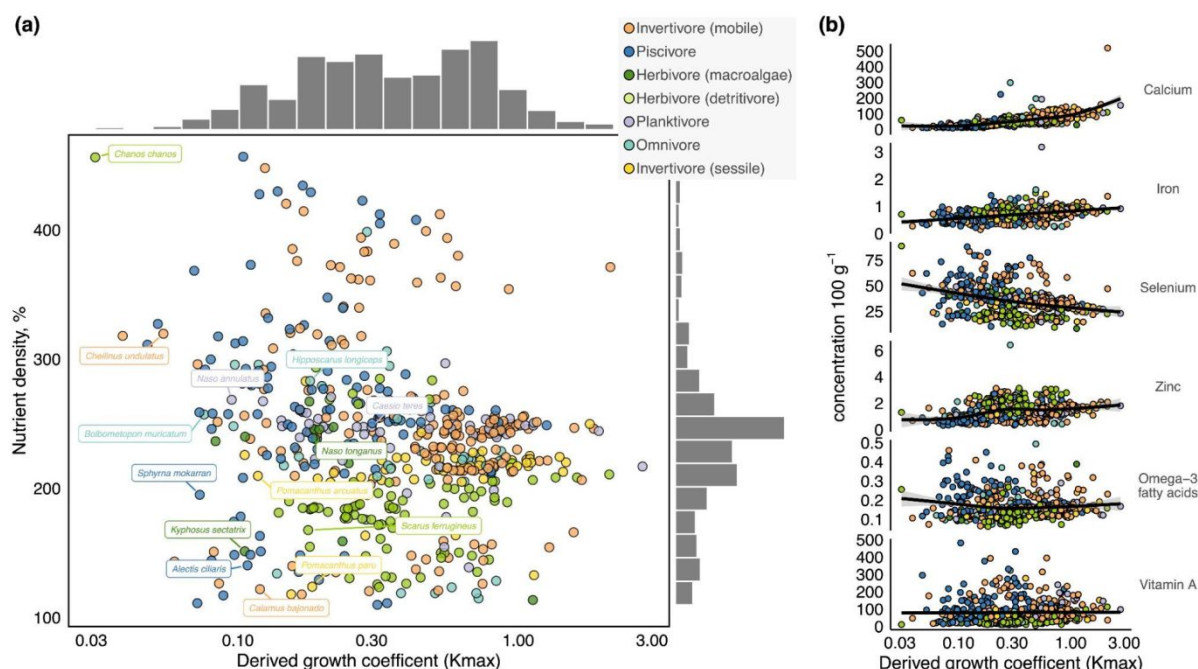


Figure 1 | Association between nutrient content and growth potential of 541 coral reef fish species. Points are individual species observed across Belize, Fiji, Madagascar, and the Solomon Islands, and Kmax is plotted on a log scale. In (a) nutrient density is the combined contribution to recommended daily women intakes of calcium, iron, selenium, zinc, omega-3 fatty acids and vitamin A [21], using reference values for adult women (18-65 years old). In (b) are each of the six nutrient concentrations, with fitted GAM smoothers (\pm 95% confidence interval). Growth coefficient Kmax is the value of growth coefficient K for each species at its theoretical maximum size, derived from the von Bertalanffy equation [14]. Labels show the top two species with highest average biomass in the dataset, for each trophic group, and marginal histograms show data distributions on each axis.

Fishery services: standing biomass, biomass turnover, and nutrient production

Species-level differences in growth rates and nutrient concentrations (Fig. 1) may not necessarily scale up to influence assemblage-level nutrient production, which is also governed by species' relative abundances. Next, we estimated standing biomass (kg ha^{-1}), biomass turnover (productivity, $\text{kg ha}^{-1} \text{ day}^{-1}$, divided by standing biomass, %), and nutrient production (mass of nutrients assimilated in fish tissue $\text{day}^{-1} \text{ ha}^{-1}$) by the reef fish assemblage at 333 sites in Belize, Fiji, Madagascar, and the Solomon Islands. Reefs supported a range of biomass levels (9 kg ha^{-1} in Madagascar to $5,937 \text{ kg ha}^{-1}$ in Fiji, Fig. 2b), and biomass production generally increased with fishable biomass (Fig. S2). Biomass turnover, however, was highly variable along the biomass gradient (1-41%), while reefs in Fiji and the Solomon Islands had the highest nutrient productivity (at $\sim 2,000 \text{ kg ha}^{-1}$ of fish biomass), particularly minerals (calcium, iron, selenium, zinc) (Fig. S2). These fishery services were provided by different fish trophic groups, with herbivorous and detritivorous fishes dominating nutrient production (mean = 34% across all six nutrients, ranging from 18-50%). Mobile invertivores were the second highest nutrient producer, with an average of 22% of the production across all nutrients, and accounted for more vitamin A production (35%) than herbivore/detritivores

(18%) (Fig. 2a). Other trophic groups had lower contributions to nutrient production, contributing an average 16% (planktivore), 13% (piscivore) and 10% (omnivore).

