Metabolic differentiation facilitates coexistence in two coral reef fish species

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*Abstract.*

Phenotypic differentiation among species determines where, when, and why species can occur and coexist. Thus, ecologists often delineate differences among species with traits that describe species’ sizes, trophic guilds, activity rates, or morphologies. However, for species with similar traits, which are most likely to compete for limiting resources, nuanced adaptations are difficult to pinpoint due to the inherent multidimensionality of species’ niches, especially for mobile animals in highly diverse ecosystems. Here, we use field surveys, morphometrics, behavioral observations, gut content DNA metabarcoding, and physiology to investigate phenotypic differentiation in two small, sympatric coral reef fish species. We show that the gobies *Fusigobius neophytus* and *Gnatholepis cauerensis* co-occur in sandy habitats throughout a coral reef lagoon in French Polynesia. While superficially similar, the two species differ in the length of their gastrointestinal tracts, their ingested prey, and their foraging rates. These differences are reflected in their metabolic rates. Furthermore, both species forage more in mixed-species vs. single-species configurations. Our results suggest that metabolic rate mirrors phenotypic adaptations across several interrelated axes of diversification. Thus, metabolic rate may provide a precisely measurable, standardized trait that can improve our understanding of ecological dynamics that govern interactions and facilitate coexistence among superficially similar species.

*Keywords: functional traits; biodiversity-ecosystem functioning; metabolic theory; niche overlap; cryptobenthic fish; limiting similarity*

Introduction

Theoretical and empirical work has demonstrated that coexistence among sympatric species requires a certain degree of niche differentiation (MacArthur and Levins 1967, Chesson 2000). Such niche differentiation usually comes with morphological, physiological, or behavioral adaptations that facilitate the exploitation of non-overlapping resources (e.g., (Schluter 1996)). Ecologists frequently seek to capture phenotypic differences through simple traits (e.g., size, diet, morphology) that reveal the ecological forces that underpin species’ abundances, distributions, and biological interactions (McGill et al. 2006, Messier et al. 2010). Indeed, trait-based ecology has offered an intuitive framework that relates species’ ecological niches to community assembly and ecological processes (Carroll et al. 2011). For plants, in particular, precisely measurable, broadly applicable, and highly responsive traits revolving around the leaf economic spectrum have shed light on how species interact and produce biomass in a changing world (Enquist et al. 2007, Díaz et al. 2016, Funk et al. 2017).

In contrast, despite great advances, trait-based approaches for animal species have largely relied on coarse categorical or semi-quantitative classifications that can overlook important ecological differences (Tscharntke et al. 2008, Mouillot et al. 2014, Wilman et al. 2014). While undoubtedly providing insights into the assembly and functioning of animal communities (Stuart-Smith et al. 2013, Gagic et al. 2015, Griffiths et al. 2015), the traits used to describe animal species, such as body size, trophic guild, morphology, or activity pattern, lack the consistency, generality, and resolution required for a fine definition of the ecological niche across taxa (Lefcheck et al. 2015, Weiss and Ray 2019). This is particularly problematic in hyperdiverse ecosystems, such as rainforests or coral reefs, in which scores of species with similar phenotypic characteristics coexist amidst an innumerable array of resources. Phenotypic differences among superficially similar species may be imperceptible when assessed with coarse categorical traits, potentially inflating perceived functional equivalence (or redundancy) within groups (Mouillot et al. 2014, Houadria et al. 2016, Cooke et al. 2019, Potapov et al. 2020). However, niche differentiation commonly occurs among members of the same functional group, with concordant phenotypic variation linked to the exploitation of distinct resources or preferences for different environmental conditions. For example, herbivorous fishes on coral reefs have long been placed into broad functional groups (Green and Bellwood 2009); yet, closer examination has yielded fine-scale differentiation among species within these functional categories across multiple ecological axes (Burkepile and Hay 2011, Rasher et al. 2013, Clements et al. 2017). Finding precise traits that accurately define functional differences will hone our understanding of animal communities.

