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RESEARCH ARTICLE

The Mechanisms Underpinning Zoogeochemistry

Rising temperature non-additively alters how different dimensions of biodiversity affect ecosystem-scale processes

Sean Pierce Richards[1] | **Maximilian H. K. Hesselbarth**[1,2] | **Jacob Edward Allgeier**[1]

[1]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA

[2]International Institute for Applied Systems Analysis (IIASA), Biodiversity Ecology and Conservation Research Group, Laxenburg, Austria

Correspondence
Sean Pierce Richards
Email: sprich@umich.edu

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Abstract

1. Improving our ability to predict when and how biodiversity mediates ecosystem processes requires greater consideration of how different dimensions of biodiversity, such as species-specific physiology or behaviour, can independently and interactively affect these processes. Global change drivers, such as increased temperature, can also alter organismal metabolism in ways that may interact with different dimensions of biodiversity, further reducing predictability.
2. Using an individual-based model of a seagrass-patch reef ecosystem, we quantified (1) how species-level physiological traits of two common reef fish, (2) foraging behaviours and (3) increasing water temperatures interacted to affect ecosystem-level primary production (PP) via consumer nutrient excretion.
3. At ambient temperature, physiology more strongly regulated ecosystem PP than behaviour, which primarily influenced where PP occurred. Increased temperature strongly independently resulted in greater ecosystem PP until a threshold whereafter ecosystem PP drastically decreased for both fish species. Temperature strongly interacted with physiology to non-additively increase ecosystem PP but only weakly interacted with behaviour due to underlying metabolic mechanisms.
4. Our study highlights the importance of species-level physiology for regulating ecological processes and that increased temperatures will alter biodiversity-ecosystem process relationships in unpredictable ways.
5. Importantly, because we quantified both the direct effects of physiology and behaviour on nutrient supply via excretion and the indirect effects of this on primary production, we were able to determine that quantifying consumer-mediated nutrient supply alone was insufficient to predict ecosystem-scale primary production.
6. Our findings emphasize that understanding the mechanisms by which biodiversity affects ecosystems requires quantifying ecosystem-scale responses, which also places findings at scales relevant for conservation.

KEYWORDS
artificial reef, behaviour, biodiversity ecosystem function, global change, individual-based modelling, physiology

1 | INTRODUCTION

It is well-established that biodiversity is an important driver of ecosystem processes (Loreau et al., 2001; Tilman et al., 2014). Yet, biodiversity is multidimensional, encompassing variation from the ecosystem level down to the genetic level. Identifying which aspects of biodiversity are important drivers of ecosystem processes is a critical challenge in ecology (Duffy, 2009; Hulot et al., 2000), particularly in biodiverse marine ecosystems (Brandl et al., 2019). Dimensions of biodiversity that have received substantial attention include between-species variation—differences among species that are captured by metrics such as species-specific physiological traits. For example, growth rate, body size and nutritional demand are often taxon-specific (Allgeier, Wenger, & Layman, 2020; Blackburn & Gaston, 1994; Kearney & White, 2012; Morais & Bellwood, 2018). These physiological traits, especially growth rate and body size, ultimately govern metabolism and individual-level processes such as consumption and excretion; in turn, these processes may exert strong control on zoogeochemical processes such as nutrient cycling, primary production and energy flow (Allgeier et al., 2021; McIntyre et al., 2007; McNaughton et al., 1997; Vanni et al., 2002).

Functional diversity, here defined as variation in multiple resource-acquisition traits within assemblages of coexisting species (Harrison et al., 2020), is another dimension of biodiversity that has important consequences for zoogeochemistry. In contrast to species physiology, functional diversity can describe traits that are commonly shared among species (i.e. functional group) (Chapin et al., 1997; Green et al., 2022; Hooper et al., 2005). For example, behavioural traits such as foraging behaviour govern how an organism moves as it acquires resources throughout an ecosystem (e.g. grazers, browsers) and thus can be important for the distribution of nutrients across ecosystems (Allgeier, Cline, et al., 2020; Ellis-Soto et al., 2021; Meyer et al., 1983; Schmitz, 2008; Schmitz et al., 2018). In fact, movement behaviour provides a mechanistic basis by which organisms may profoundly modulate zoogeochemical processes across ecosystem types (e.g. herbivore trampling grasses and soils, fish schooling around corals, herd migrations to calving sites) (Ferraro et al., 2024; Meyer et al., 1983; Schmitz et al., 2018; Schrama et al., 2013). Yet, organismal behaviour can also influence metabolism (greater movement increases metabolism) and thus, like physiological traits, can also govern ecosystem processes such as nutrient cycling and primary production (Brownscombe et al., 2017; Seibel & Drazen, 2007). While many studies focus on quantifying the relationship between biodiversity (e.g. species richness within a community) and ecosystem processes (Chapin et al., 1998; Hooper et al., 2005; Hooper & Vitousek, 1997), understanding the relative importance of other dimensions of biodiversity for driving ecosystem processes—and possibly more importantly how the ecosystem itself responds—is needed if we are to understand the mechanisms that underpin these relationships (Meyer & Leroux, 2023).

Considering how different dimensions of biodiversity affect ecosystem processes also provides the opportunity to understand potential interactions with global change. For instance, increased temperatures are particularly consequential for species that exist at the extreme edge of their thermal tolerances because they may be sensitive to shifts in temperature—especially in marine ecosystems (Pinsky et al., 2019; Sunday et al., 2010). Over prolonged temporal scales, altered temperatures may cause species responses such as adaptation or shifts in spatial distributions (Braun et al., 2023; Easterling et al., 2000; Ma et al., 2024; Perry et al., 2005). Yet, heat waves operate over shorter time scales and are projected to increase in intensity, duration and frequency, particularly in marine systems. Physiological responses to increased temperature are often described by a species-specific thermal performance curve (Rezende & Bozinovic, 2019) where metabolism increases with temperature up to some optimum after which metabolism declines (Dillon et al., 2010). Because processes such as consumption and excretion are driven by metabolism, they should follow similar trajectories provided that sufficient resources are available to satisfy energetic demands of increased metabolism; organisms may therefore modulate their foraging behaviour in response to increased temperature such that individuals spend more time searching for resources in the environment. Yet, by moving more, individual metabolism further increases, potentially changing the net amount and location of processes such as consumption and excretion. Depending on the strength of this temperature–behaviour interaction, ecosystem processes such as nutrient cycling and primary production may increase, or ultimately decrease, in response to shifts in foraging behaviour. Disentangling the interactions between ecosystem processes and species physiology, behaviour and increasing temperatures is necessary to improve mechanistic understanding of how biodiversity effects on ecosystems may be altered with future global change.

Enriching our understanding of the drivers of ecosystem processes such as nutrient cycling via consumer excretion is ecologically important but is limited because it alone provides no information about how an ecosystem responds to this resource provided by the consumers. For instance, temperature may modulate metabolic processes and excretion, but ecosystem-scale impacts may not be observed due to other biotic and abiotic interactions. Here, we quantify the relative importance of species physiology, organism foraging behaviour and changing temperature for nutrient supply via excretion and specifically focus on its implications for driving the quantity and spatial variation in ecosystem-level primary production using a model system of reef fish on patch reefs in an oligotrophic seagrass bed. Quantifying the ecological importance of different dimensions of biodiversity is challenging in field experiments (Petrovskii & Petrovskaya, 2012), especially when quantifying their implications for ecosystem-scale processes (Covino et al. 2018). Thus, here we use a spatially explicit, individual-based model (IBM) of fish populations on patch reefs to quantify the relative importance of the physiology of two dominant species of reef fish and two behavioural traits for ecosystem primary production. Specifically, we simulated populations of squirrelfish (*Holocentrus adscensionis*) and white grunts (*Haemulon plumierii*) that foraged either in the open seascape or locally around the patch reef (behaviours that typify grunts and squirrelfish, respectively). We asked the following questions:

(Q1) Does species physiology (a metric of interspecies diversity) or foraging behaviour (a metric of functional diversity) have a greater effect on ecosystem primary production?

