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High Fish Biomass and Low Nutrient Enrichment Synergistically Enhance Stability in a Seagrass Meta-Ecosystem

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ABSTRACT

Tropical seagrass ecosystems are globally imperiled due to overfishing and anthropogenic disturbances. Sustaining the services they provide will require managing resilience, particularly with increased volatility from climate change. Portfolio theory is touted as a mechanism to increase resilience in ecosystems because it takes advantage of temporal volatility in local production dynamics to increase stability at larger spatial scales. Using an individual-based model of a network of artificial reefs across multiple seagrass ecosystems that is parameterized with 15 years of field data, we demonstrate that (1) the large fish populations and the low enrichment synergistically increase portfolio effects; (2) the mechanism was via reduced local and increased meta-ecosystem stability in primary production; and (3) stability was greatest under intermediate production because nutrient enrichment reduces and fish, which have less influence on the amount of production, promote stability. Integrating common-sense management with portfolio theory can stabilize the services provided by seagrass ecosystems.

1 | Introduction

Increasing environmental uncertainty has motivated interest in managing ecosystems for resilience (Darling and Côté 2018; Moore and Schindler 2022). Portfolio theory is touted as a mechanism to increase resilience because it takes advantage of the principle that biological systems tend to be extremely variable at small scales, but if these small-scale dynamics are temporally asynchronous, their aggregate can result in increased stability at larger spatial scales (Figure 1A; dynamics referred to as portfolio effects) (Markowitz 1952). For example, Brennan et al. (2019) showed climate forcings that were spatially heterogeneous

and temporally asynchronous across numerous tributaries of the Yukon River dispersed risk experienced by two salmonid species and stabilized the production of both species across the entire river network. In this way, portfolio theory can be a powerful tool for managing resources because it can take advantage of variability at scales at which management decisions are typically implemented to increase stability at larger scales (Loreau, Mouquet, and Holt 2003; Schindler, Armstrong, and Reed 2015). Yet, effective application of portfolio theory for management requires understanding the mechanisms by which the primary drivers of variability mediate stability and at what spatial or temporal scales (McCann et al. 2021).

Maximilian H. K. Hesselbarth and Jacob E. Allgeier contributed equally.

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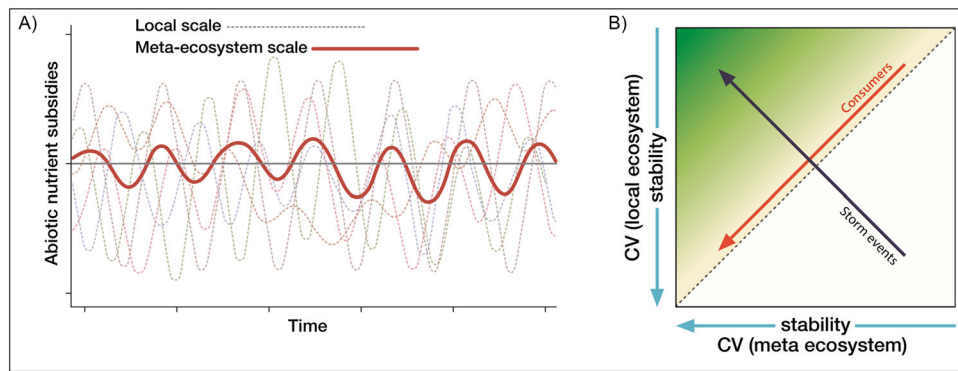
FIGURE 1 | (A) Example of portfolio effects for nutrient subsidies (nutrient enrichment) over time on local scale (dashed) and meta-ecosystem scale (solid red). (B) Hypothesized effect of anthropogenic nutrient enrichment from storm events (black arrow) and consumers (red arrow) on local (y-axis) and meta-ecosystem scale stability (x-axis) in primary production. Storm-driven variation in anthropogenic nutrient enrichment are hypothesized to increase variability in primary production among local ecosystems because some local systems would be more affected by nutrients than others, resulting in an increased CV and lower stability. Since portfolio effects are strongly scale-dependent, another scenario that could result in an increase in meta-ecosystem stability would be if storm events increased variability in primary production, but at the same time average primary production was also increasing at a greater rate. Dashed line indicates the 1:1 line, whereby any value above this line on the y-axis results in a portfolio effect (PE). Green coloration indicates hypothesized implications of PEs for primary production where darker green indicates greater production.

The high rates of ecosystem primary production (PP) in tropical coastal ecosystems (e.g., coral reefs, mangroves, seagrass beds) underpin the numerous services they provide to society, for example, carbon sequestration (Mcleod et al. 2011) and fisheries (Pikitch et al. 2004). These ecosystems are typically nutrient poor, and thus PP dynamics are strongly mediated by nutrient subsidies from anthropogenic and biotic sources (M. J. Atkinson and Falter 2003; Allgeier et al. 2014). Anthropogenic sources are typically spatially heterogeneous because watersheds along coastlines differentially allocate terrestrial runoff, for example, nutrient enrichment (de Carlo et al. 2007). They are also temporally heterogeneous because they are highly influenced by storm events that export large amounts of terrestrial nutrients to coastal waters and are predicted to become more temporally erratic and severe with climate change (Knutson et al. 2020). Spatial and temporal variability associated with storm-driven nutrient enrichment should result in high levels of instability in local PP dynamics (Figure 1B) but may stabilize PP across the aggregate system due to portfolio effects (Figure 1B; Ando and Mallory 2012).