Herbivores and mobile invertivores were therefore the largest contributors to fishery services, accounting for an average 56% of standing biomass and biomass turnover, and 40-69% of nutrient production (Fig. 2c). However, trophic group contributions varied between countries. For example, piscivores were the largest contributors to standing biomass and omega-3 and vitamin A production in Belize, whereas planktivores dominated biomass turnover and production of most nutrients in Solomon Islands (Fig. 2c). Zinc production was dominated by herbivores in all countries, likely because this nutrient is more concentrated in low-trophic species.

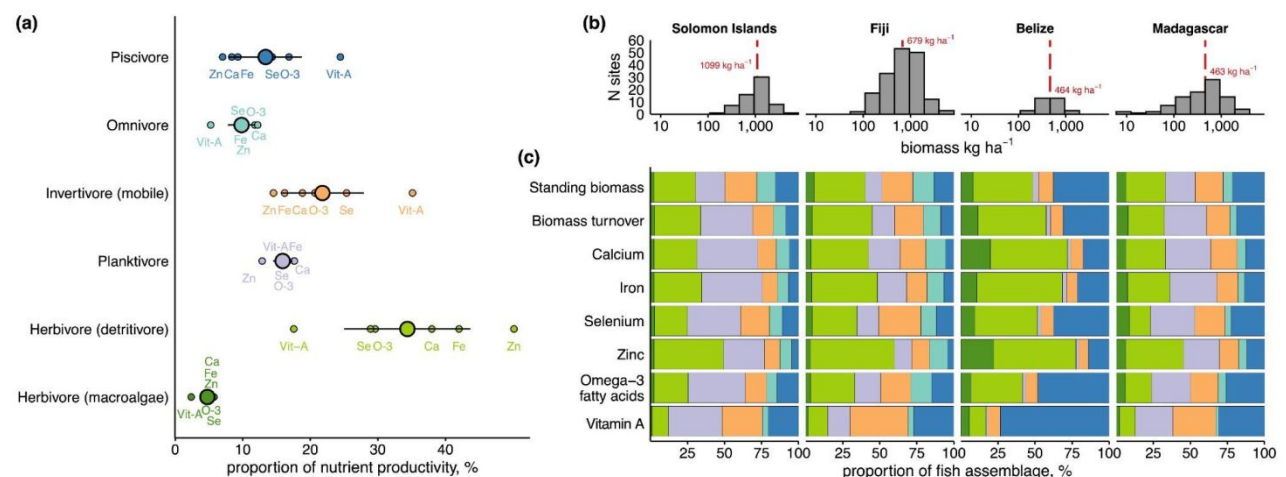


Figure 2 | Nutrient productivity of fish trophic groups. (a) is the mean contribution of each trophic group to site-level nutrient production for each nutrient (small labelled points) and the average across nutrients (large point \pm 2 SEM). (b) Histograms show log₁₀ biomass distribution across sites in each country (red dashed line is median biomass). (c) Bars show the average contribution of each trophic group to standing biomass, biomass turnover, and nutrient productivity of six nutrients, by country.

Bottom vs. top-heavy fishery services

We next fitted multivariate composition models to understand drivers of trophic group contributions to fishery services. We focus on herbivores, mobile invertivores, and piscivores because all are typically targeted by fisheries, and simplified this multivariate trophic structure by defining reefs as bottom-heavy when the relative biomass of herbivores exceeds piscivores, and top-heavy when piscivores dominate over herbivores. Standing biomass, biomass turnover, and productivity of calcium, iron, and zinc were bottom-heavy at over 96% of reefs, indicating that herbivores contributed a significant proportion of all three fishery services (Fig. 3). Only two fishing-restricted reefs had top-heavy biomass distributions (in Madagascar), whereas vitamin A production was top-heavy at 60% of reefs (Fig. 3). Belize had the most top-heavy trophic structure, where piscivores accounted for 30-60% of selenium, vitamin A, and omega-3 fatty acid production.