(Q2) How do changing temperatures directly affect primary production and modify any effects of physiology and behaviour on primary production?

We predict that physiology will more strongly affect primary production than behaviour because species-specific growth rates and body sizes constantly affect metabolism, whereas the behaviour-mediated changes in metabolism are limited to only those times when individuals move (Figure 1a,b). We also predict that primary production will increase with temperature until species' physiological tolerances are reached, and the interaction between temperature and physiology will be stronger than the interaction between temperature and behaviour because growth rate and body size largely govern metabolism, which is itself further modulated by temperature (Figure 1c–e).

2 | MATERIALS AND METHODS

IBMs are useful to understand how variation of individual-level processes such as growth, respiration and movement scale in

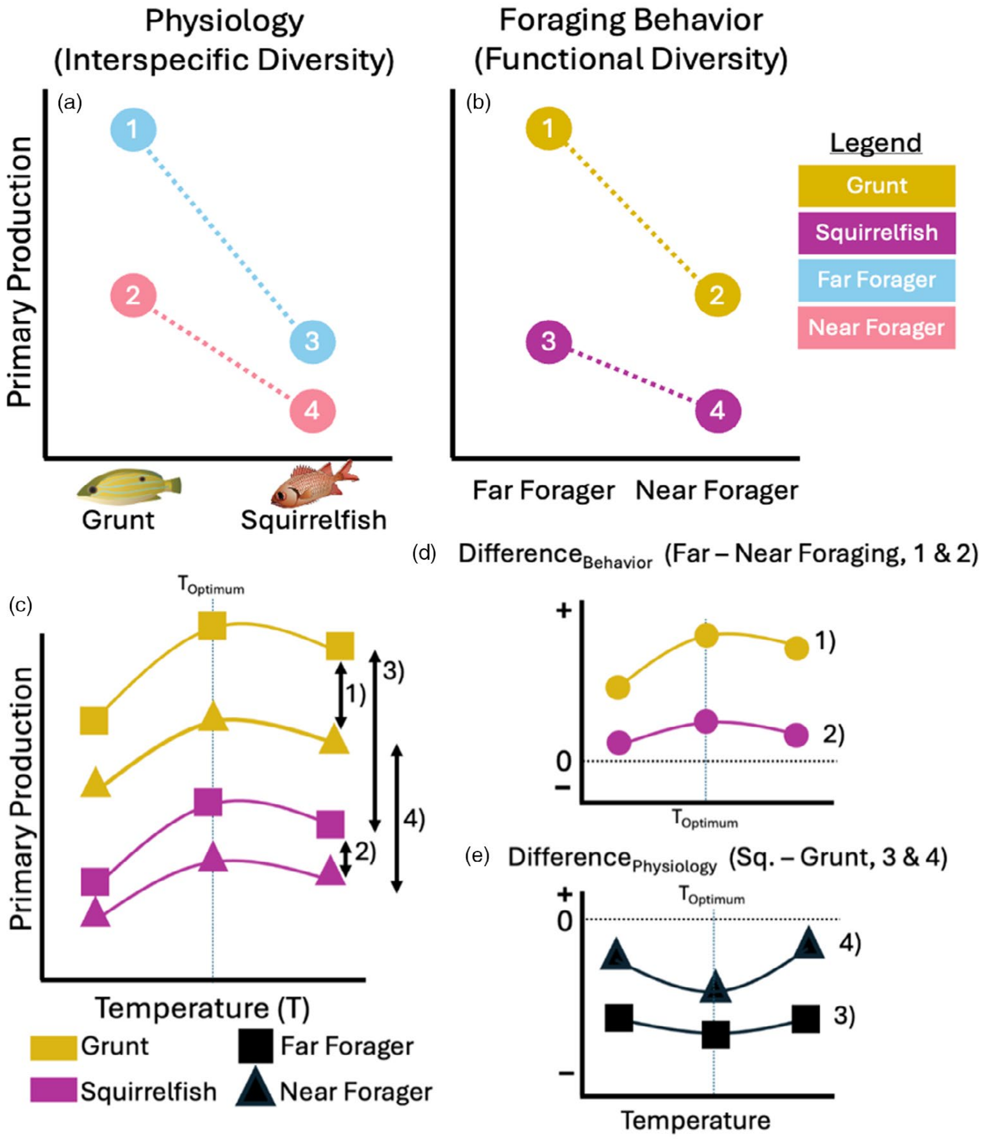

FIGURE 1 Visualization of hypotheses for research question 1 (a, b) and 2 (c–e). (a) Grunts will generate more primary production than squirrelfish because of larger body sizes. (b) Far foragers will generate more primary production than near foragers because of their increased movement and metabolisms. Enumerated points track the same datapoint represented on the different plots. Colours denote the specific physiology–behaviour combination. Lines visualize interaction effects. (c) Predicted ecosystem primary production with numbers indicating the difference between two curves. (d) Differences between behaviours (Diff$_{Behavior}$, Far—Near foraging) for grunts and squirrelfish physiologies. The numbers (1, 2) reference the differences between lines of the same colour in panel (c). (e) Differences between species physiologies (Diff$_{Physiology}$, Squirrelfish—Grunt) for Far and Near foraging behaviours. The numbers (3,4) reference the differences between lines of the same point shape in panel (c).

complex systems (e.g. populations, communities, ecosystems and networks) to impact ecosystem-level processes such as primary production across spatiotemporal scales and environmental conditions. We extended the previously published single-species IBM, Artificial Reefs in R ('arrR') (Esquivel et al., 2022) to include multiple fish species. Our IBM tracked nutrients while simulating fish movement, foraging and excretion in an oligotrophic, subtropical seagrass–patch reef ecosystem. Seagrass patches were simulated in the IBM using a single-nutrient seagrass production model conceptually based on reactive nitrogen (*Seagrass Processes*), and fish populations were simulated using bioenergetic models based on nutrient demand parameterized with empirical data (*Fish Processes*) (Allgeier, 2021). We simulated two common coral reef fish species—squirrelfish and white grunt—on patch reefs in The Bahamas that differ in their distinct physiologies and foraging behaviours. These fish represent both interspecific diversity and functional diversity since they explicitly contrast in physiology (grunts are larger and grow slower, squirrelfish are smaller and grow faster) and foraging behaviour (grunts leave the reef to forage, squirrelfish are reef-resident). All processes were simulated for 20 years using discrete 120-min timesteps to observe long-term ecosystem-scale impacts. The model environment was closed and comprised of a 50 × 50 m grid of seagrass cells with a 1-m^2 patch reef cell in the center around which fish individuals may shelter. The spatial extent and grain were selected because underlying empirical data were collected at this grain. Our model was two-dimensional because vertical space use was not a focus of this study. A full description of model processes using the Overview, Design concepts, Details (ODD) and Transparent and Comprehensive Model Evaluation (TRACE) frameworks is available in the Supporting Information (Grimm et al., 2020). All model code, written in R (R Core Team, 2024) with core functions implemented in C++ using the Rcpp package (Eddelbuettel & Francois, 2011), and analysis code is available on GitHub (https://github.com/Allgeier-Lab/arrR/tree/multi-species, https://github.com/Allgeier-Lab/Biodiv_Temp). Our study did not require ethical approval since it was simulation-based.

