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Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet and foraging microhabitat use

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Patterns of ecological specialization offer invaluable information about ecosystems. Yet, specialization is rarely quantified across several ecological niche axes and variables beyond the link between morphological and dietary specialization have received little attention. Here, we provide a quantitative evaluation of ecological specialization in a coral reef fish assemblage (f. Acanthuridae) along one fundamental and two realized niche axes. Specifically, we examined ecological specialization in 10 surgeonfish species with regards to morphology and two realized niche axes associated with diet and foraging microhabitat utilization using a recently developed multi-dimensional framework. We then investigated the potential relationships between morphological and behavioural specialization. These relationships differed markedly from the traditional ecomorphological paradigm. While morphological specialization showed no relationship with dietary specialization, it exhibited a strong relationship with foraging microhabitat specialization. However, this relationship was inverted: species with specialized morphologies were microhabitat generalists, whereas generalized morphotypes were microhabitat specialists. Interestingly, this mirrors relationships found in plant–pollinator communities and may also be applicable to other ecosystems, highlighting the potential importance of including niche axes beyond dietary specialization into ecomorphological frameworks. On coral reefs, it appears that morphotypes commonly perceived as most generalized may, in fact, be specialized in exploiting flat and easily accessible microhabitats.

1. Introduction

The fundamental characteristics of species' niches shape ecological communities across the globe. Within communities, species differ not only in their positions in niche space, but also in the respective sizes of the volumes they occupy [1]. Specialist species, often considered as taxa that occupy the smallest niche volumes, have evoked particular interest in a wide range of fields [2–4]. Ecological specialization is accepted as a key factor for countless facets of organismal biology, affecting speciation [5], species distribution patterns [6] and ecosystem functioning and stability [7]. Yet, as ecological specialization can occur on various levels (e.g. fundamental versus realized or individuals versus populations [8–10]), many aspects of its ecosystem impacts remain unresolved.

Two of the most commonly studied features of ecological specialization are morphological/physiological attributes and behavioural traits relating to foraging [2], and their respective relationships. By identifying morphological traits that directly relate to prey capture or procurement capacities, numerous studies have established strong correlations between morphological and dietary specialization in birds [11], reptiles [12], fishes [13] and mammals [14], suggesting a tight link between fundamental and realized niches and permitting the inference

of simple directional evolutionary pathways. Consequently, relating morphological features to dietary preferences has become one of the most widespread techniques used to extrapolate ecological function [15]. Ichthyologists, in particular, have made extensive use of ecomorphological techniques to interpret the ecology of fishes, especially when sustained observational studies are unfeasible [16–23].

However, in the past two decades, there have been a number of intriguing studies that have revealed high behavioural plasticity in morphologically specialized fish species [24–28]. It appears that morphological specialization in teleost fishes does not always entail dietary specialization and that, in many cases, a species' realized (dietary) niche is largely unrelated to its morphology [29,30]. One of the most striking examples of this scenario was described in African cichlids, where the apparent mismatch between morphological features and dietary niches in ecologically specialized species has been termed 'Liem's paradox' (i.e. why are morphological specialists often dietary generalists [24,31]). The most common explanation for the paradox is that specialized morphological traits enable exploitation of 'fallback foods' when preferred resources are low. It is posited that this has arisen as a result of competition-driven morphological specialization during low-resource situations, while retaining the capacity to exploit a range of preferred resources under more typical circumstances [31]. This hypothesis has been supported by both empirical and theoretical work on a wide range of taxa [32,33], and appears to be the most prevalent explanation in teleost fishes [34,35].

