

UC Santa Barbara

UC Santa Barbara Previously Published Works

Title

The importance of individual and species-level traits for trophic niches among herbivorous coral reef fishes

Permalink

<https://escholarship.org/uc/item/0v94f6w3>

Journal

Proceedings of the Royal Society B, 284(1856)

ISSN

0962-8452

Authors

Allgeier, Jacob E
Adam, Thomas C
Burkepile, Deron E

Publication Date

2017-06-14

DOI

10.1098/rspb.2017.0307

Peer reviewed

Research



Cite this article: Allgeier JE, Adam TC, Burkepile DE. 2017 The importance of individual and species-level traits for trophic niches among herbivorous coral reef fishes. *Proc. R. Soc. B* **284**: 20170307. <http://dx.doi.org/10.1098/rspb.2017.0307>

Received: 14 February 2017

Accepted: 18 May 2017

Subject Category:

Ecology

Subject Areas:

ecology

Keywords:

biodiversity, complementarity, coral reefs, fish, herbivore, parrotfish

Author for correspondence:

Jacob E. Allgeier

e-mail: zopelote@gmail.com

Electronic supplementary material is available online at rs.figshare.com.

The importance of individual and species-level traits for trophic niches among herbivorous coral reef fishes

Jacob E. Allgeier¹, Thomas C. Adam³ and Deron E. Burkepile^{2,3}

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

²The Department of Ecology, Evolution and Marine Biology, and ³Marine Science Institute, University of California, Santa Barbara, Santa Barbara, CA, USA

JEA, 0000-0002-9005-6432

Resolving how species compete and coexist within ecological communities represents a long-standing challenge in ecology. Research efforts have focused on two predominant mechanisms of species coexistence: complementarity and redundancy. But findings also support an alternative hypothesis that within-species variation may be critical for coexistence. Our study focuses on nine closely related and ecologically similar coral reef fish species to test the importance of individual- versus species-level traits in determining the size of dietary, foraging substrate, and behavioural interaction niches. Specifically, we asked: (i) what level of biological organization best describes individual-level niches? and (ii) how are herbivore community niches partitioned among species, and are niche widths driven by species- or individual-level traits? Dietary and foraging substrate niche widths were best described by species identity, but no level of taxonomy explained behavioural interactions. All three niches were dominated by only a few species, contrasting expectations of niche complementarity. Species- and individual-level traits strongly drove foraging substrate and behavioural niches, respectively, whereas the dietary niche was described by both. Our findings underscored the importance of species-level traits for community-level niches, but highlight that individual-level trait variation within a select few species may be a key driver of the overall size of niches.

1. Introduction

A principal question in ecology is: ‘how do so many kinds of animals coexist?’ [1]. At the centre of this discussion is the ecological niche; a concept that provides a basis for conceptually and quantitatively describing relative ecological roles of species, improving our understanding of how they compete and coexist [2,3]. The even partitioning of ecological niches (e.g. niche complementarity) among species may be an underlying mechanism that leads to species coexistence with substantial empirical and theoretical support [4,5]. Yet research has also provided evidence of niche overlap (i.e. niche redundancy), whereby species’ ecological roles appear redundant according to predetermined groups of functional traits [6,7]. Accordingly, identifying the specific mechanisms by which species partition an ecological niche is a topic of considerable debate in ecology.

Disentangling the importance of these proposed mechanisms becomes particularly interesting when considering sympatric animal groups that share common resources (e.g. herbivores). One of the best studied examples of this is the large mammalian herbivore community of the African savannahs [8–10]. Recent research on this diverse group found that the broad nature of traditional trophic classifications (grazers versus browsers) is misleading as to the complex nature of competition and coexistence. Instead, the authors found that important nuances in dietary preferences among, but also within species (i.e. among individuals) underpin their competition and coexistence [11]. This research suggests that further integrating the importance of the individual within the more traditional conceptualization of a species’ niche may be critical in improving our understanding of competition and coexistence of species.

Individual-level variation is a cornerstone of evolutionary theory, and has recently gained popularity among ecologists for its additionally important role in community assembly and niche partitioning [12–16]. Specifically, research has consistently shown through various measures of niche space (e.g. dietary, isotopic, spatial; [13,16,17], respectively) that within some populations, variance across niche space among individuals can be substantial relative to the variance across the entire community. As such, one hypothesis is that in some cases, understanding within-population variation may be more informative than among-population variation for questions associated with species coexistence [15].

We explore the relative importance of the individual for determining community-level niche width within a species-diverse community of sympatric herbivorous coral reef fishes. Herbivorous fishes play critical roles in coral reef ecosystems through the top-down regulation of algal communities via complementary feeding on different algal groups [18,19]. The diversity of herbivores can influence the strength of competitive interactions between corals and algae, and may be central in the resilience of coral communities following disturbances [20]. We quantified dietary, foraging substrate, and behavioural niches for approximately 18 individuals in each of nine co-occurring herbivorous species of Caribbean parrotfish using continuous behavioural observations. In doing so we were interested in addressing two primary questions:

- (i) what level of biological organization (genus, species, functional group classifications, or individual phenotype, i.e. body size) best describes individual-level niche widths? and
- (ii) how are herbivore community niches partitioned among species, and are niche widths driven by species- or individual-level traits?