Physiological traits have been identified as important descriptors of species niches (McGill et al. 2006), yet they are rarely integrated into trait-based frameworks (Wilman et al. 2014, Madin et al. 2016, Weiss and Ray 2019). Metabolic rate, in particular, can be readily compared across taxa, is precisely measurable with established techniques and protocols, and reportedly correlates with organismal characteristics (White and Kearney 2013). Here, we test whether standard (resting) and maximum metabolic rates (SMR and MMR, respectively) correlate with phenotypic differences in two cryptobenthic reef fish species. Due to their small size and inconspicuous nature, cryptobenthic fishes are poorly understood and often considered functionally equivalent (Brandl et al. 2018). However, given their important trophic role on coral reefs (Brandl et al. 2019), it is critical to understand their contributions to nutrient fluxes in tropical marine ecosystems. The common fusegoby *Fusigobius neophytus* and the eyebar goby *Gnatholepis cauerensis* (cf. *scapulostigma*; (Larson and Buckle 2012)) are widespread and sympatric across the Indo-Pacific, prefer sandy habitats in sheltered lagoons, and are of similar sizes and morphologies. We therefore test whether the metabolic profiles of the two gobies mirror differences in their anatomy, diet, or behavior, and whether phenotypic differentiation may facilitate their co-occurrence and contributions to ecosystem functioning.

Methods

We performed our study in Mo’orea, French Polynesia, using individual-based and whole-community sampling while SCUBA diving or snorkeling. For the individual-based samples, we collected both species using an anesthetic (5:1 clove-oil:ethanol solution) and small hand nets at depths of 1.5-8 m along the northern coast of the island (June/July 2018). We transferred individuals designated to the behavioral and physiological trials to flow-through seawater aquaria, and euthanized individuals for dietary and morphological analyses using a clove-oil overdose. For the community samples, fishes were collected with enclosed clove-oil stations (Ackerman and Bellwood 2002) in lagoonal and outer reef locations around the entire island between 2017 and 2020. Fishes were euthanized with a clove-oil overdose and transferred to the laboratory in an ice-water slurry. We identified, weighed, and measured all individuals. All work was performed under SFU ethics approval Protocol #1254B-17 (IMC).

*Physiological trials*

We estimated standard (resting) and maximum metabolic rates (SMR and MMR, respectively) for both species from rates of oxygen uptake using intermittent-closed respirometry (Clark et al. 2013). The respirometry setup consisted of up to eight cylindrical glass respirometry chambers (6.7 mL for small individuals, 36 mL for large individuals), of which we left one chamber empty in each run as a control for background (microbial) respiration. All chambers were fitted with fiber-optic oxygen sensors connected to an oxygen meter and logging software (FireStingO2; Pyro Science GmbH, Aachen, Germany), which recorded oxygen concentration in each chamber every 2 s. Continuously operating peristaltic pumps recirculated water inside the respirometry chambers to ensure mixing. Intermittently operating flush pumps were used to create an open period (180 s), when the chambers were flushed with fully aerated water, and a closed period (120, 180, 420, and 720 s, respectively, depending on fish/chamber sizes), during which fish oxygen uptake was recorded to calculate metabolic rate.

On the day before a respirometry trial, we moved individuals into holding tanks, where they fasted for 24 h. We then chased each individual sequentially with a dip net for at least 30 s, or until the fish was visibly exhausted, and immediately placed it into its chamber. Thus, the first post-chase recording of oxygen uptake rate was the aerobic MMR of the fish (Norin and Clark 2016). We then left all fish undisturbed in the respirometry chambers for ~23 h and calculated the SMR of each fish as the mean of the lowest 10% of all its oxygen uptake rate recordings.