As the marine analogues to cichlids in African Rift Lakes, coral reef fishes with their extreme diversity offer an outstanding opportunity to investigate ecological specialization [18]. Despite extreme morphological specialization in numerous reef fishes lineages [10], attempts to relate these features to dietary niche partitioning have had mixed success [27,36]. Herbivorous reef fishes *sensu lato* [37] provide an excellent group for exploring patterns of ecological specialization. Herbivore communities are of critical importance for the benthic structure of shallow reef environments and have been the subject of intensive research with regards to their diet [38,39], foraging behaviour [40] and evolutionary history [41]. However, patterns of ecological specialization in herbivore families have rarely been examined. This is particularly interesting given the variation in morphological diversification among and within herbivorous families [41,42], and the presence of dietary niche partitioning across distinct phylogenetic lineages [38,43,44]. Furthermore, there is evidence for subtle partitioning of feeding microhabitats in many families [43,45], which has been linked to morphological traits [42,46] but has not been considered with regards to ecological specialization, despite its potential importance in aquatic ecosystems [47]. There is, therefore, strong indication of the potential for ecological specialization in herbivorous reef fishes along three distinct, but interrelated niche axes: morphology, diet and foraging microhabitat utilization. In addition, in the light of the functional importance of herbivores in shaping benthic dynamics, and the tendency of ecological specialists to be among the first species to succumb to human-induced disturbances [7], detecting ecological specialists among herbivorous fish species may be important for coral reef management, particularly given current anthropogenic pressures [48,49].

To assess the relationship between fundamental (morphological) and realized (behavioural) specialization on coral

reefs, we examined an assemblage of 10 species of surgeonfishes (f. Acanthuridae). We first identified morphological specialization among species using external features, and then considered two distinct behavioural niche axes, diet and foraging microhabitat utilization. For each behavioural axis, we examined behavioural specialization using an individual-based multidimensional framework [45], which allows for a representation of all species along a quantitative generalist–specialist continuum. We examined the relationship between morphological specialization and the two behavioural niche axes based on three underlying hypotheses: (i) no relationship (as a null-hypothesis), (ii) a positive relationship following the 'traditional' ecomorphological paradigm where morphological specialists are behavioural specialists and (iii) an inverse relationship (potentially consistent with Liem's paradox; figure 1).

2. Material and methods

All fieldwork and sampling was conducted on reefs around Lizard Island, a mid-shelf island in the northern Great Barrier Reef (GBR), Australia (14°40'08"S 145°27'34"E). Data were collected from adult individuals of 10 surgeonfish species in four genera, *Acanthurus blochii*, *A. lineatus*, *A. nigricauda*, *A. nigrofuscus*, *A. olivaceus*, *Ctenochaetus striatus*, *Naso lituratus*, *N. unicornis*, *Zebbrasoma scopas* and *Z. velifer*. These species represent 40% of the surgeonfish species recorded from the GBR and encompass all numerically abundant species at the study site [50].

(a) Morphological characterization

Species were characterized using a set of morphological traits consisting of 19 distance-based measurements and three angle measurements. All morphological measurements were selected based on previous linkages between the morphology and functional aspects of the species' foraging ecology, such as feeding, locomotion or sensory abilities [17,51]. All values were transformed to ratios by standardizing them against head or standard length, as required (e.g. snout length ÷ head length). As none of the ratios showed a significant relationship with standard length, analyses were performed using the standardized values rather than using residuals. The average number of individuals measured for each species was 3.8 ± 0.3 (s.e.). Details are provided in reference [51]. A list of morphological features measured and their ecological significance is provided in electronic supplementary material, S1a.

(b) Diet

Specimens were collected from the reef using spearguns and barrier nets. Specimens were kept on ice, and the whole alimentary tract was removed and preserved in 10% buffered formalin within 1 h of capture. Contents were identified using microscopic analysis (4×10 magnification) along transects of a 100×100 mm grid on a Perspex plate. For detrital feeders with considerable amounts of fine organic matter in alimentary tracts, examination was performed using 10×40 magnification to allow for the identification of microalgae and other microscopic dietary items. An average of 6.6 ± 0.3 (s.e.) specimens per species were analysed. The methods are described in detail in reference [38]. A list of dietary categories and data are provided in the electronic supplementary material, S1b.

(c) Foraging microhabitat preferences

Observations on foraging microhabitat selection were carried out on SCUBA or while snorkelling (during April/May 2013). Haphazardly chosen individuals were followed until the first foray.