A key strength in our analysis is that we are using high-resolution data on 18 individuals within each species to explore the ecological importance of individual-level variation across multiple species that are traditionally considered to occupy very similar niches. Additionally, our study quantifies feeding interactions and behaviours over time for each individual, thus providing robust individual-level measures with which to test our questions. Understanding the relative importance of the individual within closely related and ecologically similar species provides an important step towards a more comprehensive understanding of how diverse assemblages of species compete and coexist for finite resources.

2. Methods

(a) Behavioural observations

We characterized the diet and foraging behaviour of nine species of parrotfishes during June and July 2013 in the Florida Keys National Marine Sanctuary (FKNMS) off Key Largo, FL, USA. Approximately 18 individuals of each species (range 16–19) were observed for 20 min each, with approximately six individuals observed at each of three separate reefs. The three study reefs were all high-relief spur and groove forereefs with very similar physical characteristics. They were chosen specifically because they contained a high diversity of habitat types and benthic communities (coral and macroalgae that are dietary items for herbivores) that were similar across sites. In this way, the three sites had very similar resource availability for the herbivorous species of interest for this study. In order to control for diurnal

variation in foraging behaviour, we conducted observations in a balanced design in three 2 h sampling intervals (10.00–12.00, 12.00–14.00 and 14.00–16.00). Focal individuals were haphazardly selected using criteria which ensured that different species were observed in the same general locations, thereby ensuring that all species had access to the same sets of resources (see [21] for further details on selection criteria). The individuals selected were representative of the size range of adult individuals of each species. Several parrotfish species are sexually dimorphic, with terminal phase males being highly territorial and aggressive towards both conspecifics and heterospecifics [22]. Thus, we focused our observations on intermediate phase fishes (which can be either male or female) for these dimorphic species to avoid confounding feeding behaviour with territoriality.

Focal fish were slowly approached by a SCUBA diver and allowed approximately 2–3 min to acclimate to the presence of the diver while their total length was estimated to the nearest cm. Upon acclimation, fish were followed closely for a period of 20 min while the diver recorded their behaviour on an underwater slate. For each bite taken by a focal fish, the diver identified the food item targeted to the lowest taxonomic level possible, with macroalgae usually identified to genus. In addition to feeding on macroalgae, focal fish frequently targeted a multi-species assemblage of diminutive filamentous algal turfs and associated detritus and microbes, which we treated as single functional group, probably resulting in an underestimation of the total niche size.

In addition to recording the food items eaten by focal fish we also recorded the type of substrate they were feeding from, categorizing each substrate as one of the following: (i) dead coral, (ii) coral pavement, (iii) boulder, (iv) rubble, or (v) ledge (for detailed information on foraging substrates see [21]). Finally, we recorded all aggressive interactions between the focal fishes and other individuals, which consisted primarily of interactions with other parrotfishes (both conspecifics and heterospecifics) and territorial damselfishes. During all behavioural observations, divers towed a GPS receiver (Garmin GPS 72) which was programmed to obtain position fixes of the focal fish at 15 s intervals, which were used to calculate the maximum linear distance moved by a fish.

(b) Statistical analysis

Individual niche widths were determined following methodologies from Bolnick *et al.* [23]. We conducted our analysis such that the total niche width (as typically thought of at the population-level) included all individuals within the sampled herbivore community under the assumption that all resources (be it feeding substrate or dietary items) were available to all individuals not just those in their respective populations. This is a reasonable assumption given that all species were observed in the same general habitat types at the same sites. Further, foraging ranges were large relative to the distribution of resources, suggesting that all species had access to a similar resource pool. Accordingly, we calculated the within individual component (WIC_i , *sensu* [23]) (for each individual using community matrices of all individuals and their diet, their foraging substrate choices, and aggressive behaviours to other sympatric species. Because bites per given dietary item was recorded for each individual, and because different species and different body sizes can differ substantially in the amount of food taken per bite, we weighted bite rate using published regressions between body size and amount ingested per bite (mg) for each of the two genera, *Scarus* and *Sparisoma* [24].

The within individual component of the herbivore community niche for each individual (WIC_i) was calculated as

$$WIC_i = P_i \times \left(- \sum_j P_{ij} \times \ln P_{ij} \right),$$

where P is a proportional matrix niche type, P_i is the proportion of all resources used by the entire herbivore community that are used by individual i , and P_{ij} is the proportion of the j th resource category in the individual i 's resource use. Bolnick *et al.* [23] used the summation of this metric across all individuals within a population to calculate the total WIC. Here we simply calculate this on the individual basis as an estimate of an individual's contribution to the total niche width of the herbivore community (herein simply referred to as 'the community'). As such, a large WIC_i indicated that an individual has a large niche.