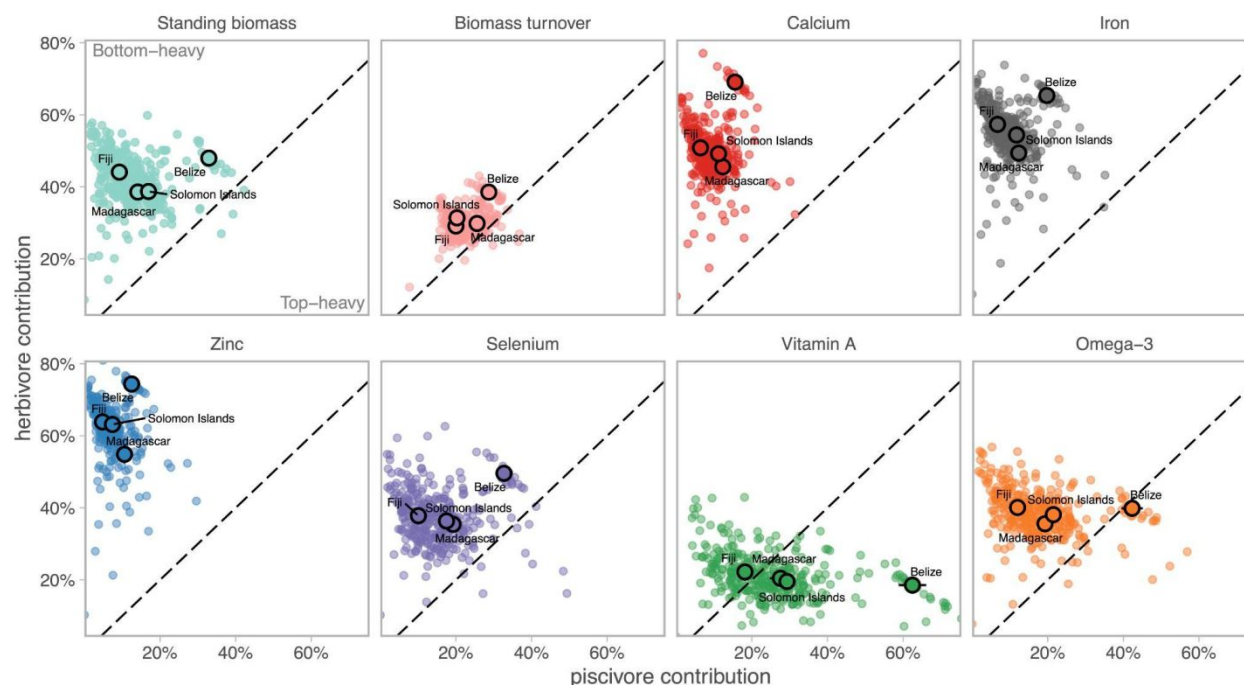


Figure 3 | Contribution of herbivores and piscivores to fishery services. Points show the posterior median predicted herbivore and piscivore contribution (%) to each fishery service, for all 333 reef sites. Bolded points represent the mean values in each country (± 2 SEM). Points in the upper-left have bottom-heavy pyramids (greater contributions from herbivores than piscivores) and points in the bottom-right have top-heavy pyramids (greater contributions from piscivores than herbivores).

Variation in the contribution of fishes to nutrient productivity was partly associated with differences in fishable biomass. For example, trophic distributions varied between Belize, Fiji and Solomon Islands, but did not change substantially along the biomass gradient within each country (Fig. S3), suggesting that unmeasured historical processes (e.g. disturbance, fishery dynamics) or biogeographic differences also govern assemblage composition of these reefs. In contrast, nutrient production in Madagascar shifted from dominance by mobile invertivores at low-biomass to herbivores at high-biomass (Fig. S3). Madagascar's reefs had the lowest biomass in the dataset, suggesting that biomass depletion due to fishing has changed trophic structure. In all four countries, nutrient production from piscivores increased with fishable biomass but, at most mid- and low-biomass reefs, piscivores accounted for less than 10% of nutrient production. However, the management regime had weak and uncertain effects on the relative contribution of fish groups (Fig. S4), with no-take areas and partially managed areas (e.g. access or gear restrictions) having similar trophic group contributions within each country (accounting for benthic effects). Only Madagascar had reefs that were openly fished, but these were similar in fish composition to no-take and restricted reefs.

Benthic composition also influenced which fish groups contributed to nutrient production. Coral cover ranged from 0-84%, with low-coral-cover reefs characterised by dominance of macroalgae (Belize, Fiji, Madagascar), rubble (Fiji, Solomon Islands), or turf algae (Solomon Islands) (Fig. S5). Nutrient contributions from herbivores increased with hard coral and

macroalgae cover, while mobile invertivores produced relatively more calcium and vitamin A as rubble increased (Fig. S6). Piscivores produced relatively fewer nutrients on reefs with more bare substrate, and more vitamin A and omega-3 fatty acids on deeper reefs (Fig. S6). These opposing benthic trends influenced the pyramid shape of fishery services. For example, only the deeper reef survey locations (>14 m, Belize and Madagascar) had top-heavy pyramids for standing biomass and biomass turnover, while reefs dominated by either coral or macroalgae (>60% cover) only supported bottom-heavy pyramids for all fishery services (Fig. S7).

