

## ECOLOGY

# Individual behavior drives ecosystem function and the impacts of harvest

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Current approaches for biodiversity conservation and management focus on sustaining high levels of diversity among species to maintain ecosystem function. We show that the diversity among individuals within a single population drives function at the ecosystem scale. Specifically, nutrient supply from individual fish differs from the population average >80% of the time, and accounting for this individual variation nearly doubles estimates of nutrients supplied to the ecosystem. We test how management (i.e., selective harvest regimes) can alter ecosystem function and find that strategies targeting more active individuals reduce nutrient supply to the ecosystem up to 69%, a greater effect than body size-selective or nonselective harvest. Findings show that movement behavior at the scale of the individual can have crucial repercussions for the functioning of an entire ecosystem, proving an important challenge to the species-centric definition of biodiversity if the conservation and management of ecosystem function is a primary goal.

## INTRODUCTION

Global efforts to conserve biodiversity are motivated by evidence that trait variability among species promotes the functionality of ecosystems and the services they provide to society (1). However, trait variability exists at many levels of biological organization, challenging ecologists to identify the specific level of organization on which conservation efforts should focus. For example, the stability of fisheries yields has been attributed to trait diversity among populations of the same species (2). Although ecologists understand that trait variation among individuals can exceed that found across all other species within a community (Fig. 1A) (3–6) and can even lead to individual-level dominance of ecological processes [e.g., disease “superspreaders”; (7)], this individual-level trait variation has been largely ignored in traditional approaches to conservation and management of ecosystem function.

Species management often assumes that individuals within populations are roughly equivalent; thus, the loss of any given individual would have similar impacts on ecological processes. For example, in marine fisheries, a common goal is to harvest populations at exploitation rates to achieve maximum sustainable yield (MSY), maintaining population sizes at some fraction of the individuals in an unfished population (8). From this perspective, if trait variation among individuals within an exploited population was negligible (as is often assumed in population models) or if harvest does not select for individual traits, the impacts of fisheries on ecosystem processes would be proportional to harvest; e.g., at 50% of the unfished population size, ecosystem function would be reduced by 50% (Fig. 1B). However, trait variation among individuals is common (4, 9), and most harvest techniques select for specific individual attributes such as body size (10) or bold behavior (11, 12). This is relevant because fisheries management now emphasizes a need for ecosystem-based approaches to improve long-term productivity of multiple exploited

species via the management of an entire ecosystem and its collection of ecological processes (13). However, trait variation is often not accounted for because of the inherent challenges associated with quantifying variation among individuals within populations. Here, we show how selective exploitation strategies interact with variation among individuals to alter ecosystem function, specifically nutrient cycling at an ecosystem scale.

We examined high-resolution movement of individuals within two populations of exploited tropical coastal marine fish species to quantify (i) the importance of individual-level movement behavior for ecosystem-scale nutrient dynamics and (ii) how harvest strategies that select for different traits affect these dynamics. In tropical coastal ecosystems, fish are an essential source of protein for millions of people (14). Fish also represent one of the largest sources of limiting nutrients for primary production via their excretion (15), fueling some of the most productive ecosystems on the planet. Fishing, largely through selective practices such as spearfishing and angling, can reduce ecosystem-scale nutrient supply from fishes in coral reefs (16) and mangroves (17). Consumer-mediated nutrient dynamics fundamentally drive nutrient dynamics and primary production in many ecosystems (18–22) through variation both among (23, 24) and within species (25–27). We take advantage of the integral link between fisheries and consumer-mediated nutrient dynamics in tropical coastal ecosystems as it provides an ideal scenario to understand the importance of individuals for ecosystem function via the mechanism of movement behavior and the associated nutrient translocation.