We were first interested in estimating the degree to which individual niche widths can be characterized by traditional taxonomic and functional classifications, or individual phenotype (body size) using simple linear models. Because of perfect collinearities among some levels of biological organization, we ran separate models for each group: genus ($n = 2$), species ($n = 9$), and functional group ($n = 2$; browsers or grazers following Adam *et al.* [21] for the same species), all of which included a covariate for the body size of each individual (fork length—FL). We additionally included a covariate for the distance (m) each fish travelled during the surveys, thus including a potentially important but often overlooked aspect of individual 'personality' [16,17]. We used model selection following Akaike information criterion, correcting for small sample sized (AICc) to determine the best-fitting model [25]. Model support for a classification would suggest that variation among individuals was best explained at this level of organization. Alternatively, lack of support at any level of organization would suggest that variation among individual niche widths is best explained at the individual level.

To understand how the community-level niche width was partitioned among species and among individuals within species we generated population-level T statistics following Violle *et al.* [15]. Specifically, to quantify how a given niche was partitioned among species we calculated the mean of the individual-level niche width (WIC_i) within each population (μ_{IP}), and the mean individual-level niche width across all individuals in the community (μ_{IC}), and took the ratio; herein $\mu_{IP/IC}$. This provides a relative measure of the importance of species-level traits for community-wide niche width. We then estimated the relative contribution of within-species individual-level traits for community-wide niche width, by calculating the variances of individual niche widths (WIC_i) within each population (σ_{IP}^2) and within the entire community (σ_{IC}^2), again taking their ratio, herein $\sigma_{IP/IC}^2$ following Violle *et al.* [15]. This provides a relative measure of the importance of within-species variation (individual-level traits) for community niche. In the case of both statistics, values greater than one indicate disproportionate importance of species-level traits ($\mu_{IP/IC}$) and within-species individual-level traits ($\sigma_{IP/IC}^2$) for total community-level niche width for each of the nine species. The relationship between these two statistics provides a way to estimate the relative importance of individual-versus species-level traits across species for community niche width. For example, in the case where $\sigma_{IP/IC}^2$ is the response variable, a slope greater than one would suggest that individual-level traits within species is more important for explaining community-level niche width than species-level traits. We tested this using simple linear regression for each niche type.

To explore any relationship between individual niche width (WIC_i) and the degree to which an individual specializes on certain dietary resources, dietary substrates, or behavioural interactions we additionally calculated an index for specialization (PS_i) following Bolnick *et al.* [23]:

$$PS_i = 1 - 0.5 \times \sum_j |P_{ij} - Q_j|,$$

where, P is a proportional matrix niche type, P_{ij} is the proportion of the j th resource category in the individual i 's resource use (all as explained above), and Q_j is the proportion of the j th

resource category in the entire herbivore community niche [23]. PS_i is a value from 0–1 where the lower the value the more specialized an individual is relative to the entire herbivore community. We then compared these values per individual with their niche size for each of the three niche types to test for correlations between the two. All analyses were conducted using R software (R Core Development Team 2012).

3. Results

Species identity best characterized variation in individual-level niche width of both community-level dietary niche and foraging substrate (table 1; figure 1). These models explained a relatively large proportion of the variation in the data, suggesting that species-level traits accurately described total variation in individual niche widths across the herbivore community. Behavioural interactions were best predicted by differences among genera, according to AICc, but the species model explained more of the variation in the data (higher R^2 , though this is probably owing to reduced degrees of freedom from the higher number of species relative to genera) (table 1; figure 1). These models explained only minor amounts of the variation in the data, suggesting that classification above the level of the individual did not explain well behavioural interactions among individuals across multiple species (table 1; figure 1). The two covariates, body size (FL) and distance travelled per individual were significant and in the best-fit model for diet and feeding substrate. Distance travelled per individual was retained in the best model for diet and behaviour. For diet, individuals that move less tended to have a larger niche, whereas individuals that moved more tended to have more interactions with other individuals. Despite this, these parameters contributed very little to model performance and alone explained approximately 12% of the variation in dietary niche and less than 8% of the variation in any of the two niches.

Applying the T statistics following [15], we found that $\sigma_{IP/IC}^2$ was typically smaller than $\mu_{IP/IC}$ suggesting that species-level traits tend to dominate over individual-level traits for community niche width. Five of the nine species had ratios greater than one and thus displayed disproportionate species- or individual-level contribution to whole-community niche across the three niche types. Interestingly, *Scarus vetula* showed disproportionate contribution (i.e. $\mu_{IP/IC}$ or $\sigma_{IP/IC}^2 > 1$) to community niche width for diet and foraging substrate, but not behavioural interactions, suggesting that one way in which *Scarus vetula* maintains such a large dietary niche is through foraging across diverse substrates. Only *Scarus guacamaia* showed disproportionate effects for dietary and behavioural interactions. *Scarus coeruleus* showed disproportionate contribution for behavioural interactions, while *Scarus coelestinus* showed disproportionate contribution for dietary niche.