Biotic subsidies from fish excretion are critical drivers of PP in tropical coastal ecosystems because fish are typically high in biomass and can supply large amounts of nutrients (Allgeier et al. 2014; Allgeier, Burkepile, and Layman 2017)—a process that can be greatly reduced by human exploitation (Allgeier et al. 2016). Fish also translocate nutrients across the seascape, for example, nutrient subsidies from foraging bouts by grunts (Haemulidae) in seagrass beds can increase nearby coral production (Meyer, Schultz, and Helfman 1983). Theory suggests that consumer-driven nutrient subsidies can stabilize local production dynamics because increased connectivity leads to a more even translocation of nutrients across the landscape (Gounand et al. 2014). Thus, in contrast to anthropogenic nutrient enrichment, the mechanism by which the consumers stabilize seascape-level production may be by increasing local stability rather than via portfolio effects (Figure 1B). Despite widespread awareness of the importance of anthropogenic nutrient enrichment and fish-derived nutri-

ents for tropical coastal ecosystems, the mechanisms by which they interact to affect the stability of local and meta-ecosystem production and, thus, how they could be managed to promote resilience to persistent small-scale perturbations remain rarely examined.

Here, using an individual-based model of a seagrass meta-ecosystem, we tested the extent to which temporal and spatial variability in two dominant nutrient sources, anthropogenic nutrient enrichment, and fish, affect the stability of PP across a network of artificial reefs (Figure 1C). Artificial reefs are a globally used fisheries management tool (Bugnot et al. 2020; Seaman 2022) and are increasingly being implemented in marine spatial planning to optimize habitat connectivity and fisheries production (Bugnot et al. 2020; Paxton et al. 2022). Recent research on artificial reefs in seagrass ecosystems revealed that aggregating fishes synergistically increase local- and ecosystem-scale PP via nutrient subsidies from fish excretion (Allgeier et al. 2018; Esquivel, Hesselbarth, and Allgeier 2022). Empirically quantifying such dynamics requires long-term datasets that are limited and often lack resolution. As such, the urgent need for effective management necessitates the use of models to direct initial strategies that should then be monitored with time (e.g., Hopf, Caselle, and White 2022). We answered three interrelated questions:

1. How do fish and anthropogenic nutrient enrichment independently influence portfolio effects?

2. How do spatial and temporal variability of these drivers interact to affect portfolio effects?

3. Do portfolio effects promote ecosystem PP?

2 | Methods

We developed a spatially explicit, mechanistic seagrass meta-ecosystem model *meta.arrR* (Figure 2; Supporting Information
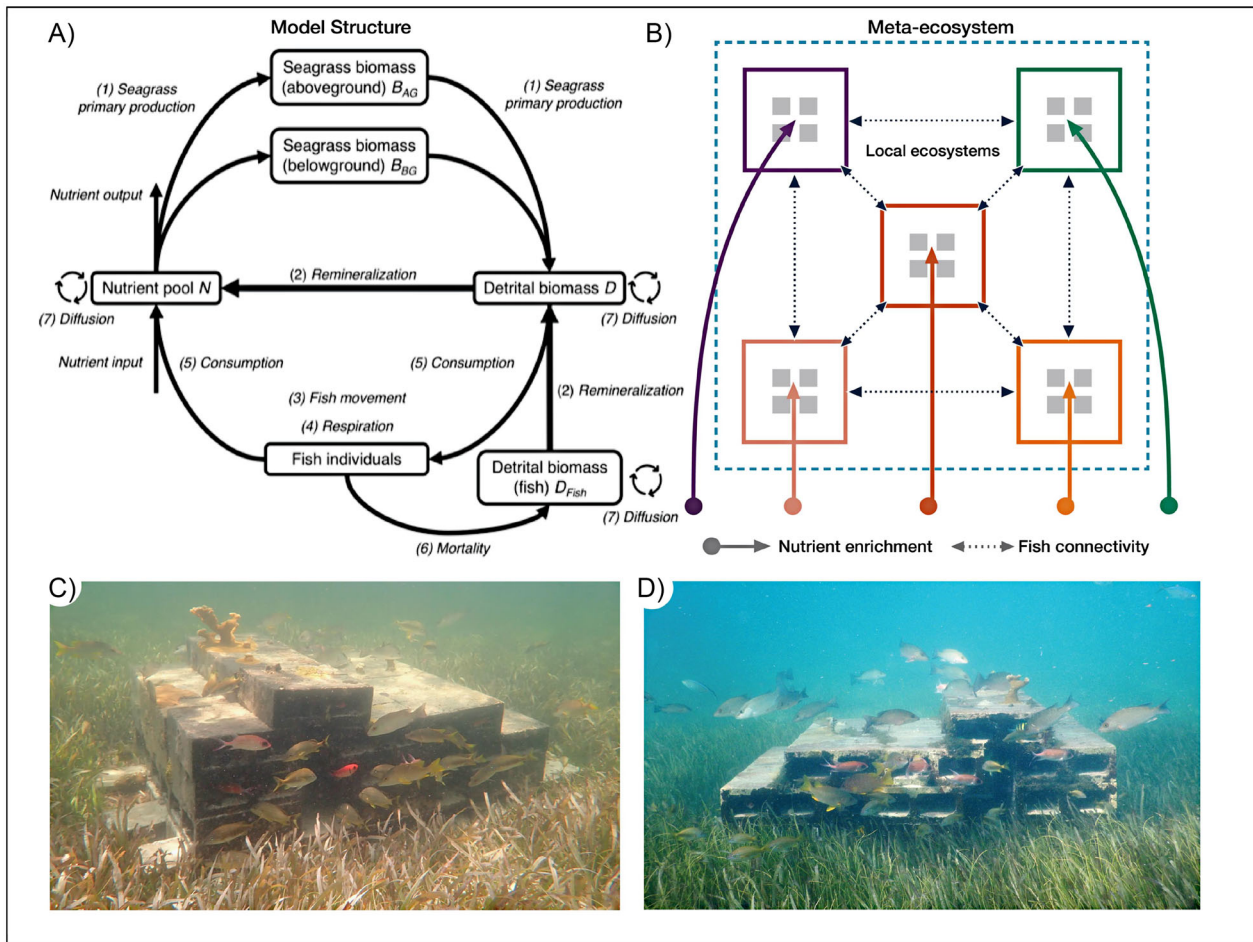
FIGURE 2 | (A) Overview of all model subprocesses and their scheduling (adapted from DeAngelis 1992). Seagrass primary production is calculated based on available nutrients in the water column, and simultaneously, seagrass biomass is sloughed to detrital biomass. The detrital biomass is remineralized to water column nutrients. Nutrients and detrital biomass are diffused among neighboring grid cells. Individual fish move throughout the model environment, and their consumption (of the detrital biomass) is determined by their respiration, which is largely influenced by body mass and movement activity. (B) Schematic for the meta-ecosystem model used in this study that includes five local ecosystems, each including an artificial reef. Each local ecosystem is connected by the movement of fish individuals (connectivity: dashed arrows) and enriched by abiotic nutrient subsidies (colored arrows originating from nutrient enrichment from outside the meta-ecosystem). The meta-ecosystem refers to all local ecosystems (light blue dashed rectangle). (C, D) Photos of experimental artificial reefs in The Bahamas studied by the authors for over 15 years. Models for this study were parameterized by extensive empirical data from this system.

S1) that consisted of a network of five connected local ecosystems, each with a single, centrally located artificial reef (Figure 2). Each local ecosystem used a spatially explicit individual-based model (Esquivel, Hesselbarth, and Allgeier 2022; Figure 2) in which individuals were a highly mobile, common, and commercially important fish species from the Caribbean, *Haemulon plumierii* (white grunt). Fish dynamics were driven by a bioenergetics model that regulated how individuals interact with the two-dimensional, 1×1 m grid-based seagrass environment via the consumption and excretion of nutrients as they move across the environment (Hanson et al. 1997; Allgeier et al. 2020). We used a single-nutrient PP model (adapted from DeAngelis 1992) of seagrass growth (not including other producers like phytoplankton) in which reactive nitrogen was the limiting factor, which allowed preferential nutrient allocation to aboveground and belowground biomass (Chapin 1980). All processes were parameterized from extensive field data from tropical seagrass ecosystems collected by the authors and, when needed, published

literature (Table S1). Importantly, modeled processes paralleled empirical findings in terms of spatial patterns and magnitude of PP (Figure S4; Table S3).

In the model, each local ecosystem received nutrient flows from (1) exogenous anthropogenic enrichment and (2) fish dynamics. Nutrient enrichment varied by the following: (1) the total amount entering the meta-ecosystem (*high*, *medium*, and *low*; Supporting Information S4; Table S2) and (2) the amount each local ecosystem received in time (herein *enrichment variation*; Figures 1A and S1; Supporting Information S4). Fish dynamics were driven by the following: (1) the total number of fish across the whole meta-ecosystem—population size (Table S2; Allgeier et al. 2014) and (2) the probability of individual fish moved from one local ecosystem to another that ranged from low to high based on previous empirical findings from similar systems (herein *connectivity*; Supporting Information S2 and S3; Figures S2 and S3; Allgeier et al. 2020).