*Morphometric analyses*

For each individual, we recorded body mass (g), total length (mm), standard length (mm), girth (diameter at the widest point in mm), and the vertical and horizontal gape width (maximum distance inside the mouth in mm) with digital calipers (0.01 mm) and a digital scale (0.001 g). For 22 individuals (10 *F. neophytus* and 12 *G. cauerensis*), we also measured the length of the gastro-intestinal tract (GIT, from the esophagus to the anus). To do so, we dissected out the gut by making an incision along the ventral side of the body under a stereomicroscope, snipping the esophagus at the highest accessible point, carefully untangling the intestinal tract, and positioning the entire GIT on a sterile petri dish. We then took a standardized, lateral photograph of the fish in the petri dish and measured the maximum length of the GIT in mm by tracing the gut in ImageJ after calibrating the scale based on the individual’s standard length.

*Dietary analyses*

To obtain dietary information, we removed the guts of 20 *F. neophytus* and 18 *G. cauerensis* in sterile conditions, as described above. Using the entire gut, we then performed DNA extractions using a DNeasy PowerSoil DNA Isolation Kit (Qiagen, Hilden, Germany). After the extractions, we sent all samples to Jonah Ventures (Boulder, Colorado) for library preparation, sequencing, and bioinformatic processing, targeting the cytochrome *c* oxidase subunit I (COI) and the chloroplast 23S rRNA gene regions (details in Appendix S1).

*Behavioral trials*

To examine foraging behavior, we performed aquarium-based feeding trials. Specifically, we set up six 30 × 38 cm plastic tanks fitted with GoPro cameras. We covered the bottom of each tank with sand (1 cm depth), the primary food source for both species, from the lagoon. To ensure homogeneity in the sand, we pooled, boiled, and redistributed the sand samples into the different aquaria. We also fitted each tank with two pieces of PVC as shelters (6 cm and 12 cm length, 1.5 cm diameter). We then placed six individual fish in each tank in three configurations: *F. neophytus* only, *G. cauerensis* only, and a mix of three *F. neophytus* and three *G. cauerensis* individuals). In total, we had 18 individuals per species and ran 9 distinct trials (three trials per configuration), with individuals being chosen randomly across trials. Before each trial, we held individuals without food for 24 h. After adding all individuals to the trial tank, we recorded foraging behavior for 30 min. We then analyzed the videos to quantify: i) the frequency of feeding (bites taken from the sandy substrate), ii) the occurrence of antagonistic behavior between individuals (one individual chasing another), and iii) the time spent sheltering in the PVC pipes. For the single-species trials, we only followed three randomly chosen individuals. In total, we performed 36 observations across all trials (18 *F. neophytus* and 18 *G. cauerensis*).

*Data analysis*

To assess coexistence patterns between the two species based on community samples, we used a joint species distribution model (jSDM). Specifically, we used a Bayesian hierarchical multivariate probit regression to determine the residual correlation coefficient of the two species (*F. neophytus* and *G. cauerensis*) after accounting for the filtering effects of habitat (Pollock et al. 2014). For metabolic rate estimates, we ran Bayesian models (Bürkner 2017) to test the effects of body mass (log10-transformed), species identity, their interaction (body mass × species), and temperature on SMR (log10-transformed) and MMR (log10-transformed). We removed two trials (one *F. neophytus*, one *G. cauerensis*) during which the temperature of the respirometry setup fell > 2.0ºC below the ambient environmental temperature (~28.5ºC), resulting in n = 15 for each species. With temperature held at the mean of 28.5ºC (full range: 27.73 – 29.32ºC), we then predicted metabolic rates across the size range of each species based on 1,000 draws from the posterior distribution. Furthermore, we predicted each species’ metabolism at the mean temperature and mean body mass of all fishes (0.714 g) (1,000 draws).

To evaluate morphological differences, we ran Bayesian models to test the effects of standard length (SL) and species identity on the horizontal and vertical gape measurements and the length of the GIT. To examine patterns of prey ingestion, we used rarefaction curves for the COI and 23S markers to visualize the number of exact sequence variants (ESVs) according to sequence abundance (Hsieh et al. 2016). Furthermore, we calculated Pianka’s index of niche overlap for the species-level predator–prey matrix of the relative read abundances (RRA) across ESVs. Then, we constructed presence–absence matrices of ESVs across all fishes for the COI and 23S markers, which we then merged into a single matrix. Using this matrix, we constructed a binary, bipartite network and computed Newman’s modularity (Newman 2006), a metric that describes network structure based on distinct clusters. Since the algorithm starts randomly (potentially resulting in different modularity results), we iterated the computation of modularity 50 times to obtain the most stable modularity computation. We then visualized module membership of all individuals in a bipartite network tree, using the Kamada-Kawai algorithm.