Using linear regression to further test the relative importance of species versus individual-level traits for community-wide niche width, we found support (i.e. 95% confidence intervals (CIs), did not overlap with one) for the importance of species-level traits for foraging substrate niches, but individual-level traits for behavioural interactions. The slope of the line for dietary niche was less than one, but did not differ significantly from one (slope = 0.88; 95% CI 0.28–1.48) suggesting the importance of both species- and individual-level trait variation.

Finally, because we were interested in the possible relationship between individual niche width (WIC_i) and degree of specialization (PS_i), we assessed the degree of

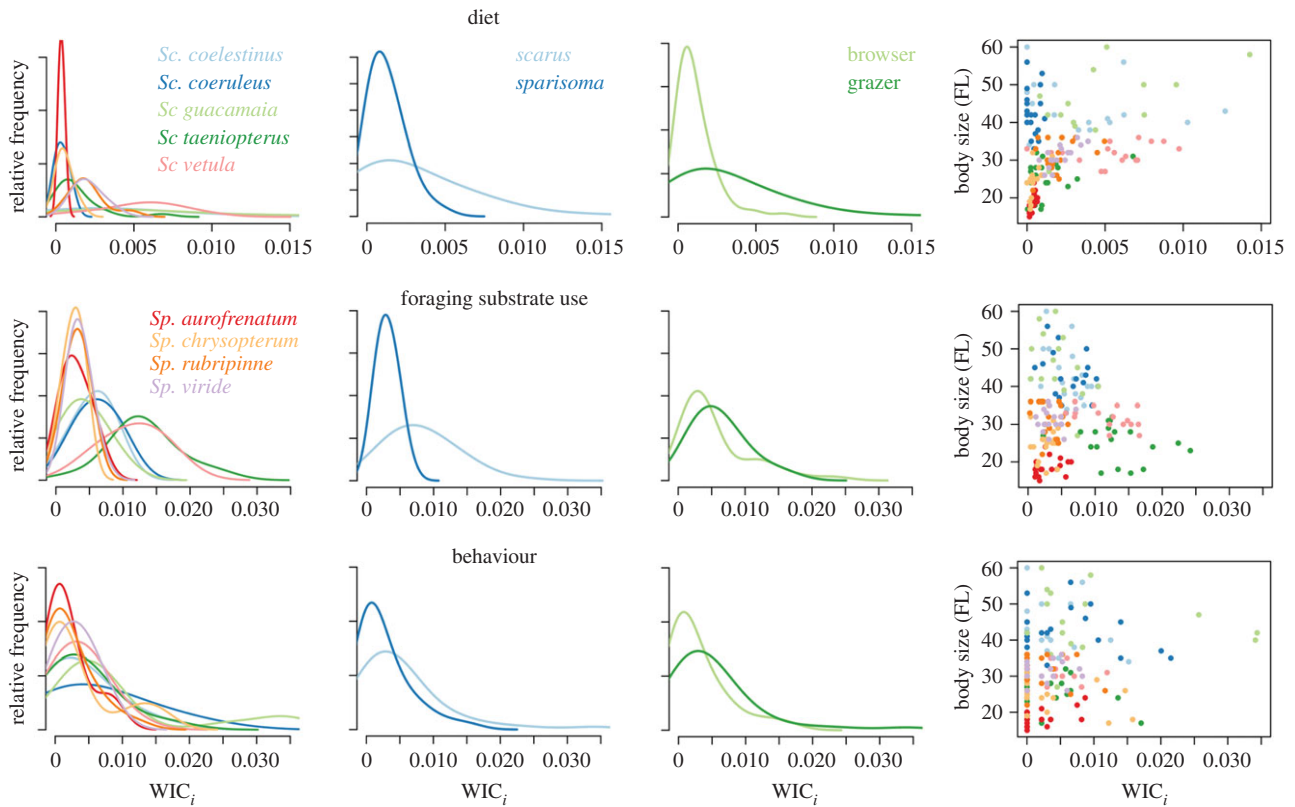


Figure 1. Frequency histograms of all within individual niche widths (WIC_i) separated out at the three levels of biological organization of interested (genus, species and feeding group), as well as by the relative body size of all the individuals (organized by species). (Online version in colour.)

Table 1. Results from linear models showing relative support for the importance of different levels of biological organization for describing individual-level niche widths across the herbivore community for the three niche types. (Levels in bold indicate the classification level that was the best model. Model parameter are as follows: int, intercept; distance, the distance each fish moved during the observation period; FL, fork length of individual.)

niche type	classification level	int	distance	FL	logLik	R-squared	AICc
dietary	genus	-6.65	-0.005	0.03	-147.35	0.26	305.09
	species	-6.95	-0.003	0.02	-100.00	0.65	226.13
	feeding guild	-6.64	-0.005	0.02	-145.16	0.29	300.72
foraging substrate	genus	-3.81	-0.002	-0.02	-102.89	0.58	216.18
	species	-5.22	n.a.	-0.02	-90.70	0.66	205.19
	feeding guild	-5.16	-0.003	n.a.	-151.30	0.09	310.85
behavioural interactions	genus	-5.76	0.005	n.a.	-222.10	0.10	452.45
	species	-5.73	0.005	-0.03	-215.51	0.17	457.13
	feeding guild	-6.18	0.005	n.a.	-222.76	0.09	453.78

correlation between the two metrics. PS_i (the smaller the value the more specialize the individual) and WIC_i showed positive correlations for foraging substrate and behavioural interactions niches ($r = 0.53, 0.50$, respectively, p -values both < 0.001) but not for dietary niche (p -value = 0.53). Thus, fishes with small foraging substrate and behavioural interaction niches tended to also be substrate and behavioural specialists, but this trend did not hold for dietary niche.