We quantified the effect of (1) nutrient enrichment that varied by total amount and spatially across the network and (2) fish dynamics that varied by population size and connectivity on the local ecosystem and meta-ecosystem total seagrass PP (gDW d^{-1} m^{-2}; Supporting Information S5). Total PP consists of both aboveground and belowground components (total PP = aboveground PP + belowground PP; belowground PP strongly correlates with total PP because it constitutes the majority of biomass and thus is not included herein; Figure S5). Stability was quantified at the local scale by calculating the mean coefficient of variation of PP in each local system ($CV\alpha$) and at the meta-ecosystem scale by calculating the coefficient of variation of the summed PP of all systems ($CV\gamma$) (Wang and Loreau 2014), where a lower CV indicates greater stability (Supporting Information S6). Portfolio effects associated with PP were quantified by the ratio of $CV\alpha$ and $CV\gamma$, where higher values indicate that PP across all local systems was more stable than the average local ecosystem PP, that is, a stronger portfolio effect (Wang and Loreau 2014, 2016). Synchrony was calculated by dividing the sum of the covariances in PP among local ecosystems by the summed square root of the variance in PP within each local ecosystem squared (Wang and Loreau 2014).

3 | Results

3.1 | How Do Consumers and Anthropogenic Nutrient Enrichment Independently Influence Portfolio Effects?

Nutrient enrichment and fish dynamics independently and consistently promoted portfolio effects (portfolio effect > 1; Figure 3A). Fish dynamics drove stronger portfolio effects than nutrient enrichment (Figure 3A), but the magnitude of their effects on stability ($CV\alpha$ and $CV\gamma$) was comparable (Figure 3C,D). Increases in fish population size (1) had a greater positive effect on portfolio effects than increases in fish connectivity (Figure 3B), (2) increased local and meta-ecosystem stability for aboveground PP (negative effects on $CV\alpha$ and $CV\gamma$; Figures 3C and S6), and (3) reduced local and increased meta-ecosystem stability for total PP (positive effects on $CV\alpha$ and negative effects on $CV\gamma$; Figures 3D and S6). Fish connectivity increased locally but had little effect on meta-ecosystem stability for both aboveground and total PP (Figures 3C,D and S6). Variation in nutrient enrichment (1) always reduced local and meta-ecosystem stability of PP and (2) had a greater effect than the amount of nutrients that always increased local and meta-ecosystem stability (with very little effect on meta-ecosystem stability of total PP). This resulted in an overall weakening of portfolio effects with increased variation and total nutrients (Figures 3C,D and S7).

3.2 | How Does Spatial and Temporal Variability of Consumers and Anthropogenic Nutrient Enrichment Interact to Affect Portfolio Effects?

When fish dynamics and nutrient enrichment were both included in the model, nutrient enrichment had similar (for total PP) and greater (for aboveground PP) effects on portfolio effects as fish dynamics (Figure 4Ai,ii). Specifically, the highest portfolio effect values were found when nutrient enrichment was

low and fish populations were high (Figures 4Bii,iv and 3C). The mechanism by which high portfolio effects occurred was that lowering levels of nutrient enrichment in the presence of fish reduced local and increased meta-ecosystem stability (increased $CV\alpha$ and reduced $CV\gamma$; Figure 4B)—a mechanism that supports theoretical expectations. Importantly, this mechanism (reduced local and increased meta-ecosystem stability) was strongest for total PP under conditions of increasing fish populations across all levels of variation in nutrient enrichment (Figure S9).

Exploring the synchrony of PP dynamics provided further support for theoretical expectations of the mechanisms that generate strong portfolio effects, whereby the expectation is that the greatest portfolio effects will be found under conditions of highly variable and asynchronous dynamics across local systems. We found that increased nutrient enrichment increased synchrony and greater fish population sizes reduced synchrony in PP across local ecosystems reduced and increased portfolio effects, respectively (Figures S10 and S11). These mechanisms resulted in a synergistic interaction between fish dynamics and nutrient enrichment, whereby fish populations always buffered against the negative effect of nutrient enrichment and increased portfolio effects (Figure 4C). A control model with no fish movement and consistent nutrient input demonstrated that the mechanisms by which these factors mediate portfolio effects across the seagrass meta-ecosystem are not a function of the innate dynamics in our model (Figure S12).

3.3 | Do Portfolio Effects Promote Ecosystem Primary Production?

Portfolio effects did not strongly influence total and aboveground PP. Both total and aboveground PP were highest at low and intermediate portfolio effects, respectively (Figure 4). Instead, PP was driven primarily by the amount of nutrient enrichment and the size of the fish population for aboveground PP (Figure 5A) and almost exclusively by the amount of nutrient enrichment for total PP (Figure 5B). Neither variation in nutrient enrichment nor fish connectivity had strong effects on total or aboveground PP (Figure 5A,B). Interestingly, aboveground PP was positively affected by greater local and meta-ecosystem stability (Figure 5A), but total PP was relatively invariant to stability at either scale (Figure 5B). These trends emerged because enrichment was the primary driver of production, but fish populations, which have a weaker influence on PP per se, had stronger effects on measures of stability.