Finally, we tested the effects of species identity, mixed- vs. single-species configurations, and their two-way interaction on bite rates from the aquarium trials using a Bayesian linear model with a negative binomial error distribution. We also ran the model with a random effect for each trial and tested for differences in model performance using leave-one-out (LOO) cross validation. We predicted bite rates per min based on 1,000 draws from the posterior. We performed all analyses in *R* (R Core Team 2019) (see Appendix 2 and *R* code for detail).

Results

The two gobies frequently co-occurred throughout the lagoon around Mo’orea but were absent from the exposed forereef. Accordingly, the probit model showed a strong effect of habitat for both species (*F. neophytus*: *Slope* = -59.79 [-94.76 lower 95% credible interval, -34.39 upper 95% credible interval]; *G. cauerensis*: *Slope* = -78.31 [-99.32, -63.21]), but the median residual correlation coefficient was also positive (0.466), indicating no negative biotic interactions between the two species within their environmental niches (Fig. 1).

The two species differed substantially in their metabolic profiles (Fig. 2). A predictably strong scaling relationship existed between individual metabolic rates and body mass, with similar slopes (metabolic scaling exponents) in both species for SMR (*F. neophytus* = 0.62 [0.48, 0.77]; *G. cauerensis* = 0.57 [0.35, 0.69]) and MMR (*F. neophytus* = 0.59 [0.36, 0.82]; *G. cauerensis* = 0.62 [0.39, 0.92]). However, the intercept (metabolic level, back-transformed) was substantially higher for *G. cauerensis* than *F. neophytus* for both SMR (*F. neophytus* = 0.124 [0.114, 0.134] mg O2 h-1;*G. cauerensis* = 0.147 [0.128, 0.169] mg O2 h-1) and MMR (*F. neophytus* = 0.281 [0.246, 0.318] mg O2 h-1;*G. cauerensis* = 0.449 [0.344, 0.529] mg O2 h-1) (Fig. 2A,B). At their mean body mass (0.714 g), the SMR of *G. cauerensis* was 19.80% [7.92%, 31.68%] higher than that of *F. neophytus*, while the MMR of *G. cauerensis* was 56.96% [34.35%, 83.91%] higher than that of *F. neophytus* (Fig. 2C,D).

Horizontal and vertical gape increased with SL, but neither differed between the species (Appendix S3). In contrast, the GIT of *G. cauerensis* was roughly twice as long as that of *F. neophytus* at their median SL (*F. neophytus* = 19.2 [14.8, 24.1] mm; *G. cauerensis* = 37.5 [33.3, 41.6] mm), while the girth was slightly narrower for *G. cauerensis* (*F. neophytus* = 4.88 [4.74, 5.01] mm; *G. cauerensis* = 4.61 [4.45, 4.78] mm) (Appendix S3, Fig. S1).