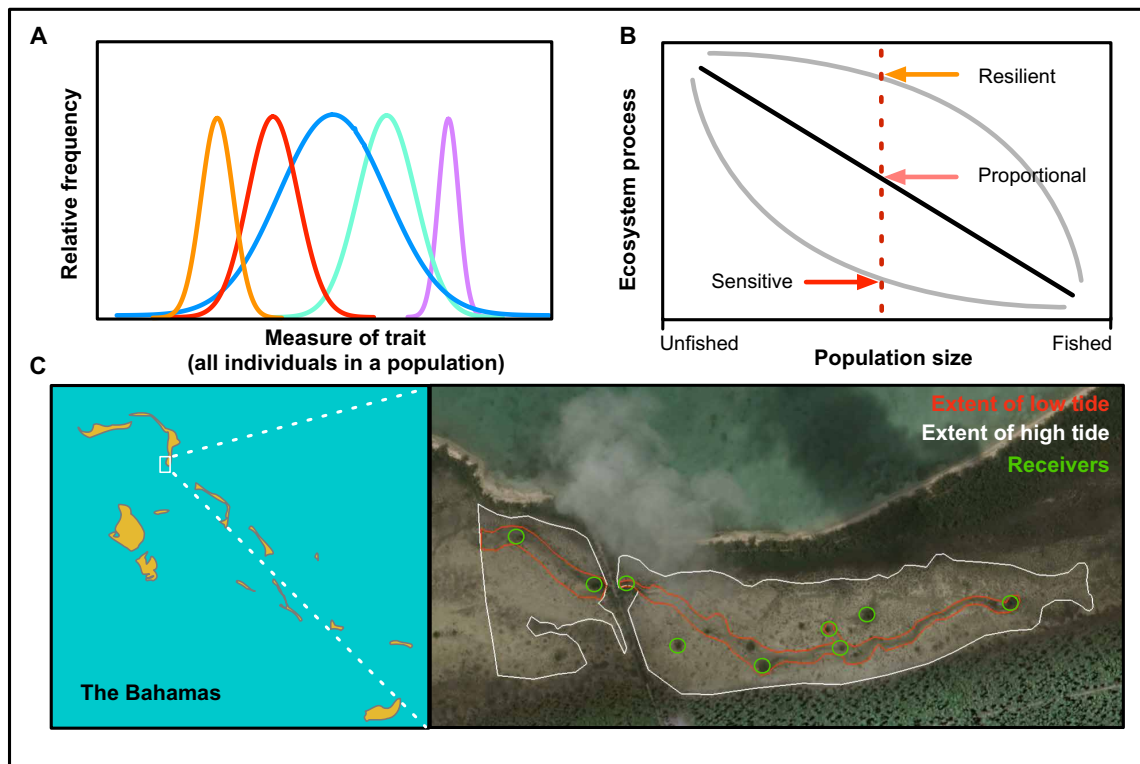
## RESULTS/DISCUSSION

Our first objective was to quantify individual-level variation in movement behavior within the two populations. We used acoustic telemetry to monitor the movement of generalist species, gray snapper (*Lutjanus griseus*) and cubera snapper (*Lutjanus cyanopterus*), in a mangrove estuary in The Bahamas (Fig. 1C and Materials and Methods). The estuary is shallow (<1 m), tidally dominated (i.e., no riverine input) with nine refugia holes (3- to 5-m diameter by 1- to 3-m depth—this accounted for all the areas in the estuary sufficiently large to provide shelter for fishes) in which stationary receivers

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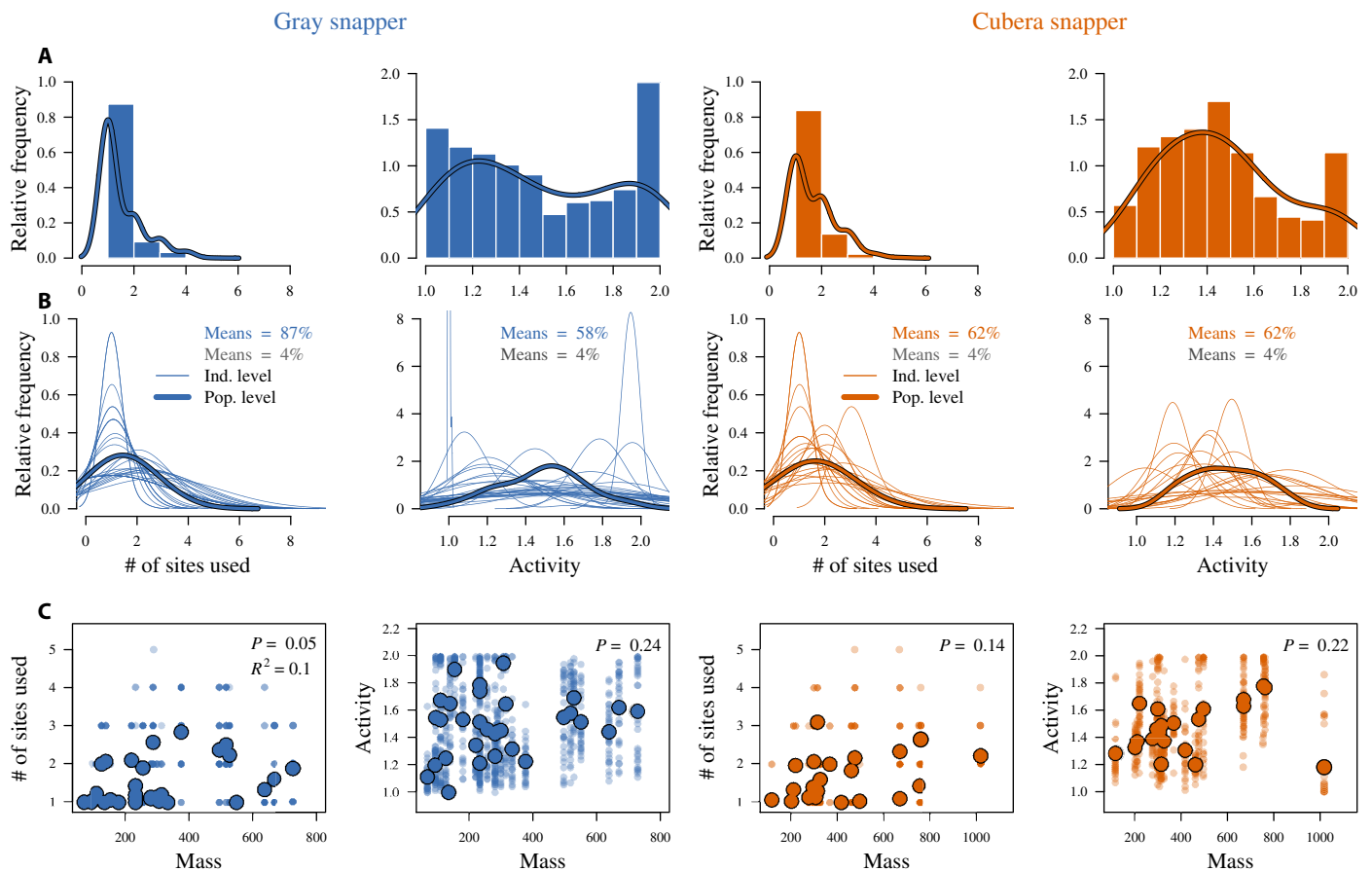
**Fig. 1. Conceptual basis for study and map of study system.** (A) Population-level measures of trait variation for different species (colors) in a community, illustrating that variation among individuals within a single population (e.g., blue line) can exceed that of the entire community. (B) Selective harvest (gray lines) may have differential effects on ecosystem processes (being resilient or sensitive to certain harvest techniques), depending on how and what traits are selected for relative to nonselective harvest (i.e., random removal; black line). Dashed line represents a harvest rate that could result in various consequences for ecosystem processes. (C) Map of Abaco Island, The Bahamas, and satellite image of study location, a mangrove-lined estuary (~11.5 ha; 25°56'28"N, 77°16'26"W). White lines indicate the maximum extent of high tide, red lines indicate the minimum extent of low tide, and green circles indicate acoustic receiver locations.