4. Discussion

Resolving how species compete and coexist within ecological communities represents a long-standing challenge in ecology. This task is particularly salient when considering the

ecological ramifications of species loss in communities with high levels of species diversity in the wake of a current global mass extinction event [26]. Our study seeks to provide insight to this problem by quantifying niche partitioning across a relatively large number of individuals within nine species in a diverse coral reef fish community. We found mixed support for the importance of different levels of biological organization for characterizing the three ecological niches of interest. Species identity was a relatively strong predictor of both diet breadth and foraging substrate across the nine closely related parrotfish. This finding provides compelling support for the importance of taxonomic identity, and thus biodiversity, for characterizing the trophic role and habitat use of species, particularly in light of the fact that feeding

guild classification was a poor descriptor of these niches. By contrast, no level of biological organization described well behavioural interactions, but instead they were nearly entirely driven by strong individual-level variation among a single dominant species. Further, additional individual-level attributes such as body size and the relative distance travelled while foraging had relatively little influence on all three niches, highlighting the potential idiosyncratic nature of individual ‘personalities’. Our findings collectively underscored the importance of species-level traits for niche partitioning, but that individual-level trait variation with a select few species is a key driver of niche width across this diverse, but taxonomically similar group of herbivores.

Understanding how an ecological niche is partitioned among species and within species allows insight into the relative strength of niche complementarity among species, and whether species and/or individuals tend to be more generalist or specialist. Characterizing species in these terms has been a common theme in ecology for decades, and may be particularly useful in the context of predicting ecological ramifications of species loss for ecosystem function [12,27,28]. Species that have dominant species-level traits would typically be considered ecological generalists in that they occupy a large portion of the total niche of the community [23]. Yet within a dominant species, individuals may vary in their degree of specialization, ranging from generalists, using a wide range of the available resources, or specialists, using only a small subset of these resources [23].

Our analysis allows us to estimate both the degree to which a species has disproportionate influence on an ecological niche ($\mu_{IP/IC}$ and $\sigma_{IP/IC}^2$), but also the degree to which individuals within these species are characterized as having specialist or generalist traits (PS_i index). For example, *Scarus vetula* has strong influence on the herbivore community dietary and foraging substrate niche, in that the mean niche of the individuals in that species were substantially higher than the mean across all individuals in the entire community ($\mu_{IP/IC} > 1$). This suggests that this species consumes a large proportion of the total community-wide dietary resources. Yet when we consider the individuals within this species, we can see that although there is relatively low degree of variation in niche widths across individuals ($\sigma_{IP/IC}^2 < 1$), these individuals still span a relatively broad range of specialization (0.31–0.92; mean = 0.62 ± 0.20). In this case, some individuals are strong generalists (0.92) and others are more specialized (0.31) in their feeding. These findings are congruent with the natural history of this species because they are large bodied individuals that, owing to their size, inherently consume a large proportion of the total community-level dietary resources. Yet despite the large quantity of food consumed, some individuals within this species feed across a large range of the dietary items used by the whole community making them dietary generalists, whereas others only feed on a small subset of these items making them dietary specialists.

In this context, the proportion of total resources that an individual uses has strong influence on their niche width (see methods for equation), explaining why the largest individuals in our dataset tended to have the largest dietary niche width (figure 1). Yet the body size of an individual, nor their relative niche size, does not necessarily dictate their degree of specialization. For example, *Scarus guacamaia* has a very disproportionate influence on the size of the community-level dietary niche (high $\mu_{IP/IC}$), with very high among-individual variation in niche sizes (high $\sigma_{IP/IC}^2$;

figure 2). Despite this, all individuals of this species appear to be ecological generalists relative to the entire herbivore community (high PS_i ; figure 2c), irrespective of their niche width (WIC_i). Thus, individuals within this species are consistent in the relatively high diversity of dietary resources they consume, but vary in the relative amount that they are consuming. By contrast, individuals within the species *Sparisoma aurofrenatum* and *Sparisoma chrysopterum* have consistently small individual niche sizes yet span a broad spectrum in their degree of specialization (i.e. they consume a relatively small amount, but have relatively diverse diets among individuals), underscoring how specialization and niche size are not necessarily strong correlates.