Furthermore, the two species differed in their ingestion of animal (identified with the COI marker) and autotroph (identified with the 23S marker) prey items. COI gut content metabarcoding yielded 51 distinct ESVs (i.e., prey items) across the two goby species. Only five (of 20) *F. neophytus* ingested animal prey items; in contrast, 14 (of 18) *G. cauerensis* ingested animal prey items. 23S gut content metabarcoding revealed 1,500 distinct ESVs, and all but two individuals (one *F. neophytus*, one *G. cauerensis*) ingested autotrophic prey items. Both species ingested similarly high relative abundances of diatoms (phylum Bacillariophyta), but *G. cauerensis* ingested a higher proportion of algae in the phylum Cryptophyta, whereas *F. neophytus* ingested a higher relative abundance of unidentified autotrophic material (Appendix S3, Fig. S2). The rarefaction showed that *G. cauerensis* ingested a markedly higher diversity and abundance of animal prey items, while *F. neophytus* ingested a higher diversity and abundance of autotrophic prey items (Fig. 3A,B). Pianka’s niche overlap index was 0.369 based on the COI gut content metabarcoding data and 0.423 based on the 23S data. The trophic network constructed from the combined presence–absence matrix of COI and 23S ESVs was compartmentalized into five distinct modules in the consensus computation (modularity = 0.351). The five modules were divided into two modules (I and II) dominated by *G. cauerensis* and three modules (III, IV, V) dominated by *F. neophytus*. Only one *F. neophytus* individual was assigned to modules I and II (which contained 12 *G. cauerensis*), while five *G. cauerensis* spread across the three modules that contained the remaining 18 *F. neophytus* (Fig. 3C).

Finally, the ecological differences in physiology, anatomy, and diet were also reflected in differences in the foraging behavior between the two species (Fig. 4). *G. cauerensis* always took more bites than *F. neophytus*. While *F. neophytus* foraged least in the single-species setting (0.033 [0.013, 0.081] bites min-1), they took at least an order of magnitude more bites when mixed with *G. cauerensis* (0.606 [0.336, 1.235] bites min-1). Similarly, *G. cauerensis* took twice as many bites in the mixed-species treatment (10.785 [6.070, 22.188] bites min-1) than when only kept with conspecifics (5.887 [3.374, 11.795] bites min-1). Two-thirds of aggressive interactions (27 out of 39) were initiated by *F. neophytus* (74.1% directed at conspecifics during the single-species trials). Chases initiated by *F. neophytus* in mixed-species treatments were directed at *G. cauerensis* (57.1%) and *F. neophytus* (42.9%). In turn, 12 chases (30%) were initiated by *G. cauerensis*, all during mixed-species trials. 11 (91.7%) of these were directed at conspecifics.

Discussion

Phenotypic variation among species determines their biotic interactions, ecological role, and response to changing environmental conditions. Yet, species’ phenotypes are inherently multidimensional and shaped by the interplay of morphological, physiological, and behavioral adaptations. Here, we show that species-specific variation in metabolic rate mirrors phenotypic differentiation in two cryptobenthic coral reef fishes. Specifically, metabolic differences in two sympatric, sand-dwelling gobies (*Fusigobius neophytus* and *Gnatholepis cauerensis*) reflect divergences in morphological, dietary, and behavioral traits. This partitioning, in turn, appears to enables the coexistence of the two species in a seemingly homogeneous sandy habitat.

Our results reveal that sympatric, sand-dwelling gobies can differ markedly in their ecological niches. Near-reef sandy habitats harbor diverse assemblages of small, benthic fishes that are superficially similar (Syms and Jones 2004), until examined more closely. In the western Atlantic, for example, *Gnatholepis thompsoni* differs in its dentition, foraging behavior, and prey ingestion from other sand-dwelling gobies in the genus *Coryphopterus* (Kramer et al. 2009), a genus close to *Fusigobius* (Thacker and Cole 2002, Thacker and Roje 2011). Our examination of the Indo-Pacific *F. neophytus* and *G. cauerensis* indicates similarly strong phenotypic differences, suggesting a marked difference in the lifestyles of the two fishes.