were located (Fig. 1C). During low tide events, fishes were restricted to refugia holes, whereas during high tide cycles, fishes were able to move freely throughout the estuary to forage (Fig. 1C).

We measured two behavioral traits for each individual: the number of sites used per day and the activity rate per day (a measure of swimming and foraging time; Fig. 2A and Materials and Methods). A typical population-level approach would assume that the mean across all individuals for each day generally reflects individual-level traits. We tested this assumption by comparing the population-level distributions (i.e., sites used per day and activity rate per day averaged across individuals, representing the population-level mean) to each individual-level distribution (i.e., sites used per day and activity rate per day for a single individual) using *t* tests. Between 62 and 86% of individual-level distributions of per-day activity and site use differed from the population-level distributions (Fig. 2B). For comparison, simulated individuals (generated by sampling from normal distributions of activity and site use; Materials and Methods) only differed from population-level distributions 4 to 5% of the time. Neither attribute of behavior was well predicted by body size (Fig. 2C), a finding that is particularly unexpected given that it is commonly assumed that larger animals have a greater tendency for movement (28). These results demonstrate strong individual-level variation in two behavioral traits that are not otherwise well predicted by population-level means or a commonly used ecological covariate (body size). Similar findings in a variety of systems, including various freshwater

species of fishes and zooplankton [see (4)] and herbivorous fishes on coral reefs (29), have stimulated interest in the integrative effects of behavioral traits for ecosystem-scale processes (4, 5).

Our second objective was to scale-up from basic movement attributes to quantify how individual-level variation in behavior influences ecosystem-scale nutrient dynamics. We developed models to “energetically track” individuals over time and estimate their total supply (net excretion) of nitrogen (N) and the extent to which they move N across the ecosystem (translocation). To do this, we constructed bioenergetics models for each individual fish using a genus-specific (*Lutjanus*) model that was parameterized for each individual’s body size (30). These models were applied to time series of individual fish to estimate excretion rates at 20-min time steps for 30 days. At every time step, models were updated on the basis of physiological and environmental attributes that would influence an individual’s metabolic rates: (i) the individual’s current activity (foraging or within a refugia hole, i.e., increased or resting metabolism, respectively) and (ii) the temperature of the surrounding water given an individual’s location (changing over time and space; Materials and Methods). We again used *t* tests to test how well population-level distributions (i.e., the population-level mean generated by averaging across all individuals for each day) were representative of individual-level trait distributions, this time for N supply and translocation. Between 81 and 95% of individual-level distributions differed from that of the population (Fig. 1, Materials and Methods, and fig. S1). Compared to the