4 | Discussion

Given the increase in frequency and magnitude by which anthropogenic disturbances are impacting ecosystems independently and interactively, managers are seeking to implement mechanisms that increase stability and resilience by either helping ecosystems resist changes to, or recover from, disturbances. Promoting portfolio effects offers one mechanism to maintain the services an ecosystem provides and thus promote stability in the face of erratic but persistent perturbations by considering the scale at which the perturbations impact ecosystems. Our
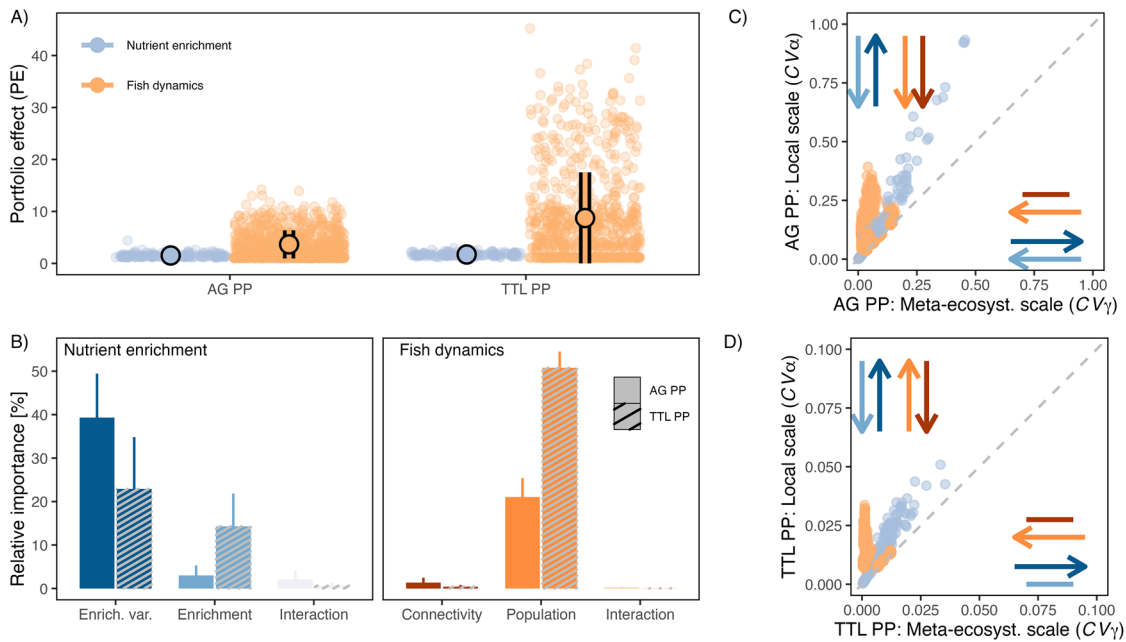
FIGURE 3 | (A) Mean portfolio effects of aboveground (AG PP) and total (TTL PP) primary production for models that include nutrient enrichment (no fish) and fish dynamics (no anthropogenic nutrient enrichment). Circles indicate the mean and error bars indicate standard deviation. (B) The relative importance, that is, contribution to model R^2, of explanatory variables for portfolio effects (PE = $CV\alpha/CV\gamma$) associated with nutrient enrichment alone (blue colors) and fish dynamics alone (orange colors). AG and TTL indicate models for aboveground and total primary production, respectively. "Enrich. var." indicates the variability of abiotic nutrient enrichment to different local systems. "Enrichment" indicates the total amount of abiotic nutrients being supplied to the whole system, for example, high, medium, and low. (C, D) demonstrate model outputs to allow comparison with our hypotheses from Figure 1B. Specifically, they show the plotted values from model simulations (colored datapoints) for the coefficient of variation on local ($CV\alpha$) and meta-ecosystem scales ($CV\gamma$) for aboveground (AG PP) and total (TTL PP) primary production, respectively. The dashed line indicates the 1:1 line—datapoints above this line indicate portfolio effects. Arrows in C and D indicate the direction of change in CV with increased nutrient enrichment (Enrichment var or Enrichment; blue arrows) and fish dynamics (connectivity or population; orange arrows) for the respective explanatory variables found in B and are identified by color—a flat line indicates no or little effect on CV.

study provides a novel advance on how this approach may be implemented in fragmented coastal ecosystems because it identifies the mechanisms by which (1) volatile climate-driven storms that cause spatially and temporally heterogeneous nutrient enrichment and (2) diminishing fish populations independently and interactively influence stability at local and meta-ecosystem scales. Specifically, we show that erratic nutrient enrichment reduces the stability of local and meta-ecosystem seagrass production, but high fish biomass, that is, reflecting what has been observed in empirical systems (Andskog, Layman, and Allgeier 2023), has an interactive effect that synergistically increases portfolio effects primarily by increasing meta-ecosystems stability. Importantly, our model does not assess stability in the context of extremely large disturbances and does not fully reflect the complexities of the real world. Nonetheless, we underscore that the urgency for conservation in coastal ecosystems necessitates models such as ours to inform initial conservation strategies that can be implemented and studied in an adaptive management framework.