Discussion

Empirical analysis of trophic distributions can help to delineate the structure and function of coral reef food webs, revealing ecological rules [2], environmental forcing [9], and human impacts [7]. Yet coral reef fish assemblages have largely been described using static measures of ecosystem state (e.g. fish biomass), potentially obscuring contributions from lower trophic levels to ecosystem productivity [12,26] and fisheries catch [27]. Here we combined species-level growth rate and nutrient concentrations with underwater surveys to show that herbivores and mobile invertivores dominate trophic structure on coral reefs, which is consistent with theoretical expectations [2] and previous empirical studies [7,28]. We also showed that biomass turnover and nutrient production by fishes are more bottom-heavy than fishable biomass, further underlining the importance of lower trophic levels in channelling benthic production and nutrients through reef food webs, as well as supporting coastal fisheries.

At the species-level, nutrient density and biomass production were weakly associated, but this was partly because nutrient density (an aggregate metric of nutrient concentrations) obscured relationships between growth rate and concentrations of individual nutrients. Empirical models show that reef fish growth rates are fastest in small-bodied species [29,30] and higher in herbivores and piscivores [14], whereas nutrient concentration varies predictably with body size and traits such as trophic level and diet [5,13]. We found that size-linked nutrients such as calcium, iron, and zinc were more concentrated in species with fast biomass turnover, possibly reflecting stronger input of minerals at the base of marine food webs. Selenium, in contrast, was more concentrated in slow-growing species, likely because these species also typically occupy deeper habitats [5], whereas omega-3 fatty acids and vitamin A concentrations had weak associations with species' potential biomass turnover.

Species-level nutrient and growth rate values must be combined with abundance or biomass data to understand nutrient flux and productivity at the scale of reef fish assemblages [16]. We integrated growth rate, nutrients, and biomass to assess the contribution of fish trophic groups to three fishery services provided by coral reefs (standing biomass, biomass turnover, nutrient production). Fishery services were bottom-heavy at most reefs, but the relative contribution of trophic groups to fishery services also varied regionally, between Pacific (Fiji, Solomon Islands), Indian Ocean (Madagascar), and Caribbean (Belize) reefs. In Belize, for example, browsing herbivores had highest biomass, likely because macroalgae was present at

all reefs (Fig. S5), suggesting that fishery services at macroalgae-dominated reefs are dominated by browser species. Fiji had the most bottom-heavy trophic pyramids, suggesting that these reefs have particularly high benthic productivity, with both algal and coral regimes supporting high biomass turnover of herbivorous species. These regional differences are likely linked to abiotic processes that constrain energy and nutrient flux through reef food webs (e.g. temperature, irradiance, upwelling) [9,12], disturbance history (e.g. fishing, thermal stress) [31], and intrinsic regional differences in community composition. Analyses that quantify abiotic influences on benthic and pelagic primary production, fishing intensity on different trophic groups, and energy flux through food webs are required to fully understand regional variability in coral reef trophic structure. Such assemblage-level analyses of rate-based ecosystem metrics (e.g. productivity) will help to inform understanding of general patterns in the structure and composition of food webs [32].

Analyses of coral reef trophic structure have largely focused on biomass gradients [7,8,28], but here we also assessed links between benthic composition and the relative abundance of fish trophic groups. Surveyed reefs supported a mix of coral, rubble, and algae-dominated habitats (Fig. S5), and bottom-heavy trophic pyramids were also prevalent in all of these benthic regimes. These sites have experienced recent disturbances to reef habitat, such as cyclones and coral bleaching, but these did not appear to substantially change trophic group contributions to fishery services. Such modelling of habitat drivers of fish trophic groups can provide information for adapting management to future reefscales. For example, we found that shifts to rubble dominance increased the contribution of mobile invertivores to nutrient production, consistent with increases in goatfish (Mullidae) populations after coral declines [33]. Gears targeting these species could help maintain nutritious catches from fisheries after coral mortality events, but this should be informed by knowledge on which species groups are preferentially targeted by fishers, and consumed locally. In contrast, nutrient production from reef herbivores increased with coral and algal cover, adding further evidence that herbivores are likely to play a key role in supporting food security on both coral-dominated and degraded reefs [13,26,34].