2.1 | Seagrass processes

Each 1-m^2 cell of the model environment had five nutrient pools: above-ground (AG) seagrass biomass, below-ground (BG) seagrass biomass, water-column nutrients, detritus biomass and detrital fish biomass (Figure S1). Nutrients flowed through the pools, thereby driving seagrass production, by the following processes once per day (equivalent to 12 model timesteps). (1) Water-column nutrients, the primary source of nutrients for marine autotrophs, were assimilated by both AG and BG seagrass and differentially allocated to AG or BG production whereby, below a certain biomass threshold, BG was prioritized over AG production. (2) A proportion of seagrass biomass was sloughed to the detrital pool. (3) A proportion of detrital biomass was remineralized into water-column nutrients. (4) Lastly, proportions of the nutrient and detritus pools were diffused among neighbouring cells at every iteration to more closely model water-column dynamics (see ODD in Supporting Information for further information). Finally, due to data limitation, the seagrass production model did not account for seagrass physiological responses to temperature, which could certainly improve our model.

2.2 | Fish processes

Fish individuals were regulated by nutrients, not energy, to reliably approximate nutrient excretion (Schiettekatte et al., 2020). For each model timestep, fish individuals interacted with the seagrass environment while undergoing four major processes according to their species-specific parameters (see *Species Physiology* below): (1) Fish moved stochastically throughout the environment according to two mutually exclusive foraging behaviours (near the reef, farther from the reef—see *Movement Behaviours*) that controlled where individuals consumed resources (detrital pool). (2) Fish respired according to their current biomass, activity, and ambient temperature. (3) Fish grew according to their continuous, nonlinear Von Bertalanffy growth functions by consuming detrital nutrients, which are apportioned to growth and the remaining nutrients are excreted and egested back to the water column (and ultimately taken up by seagrass for production). The fish in our model often consume invertebrates, but our model did not have invertebrates because of lacking data on invertebrate densities. As such, fish consumed nutrients directly from the detrital pool sufficient to meet their nutrient demand after accounting for nutrient loss from trophic transfers (the fish normally eat invertebrates that are at least one trophic level above the seagrass) and egestion. (4) Fish potentially experienced two sources of mortality (i) when body length approached species-specific maximum size, or (ii) when food resources were insufficient for survival (see Supporting Information, for further information). In both cases, individuals that died were replaced as juvenile fish, and remaining fish biomass from the deceased individual was returned to the detrital fish biomass pool, which was decomposed into general detrital biomass concurrently with remineralization (although at different rates). Because we were only interested in ecosystem processes, we did not simulate population dynamics (Figure S1).

2.3 | Species physiology

Species physiology was implemented into the bioenergetic models through the following species-specific parameters or functions: length–weight relationships (Munsterman, unpublished data), growth rate (Froese & Pauly, 2024), maximum body size (Froese & Pauly, 2024), body nutrient content (Allgeier et al., 2015) and organismal respiration (Hanson et al., 1994). Respiration parameters described nonlinear metabolic responses to increasing temperature that mirrored thermal performance curves. No species-specific data were available for respiration parameters, so both species received the same respiration parameters (Yellow Perch—Hanson et al., 1994) for the bioenergetic models rather than arbitrarily choosing different values (Hanson et al., 1994). Assimilation efficiency may also vary with temperature and could modulate the relationship between consumption and excretion (Shelley & Johnson, 2022) but was not simulated due to limited data. Importantly, these parameters have been previously shown to generate model outcomes that accurately reflect empirical data collected in this system (Esquivel et al., 2022; Hesselbarth & Allgeier, 2024; Munsterman et al., 2024). Further descriptions of all model processes and core parameters can be found in Esquivel et al. (2022), Munsterman et al. (2024) and the Supporting Information. Any values there were updated values based on improved empirical data are reported in Table S1.

2.4 | Movement Behaviours

Two distinct fish movement behaviours were simulated. These behaviours were unrelated to species physiology and characterize the behaviour of the two common reef fish used in our study: grunts typically forage away from the reef on which they shelter (Far-foraging), squirrelfish typically forage proximally to the reef on which they shelter (Near-foraging). Although behaviour can mean many things, for example diet, schooling, migration, movement behaviour, in particular, is important for ecosystem processes because it directly affected where individuals consumed resources and excreted nutrients (Allgeier, Cline, et al., 2020). Individual movement behaviour was either: (1) Far-Foraging—individuals left the reef to forage, moved stochastically in the open seagrass while consuming food and filling energy reserves, and returned to shelter at the reef until these reserves were depleted; or (2) Near-Foraging—individuals constantly sheltered and consumed local food resources at the reef. Metabolic costs of movement behaviour were simulated using an activity modifier that modulated metabolic costs according to movement distance (Hanson et al. 1994, Allgeier, Cline, et al., 2020); thus, far-foraging fish had higher activity than near-foraging fish meaning they had higher energetic demands and excretion rates.

2.5 | Simulations

Populations of 20, 40 and 80 fish were simulated in the model environment based on empirical population estimates from experimental reefs in The Bahamas (Allgeier et al., 2013). Abundance was constrained to preserve variation in population size structure and retain species-specific size–metabolism relationships. To isolate the importance of physiology and behaviour, the simulated population was entirely composed of one of the two fish species (i.e. squirrelfish or grunts; Figure 2) with one of two behaviours (i.e. far-foraging or near-foraging; Figure 2). Starting water column and detrital nutrients were initialized to remain stable in the absence of fish (Esquivel et al., 2022). A burn-in phase (wherein no fish processes were simulated) was used for 10% of the total model time (2 of 20 total years) to further ensure the model environment was stable. Each model scenario (Figure 2) was replicated 40 times.

We conducted a sensitivity analysis of the IBM to identify key parameters that may influence model results. Specifically, we first performed a local sensitivity analysis by individually varying 22 total parameters that influence the following components of the model: seagrass nutrient content and production allocation, diffusion and mineralization rates, movement distance, growth rate and respiration rates. Most parameters were simulated by increasing or reducing the initial value by 5%, that is a + − 10% range. The ranges for optimum and maximum temperatures of the respiration function were constrained to more realistic values (Optimum: 32, 34, 36, 38, 39; Maximum: 37, 38, 40, 42, 44). Sensitivity analysis scenarios simulated populations of 40 grunt and squirrelfish individuals for 20 total years, 10% of which was a burn-in period to ensure stabilized processes, and each scenario was replicated 10 times. Second, we conducted a more advanced sensitivity analysis by identifying key parameters that generated a change in model outputs (primary production and primary production per unit biomass—see below—at the ecosystem, reef and open seagrass scales) was greater than 5% relative to model outputs for initial parameters. We performed a Sobol global sensitivity analysis (Sobol' et al., 2007) to identify potential interactions between the key parameters. Parameters were sampled using Latin hypercube sampling ($n = 250$, Mckay et al., 2000). Since maximum respiration temperature must be greater than optimum respiration temperature, we performed two Sobol global sensitivity analyses where maximum respiration temperature was allowed to vary ±10% while optimum respiration temperature was varied −10% (and vice versa).

We tested our hypotheses with two response variables—total primary production (AG + BG production g $\text{day}^{-1}\,\text{m}^{-2}$—herein PP) and primary production per unit biomass of the total fish population biomass (g $\text{day}^{-1}\,\text{m}^{-2}\,\text{g Fish}^{-1}$—herein PPB). Quantifying PPB allowed us to account for differences in total biomass for populations of the two fish species with the same abundance since grunts could attain larger maximum body sizes than squirrelfish (an important species-specific physiological trait that we did not want to constrain) and therefore have greater population biomass. Average total population biomass was calculated at the final timestep to account for variation during the model run. PPB can be interpreted as the efficiency by which fish populations influenced PP. At the end of each model run, PP and PPB were calculated for the entire 50 × 50 m model environment. Because differences in movement behaviour may change the spatial distribution of nutrient supply and, in turn, primary production, we also separated ecosystem production into reef (within five meters of the reef) and open seagrass (beyond five metres from the reef) production (Figure 2, Allgeier, unpublished data). To test our first hypothesis (Figure 1a,b), we simulated four independent populations in a full factorial combination of physiology and behaviour at the mean annual water temperature of the field site in The Bahamas where empirical research that informed this model was conducted, 26°C (Allgeier, unpublished data; 'Aqualink' 2022) (Figure 2). To test