A central finding from our study was the strength by which fish dynamics and nutrient enrichment interacted to mediate production dynamics and stability at local and meta-ecosystem scales. In isolation, fish dynamics drove the strongest portfolio effects because larger populations moving across the local ecosystems, irrespective of levels of connectivity, reduced local and increased

meta-ecosystem stability of total PP (Figure 3D). In contrast, portfolio effects driven by the independent effects of nutrient enrichment were mediated primarily by spatial variation in the distribution of nutrients that decreased both local and meta-ecosystem stability (Figure 3C,D). However, when modeled in conjunction, the interaction between nutrient enrichment and fish population size was synergistic, whereby the positive effect of fish population size on portfolio effects was disproportionately greater when nutrient enrichment levels were low relative to when they were high. This occurred because (1) high levels of enrichment stabilized dynamics at both scales and (2) fish population size reduced stability at the local scale but contributed to greater stability at the meta-ecosystem scale. The importance of these factors was highlighted by our control model that showed the innate dynamics of our model did not influence the stability of PP at any scale or portfolio effects across the meta-ecosystem, emphasizing the importance of fish and nutrient enrichment as drivers of stability in these seagrass ecosystems. Our findings underscore that integrating traditional conservation efforts to reduce nutrient enrichment and overfishing, with multiple, connected management units could increase the stability of the services provided by the aggregate system even in the face of anthropogenic disturbances.

A counterintuitive outcome of our study was the relatively weak role of fish connectivity in maintaining measures of stability
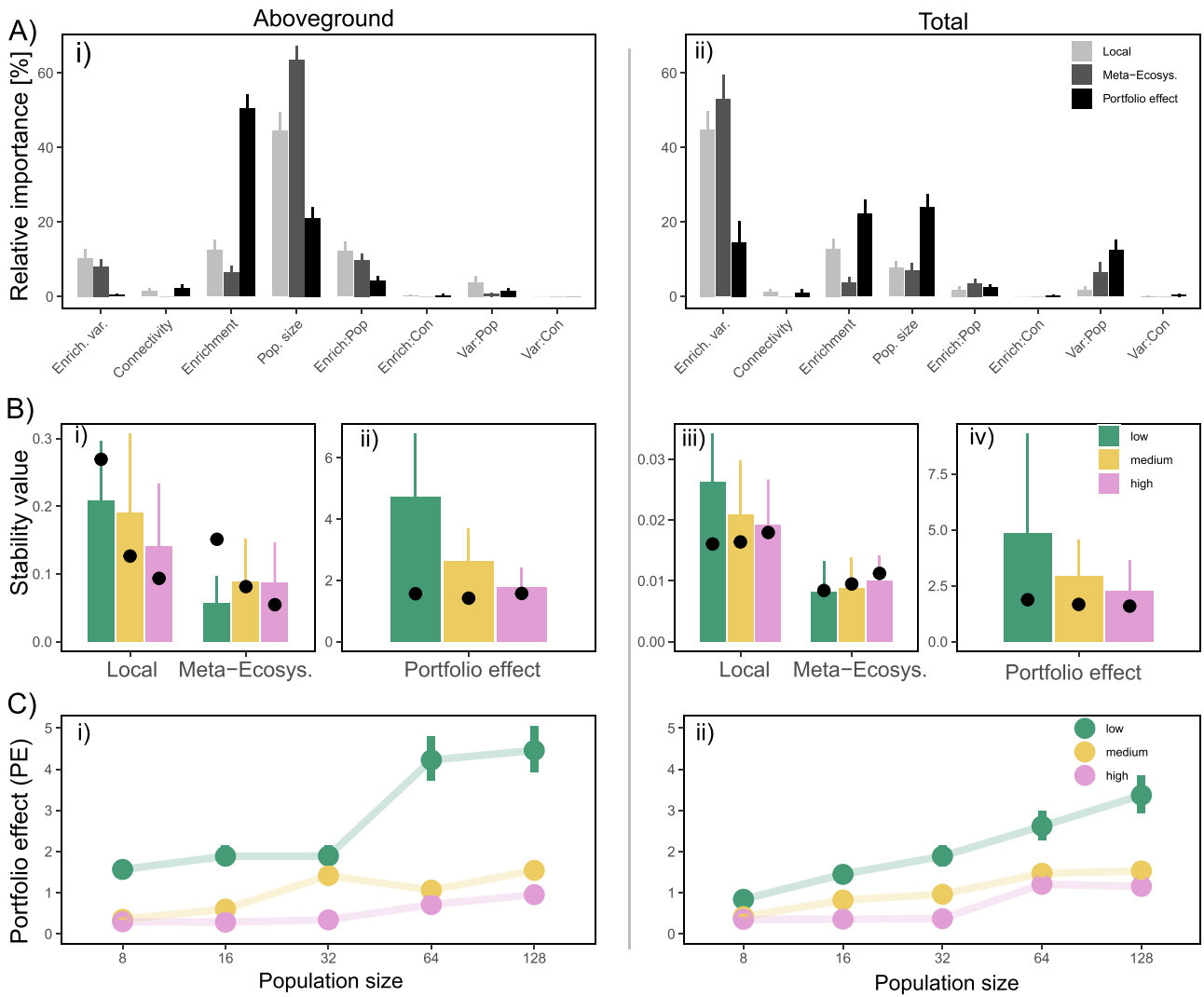
FIGURE 4 | (A) The relative importance, that is, contribution to the model R^2, of different predictor variables from the best linear model (based on AICc) explaining variation in different measures of stability (local, meta-ecosystem scale, and portfolio effects—noted by bars with different markings) for aboveground (Ai) and total primary production (Aii). Models included variation in nutrient enrichment and fish dynamics. (B) Mean estimates of local and meta-ecosystem stability as a measure of *CV*—the lower the value, the greater the stability (Bi, iii) and portfolio effects—the higher the value, the stronger the PEs (Bii, iv) for aboveground (Bi, ii) and total (Biii, iv) primary production at each level of nutrient enrichment (indicated by color). Error bars indicate standard deviation. The solid black points identify the relative values when simulations do not include fish dynamics (determined in Question 1—see Figure 2A,C,D), demonstrating that fish consistently strengthen portfolio effects (and other measures of stability). (C) Marginal means for portfolio effects at different levels of fish population size and nutrient enrichment for aboveground (i) and total primary production (ii).