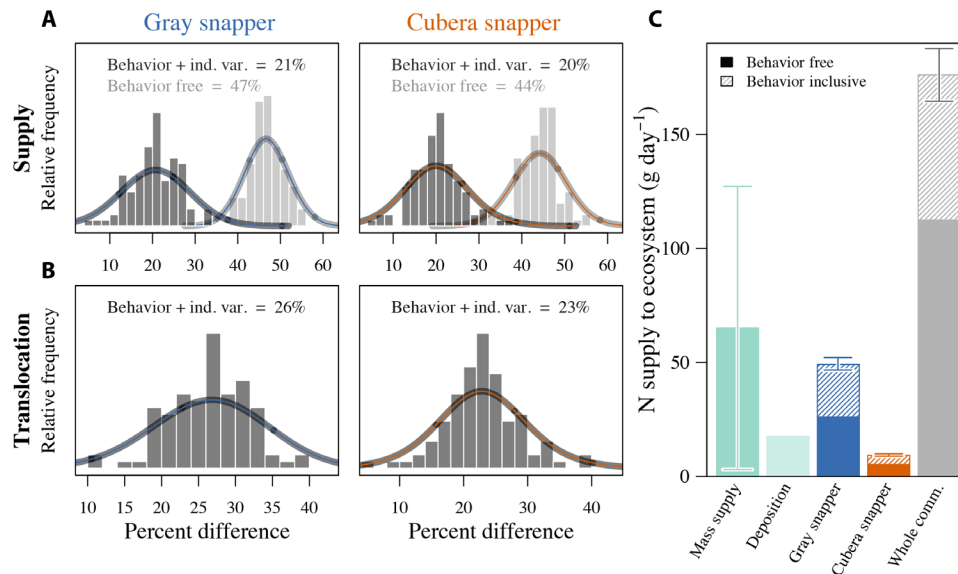


**Fig. 2. Individual behavioral traits strongly differ from population-level means.** (A) Histograms of raw data on site use per day and activity per day (time spent foraging) for both the gray and cubera snapper (blue and orange, respectively). Bars and associated dark lines indicate frequency of events within populations. (B) Individual-level site use per day and activity per day. Thin colored lines represent distributions of daily behavioral traits for each observed individual. Thick colored lines represent the population-level distribution (means across all individuals per day). Values associated with "Means" indicate the percentage of individual-level distributions that differ from the population-level means. These tests were run for the observed data (indicated by the colored text) and for simulated individuals that were generated by sampling randomly from normal distributions of site use per day and activity per day (indicated by gray text; distributions are not shown here for simplicity; Materials and Methods). (C) Site use and activity in relation to body size according to individual-level daily estimates (smaller transparent circles) and daily means across all individuals (larger circles with black outline).  $P$  values indicate the significance of the relationship between body size and mean behavioral trait.  $R^2$  is indicated when the relationship is significant.

simple measures of behavior (site use per day and activity rate per day; 62 to 86%), these findings show that scaling additional physiological factors (metabolism and body size) to estimate the influence of individuals on ecosystem processes substantially magnifies the discrepancy between individuals and their population-level means. For context, we simulated individual fish with body sizes sampled from the distributions of the observed populations, and behavior being determined by sampling from normal distributions of activity (Materials and Methods). We found that 67 to 91% of simulated individuals differed from their population-level means for both N supply and translocation. These results extend our findings that individual-level behavioral traits are poorly captured at the population level and show that individual-level impacts on ecosystem function are even more pronounced because of the additional variation associated with individual-level physiological attributes.

Scaling individual-level processes to estimate population-level nutrient supply (Materials and Methods) showed that the gray and cubera snapper populations contributed 52 and 10.9 g N day<sup>-1</sup>, 44 to

47% greater, respectively, than from simulated populations in which behavior was not accounted for (i.e., individual-level models were informed only by body size and not by movement-based metabolism) (Fig. 3). Even when accounting for behavior (i.e., individual-level models are informed by body size- and movement-based metabolism; Materials and Methods), the simulated populations still underestimated N supply and translocation by 20 to 26% relative to the observed populations (Fig. 3), that is, relative to the estimates generated from models parameterized by observed movement and body size of individuals in the two populations. These findings are particularly notable considering the degree to which our simulations were informed by the observed population-level demographics (i.e., observed data) and captured similarly high levels of individual-level variation in N supply and translocation (67 to 91%) relative to the observed individuals (81 to 95%). Scaling-up ecological processes from the individual to the ecosystem is a widely used approach in ecology and is increasingly being applied to understand how anthropogenic changes may influence ecosystem-scale processes (31). Our results



**Fig. 3. Individual behavior affects nutrient supply and translocation and ecosystem-level nutrient dynamics.** (A and B) Distributions of the percent difference between observed estimates of population-level N supply per day (A) and N translocation per day (amount of N distributed across the estuary) (B) and populations simulated using models that are informed by the observed populations and incorporate behavior- and individual-level variation (“Behavior + ind. var.”—black bars and text) and behavior-free models that are informed only by the body size distributions of the observed populations (“Behavior free”—light gray bars and text). Values associated with text represent median differences between observed and simulated data. (C) Primary sources of N ( $\text{NH}_4^+$ ) supply ( $\text{g day}^{-1}$ ) to the ecosystem: mass supply—calculated as the difference between net input and output from the system due to tidal flushing (Materials and Methods), deposition from rainfall, gray and cubera snapper, and the whole community (all species + gray and cubera snapper; Materials and Methods). Dashed portions of bars indicate estimated contribution of net supply due to behavior. Error bars associated with mass supply indicate the maximum (upper) and minimum (lower) estimates (see Materials and Methods). Error bars for population and community estimates represent 1 SD generated through bootstrapping procedures (Materials and Methods).

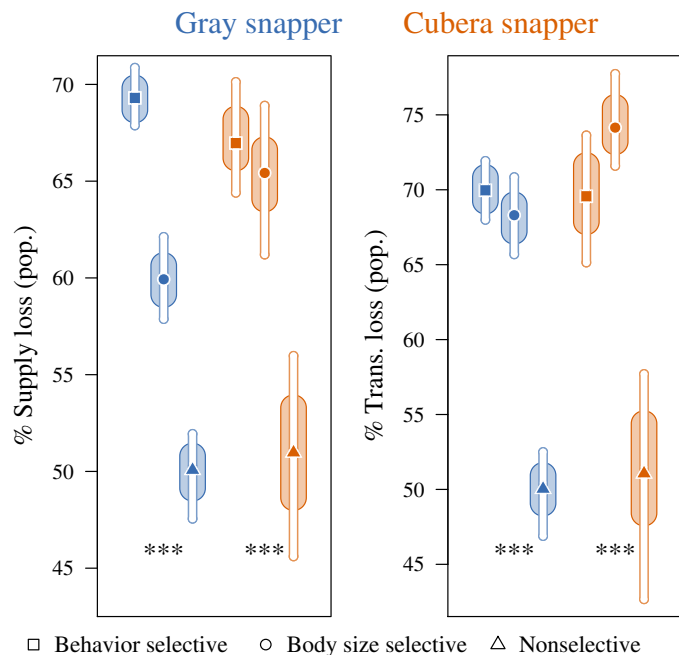
signal that interpreting results from this approach must be done cautiously, and where possible, empirical data should be used to inform individual distributions especially if the processes being scaled are influenced by behavioral or physiological traits.