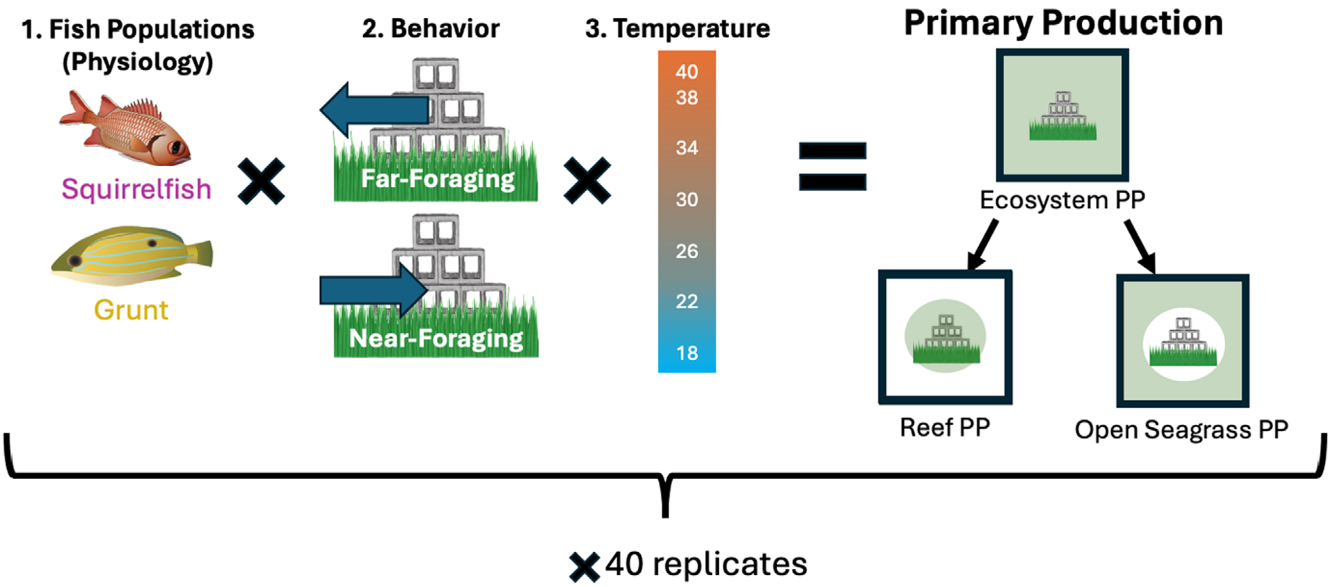

FIGURE 2 Conceptual diagram of simulation experiment including scenarios and metrics. Physiologies differed by growth rates, maximum body size, body nutrient content, and length-weight relationships. Behaviours were either far- or near-foraging relative to the reef. Illustrations by K. S. Munsterman.

our second hypothesis (Figure 1c–e), we used the same factorial combinates as for the first hypothesis but simulated them ranging from extreme low to high water temperatures: 18°C, 22°C, 26°C, 30°C, 34°C, 38°C and 40°C (Figure 2).

Because simulation experiments can produce an infinite number of replicates, frequentist significance tests are not applicable (White et al., 2014); however, we reported average values and 95% confidence intervals for each treatment to determine whether there were ecologically meaningful differences among treatments. To highlight any cryptic interactions among physiology, behaviour, and temperature in our second hypothesis, we quantified the mean differences between behaviours ($\text{Diff}_{\text{Behavior}} = \text{PP}_{\text{Far-Forage}} - \text{PP}_{\text{Near-Forage}}$; Figure 1d) and physiologies ($\text{Diff}_{\text{Physiology}} = \text{PP}_{\text{Squirrelfish}} - \text{PP}_{\text{Grunt}}$; Figure 1e) for both PP and PPB at each temperature level. Specifically, we calculated $\text{Diff}_{\text{Behavior}}$ for both squirrelfish and grunts and $\text{Diff}_{\text{Physiology}}$ for both far- and near-foragers. This produced a relative metric whereby positive differences indicated stronger effects of far-foragers and squirrelfish. Likewise, negative differences indicated stronger effects of near-foragers and grunts. Variation in differences across the temperature gradient illustrated interactions with temperature. This also allowed us to examine whether physiology modulated the effects of temperature and behaviour on PP and PPB by showing if trends in $\text{Diff}_{\text{Behavior}}$ across temperature were different for squirrelfish and grunts (and vice versa).

3 | RESULTS

To account for potential effects of total fish biomass, all models were run for population sizes of 20, 40, and 80 individuals; however, herein we present only results for runs with 40 individuals for two reasons. First, 40 individuals is an abundance that is common on experimental patch reefs in The Bahamas (Allgeier et al., 2013); second, all results were either consistent across all population sizes (Q1), or there were minor differences across population sizes, but the overall trends were comparable (Q2). Results for all population sizes are presented in Figures S2–S7 (Richards et al. 2026). Plots of PP and PPB with 95% confidence intervals are presented in Supporting Information because confidence intervals were small relative to the mean values (Figure S8).

3.1 | Sensitivity analysis

The local sensitivity analysis revealed that ecosystem, reef, and open seagrass PP were sensitive to four, six and two parameters (seven unique parameters), respectively, whereby ±5% of the parameter resulted in a > 5% change in model output. These parameters were: above-ground seagrass nutrient content, proportion of seagrass biomass sloughed to detrital biomass, slope and intercept of respiration function, maximum and optimum respiration temperature, and the rate at which respiration increases over low water temperature. Ecosystem, reef and open seagrass PPB were sensitive to the same parameters as their PP counterparts, respectively (Table S2).

The Sobol global sensitivity analysis did not identify any interactions among the seven significant parameters identified in the local sensitivity analysis (total effects were not significantly different from main effects). The optimum respiration temperature, proportion of seagrass biomass sloughed, slope of respiration function and above-ground seagrass nutrient content had the largest effect sizes across all model responses (Figures S9 and S10).

3.2 | Q1: Does species physiology or behaviour have a greater effect on ecosystem primary production?

At average water temperature (26°C), there were strong effects of species physiology and weak effects of behaviour on ecosystem-level PP, yet the effect of behaviour on PP near the reef and in open seagrass was stronger than that on ecosystem-level PP (Figure 3a). Specifically, grunts had a greater positive effect on PP than squirrelfish at all scales, and far-foraging behaviour had a greater positive effect on PP than near-foraging behaviour at the ecosystem and open seagrass scales (Figure 3a). However, there was not an ecologically meaningful difference in the effect of grunt foraging behaviour on ecosystem-scale PP because the 95% confidence intervals overlapped (Figure S8A).

As with net effects on PP, species physiology had a greater effect than behaviour on PPB (Figure 3b). Squirrelfish populations increased PPB more than grunts (Figure 3b) in contrast to their relative effects on PP because squirrelfish had higher metabolisms (higher growth rates, smaller body size) and thus excreted more nutrients per unit mass (Figure S11). Behaviour did not have ecologically meaningful effects on the efficiency by which the populations affected ecosystem-scale PP but did for reef- and open seagrass-scale PP (PPB—Figure 3b; Figure S8D–F).

3.3 | Q2: How do changing temperatures directly affect primary production and modify any effects of physiology and behaviour on primary production?