In fishes, interspecific variation in gut length often correlates with variation in broad trophic categories, with longer gastrointestinal tracts from planktivores to carnivores to omnivores and herbivores (Elliott and Bellwood 2003, Wagner et al. 2009, Wilson and Castro 2010). This pattern is, at least in part, driven by the nutritional challenges of digesting plant material (Choat and Clements 1998), and it roughly holds true across some species of coral reef gobies, with the herbivorous species having the longest guts (Hernaman et al. 2009). The gut of *G. cauerensis* was twice as long as the gut of *F. neophytus*. However, the relationship between comparative gut length and the ingested biota of the two species is counterintuitive: *G. cauerensis* ingested more animal material, while *F. neophytus* ingested more plant material. Although ingested biota is not a strict indication of trophic ecology (Casey et al. 2019), our results show a pattern opposite than predicted by differences in gut length. Similarly, in accordance with previous investigations of bite rates in gobies (Hernaman et al. 2009), *G. cauerensis* foraged at a significantly higher rate than *F. neophytus*. Yet, more active lifestyles are commonly associated with shorter gastrointestinal tracts across trophically similar fishes (Fu et al. 2009), and species that rely on plant material for nutrition generally have high foraging rates (Choat and Clements 1998). Thus, relationships between gut length, foraging activity, and the nature of ingested prey items in the two studied gobies appear to contradict expectations strictly based on digestive physiology across trophic groups.

However, within the same trophic group, the length of the intestinal tract may not correspond to finer-scale dietary differences (Kramer and Bryant 1995) although it can be overridden by phylogenetic history (German and Horn 2006). The genus *Gnatholepis* is placed within the Gobionellinae, a lineage of herbivorous and omnivorous genera predominantly associated with brackish, low-flow habitats (Thacker and Roje 2011), which may explain the comparatively long gut of *G. cauerensis*. In contrast, *F. neophytus* is placed close to the genus *Corphyopterus*, which is predominantly carnivorous and occasionally planktonic (Thacker and Cole 2002, Kramer et al. 2009) and possibly drives the shorter gut lengths in *Fusigobius* despite their predominant ingestion of algae. Notably, *F. neophytus* has previously been listed as a micro-crustacean feeder, while also ingesting large amounts of organic detritus (Nakamura et al. 2003). Organic detritus has a high prevalence of diatoms (Wilson et al. 2001), which were common in the guts of *F. neophytus*. Overall, the phenotypic differentiation between *G. cauerensis* and *F. neophytus*, albeit apparent across multiple niche axes, is clearly riddled with convoluted signals arising from evolutionary history, cryptic dietary items, and complex interrelated processes that drive foraging strategies and digestive physiology.

An energetic perspective, as provided by the metabolic differences between the two species, can help us understand this complex, multidimensional mosaic of trait differentiation, and it highlights the potential of metabolic rate to serve as a proxy for phenotypic variability among species. The comparatively low metabolism of *F. neophytus* aligns with the species’ short GIT, low foraging rates, and high ingestion of autotrophs. The higher metabolism of *G. cauerensis* matches the species’ continuous and active foraging strategy, long GIT, and mixed diet of animal and autotroph material. The GIT and its associated organs can account for 40% of the vertebrate metabolism (Cant et al. 1996), and there are strong, intuitive metabolic ramifications of active, continuous foraging vs. passive prey ingestion, independent of digestion costs, such as sit-and-wait ambush predation (Fu et al. 2009, Killen et al. 2016). Furthermore, the prevalence of animal prey ingestion corresponds to elevated metabolic rates (Muñoz-Garcia and Williams 2005). While these examples emphasize the potential of metabolism to serve as a proxy of phenotypic differentiation, they are almost exclusively based on either intraspecific comparisons or assessments across broad, coarse groups of organisms. Our results, in turn, indicate that metabolism also provides a detailed account of nuanced ecological differences between species that broadly overlap in body size, morphology, habitat, and ecology.

The capacity of metabolic rate to represent fine-scale phenotypic variation between the two study species holds promise for our understanding of coexistence dynamics and ecosystem functioning. In our feeding trials, both species foraged more frequently in mixed-species groups, which indicates that the metabolic differences between the two species might allow a relaxation of interspecific competition and may permit stable coexistence, ultimately enhancing the energetic efficiency with which prey are converted to body mass in mixed assemblages of sand-dwelling gobies. This is supported by population dynamics of sand-dwelling gobies in the Caribbean, in which strong intraspecific density-dependence reduces the growth, survival, health, and body condition of individuals (Forrester and Steele 2004). Specifically, in mixed-species assemblages, individual growth of *G. thompsoni* and *C. glaucofraenum* exceeded growth in single-species groups (Forrester et al. 2006), and intraspecific competition for food and shelter is more limiting than competition between species (Forrester and Steele 2004, Forrester et al. 2006). Based on our study, it is likely that these Caribbean gobies would also display distinct metabolic profiles and phenotypic differentiation across multiple axes.