Placing our findings into the context of the whole ecosystem, we found that the observed gray and cubera snapper populations supplied ~97% of the mass supply of N to the estuary, including N supply from tidal flushing and N deposition (Fig. 3B and Materials and Methods). Scaling the behavior-inclusive estimates to the whole fish community reveals that fish can contribute up to two times the total mass supply of N to the system (Fig. 3B and Materials and Methods). Animals are widely recognized to contribute substantially to nutrient budgets in many ecosystems (18, 20, 21, 32–34). However, in tropical coastal ecosystems where primary production is often limited by both N and phosphorus (P) (35–37), the relevance of fish community-level nutrient supply rates compared to other sources has been uncertain, although estimated to be substantial (15). Here, we show that approaches that do not account for behavior-mediated changes in metabolism substantially underestimate the contribution by consumers to ecosystem nutrient budgets.

The importance of intraspecific variation in behavior for ecosystem function demonstrated here suggests that if ecosystem-based management is a priority, the ecological ramifications of harvesting strategies may need to be reconsidered. Gray snapper and cubera snapper support important commercial and subsistence fisheries throughout the Caribbean and are traditionally harvested via spearing and angling (38). These harvest techniques are used throughout coastal ecosystems globally and are typically selective for large body size [e.g., spearing (39)] and bolder or more active individuals [e.g.,

angling (40) and, to some extent, spearing (12)]. We tested how our findings are relevant for ecosystem-based management of these two fisheries under a range of conditions of harvesting at MSY, where populations are typically maintained between 30 and 70% of their unfished size (Materials and Methods and figs. S3 and S4). Simulated harvest of unexploited populations (such as those in our study) to 50% of their unfished abundance (e.g., Fig. 1B) reduced nutrient supply and translocation by as much as 69% for cubera and 74% for gray snapper (Fig. 4). In all cases, selective harvest strategies reduced N supply or translocation by 10 to 24% more compared to nonselective harvest, i.e., random removal of individuals (Fig. 4).

A key result from this analysis is that behavior-selective harvest had the largest effect on nutrient supply in all cases with the exception of translocation of nutrients by cubera snapper. This finding underscores the importance of behavior, more than body size, for mediating nutrient dynamics in the presence of fishing. This is at first counterintuitive given the strong support for the importance of body size on nutrient supply in previous work (18, 23, 24) as well as in this study. For example, here we found that body size was the strongest predictor of individual-level nutrient supply across both populations (Materials and Methods and table S4), whereas activity was the second strongest predictor and synergistically interacted with body size (Materials and Methods and table S4). This positive interaction strongly influences the behavior-selective harvest of individuals because even though behavior-selective fishing selected more for medium-sized individuals (the largest individuals are not the most active; Fig. 2C), these individuals supply more nutrients, on average, because of their increased activity. Body size is a widely used metric for scaling ecological processes, but our findings show that additional



**Fig. 4. Selective harvest disproportionately reduces ecosystem-level nutrient supply.** Reductions in population level of N supply and translocation for gray and cubera snapper (blue and orange, respectively) from selective and nonselective harvest of 50% of individuals from unfished populations. Asterisks (\*\*\*) indicate all values are significantly different [ $P < 0.01$ ; analysis of variance (ANOVA) with Tukey post hoc test]. Behavior selective and body size selective represent fishing that selects against active individuals and large individuals, respectively. We carried out simulated fishing by removing the top 50% of active and large individuals for angling and spearing, respectively. Nonselective is fishing with random removal (see Materials and Methods and figs. S3 and S4 for results for harvest at 30 to 70%).

individual-level traits should be considered in light of how they can interact to produce alternative outcomes for ecosystems.

While much of our focus has been on the net N supply to the system, the importance of N translocation is also important, especially in nutrient-poor tropical coastal ecosystems (41). For example, the translocation of nutrients by grunts (*Haemulidae* spp.) from seagrass beds to coral reefs can increase the growth rate of coral by 70% (42). Similarly, in our study system, an individual fish that moves frequently or far will disproportionately translocate nutrients relative to other individuals. This likely also has a disproportionate influence on primary production because the producers receiving the nutrients from this individual would otherwise receive very little due to low ambient availability in this system (35). The translocation of nutrients by animals, however, is a critical ecosystem function that extends well beyond nutrient-poor ecosystems, e.g., grasslands (43), lakes (20), and rivers (44); thus, selective removal of more mobile animals should be recognized as a cryptic consequence of exploitation in many ecosystems.