Managing trophic structure of fishery services

Contributions to nutrient productivity remained relatively constant along biomass and trophic group gradients in Belize, Fiji, and Solomon Islands, and between protected and partially managed reefs (Fig. S4). These patterns are similar to those observed on Indian Ocean [28] and Indonesian reefs [8], where most reefs were dominated by invertivores and herbivores, but fish composition shifts from convex (dominated by mid-trophic levels) to concave (dominated by low and high trophic levels) trophic structures as community fish biomass increases [7]. However, fishing levels that deplete fish biomass below 100 kg ha⁻¹ can release benthic invertebrate populations such as sea urchins, promoting dominance of invertebrate energy pathways in reef food webs [7]. Madagascar had the only openly-fished reefs in the dataset and, with some reefs supporting less than 100 kg ha⁻¹ of fishable biomass, likely experienced very high levels of fishing pressure. At these low-biomass reefs, mobile invertivores replaced herbivores as the dominant nutrient producers, suggesting these food

webs are primarily supported by invertebrate energy pathways, creating losses in nutritious catch from herbivorous species.

Reefs in Belize, Fiji and Solomon Islands had fishable biomass above 100 kg ha⁻¹ and also maintained trophic structure across their biomass gradient. Such consistency mirrors findings from a recent global reef analysis [12], indicating that regulating fishing to avoid biomass depletion can be an effective method of protecting fish trophic structure. We note that 100 kg ha⁻¹ is likely an extreme biomass depletion, below the 300-600 kg ha⁻¹ that is recommended to avoid fishery collapse [28]. Yet in the four countries analysed here, reefs were managed using diverse fishing regulations (e.g. gear restrictions, area and time closures), and most reefs likely experienced moderate to high fishing effort, suggesting that all management forms are effective in protecting species supplying fishery services. Indeed, no-take areas had similar trophic structure to ‘partially’ managed reefs, supporting evidence that both conservation and fishing goals can be achieved through gear and area closures [8], whereas open-access reefs in Madagascar experienced extreme biomass depletion and disrupted trophic structure.

Such alignment of conservation and fishing goals is particularly relevant for herbivorous species that are targeted in fisheries across the tropics [35] but also have key functional roles in promoting coral settlement through grazing of detritus and algae on reef substrate [36]. Maintaining sustainable fishing of herbivore populations while protecting ecosystem functioning is thus a central challenge for fisheries management on coral reefs [37,38]. Our results suggest that ‘partial’ fishing management in Belize, Fiji, Solomon Islands successfully protects function and fishing of herbivorous fishes. Indeed, herbivore populations may experience light exploitation and continue to exert grazing pressure on reef substrate [39], provided fishing effort is regulated above biomass thresholds [28] and herbivores have sufficient time to recover from biomass depletion [40].

Despite implementation of fishery restrictions at most reefs, piscivores were rarely observed and generally had minor contributions to biomass turnover and nutrient production. Top-heavy fishery services (i.e. dominated by piscivores) were only observed for vitamin A in Belize or on reefs with high fishable biomass. These patterns underline the diminished functional importance of piscivores in fished seascapes and small protected areas [7,28,41,42], and suggest that these species contribute less than other reef fishes to fisheries catch or tropical seafood supply, even on lightly-fished reefs. However, small-scale coastal fishers also target fishes in habitats connected to coral reefs (e.g. seagrass, mangrove) [43,44] that were not included in this analysis, and both fisher effort and species selectivity can vary spatially on reefs [45]. Further understanding of the contributions of trophic groups to fishery services should integrate ecological surveys from other habitats, using catch composition data to help ensure key non-reef stocks are included alongside coral reef fishes. For example, small-scale fishers in Western Province, Solomon Islands target up to 382 species, but only 56% of these were observed in these reef surveys, leaving 216 species either not observed on reefs or likely caught in other habitats (e.g. pelagic fish: Carangidae, Corhyphaenidae). Nutrition-sensitive fisheries management, which prioritises catch of nutrients rather than

biomass [46], could therefore focus on regulating herbivore and mobile-invertivore fisheries that produce the majority of biomass and nutrients. Indeed, gear-based management is already effective at reducing capture of rare, non-target species [47], and can now be combined with predicted nutrient concentrations to recommend gears that can supply long-term sustainable catch to maximise reef nutrient yields [48].