We found substantial variation in species-level contribution to the community-level niche for all three niche types. The fact that a few species tended to have disproportionate influence on the community-level niche provides some support for ecological dominance (or functional redundancy) and thus contrasts expectations of niche complementarity [4,28–30]. However, it is important to note that, while the individuals we observed within each species were representative of the range of body sizes found within these coral reefs, our analysis is not weighted for the relative abundance of the species relative to one another. For example, although *Scarus guacamaia* had strong *per capita* dominance in both the dietary and behavioural niche, this may not be reflective of their net ecological-scale impacts given their low abundance relative to other species. By contrast, *Sparisoma aurofrenatum* had substantially smaller effects on all niches than *Scarus guacamaia*, but are greater than an order of magnitude more abundant [20,21] on the same reefs where our observations were conducted. Thus, the *per capita* strength of a species effect on a particular niche may be offset by their abundance relative to other species within this same system.

We also found substantial differences in the degree to which individual-level traits within species contributed to the community-level niche. This finding is consistent with recent research on large mammalian herbivores in African savannahs showing high within-species variation in dietary niche [11], and emerging ideas of the importance of within-species variation as a potential mechanism for coexistence [13,15]. The relationship between $\sigma_{IP/IC}^2$ and $\mu_{IP/IC}$ compares the relative importance of species-level traits to the relative importance of within-species individual-level traits, and thus the slope of this relationship provides a useful metric to quantify the overall importance of within-species variation in niche width. In this context, when the slope is greater than one, individual-level traits (i.e. the variation among individuals within species) are more important for the community niche than species-level traits.

Interestingly, large variation was found for the relative importance of individual *and* species-level traits in the dietary niche, i.e. the CIs of the slope did not significantly differ from one (slope = 0.91; 95% CI 0.2–1.63); a finding that is congruent with previous research showing substantial variation in dietary preferences within and among species [12,14,31–34]. By contrast, species were highly selective of substrates on which they foraged with little variation among the individuals within these species. This finding is potentially revealing as to how species that share similar resources can coexist. Although species seem to overlap substantially in the dietary items they consume, they appear to be highly selective of where spatially they are consuming these items. Finally, behavioural interactions between individuals (typically of different species)