at the local and meta-ecosystem scale. There is an increase in interest in the role of consumers in mediating ecosystem dynamics in freshwater (C. L. Atkinson et al. 2017), marine (Allgeier, Burkepile, and Layman 2017; Bianchi et al. 2021), and terrestrial ecosystems (Schmitz et al. 2018), and their role as drivers of nutrient and energy pathways is also central to recent theoretical advances in meta-ecosystem theory (Marleau et al. 2010; Marleau, Guichard, and Loreau 2015; Gounand et al. 2014; Ellis-Soto et al. 2021; Peller, Marleau, and Guichard 2021; Rizzuto et al. 2024). Our study provides novel perspectives on the role of consumer movement because instead of the more typical approach focusing on dispersal (Harrison et al. 2020), we focus on the foraging behavior of a common and commercially important fish species (*H. plumierii*) that is a critical driver of nutrient flow in these ecosystems (Odgen and Ehrlich 1977; Meyer, Schultz, and

Helfman 1983; Allgeier et al. 2014) and a key driver of PP around artificial reefs in seagrass beds in the Caribbean (Allgeier et al. 2018; Andskog, Layman, and Allgeier 2023).

We hypothesize that fish connectivity had weak effects on measures of stability because of the mechanisms by which *Thalassia testudinum*, the dominant seagrass species in the Caribbean and in our model environment, allocates nutrients for production. This species persists in low-nutrient environments and, when exposed to surplus nutrients, allocates them first to belowground production (Layman, Allgeier, and Montaña 2016). Only when belowground production reaches a certain capacity (Layman, Allgeier, and Montaña 2016; Esquivel, Hesselbarth, and Allgeier 2022) are nutrients then allocated to aboveground dynamics. This allocation scheme, which is common among
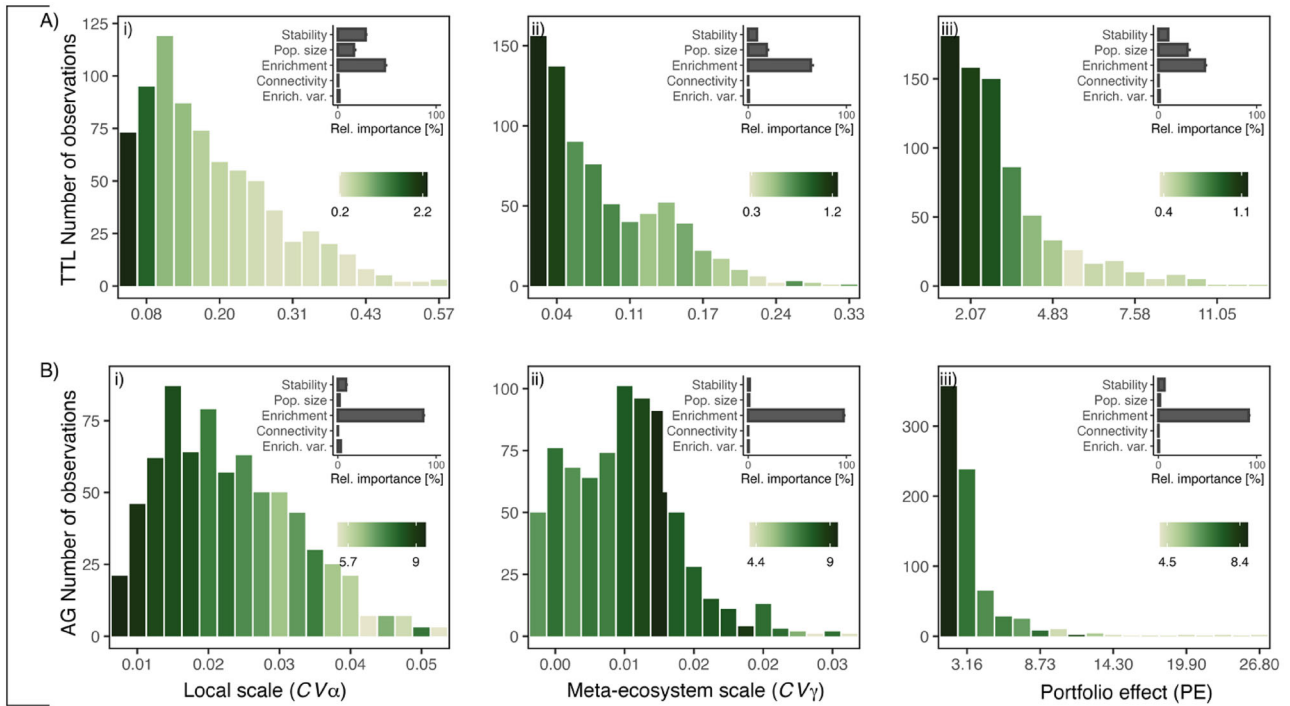
FIGURE 5 | Histograms of local ($CV\alpha$), meta-ecosystem scale ($CV\gamma$) stability, and portfolio effects for aboveground (A) and total (B) primary production from all model runs that include all combinations of variation in nutrient enrichment and fish dynamics ($n = 750$). Green color on each plot indicated the relative primary production ($g\,m^{-2}\,day^{-1}$) at each level of stability. Inset figures indicate the relative importance, that is, contribution to the model R^2, of the model (primary production $\sim CV$/portfolio effect + nutrient enrichment + spatial variation + population size + connectivity). Parameters not shown on the plot indicate lack of significance.