Future directions

Our study provides a framework for estimating nutrient productivity from fish survey data using publicly-available statistical predictions of fish growth rates [10] and nutrient concentrations [17]. Nutrient productivity measures the turnover of nutrients between trophic levels, offering insights into nutrient flux in reef food webs and providing a new approach for quantifying food provisioning from coral reefs. This rate-based metric unites concepts from food systems, ecology, and fisheries theory, and is complementary to emerging research on reef fish productivity [12,15,26] and elemental flux [16]. We used statistical models fitted to published data to make statistical predictions of nutrient concentrations in reef fish species, which is necessary for estimating assemblage-level nutrient productivity in diverse and data-limited reef fishes. Future research will need to consider potential for environmental variation to influence nutrient concentrations in fish [13,49], and how such intraspecific variation might have knock-on effects for nutrient flux through reef food webs.

We analysed trophic groups of fish with similar diets and behaviours that are relevant to fisheries (herbivores, piscivore, mobile invertivores) [8], whereas previous large-scale analyses delineated reef fish pyramids using trophic levels [7,12]. Since fisheries management typically focuses on species or gear restrictions that affect catch selection, we suggest regulating fishing using trophic groups (vs. trophic levels). This approach also avoids issues arising from assigning a single trophic level to species with diverse (e.g. ‘nominal’ herbivores [50]) and variable diets (e.g. ontogenetic shifts [51,52]). Our analysis also focused on reef fish species observed in ecological surveys, but not invertebrates that contribute to energy and nutrient flux in coral reef food webs [53], particularly in rubble habitats. Analysis of entire food webs (i.e. fish, invertebrates, and primary producers) is a longstanding challenge in coral reef science, owing to high turnover of small, cryptic species [29] and high biomass of mobile top predators [9], both of which are difficult to census accurately at comparable spatio-temporal scales. Our results suggest that invertebrate biomass (or population turnover) was higher on rubble and low-biomass reefs that supported the largest (relative) biomass of mobile invertivores. Further analysis of the contribution of invertebrates to coral reef biomass, biomass turnover and nutrient production will considerably develop understanding of energy flow in reef food webs.

Conclusion

Our analysis of coral reefs in four countries spanning the tropics showed the dominance of low trophic-level fishes in standing biomass, biomass production, and nutrient production. Coral reef herbivores are likely to be the primary contributor to fisheries services across

diverse (and disturbed) benthic habitats, fisheries management strategies, and at reefs with varying biomass levels, underlining their importance for tropical food security. Here, reefs that avoided extreme biomass depletion (i.e. $>100 \text{ kg ha}^{-1}$) maintained herbivore dominance, affirming the potential for fisheries management to reach biomass thresholds [28], ecosystem functions, and nutritious fisheries catches. Higher biomass thresholds ($300\text{--}600 \text{ kg ha}^{-1}$) near maximum sustainable yields will have additional benefits for ecosystem-level sustainability targets, as recommended by large-scale analyses of both fished and remote reefs [8,28,54]. We also found that the trophic structure of reef fishery services was resilient to different management strategies (e.g. gear and access restrictions, no-take areas), supporting use of culturally and socially appropriate management that permits fishing. Our framework provides an interdisciplinary approach that integrates theory across ecology, human health, and fisheries science, helping focus efforts on protecting and maximising sustainable seafood supply to food-insecure communities [6,55].