An ideal conservation scenario would be that nutrient supply is minimally reduced from harvesting to maintain MSY (Fig. 1B; “resilient scenario”). However, our study shows that the reduction in biomass and loss of individual-level behavioral characteristics due to fishing are greater than proportional, thus discouraging selective fishing, even when harvesting to maintain population sizes that are considered sustainable from an MSY perspective (Materials and Methods and figs. S3 and S4). These results pose an important challenge to

conservation because fisheries are essential for the livelihoods of millions of people globally, and thus, only in limited cases is the cessation or reduction in fishing an option. More generally, our results challenge the species-centric definition of biodiversity and provide evidence that the role of individuals may need to be further reconciled in how we approach conservation and the maintenance of ecosystem function.

## MATERIALS AND METHODS

### Study system

The research site was a mangrove-lined estuary located on Abaco Island, The Bahamas called Cross Harbour (25°56′28″N, 77°16′26″W). Food web structure and dynamics (45–52), nutrient dynamics (17, 35, 53–55), and movement of gray and schoolmaster snapper (56) have been previously studied by the authors in these systems. Bahamian mangrove-lined estuaries, locally called tidal creeks, are characterized by low physical relief and no riverine input, thus are completely tidally dominated. The study area represented ~11.5 km<sup>2</sup> of the entire estuary, which was ~30 km<sup>2</sup>, estimated using Google Earth software. The study area was chosen on the basis of the availability of predator refugia holes (herein referred to as refugia holes) and was delineated on the basis of the extent of fish habitat determined from visual surveys conducted by the authors. Refugia holes are depressions in the shallow seascape (3 to 5 m in diameter and 1 to 3 m deep) in which fishes can shelter during low tide events when the majority of the estuary (i.e., areas other than the refugia) is devoid of water.

### Telemetry

A total of 33 gray snapper and 25 cubera snapper were tagged with Vemco acoustic transmitters (V7 and V9) between July 2006 and February 2007 (not all fish were used in the subsequent analysis—see the Supplementary Materials for detailed tagging procedures). Fish were caught with hook and line or traps. Standard length was recorded for each individual. Nine receivers (Vemco VR2W) were placed within each of the refugia holes throughout the study site. Receivers can detect acoustic transmissions that are unique to each transmitter placed inside of individual fish. The detection range of the transmitters is ~50 to 150 m, depending on water clarity, depth, and potential obstruction from objects, e.g., in this system, mangrove roots or seagrass (personal observation by J. E. Allgeier and C. A. Layman). Receivers were moored at the bottom of the refugium hole and had a detection range of ~0.5 to 5 m extending beyond the perimeter of the refugia. Our assumption, which was based on extensive visual surveys, hundreds of hours of personal observation, and prey fish tethering experiments conducted by J. E. Allgeier and C. A. Layman, was that when fish were not detected by our receivers, they were outside of the refugia holes and actively foraging. The ability of receivers to detect fish on the perimeters of the refugia holes suggests that if anything, our analysis is conservative as it underestimates the amount of time fishes were foraging (and thus increasing their individual effects on nutrient dynamics). Data from receivers were downloaded opportunistically by the authors.

### Calculating behavioral traits—Activity and site use per day

We generated a full time series of data for each fish whereby a location (refugium hole) or the absence of detection (foraging) was recorded at every 20-min window of time for 30 days each. Thirty days was

selected because it was the longest time frame for which we had continuous coverage of the largest number of our tagged fish (i.e., 31 and 21 for gray snapper and cubera snapper, respectively). All but six fish time series took place between January and February 2007. The other six took place between June and September 2007. In an ideal scenario, all fish movement data would have been from the exact same days, but idiosyncrasies in their behavior, e.g., fish at times left the entire estuary (often captured by additional receivers we had throughout the area), rendered this difficult and would have substantially reduced the number of days for which we had overlapping data for a maximum number of fish. Instead, for the purposes of this study, we felt it was optimal that fish had the same number of days (and as many as possible) of movement data for which basic parameters could be estimated.

Calculating the behavioral traits consisted of (i) counting the number of different sites visited by each individual fish for each day (site use; sites 1 to 9) and (ii) summing up the total amount of time that fish were either inactive (detected by a receiver in a given refugium hole) or active (not detected and thus assumed to be swimming and/or foraging outside of the refugia). Activity was binary (1 = not swimming in refugia or 2 = swimming outside of refugia), consistent with the activity parameter used in bioenergetics models (57, 58). A binary value for activity is an oversimplification of the “true” activity of a fish, but given this binary value was assigned for every 20-min window of time for 30 days, over greater time scales (e.g., 1 hour), this variable becomes a continuum between 1 and 2. Thus, we generated distributions of site use and activity per day for each individual to test the hypothesis that individual-level behavior was well described by the population-level means (mean daily activity or site use across individuals within a population). To do this, we used *t* tests to determine whether the means of each individual-level distribution differed from that of the population-level distributions (Fig. 2).

For purposes of comparison, we generated simulations whereby the same number of individuals for gray and cubera snapper populations (31 and 21, respectively) was created to test whether the observed individuals differed from null expectations that individuals are represented by population-level normal distributions of activity and site use. Specifically, time series were generated for each fish by randomly sampling from normal distributions of activity (1–2) and site use (1–9) for each day for each individual. This process was repeated such that we generated 100 simulated populations of gray snapper (with 31 individuals each) and cubera snapper (with 21 individuals each). For each simulated population, we tested how well the population-level distribution captured the individual-level traits (the same test as conducted on the observed data). We used *t* tests to quantify the proportion of individual-level distributions (activity or site use per day per individual) that differed from the population-level distributions (means across all individual per day). Results from these tests are reported in Fig. 2.