Functional trait-based ecology offers many insights into the processes that govern community assembly and functioning (McGill et al. 2006). While physiological traits are implicitly integrated into the plant economic leaf spectrum (Funk et al. 2017), they have rarely been used to explain coexistence, assembly, and functioning of animal communities (Start et al. 2018). Our results highlight the potential power of metabolic traits (standard and maximum metabolic rates) to collapse ecological differentiation across major phenotypic axes that may be influenced by a variety of competing dynamics (e.g., evolutionary history, nutritional challenges, diet shifts). Examining consumer communities through a metabolic lens may therefore reveal important differentiation among species that are presently considered functionally equivalent (e.g. (Mouillot et al. 2014, Houadria et al. 2016, Cooke et al. 2019, Potapov et al. 2020)). This differentiation, in turn, impacts overarching ecological processes that determine ecosystem functioning (Brown et al. 2004). Given the speed with which biological assemblages are undergoing global changes, new means to understand these dynamics are a vital goal in ecology.

ACKNOWLEDGEMENTS

We thank the staff of the CRIOBE, G. Martineau, S. Degregori, and H. Yan for field assistance. Funding was provided by the BNP Paribas Foundation (VP), Agence National de la Recherche (VP & SJB), Natural Science and Engineering Research Council of Canada (IMC & SJB), and Danish Council for Independent Research (TN; DFF-4181-00297). SJB was supported by an NSERC Banting Fellowship and JMC by a Make Our Planet Great Again Grant. All code and data to reproduce the results are included in the submission and will be made available on a public repository upon acceptance.

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Figure Legends

Fig. 1. (**A**) Map of Mo’orea, French Polynesia, with the occurrences of the two goby species indicated for samples taken in the lagoon (circle) and on the slope (triangle). Empty symbols indicate the absence of both species, while blue (*F. neophytus*) and gold (*G. cauerensis*) symbols indicate the presence of the respective species. Symbols are scaled by the log+1 of the abundance in each sample. (**B**) Predicted probabilities of occurrence for the two species, based on a jSDM. Symbols indicate habitat type, while contours delineate the density distribution of samples.

Fig. 2. Relationship between (**A**) standard metabolic rate (SMR) and (**B**) maximum metabolic rate (MMR) and body mass for *F. neophytus* (blue circles) and *G. cauerensis* (gold diamonds). (**C**) Lines represent 100 fitted draws from the model posterior and (**D**) depict posterior predictions for species-specific SMR and MMR estimates at the overall mean body mass (0.714 g). Dashed and dotted lines and the opacity of the density curves represent the median and 95% percentiles, respectively.

Fig. 3. Rarefaction curves showing the number of ESVs according to sequence abundance for (**A**) COI gut content metabarcoding and (**B**) 23S gut content metabarcoding for *F. neophytus* (blue) and *G. cauerensis* (gold). Solid lines indicate interpolated, empirical estimates, while dashed lines indicate extrapolation to the maximum sequence abundance observed across the two species. (**C**) Trophic network plot with individual fishes highlighted with colored shapes, and the end points of the interaction lines representing distinct prey items. Shapes indicate module membership, while colors indicate species (blue = *F. neophytus*; yellow = *G. cauerensis*).

Fig. 4. Behavioral patterns of the two species in mixed- and single-species treatments. Violin plots represent the predictions from a Bayesian two-way interaction model, with the 0.025, 0.5, and 0.975 quantiles indicated, while blue circles (*F. neophytus*) and gold diamonds (*G. cauerensis*) depict the raw data obtained from the feeding trials.