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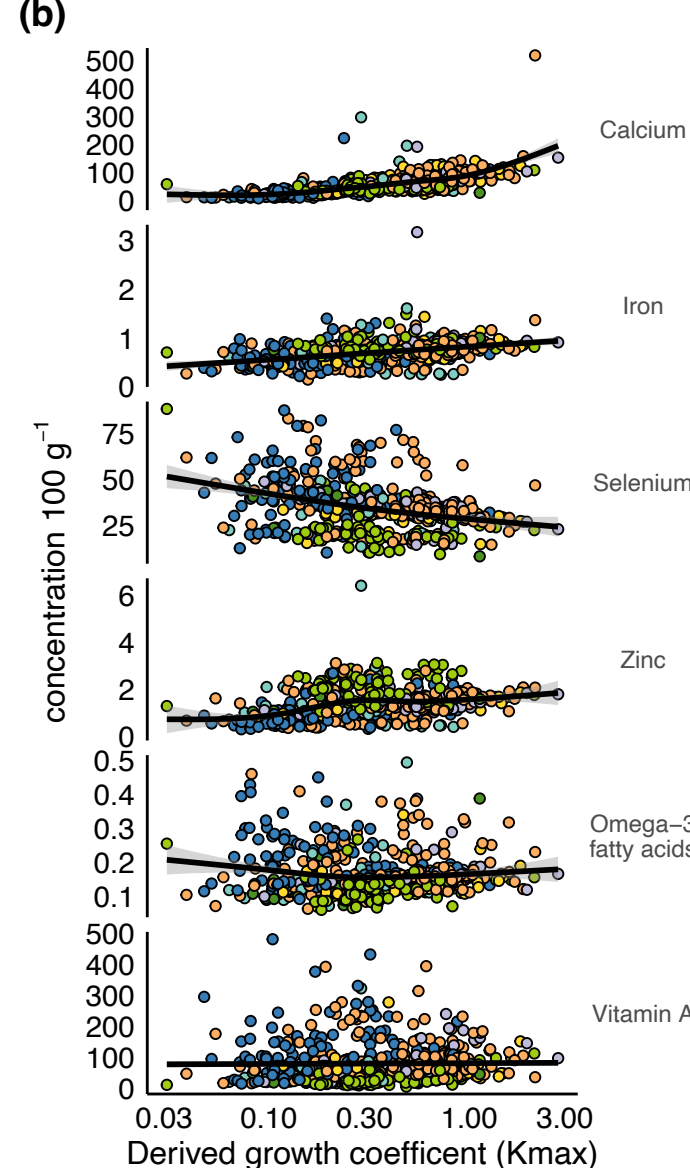
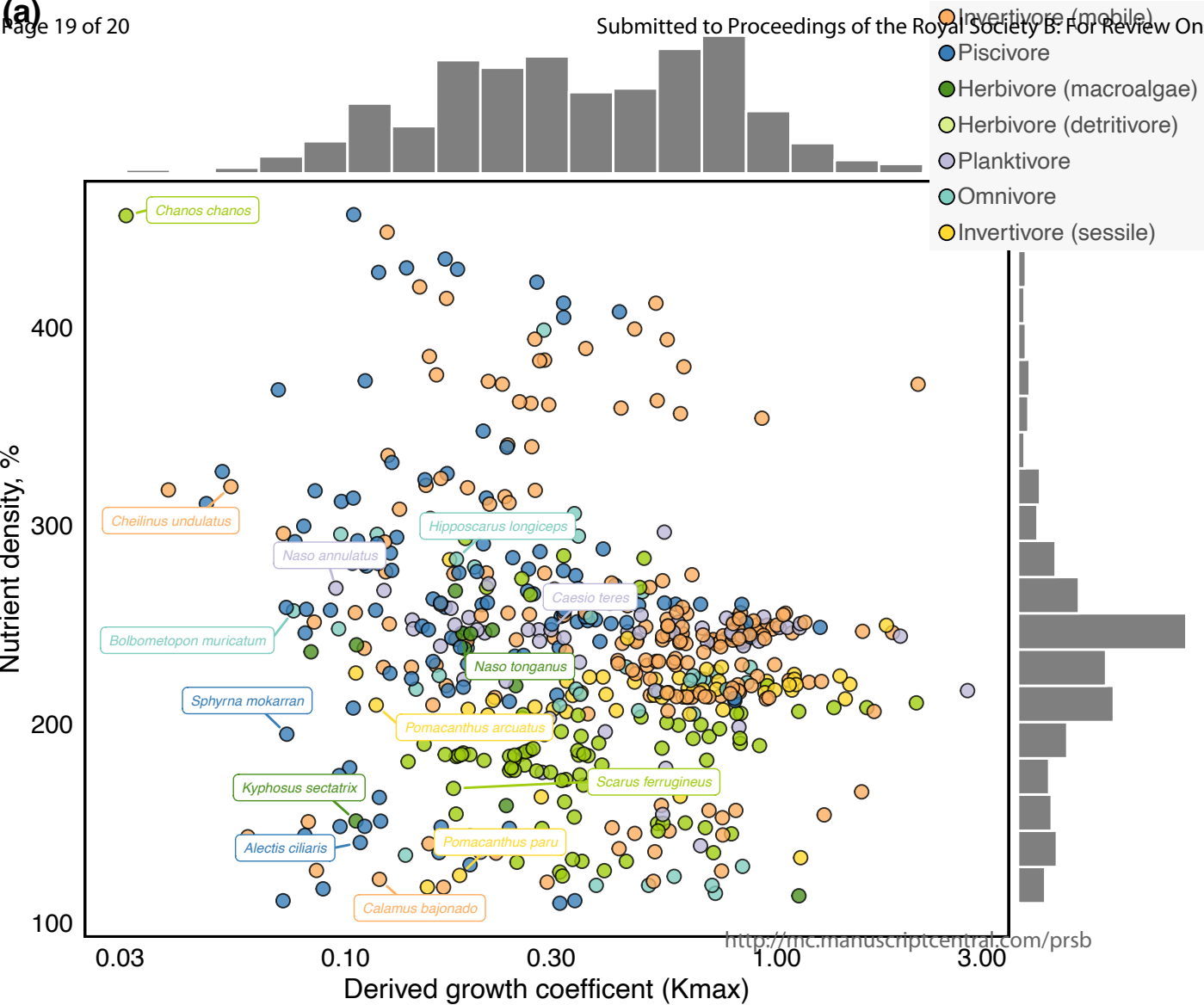
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