### Community and population surveys

An important aspect of this research is to scale findings to the ecosystem. We estimated population sizes for gray and cubera snapper through visual surveys in two ways. First, repeated visual surveys were conducted in each refugia during low tide events using snorkel surveys in which all fish were exhaustively counted (surveys were not timed). Similar techniques have been used by the authors (J. E. Allgeier and C. A. Layman) on artificial reefs in nearby seagrass ecosystems (59–61).

Estimates were averaged across all dates and summed across all refugia holes to get a mean total number of fish (all species) within the refugia holes. Second, walking transects (50 m by 2 m) were conducted during low tide to estimate fish densities in regions of the estuary that were not within refugia, but that fish could access during low tide events—i.e., the primary water channels. These estimates were averaged across sampling dates and scaled-up to the low tide area of the tidal creek to estimate the average number of fish (all species) outside of the refugia holes during low tide. In doing so, we were able to estimate fish densities at low tide in the only two habitat types that fish could possibly occupy. Estimates (mean densities in refugia at low tide + mean densities outside refugia at low tide) were summed to get a single population size estimate for each species. All surveys ( $n = 21$ ) were conducted by C. A. Layman between 23 January 2006 and 21 September 2006. We are confident that these estimates are, if anything, conservative for two reasons: (i) Our estimates of fish density in each hole are most certainly underestimates versus overestimates, and (ii) for many species of fish, individuals will often emigrate into estuaries at high tide (62, 63). To understand potential error associated with our population-level estimates, we used a bootstrapping technique whereby we iterated through the data 1000 times, each time removing a single survey date (see error bars associated with Fig. 3) and then following the same procedure of averaging across all remaining dates and summing across the snorkel surveys and the walking transects. Surveys resulted in an estimate of  $488 \pm 27$  SD gray snapper and  $68 \pm 4$  SD cubera snapper for the upper portion of the estuary (Fig. 1). These estimates suggest that 6% of gray and 34% of cubera snapper populations were tagged for movement analysis.

To estimate the contribution of the entire community (i.e., all other species) for N supply to the system, we used the fish community survey data to estimate community-level biomass and supply of  $\text{NH}_4^+$  (table S1). Specifically, using data previously collected from the system for past food web studies (64) and this study, we generated body size distributions (assumed to be log normal) for each species within our surveys. Sampling from these body size distributions, we generated 100 different populations for each species. These body sizes were converted to mass using published length-weight relationships (30, 65). We then estimated daily excretion rates of  $\text{NH}_4^+$  for each individual based on the published relationships from Allgeier *et al.* (24) and aggregated to estimate the community-level  $\text{NH}_4^+$  supply (table S1). To understand potential error associated with our population-level estimates, we again used a bootstrapping technique whereby we iterated through the data 1000 times, each time removing a single survey date (see error bars associated with Fig. 3). Mean fish community N supply over the 100 iterations was  $79.8 \pm 5.9$  SD  $\text{g NH}_4^+ \text{ day}^{-1}$ —not including the estimates for gray and cubera snapper generated from this study—see methods below.

### Scaling individual-level physiological processes onto behavioral traits

We used a bioenergetics approach to energetically track individuals over time in our study system. This approach allowed us to combine knowledge about basic behavioral traits or attributes of individual fish with physiological parameters of those fish to estimate their combined effects on nutrient supply and translocation via excretion of waste products. Bioenergetics models (57, 58) were built based on previous models used to estimate excretion rates of N for *Lutjanidae* (61) and empirically parameterized by data from Allgeier *et al.* (24). To do this, we constructed individual specific bioenergetics models

(the same base model but with each individual's body mass) that were serially updated every 20 min based on two primary factors. First, if a fish was assumed to be "active" (i.e., it was not detected in a refugia hole), the activity parameter was up-regulated from basal metabolism of 1 to active metabolism of 2 (58). Second, given the influence of temperature on metabolic processes (57, 58), we allowed water temperature to vary based on the fish's location in the estuary. To do this, we placed temperature loggers (Hobo brand) in six locations within the estuary for the extent of the study period: three in commonly used refugia holes and three in shallow areas that would vary in their degree of access due to different tidal stages. These data were then used to update the individual-specific models whereby when fish were detected within a refugia, we used refugia-specific temperature data when possible and average refugia temperature data when not. When fish were not detected by our receivers, model temperature was the average across the three temperature loggers in shallow sites. There were periods of time for which logger data were incomplete (e.g., when loggers were removed to change batteries, download, or if a logger failed). These time periods were often short (i.e., minutes to hours), but to assure a complete time series of temperatures, we generated correlations from the nearest logger and used linear coefficients to interpolate temperatures for the incomplete time periods. Statistical models testing for the most important factors explaining daily individual-level N show that temperature was third in parameter importance behind body size and activity (standardized parameter effect sizes: 0.74, 0.34, and 0.18, respectively), and thus, we expect the subtle variation caused by this approach had minimum influence on our findings.

Using this approach, we calculated both N supply and translocation (i.e., the movement of nutrients across the estuary when fish were not resting in refugia) by individuals to the ecosystem. Specifically, N supply was calculated as the sum of N excretion per individual over time. N translocation was quantified as the sum of N excretion per individual only during the time when the individual was foraging (i.e., when the fish was active).