Figure 1

A close up of a map

Description automatically generated

Figure 2

A close up of a map

Description automatically generated

Figure 3

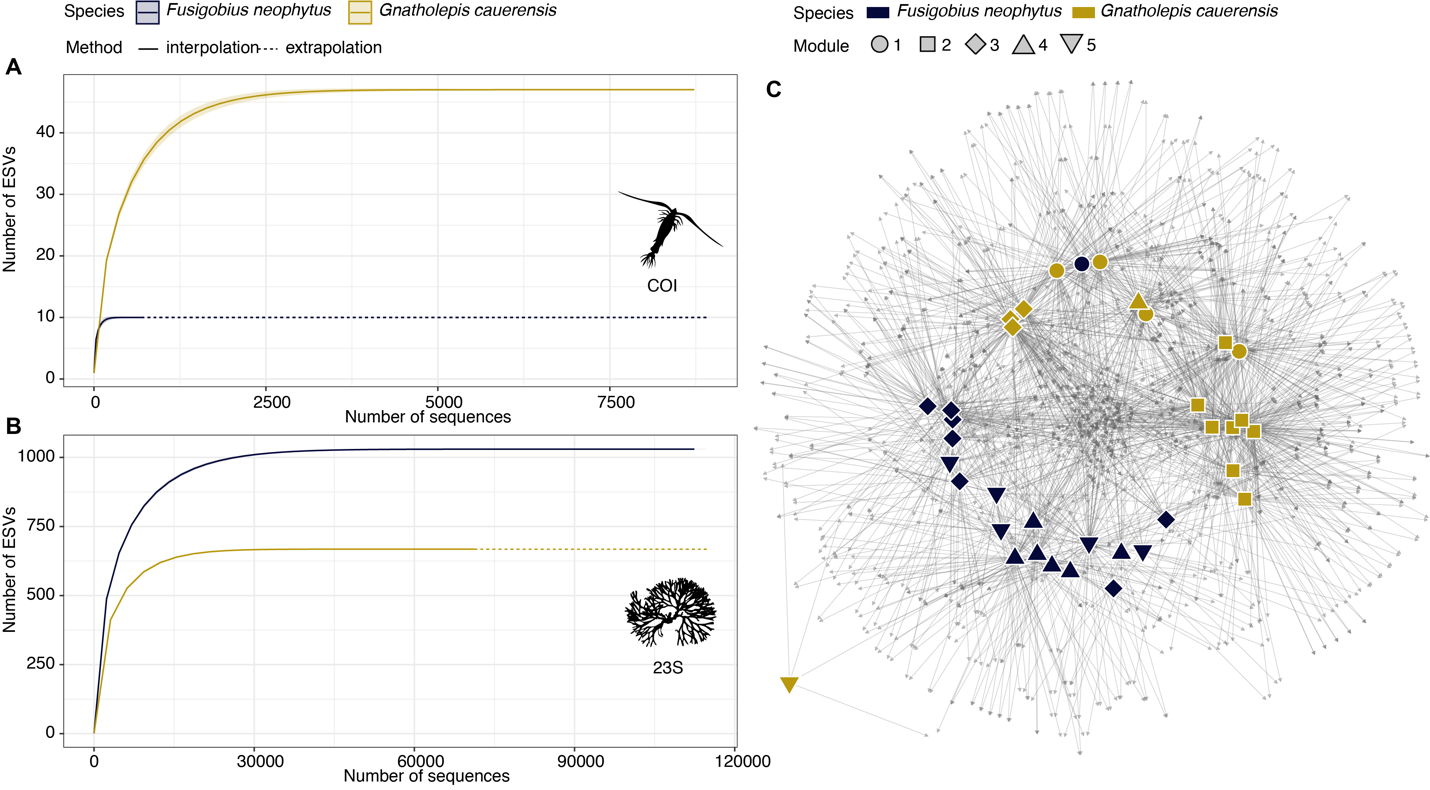
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Figure 4

A screenshot of a video game

Description automatically generated