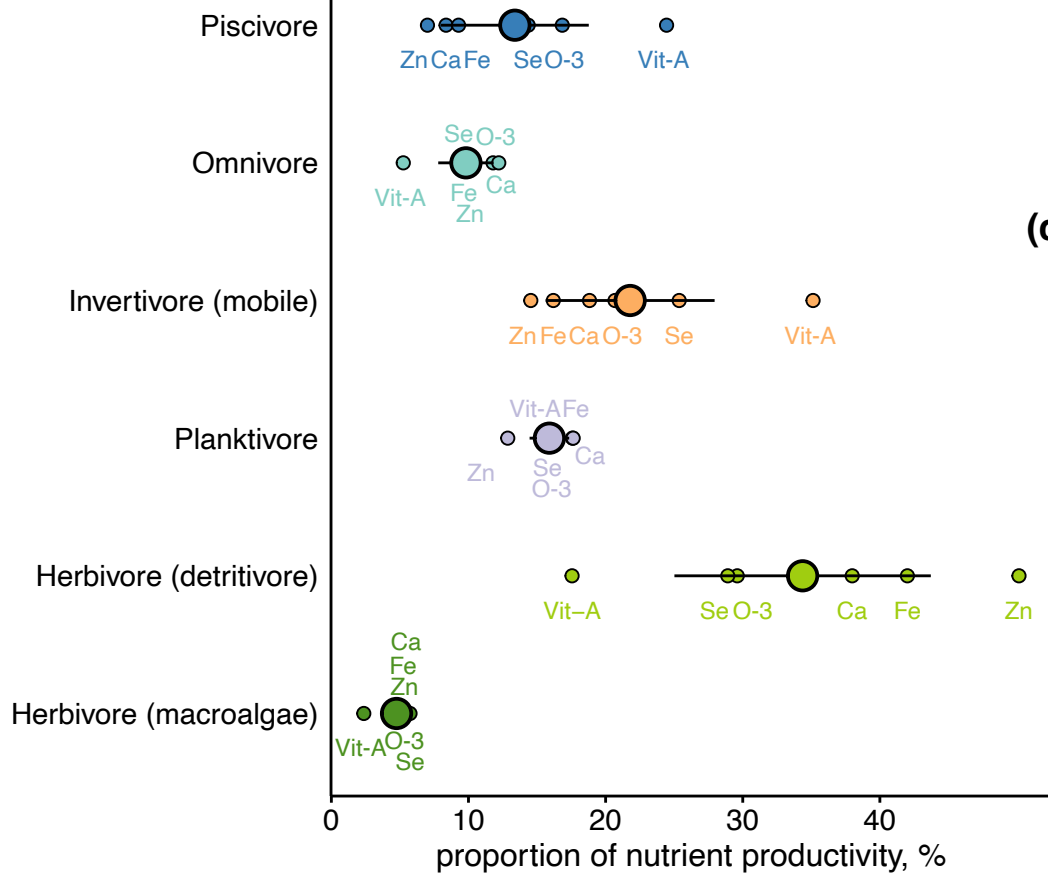
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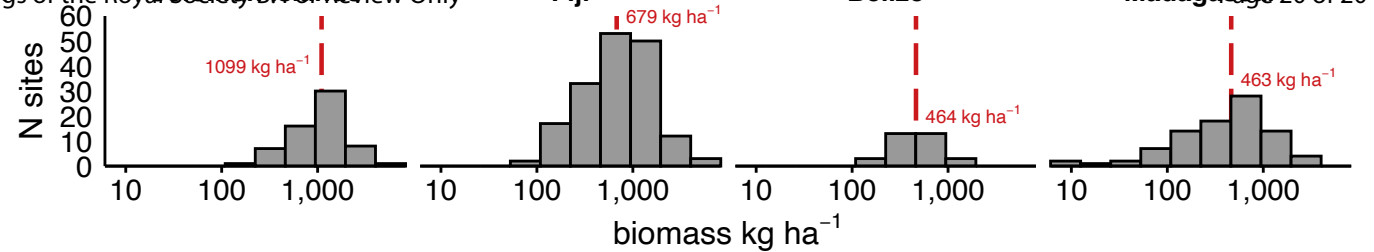
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