The relative importance of species physiology versus behaviour across a gradient of temperatures was consistent with findings from Q1. Specifically, at almost every temperature level, grunts had a greater positive effect on PP than squirrelfish, and far-foragers generated more PP than near-foragers at the open seagrass scale (Figure 4a). Similarly, the effect of behaviour on ecosystem-scale PP

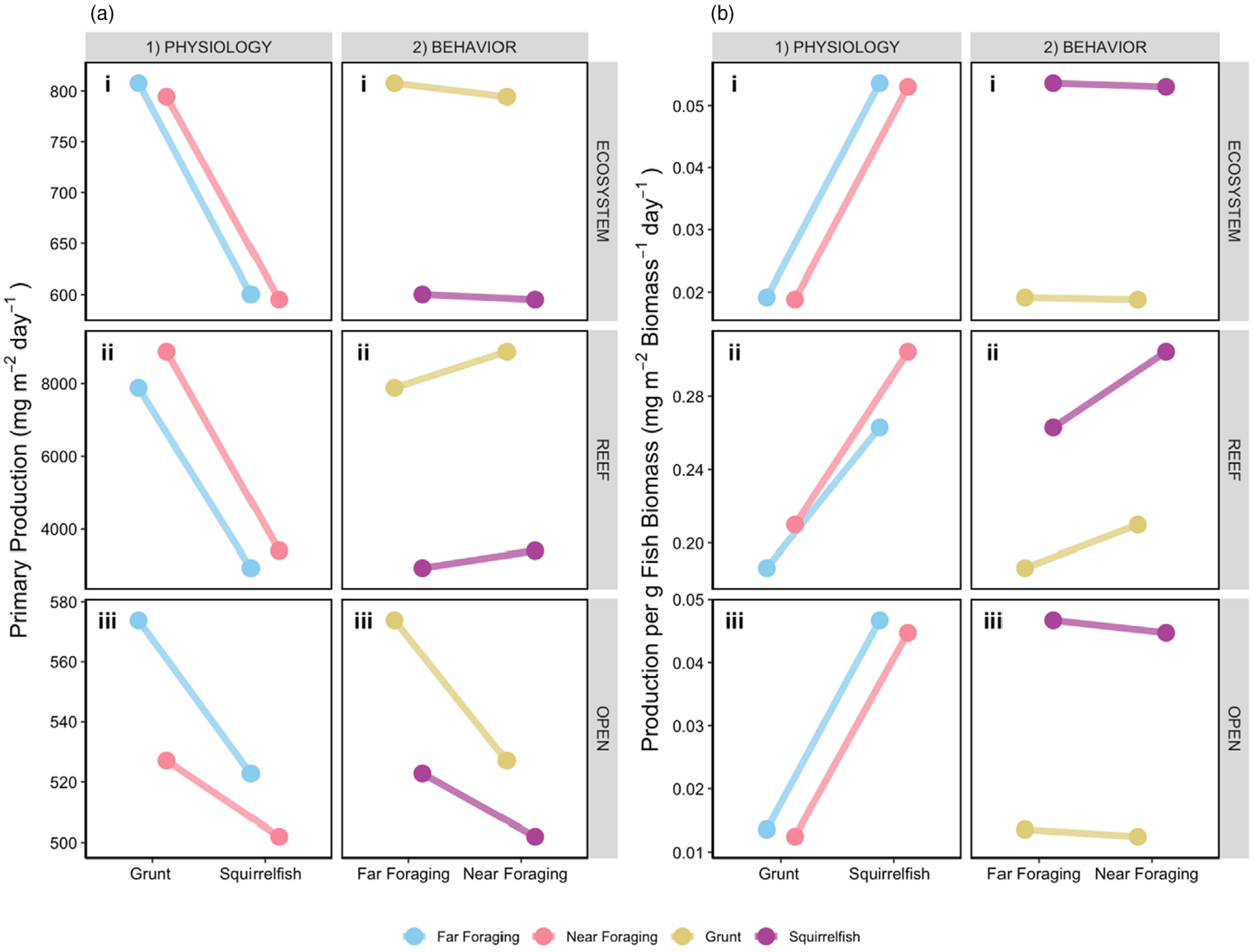

FIGURE 3 Interaction plots of mean (a) seagrass primary production (PP) and (b) PP per unit fish biomass (PPB). Colours indicate subsets of categories on the x axis. Rows indicate different spatial subsets of the model environment, and columns indicate the relevant comparison. Physiology and behaviour columns visualize the same data with different x-axes to highlight the greater effects of physiology relative to behaviour. Note differences in scales among panels.

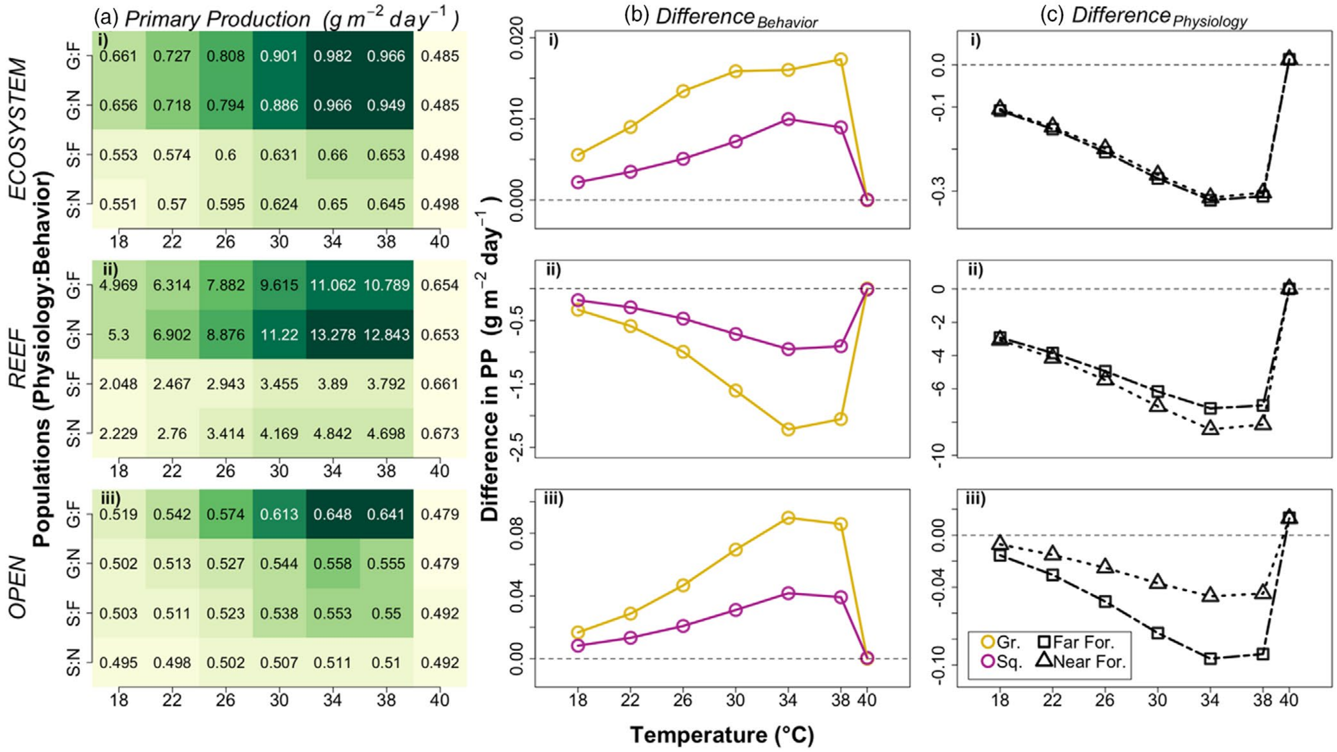

FIGURE 4 (a) Effects of temperature on the relative importance of physiology and behaviour for primary production. Physiology is either grunt (G) or squirrelfish (S), and behaviour is either far-foraging (F) or near-foraging (N). Values within cells are average primary productivity. Darker green colours indicate greater primary production. (b) The difference in the effect of behaviour on net PP for each species, for example the difference between a grunt that forages far and a grunt that forages near the reef. (c) The differences in the effect of species for net PP for each behaviour, for example the difference between a far-forager that is a grunt (Gr.) and a far-forager that is a squirrelfish (Sq.). Note differences in scales among panels.

was not ecologically meaningful across all temperatures (Figure S8A). Also consistent with Q1, squirrelfish were more efficient at generating PP per unit mass (PPB) than grunts at every temperature level for the entire ecosystem, near the reef and open seagrass. Behaviour had strong effects on PPB near the reef and became ecologically meaningful in the open seagrass at intermediate temperatures (Figure 5a; Figure S8E,F).