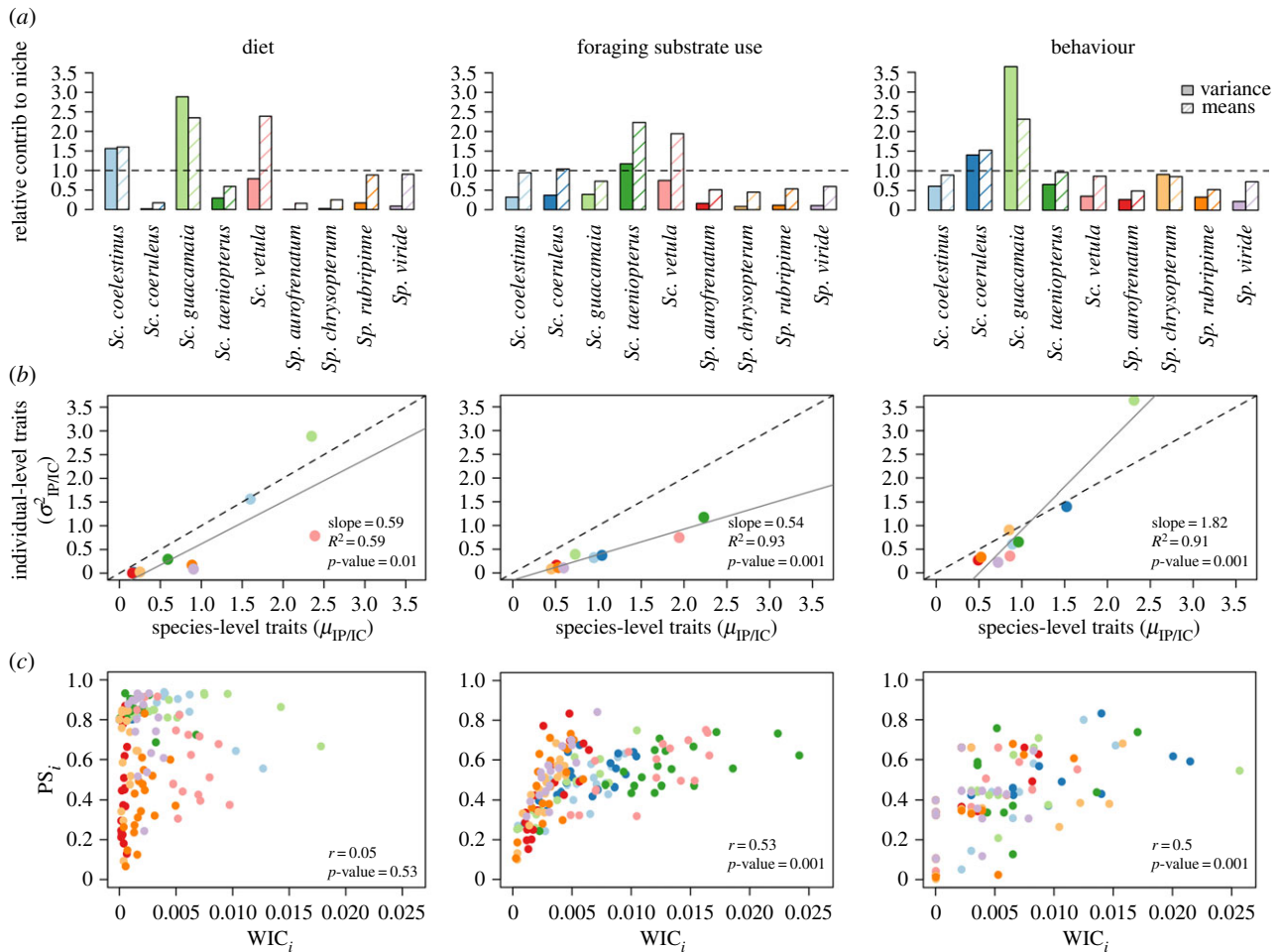


Figure 2. (a) Barplots shows the relative contribution to the three community niche types with respect to individual-level traits ($\sigma_{IP/IC}^2$ variance—solid bars), and species-level traits ($\mu_{IP/IC}$ means—stripped bars). Dashed line indicates the point at which traits are disproportionate relative to the community. (b) Bipolots showing the relationship between $\sigma_{IP/IC}^2$ and $\mu_{IP/IC}$. Regression with slope greater than one indicates the importance of individual-level over species-level traits for the three niche types. Note some data points on (c) are obscured by other data points. (Online version in colour.)

highlight the importance of strong individual-level traits, whereby a single *Scarus guacamai* was nearly entirely dominant, e.g. the slope is greater than one if this species is removed from the relationship, but it does not significantly differ from one (slope = 1.1; 95% CI 0.54–1.69, $R^2 = 0.75$, p -value = 0.003).

Dietary interactions have long been of central interest to ecologists and have subsequently been the focus of many studies seeking to identify individual-level variation within species or populations (see review by [23]). Yet, increasing our understanding of how animals coexist requires refined understanding of interactions beyond what they eat [13,15–17]. Our study highlights the importance of considering multiple traits by showing that despite relatively high dietary overlap, in part owing to high variation in individual-level niches, a potentially important reason why these herbivorous fishes are able to partition finite resources and minimize competition is the high levels of selection in foraging substrate that is relatively constrained across all nine species. Yet, there are many other co-occurring species in coral reef fish communities and behavioural variation may exceed the timescales of our observations. Thus, while our findings shed light on the questions of resource partitioning and competition among herbivorous reef fishes, further studies are needed to test whether similar patterns hold across different guilds of reef fishes and over various time scales of observation.

Our study highlights that the leading mechanisms for coexistence, i.e. complementarity, may be over simplistic, largely because the substantial variation that exists within species needs to further be considered. We provide some support for the ecological notion of dominance in that for all three niches of interest, only a select few species had disproportionate influence on community niche width in the context of both species- or individual-level traits. Further, while our study provides strong evidence for the importance of biodiversity at the species-level, it also highlights the need to extend concepts of biodiversity beyond traditional levels of organization to include the importance of variation among individuals within this taxonomic unit.

Ethics. This study meets the terms of the ethics committee at the institution for whom the study was conducted. The work was conducted at the Florida Keys National Marine Sanctuary under permit no. FKNMS-2013-058.

Data accessibility. Data will be made accessible in full as an electronic supplementary material.

Authors' contributions. T.C.A. and D.E.B. designed field research. T.C.A. conducted field research. J.E.A. conducted statistical analysis and wrote initial draft. All authors contributed on subsequent drafts.

Competing interests. We declare we have no competing interests.

Funding. Data collection was supported by a grant from NOAA's Coral Reef Conservation Program to D.E.B. and B.I. Ruttenberg.