plants in nutrient-poor environments (Chapin 1980), can buffer production dynamics from short-term variability because excess nutrients stored in the roots can maintain production when nutrient availability is low. Thus, to some extent, these dynamics decoupled the temporal scales between enrichment from fish moving into local ecosystems and seagrass growth. It is also the reason that total PP is generally more stable than aboveground PP, as belowground PP accounts for the majority of the total production in these systems. In contrast to connectivity, larger fish populations destabilized local total PP simply because the number of fish in local ecosystems varied temporally (even though their total number was always consistent because fish did not emigrate from or immigrate to the meta-ecosystems).

Portfolio theory typically focuses on the stabilization of some measure of returns over time but is often not related directly to the total productivity of a system (Nie et al. 2023). Understanding the nature of this relationship is relevant when considering the implications of portfolio effects for ecosystem services, as most services are underpinned by the PP of an ecosystem. We found that portfolio effects are strongest under low and intermediate production, and this is driven primarily by the relative amount of nutrient enrichment to the system. This is consistent with our findings that portfolio effects are highest with high fish population sizes and low nutrient enrichment. Interestingly, the mechanisms by which this occurred in our study are twofold: (1) the amount of nutrient enrichment had weak stabilizing effects on local ecosystem production (stabilizing primarily through belowground production), which in turn led to reductions in portfolio effects (Figure S8) and (2) variability in nutrient enrichment

destabilized local production, as predicted, but concomitantly also destabilized meta-ecosystem stability, thus reducing portfolio effects (Figure S8). In contrast, fish-mediated nutrients, which at the highest input levels were similar to that of the lowest anthropogenic nutrient input rates, were always a stabilizing force for seagrass at the meta-ecosystem scale. These findings suggest an important trade-off between maintaining high stability in production and high production in AR-seagrass systems.

A key strength of our study is that we use robust system-specific empirical data on fish energetics and movement, seagrass production dynamics, and nutrient enrichment rates to parameterize the models. Yet, for this same reason, caution should be taken when extrapolating specific findings to other systems. For example, the physiological parameters associated with seagrass may not be appropriate for temperate seagrass ecosystems. Nonetheless, findings from our study are relevant for the restoration and management of oligotrophic tropical coastal ecosystems in two key ways. First, we show that fish dynamics consistently promote portfolio effects according to theoretical expectations and that these dynamics synergistically promote portfolio effects when they occur in conjunction with nutrient enrichment dynamics. Therefore, our findings suggest that in oligotrophic tropical coastal ecosystems maintaining fish populations represents a management priority over reducing anthropogenic nutrient enrichment, but that management efforts will be maximized with efforts that also reduce nutrient enrichment. Second, seagrass ecosystems are globally threatened and increasingly fragmented, which require conservation efforts to adapt if they are to work with ever-reducing management unit

size. We show that artificial reefs, because they promote fish aggregations, provide a useful mechanism to increase productivity in small seagrass patches with yet unquantified potential to increase seagrass extent and that spatially coupling these patches in a meta-ecosystem framework can greatly promote stability in the services the aggregate ecosystem can provide. Collectively, these findings provide a useful roadmap for implementing needed marine spatial planning or networks of marine protected areas in one of the most impaired ecosystem types globally.

Author Contributions

Both authors contributed to the development of concepts, questions, model structure, and statistical analysis. M.H.K.H. coded the model and performed statistical analyses. Both authors wrote the manuscript.

Data Availability Statement

All analysis codes can be found at https://doi.org/10.5281/zenodo.10671464. All model source code can be found at https://github.com/Allgeier-Lab/meta.arrR.

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Supporting Information

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