Irrespective of physiology or behaviour, the relationships between temperature and PP and PPB mirrored thermal performance curves such that both PP and PPB increased with temperature until 34°C whereafter both decreased precipitously to a minimum PP and PPB at 40°C (Figures 4a and 5a). At the thermal extremes (18°C and 40°C), there were few ecologically meaningful effects of behaviour (Figures 4a and 5a; Figure S8). This result was consistent for the entire ecosystem, near the reef and in open seagrass.

The effect of behaviour on PP and PPB (i.e. Diff$_{\text{Behavior}}$) changed notably across the temperature gradient although the magnitude of the effect was relatively small compared to total PP. Diff$_{\text{Behavior}}$ was greater for grunts than for squirrelfish when considering PP but was reversed when considering PPB. Interestingly, Diff$_{\text{Behavior}}$ for both PP and PPB had a distinct nonlinear relationship with temperature that resembled a thermal performance curve demonstrating an interaction whereby the effect of behaviour changed across different temperatures. The fact that the lines for squirrelfish and grunts did not map directly onto one another for Diff$_{\text{Behavior}}$ suggested a three-way interaction between temperature, behaviour and physiology whereby the effect of behaviour was different for each species and these differences changed across temperature (Figures 4b and 5b). However, upon examining organismal metabolism using the total amount of consumer-derived nutrients (the established driver of PP and PPB), there were relatively small differences in the total amount of excreted nutrients between behaviour types across the temperature range (Figure S11). This instead showed that behaviour was simply a scalar for metabolism that only became relevant when placed in the context of physiology's effect on metabolism.

In contrast, although Diff$_{\text{Physiology}}$ for PP and PPB also followed a similar thermal performance curve pattern, the magnitude of the difference was much greater than for Diff$_{\text{Behavior}}$ and accounted for more of total PP, demonstrating strong effects of physiology on PP and PPB that interacted with increasing temperatures (Figures 4c and 5c). Diff$_{\text{Physiology}}$ was relatively similar for far- and near-foraging behaviours at the ecosystem-level (no three-way interaction) but was different near the reef and in the open seagrass, suggesting a three-way interaction and providing support that the effects of behaviour were largely associated with where PP occurred (i.e. the reef) and not the total PP in the ecosystem (Figures 4c and 5c).

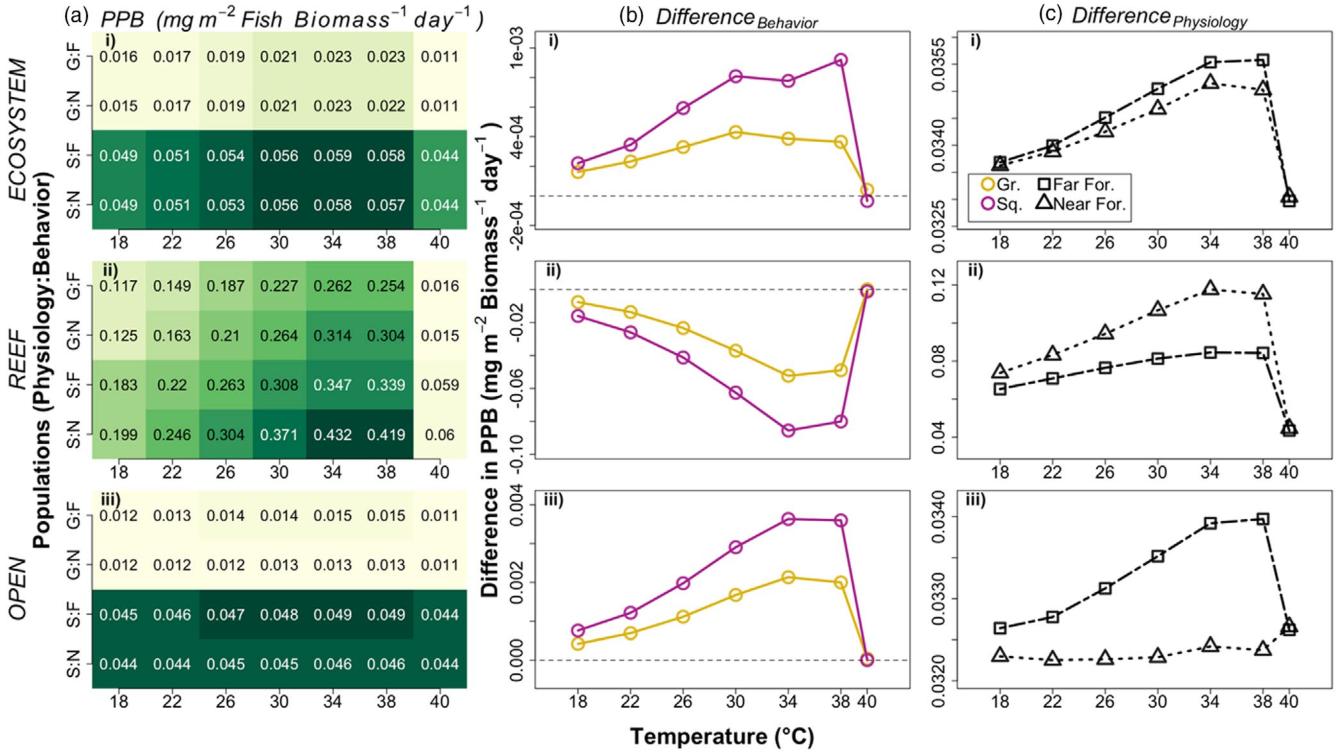

FIGURE 5 (a) Effects of temperature on the relative importance of physiology and behaviour for primary production per unit biomass (PPB). Physiology is either grunt (G) or squirrelfish (S), and behaviour is either far-foraging (F) or near-foraging (N). Values within cells are average PPB. Darker green colours indicate greater PPB. (b) The difference in the effect of behaviour on net PPB for each species, e.g., the difference between a grunt that forages far and a grunt that forages near the reef. (c) The differences in the effect of species for net PPB for each behaviour, for example the difference between a far-forager that is a grunt and a far-forager that is a squirrelfish. Note differences in scales among panels.

4 | DISCUSSION

The relationships between biodiversity and ecosystem processes are complex, and our understanding of them is constantly evolving (Cardinale et al., 2012; Johnson et al., 2024; Reiss et al., 2009; Wardle, 2016). Yet, a mechanistic understanding of how different dimensions of biodiversity drive ecosystem function is essential because conservation efficacy can vary based on the prioritized conservation target (e.g. species or functional richness, evenness, ecosystem function, trophic structure) (Dade et al., 2019). Adding to this, global change is severely affecting many dimensions of biodiversity simultaneously as well as the climate in which they persist. Thus, understanding not only biodiversity-ecosystem process relationships but also how the mechanisms themselves may be shifting under global change is critical for ensuring effective conservation measures in future (Sage, 2020). Designing empirical experiments that isolate the different dimensions of biodiversity from one another and can quantify their effects at scales relevant for conservation is challenging if not impossible (Schindler, 1998; Testa et al., 2017). Thus, we took advantage of a well-vetted ecosystem model that is (1) underpinned by extensive empirical data of a subtropical ecosystem in which many species exist near their thermal extremes, (2) has the flexibility to factorially manipulate the individually modelled consumers and (3) allows processes to be quantified at the scale of the ecosystem (Esquivel et al., 2022). An important contribution of our study is that we extend understanding of how two dimensions of biodiversity affect the ecosystem by quantifying both the ecologically relevant ecosystem processes (nutrient supply) and actual responses from the ecosystem itself (primary production), which are potentially more valuable for conservation. Our study demonstrates that both dimensions of biodiversity we studied have significant but unequal effects on ecosystem-scale processes and that they non-additively interact with increasing warmer temperatures in seagrass-patch reef ecosystems.