1. Hutchinson G. 1959 Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**, 145–159. (doi:10.1086/282070)
2. Elton CS. 1927 *Animal ecology*. London, UK: Sidgwick and Jackson.
3. Liebold MA. 1995 The niche concept revisited: mechanistic models and community context. *Ecology* **76**, 1371–1382. (doi:10.2307/1938141)
4. Loreau M, Hector A. 2001 Partitioning selection and complementarity in biodiversity experiments. *Nature* **413**, 548. (doi:10.1038/35097128)
5. Loreau M. 2004 Does functional redundancy exist? *Oikos* **104**, 606–611. (doi:10.1111/j.0030-1299.2004.12685.x)
6. Villéger S, Navack-Gottshall PM, Moullot D. 2011 The multidimensionality of the niche reveals functional diversity changes in benthic marine biotas across geological time. *Ecol. Lett.* **14**, 561–568. (doi:10.1111/j.1461-0248.2011.01618.x)
7. Moullot D *et al.* 2014 Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proc. Natl Acad. Sci. USA* **111**, 13 757–13 762. (doi:10.1073/pnas.1317625111)
8. McNaughton SJ. 1978 Stability and diversity of ecological communities. *Nature* **274**, 251–253. (doi:10.1038/274251a0)
9. Ambrose SH, DeNiro MJ. 1986 The isotopic ecology of East-African mammals. *Oecologia* **69**, 395–406. (doi:10.1007/BF00377062)
10. McNaughton SJ, Ruess RW, Seagle SW. 1988 Large mammals and process dynamics in African ecosystems. *Bioscience* **38**, 794–800. (doi:10.2307/1310789)
11. Kartzinel TR, Chen PA, Coverdale TC, Erickson DL, Kress WJ, Kuzmina ML, Rubenstein DI, Wang W, Pringle RM. 2015 DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proc. Natl Acad. Sci. USA* **112**, 8019–8024. (doi:10.1073/pnas.1503283112)
12. Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML. 2003 The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.* **161**, 1–28. (doi:10.1086/343878)
13. Bolnick DI *et al.* 2011 Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* **26**, 183–192. (doi:10.1016/j.tree.2011.01.009)
14. Araújo MS, Bolnick DI, Layman CA. 2011 The ecological causes of individual specialisation. *Ecol. Lett.* **14**, 948–958. (doi:10.1111/j.1461-0248.2011.01662.x)
15. Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J. 2012 The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* **27**, 244–252. (doi:10.1016/j.tree.2011.11.014)
16. Toscano BJ, Gownaris NJ, Heerhartz SM, Monaco CJ. 2016 Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia* **182**, 55–69. (doi:10.1007/s00442-016-3648-8)
17. Spiegel O, Leu ST, Bull CM, Sih A. 2017 What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecol. Lett.* **20**, 3–18. (doi:10.1111/ele.12708)
18. Burkepile DE, Hay ME. 2008 Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proc. Natl Acad. Sci. USA* **105**, 16 201–16 206. (doi:10.1073/pnas.0801946105)
19. Rasher DB, Hoey AS, Hay ME. 2013 Consumer diversity interacts with prey defenses to drive ecosystem function. *Ecology* **94**, 1347–1358. (doi:10.1890/12-0389.1)
20. Adam T, Burkepile D, Ruttenberg B, Paddock M. 2015 Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar. Ecol. Prog. Ser.* **520**, 1–20. (doi:10.3354/meps11170)
21. Adam TC, Kelley M, Ruttenberg BI, Burkepile DE. 2015 Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia* **179**, 1173–1185. (doi:10.1007/s00442-015-3406-3)
22. Robertson R, Warner RR. 1978 *Sexual patterns in the labroid fishes of the Western Caribbean, II, the parrotfishes (Scaridae)*. *Smithsonian Contributions to Zoology*, pp. 1–26. Washington, DC: Smithsonian Institution Press.
23. Bolnick DI, Yang LH, Fordyce JA, Davis JM, Svanback R. 2002 Measuring individual-level resource specialization. *Ecology* **83**, 2936–2941. (doi:10.1890/0012-9658(2002)083[2936:MILRS]2.0.CO;2)
24. Bruggemann JH, Kuyper MWM, Breeman AM. 1994 Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viridae* (Scaridae). *Mar. Ecol. Prog. Ser.* **112**, 51–66. (doi:10.3354/meps112051)
25. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference: a practical information theoretic approach*, 2nd edn. New York, NY: Springer-Verlag.
26. Barnosky AD *et al.* 2011 Has the Earth's sixth mass extinction already arrived? *Nature* **471**, 51–57. (doi:10.1038/nature09678)
27. Roughgarden J. 1972 Evolution of niche width. *Am. Nat.* **106**, 683–718. (doi:10.1086/282807)
28. Gravel D, Bell T, Barbera C, Bouvier T, Pommier T, Venail P, Mouquet N. 2011 Experimental niche evolution alters the strength of the diversity-productivity relationship. *Nature* **469**, 89–92. (doi:10.1038/nature09592)
29. Petchey OL, McPhearson PT, Casey TM, Morin PJ. 1999 Environmental warming alters food-web structure and ecosystem function. *Nature* **402**, 69–72. (doi:10.1038/47023)
30. Dimitrakopoulos PG, Schmid B. 2004 Biodiversity effects increase linearly with biotope space. *Ecol. Lett.* **7**, 574–583. (doi:10.1111/j.1461-0248.2004.00607.x)
31. Bolnick DI, Svanback R, Araújo MS, Persson L. 2007 Comparative support for the niche variation hypothesis that more generalized populations also are more heterogeneous. *Proc. Natl Acad. Sci. USA* **104**, 10 075–10 079. (doi:10.1073/pnas.0703743104)
32. Layman CA, Quattrochi JP, Peyer CM, Allgeier JE. 2007 Niche width collapse in a resilient top predator following ecosystem fragmentation. *Ecol. Lett.* **10**, 937–944. (doi:10.1111/j.1461-0248.2007.01087.x)
33. Araújo MS, Bolnick DI, Machado G, Giarretta AA, dos Reis SF. 2007 Using $\delta^{13}\text{C}$ stable isotopes to quantify individual-level diet variation. *Oecologia* **152**, 643–654. (doi:10.1007/s00442-007-0687-1)
34. Streicker DG, Allgeier JE. 2016 Foraging choices of vampire bats in diverse landscapes: potential implications for land-use change and disease transmission. *J. Appl. Ecol.* **53**, 1280–1288. (doi:10.1111/1365-2664.12690)