### Scaling individual-level processes of N supply and translocation to the population

Population-level abundance estimates based on our field surveys indicated that the gray and cubera snapper populations within our study area were 488 and 68, respectively. To scale up the individual-level processes to the whole population, we used a resampling method to generate 100 different populations (per species) whereby individuals were randomly selected with replacement from the observed individuals. These resampled populations were then used to estimate the extent to which individual-level variation influenced population-level N supply and translocation (Fig. 3 and fig. S1).

We used simulation to test how base assumptions of activity (i.e., that daily activity is normally distributed) determine the degree to which individuals deviate from their population-level means and, in turn, how this may affect ecosystem-scale processes of N supply and translocation. A goal of these simulations was to test how effective different assumptions about behavior were at predicting the observed behavior in our telemetry study. To do this, we generated simulations at two levels of realism: with and without including individual behavior, herein referred to as "behavior inclusive" and "behavior free," respectively. For the behavior-free simulations, body size was the only factor that varied among individuals; all other parameters were constant across time under the assumption that individuals do

not move at all (activity parameter = 1). For the behavior-inclusive simulations, individuals were differentiated by body size and activity. In these cases, models were updated at each 20-min time step (similar to how we modeled the observed individuals), but in this case, parameters for activity were randomly sampled from normal distributions (i.e., daily activity level is represented as a number between 1 and 2). Simulated individual's body size (i.e., 488 and 68, for gray and cubera snapper, respectively) was determined by drawing from the log-normal distribution of body sizes based on the population demographics of the respective observed population (i.e., using the real data for the gray and cubera snapper). In all cases, we used the same bioenergetics model framework to energetically track individuals through time. For simulations, we held water temperature constant at the mean temperature across the study time frame (24°C)—this is a generally conservative approach given that the mean temperature experienced by the observed individual fish was  $25.5 \pm 0.79^\circ\text{C}$  SD.

### Estimating additional sources of N to the ecosystem

To place our findings in the context of the entire ecosystem, we estimated the amount of N supplied to the system in two ways: (i) We estimated mass nutrient supply to the system driven by tidal flushing and (ii) N deposition. Detailed methods used to calculate sources of N to the ecosystem can be found in the Supplementary Materials. Bahamian islands have no freshwater rivers and streams due to their karst geology and flat topography (38). As such, Bahamian estuaries receive water primarily from the ocean via tidal oscillations, which occur twice daily, as well as through direct rainfall. They may also receive N from biological N fixation; however, we did not include this in our study because of the relative paucity of data on this source of N and findings that N fixation can at times be countered by denitrification in mangrove ecosystem sediments (thus, depending on this amount, our estimate of all other sources of N to the system could be an underestimate) (66). Our previous work has shown these Bahamian estuarine ecosystems to have extremely low availability of ambient nutrients in the water column (35, 53).

### Simulated fishing

Both species were fished using simulation under three different scenarios: (i) behavior selective: removing individual fish in rank order from the most active to the least; (ii) body size selective: removing individual fish in rank order from the largest to the smallest; and (iii) nonselective: removing individuals randomly from the population. Accurately estimating the population size that produces MSY requires information (i.e., population-level growth rates or stock-recruitment relationships) beyond the scope of this study but generally falls between 30 and 70% of the unfished population size (67). As such, we fished all populations using simulations where we removed 30, 40, 50, 60, and 70% of individuals (not biomass) from the populations to provide a range of fishing pressure that likely encompasses most species (figs. S3 and S4), whereby the removal of individuals was either selective, removing the most active or largest, or random. On the basis of the recommendations of Punt *et al.* (67) for simplicity, in the main text, we only presented fishing where MSY occurred when removing 50% of the individuals. For each species and harvest technique, fishing was conducted iteratively on the 100 populations that were generated through resampling techniques described above (also used to estimate population-level contribution to supply

and translocation), See figs. S3 and S4 for results from fishing where we removed 30, 40, 60, and 70% of the individuals.

### Statistical models testing body size effects

We used linear mixed-effects models to test for the relative importance of body size, temperature, and activity for individual-level nutrient supply by both gray and cubera. The global model was

$$\text{Log}(N_{\text{EXC}}) \sim \text{body mass} + \text{activity} + \text{body mass} * \text{activity} \\ + \text{temperature} + (1|\text{species}) + (1|\text{fishID}) + (1|\text{date})$$

Whereby, excretion ( $N_{\text{EXC}}$ ) was the grams supplied per fish per day. We included species and fishID (a unique ID for each individual) and date as random effects, as we were most interested in the effect sizes of the fixed effects: body mass (log transformed), activity (mean per day), and temperature (mean per day). All values were standardized to allow direct comparisons among parameter estimates (table S4). The package lme4 in R (68) was used to run the model.

### SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/9/eaax8329/DC1>

Specific tagging procedures

Estimating additional sources of N to the ecosystem

Table S1. List of species and specific parameters used to scale population estimates.

Table S2. Time series of ambient availability of N from the mouth of a tidal creek in The Bahamas.

Table S3. N deposition rates.

Table S4. Model statistics for testing body size effects.

Fig. S1. Importance of individual behavior for ecosystem-level nutrient supply and translocation.

Fig. S2. Image of the study system.

Fig. S3. Selective harvest disproportionately reduces ecosystem-level nutrient supply.

Fig. S4. Selective harvest disproportionately reduces ecosystem-level nutrient translocation.

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