A central finding of our study was that primary production was more strongly affected by species physiology than organismal behaviour. Fully understanding this result requires disentangling how two key features of physiology, body size and growth rates, interactively influence metabolism and thus mediate nutrient recycling via excretion. Small fish have higher metabolisms and excrete more nutrients per unit mass, but large fish can supply more total nutrients due to larger body sizes; thus, total nutrients supplied via excretion increase with the size of the fish (Allgeier et al., 2015; Vanni & McIntyre, 2016). For our simulation study, we compared the effects of grunts and squirrelfish based on equal abundances and not biomass because body size is a species-level physiological trait and controlling for biomass would require strongly restricting body size for grunts since they have a larger maximum size than squirrelfish. As a result, grunts attained greater biomass and thus supplied more nutrients than squirrelfish at the same abundance, thereby enhancing PP more than squirrelfish. However, since squirrelfish were on average smaller and since smaller fish have a higher metabolism, they supplied more nutrients per unit biomass, which was reflected in the higher efficiency of PP per unit biomass (PPB). Adding to this, squirrelfish also have higher growth rates than grunts, which further increase metabolic rates and thus also contributed to their greater effect on PPB. These results suggest that if the maintenance of ecological processes is a focus of conservation, then population size structure and how biomass is distributed in the population should be points of consideration (Munsterman et al., 2024).

We found that behaviour had a weaker effect on ecosystem-scale PP than species physiology but had strong effects on the spatial distribution of PP within the ecosystem. We predicted that far-foraging fish populations would enhance ecosystem-scale PP because greater individual activity should increase the total nutrient supply from fish due to heightened metabolism (Allgeier, Cline, et al., 2020; Brownscombe et al., 2017). The total amount of nutrients supplied via excretion was, indeed, higher for far-foraging fish than for near-foraging fish (Figure S11), but the increase in nutrients was not sufficiently strong to elicit a noticeable effect on ecosystem-level PP. This is because seagrass production in the *Thalassia testudinum* (TT)-dominated system has been shown to be highly regulated by nutrient allocation rules (Layman et al., 2016), and our model reflects this empirical understanding. Specifically, under low ambient availability of nutrients, seagrass shunt most nutrients to below-ground production. As nutrient availability increases, the plant allocates more nutrients to above-ground production which can accelerate nonlinearly because of increased uptake rates with greater above-ground biomass (Esquivel et al., 2022; Layman et al., 2016). In our study, even though far-foraging behaviour did increase nutrient supply at the ecosystem-scale or PP farther from the reef, nutrients were never sufficiently concentrated in any single area to initiate nonlinear above-ground production dynamics and thus did not increase ecosystem-level production (note we did not include any shifts in seagrass community composition in our model, but empirical results from the study system show the primary effect on the seagrass community is *on T. testudinum* biomass and density, (Allgeier et al., 2018)). Said dynamics could be initiated with sufficient movement to proximal patch reefs (although this was not tested here to control for variable occupancy of different reef sites). Studies of large ungulates in terrestrial systems have examined the effects of movement on consumer-mediated nutrient redistribution, demonstrating that such nutrients were concentrated in high-use areas such as bedding sites and trails (Murray et al., 2014), which can be utilized by other organisms (Veldhuis et al., 2018) and facilitate feedbacks and biogeochemical hotspots that fuel ecosystem processes (Ferraro et al., 2024). Our findings fit into an established framework that considers how the quantity, quality, timing and duration of consumer-mediated nutrient input affects ecosystem responses (Subalusky & Post, 2019) and emphasize that quantifying the ecosystem response to processes such as consumption or excretion, as opposed to these processes alone, is important to fully understand the ecosystem-level implications of consumer biodiversity.

Climate change is rapidly affecting ecosystems globally, with clear consequences for marine ecosystems (Burrows et al., 2011; Lenoir et al., 2020; Pinsky et al., 2019; Poloczanska et al., 2013). We identified three important interactions among physiology, behaviour and temperature: (1) the effect of physiology on PP was greater with increased temperature, (2) the effect of behaviour on PP was greater with increased temperature and (3) the effect of physiology was greater with increased temperature and varied between behaviours. These non-additive effects likely emerged because the three factors all independently regulated organism respiration, and thus consumption and excretion, in different ways whereby: (1) species physiology governed metabolic costs according to a nonlinear growth function determined by species growth rate and maximum body size, (2) temperature changed individual metabolisms according to a non-linear temperature response function and (3) foraging behaviour modulated individual movement, which acted as a scalar on any existing metabolic costs. The physiology–temperature interaction was the strongest and most non-additive because it compounded two nonlinear relationships—the metabolic response to temperature and metabolic costs from species-specific growth functions—resulting in substantial increases in individual excretion (Figure S11). In comparison, the behaviour–temperature and physiology–behaviour–temperature interactions were much weaker because outcomes were largely reflections of physiological effects that were amplified through behaviour's effect on metabolism. Specifically, far-foraging behaviour resulted in more movement than the near-foraging behaviour, leading to augmented individual activity that scaled metabolism already affected by physiology. Although foraging behaviour may not drive non-additive interaction effects on ecosystem primary production, it is still important to consider behaviour in the context of ecosystem function because other behavioural characteristics such as diet that were not simulated herein could potentially interact with temperature and increases in individual consumption from greater temperatures and physiological changes may have unpredictable effects on movement (Alfonso et al., 2021). For example, individuals may leave the system, change their foraging behaviour, or overgraze with significant repercussions for ecosystem processes—all of which we were not able to account for in our model due to the lack of empirical data on which to base these responses.

Animals mediate ecosystem-scale nutrient cycling and carbon dynamics, yet multiple mechanisms may explain how animals underpin these zoogeochemical processes (Meyer & Leroux, 2023; Schmitz et al., 2018). Major advances have identified two dimensions of biodiversity—organismal behaviour (e.g. foraging, birthing, site fidelity) and species physiology (e.g. growth rate, respiration, biomass)—as key mechanisms of zoogeochemistry, but comparisons isolating the relative importance of each dimension of biodiversity remain lacking (Allgeier et al., 2021; Ferraro et al., 2024). Distilling the independent and interactive effects of these mechanisms on zoogeochemical processes is necessary to resolve long-standing debates in ecology (Duffy, 2009; Hulot et al., 2000; Schmitz et al., 2018). In this study, we found that both dimensions of biodiversity exhibited ecologically meaningful effects whereby foraging behaviour modulated the distribution of primary production within the ecosystem and species physiology exerted even greater control over ecosystem-scale primary production. Our study provides further support for the conservation of biodiversity but underscores the importance of considering which ecosystem processes conservation should target and how biodiversity-ecosystem process relationships may change as the planet continues to warm.

Spatially explicit IBMs are a powerful tool to test ecologically relevant questions that are challenging to conduct experimentally in situ (e.g. Grimm et al., 2017; Tao et al., 2024; Zheng et al., 2024). Yet, there are inherent constraints to the realism of such simulations. There were three primary limitations in our study. First, our model environment was closed, and individuals neither immigrated nor emigrated from the simulation environment. This assumption may be unrealistic but allowed us to specifically isolate the effect of the key factors of interest without confounding nutrient inputs or losses. Second, to isolate the effects of each dimension of biodiversity, we were forced to simulate independent fish populations rather than interacting fish communities of both species. Although unrealistic, this allowed us to isolate the effects of species physiology and behaviour that would otherwise have been confounded in a community of both species. Third, although the bioenergetic models that underpin species physiology were parameterized with substantial species-level data, we were unable to acquire species-specific respiration parameters because they were unavailable in the literature and are challenging to obtain empirically (Rummer et al., 2016). Respiration-related parameters comprised most of the parameters identified in the local and global sensitivity analyses, so improving species-specific respiration data would further inform our conclusions about ecological processes.

Although using the same respiration parameters for both fish limits comparisons of the two species' physiology, especially in the context of temperature change, arbitrarily selecting different respiration parameters would introduce additional uncertainty and potentially confound our findings. Our results produced an expected thermal performance curve, albeit with excretion (Figure S11) and primary production as proxies (Figures 4a and 5a), demonstrating that these respiration parameters are indeed sufficient to replicate realistic trends (Rezende & Bozinovic, 2019). Further, even with identical respiration parameters, there are observable differences among the two fish species in excretion (Figure S11) and primary production (Figures 4a and 5a) because of interactions with other well-parameterized physiological components such as growth rates and body size. We expect that the effects of species physiology and behaviour on PP will remain robust even though estimates of PP may change as parameterization of metabolic responses of fish and seagrass improves.

The maintenance of biodiversity is a long-standing goal of conservation, but achieving effective policy and management requires robust scientific evidence of how biodiversity impacts ecosystems. Our study identifies three key challenges that, if addressed, can increase the applicability of biodiversity research for conservation and policy. First, we show that quantifying the flux of nutrients provided by fishes is not sufficient to understand their impacts on the ecosystem because of, often cryptic, nutrient allocation dynamics by seagrass. This underscores the need to measure beyond processes provided by consumers and include how the ecosystem responds to these processes. Second, we show that both dimensions of biodiversity that we explored were important for different aspects of ecosystem PP, but that species-specific physiology has by far the strongest effects on ecosystem PP. Finally, our study shows that the effects of all dimensions of biodiversity on ecosystem PP unpredictably change under scenarios of realistic increases in temperature because of the nonlinear way temperature affects metabolism and its non-additive interactions with behaviour and species physiology. Our study provides strong support for the species-level approach to biodiversity conservation but likewise clearly illustrates the need to consider which ecosystem processes conservation should target and how biodiversity–ecosystem process relationships may change as the planet continues to warm.

AUTHOR CONTRIBUTIONS

Sean P. Richards and Jacob E. Allgeier conceived the project with important contributions from Maximilian H.K. Hesselbarth during implementation. Sean P. Richards coded an updated model and conducted analyses with input from Maximilian H.K. Hesselbarth and Jacob E. Allgeier. Sean P. Richards drafted the initial manuscript with substantial contributions from Jacob E. Allgeier and Maximilian H.K. Hesselbarth. All authors gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from GitHub: https://github.com/Allgeier-Lab/Biodiv_Temp. Analysis reported in this article can be reproduced using scripts available on GitHub. All individual-based model code may be found on GitHub: https://github.com/Allgeier-Lab/arrR/tree/multi-species.

STATEMENT ON INCLUSION

Our study was a modelling experiment based on over 15 years of empirical research conducted in The Bahamas. Although no local data were collected for this experiment, our group has partnered extensively with local organizations and fishing communities in The Bahamas to conduct our research, creating employment and outreach opportunities that have enriched our science.

ORCID

Sean Pierce Richards https://orcid.org/0000-0001-8707-1220
Maximilian H. K. Hesselbarth https://orcid.org/0000-0003-1125-9918
Jacob Edward Allgeier https://orcid.org/0000-0002-9005-6432

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Values for all individual-based model parameters.

Table S2. Results of local sensitivity analysis. Parameters were changed one at a time across a ±10% range in 5% increments. No results are reported for changes in model outputs that were less than 5%. Reported outputs are for populations of 40 grunt and squirrelfish individuals, respectively. PP, primary production; PPB, primary production per unit biomass.

Figure S1. Conceptual overview of all model subprocesses (from Esquivel et al., 2022).

Figure S2. Q1 results for 20 individuals. Interaction plots of mean (A) seagrass primary production (PP) and (B) PP per unit fish biomass (PPB). Colours indicate subsets of categories on the x axis. Rows indicate different spatial subsets of the model environment. Columns indicate the relevant comparison. Physiology and behaviour columns visualize the same data with different x-axes to highlight the greater effects of physiology relative to behaviour.

Figure S3. Q1 results for 80 individuals. Interaction plots of mean (A) seagrass primary production (PP) and (B) PP per unit fish biomass (PPB). Colours indicate subsets of categories on the x axis. Rows indicate different spatial subsets of the model environment. Columns indicate the relevant comparison. Physiology and behaviour columns visualize the same data with different x-axes to highlight the greater effects of physiology relative to behaviour.

Figure S4. Q2 PP results for 20 individuals. (A) Effects of temperature on the relative importance of behaviour and physiology for primary production. Physiology is either grunt (G) or squirrelfish (S), and behaviour is either far-foraging (F) or near-foraging (N). Values within cells are average primary productivity. Darker green colours indicate greater primary productivity. (B) The difference in the effect of behaviour on net PP for each species, e.g., the difference between a grunt that forages far and a grunt that forages near the reef. (C) The differences in the effect of species for net PP for each behaviour, for example the difference between a far-forager that is a grunt (Gr.) and a far-forager that is a squirrelfish (Sq.).

Figure S5. Q2 PP results for 80 individuals. (A) Effects of temperature on the relative importance of behaviour and physiology for primary production. Physiology is either grunt (G) or squirrelfish (S), and behaviour is either far-foraging (F) or near-foraging (N). Values within cells are average primary productivity. Darker green colours indicate greater primary productivity. (B) The difference in the effect of behaviour on net PP for each species, e.g., the difference between a grunt that forages far and a grunt that forages near the reef. (C) The differences in the effect of species for net PP for each behaviour, e.g., the difference between a far-forager that is a grunt (Gr.) and a far-forager that is a squirrelfish (Sq.).

Figure S6. Q2 PPB results for 20 individuals. (A) Effects of temperature on the relative importance of behaviour and physiology for primary production per unit biomass (PPB). Physiology is either grunt (G) or squirrelfish (S), and behaviour is either far-foraging (F) or near-foraging (N). Values within cells are average PPB. Darker green colours indicate greater PPB. (B) The difference in the effect of behaviour on net PPB for each species, for example the difference between a grunt that forages far and a grunt that forages near the reef. (C) The differences in the effect of species for net PPB for each behaviour, for example the difference between a far-forager that is a grunt and a far-forager that is a squirrelfish.

Figure S7. Q2 PPB results for 80 individuals. (A) Effects of temperature on the relative importance of behaviour and physiology for primary production per unit biomass (PPB). Physiology is either grunt (G) or squirrelfish (S), and behaviour is either far-foraging (F) or near-foraging (N). Values within cells are average PPB. Darker green colours indicate greater PPB. (B) The difference in the effect of behaviour on net PPB for each species, for example the difference between a grunt that forages far and a grunt that forages near the reef. (C) The differences in the effect of species for net PPB for each behaviour, for example the difference between a far-forager that is a grunt and a far-forager that is a squirrelfish.

Figure S8. Total primary production and primary production per unit biomass (mean ± 2 standard deviations) for grunts squirrelfish that forage far and near across a gradient of temperature. Overlapping error bars suggest differences between treatments are not ecologically meaningful. Points are intentionally small to visualize error bars.

Figure S9. Main (blue) and total (orange) effect of the Sobol sensitivity analysis including maximum respiration temperature. Only parameters that generated a >5% change in model outputs (total, reef, and open seagrass primary production and primary production per unit biomass–PPB) for a 5% were included. Parameters were sampled using Latin hypercube sampling ($n = 250$).

Figure S10. Main (blue) and total (orange) effect of the Sobol sensitivity analysis including optimum respiration temperature. Only parameters that generated a >5% change in model outputs (total, reef and open seagrass primary production and primary production per unit biomass—PPB) were included. Parameters were sampled using Latin hypercube sampling ($n=250$).

Figure S11. Total excretion for grunts squirrelfish that forage far and near across a gradient of temperature over the entire model run (20 years).

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