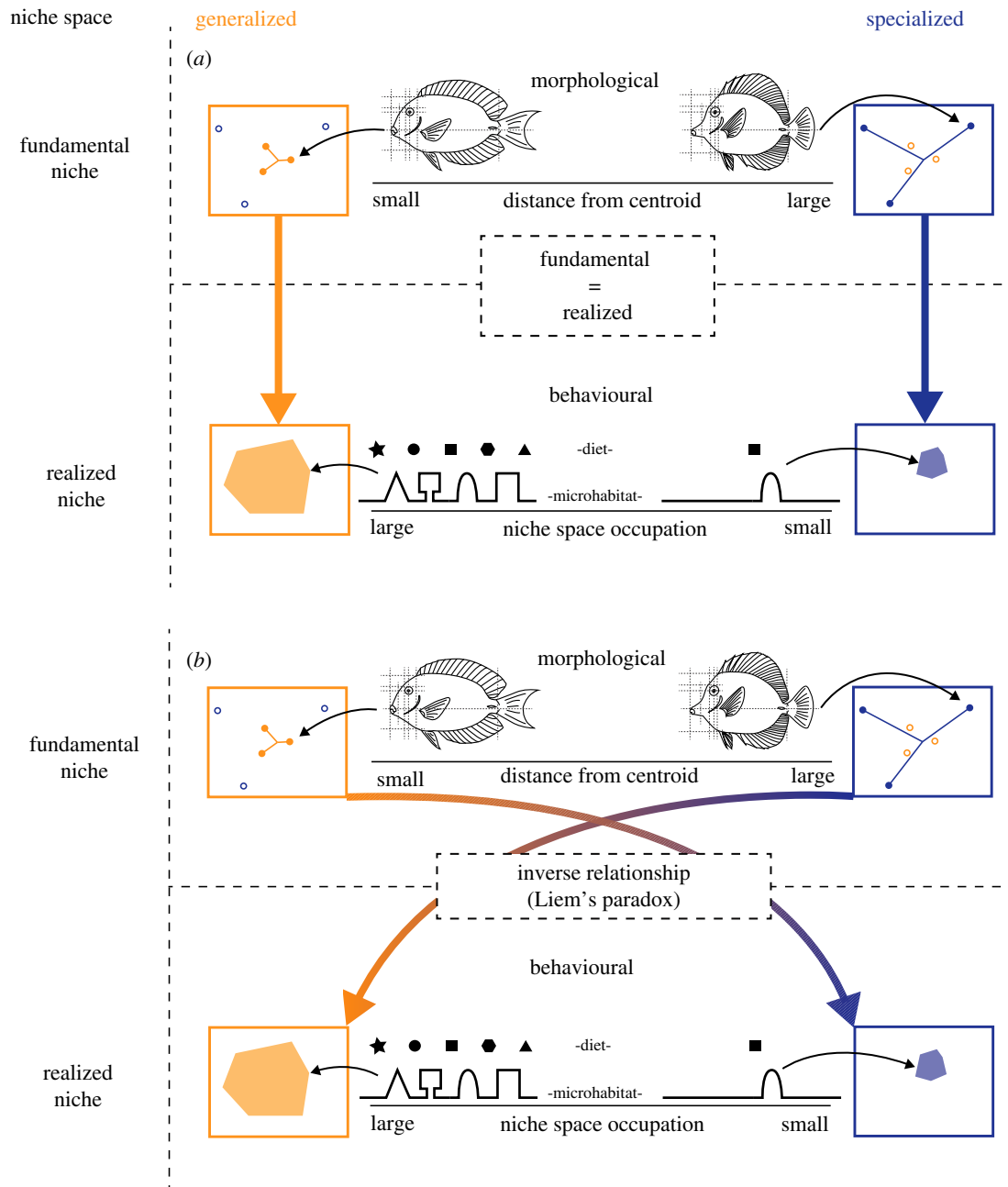


Figure 1. A conceptual synthesis of the potential relationships between fundamental (morphological) and realized (behavioural, i.e. diet (filled symbols) or foraging microhabitat utilization (open symbols)) specialization in surgeonfishes. The three hypotheses were (i) no relationship between morphological and behavioural specialization (not figured), (ii) morphological specialists are behavioural specialists (a) or (iii) morphological specialists are behavioural generalists and vice versa, potentially consistent with a phenomenon termed Liem's paradox (b). (Online version in colour.)

Then, the surface orientation and accessibility (open horizontal (A), open vertical (B), underside (C), concealed vertical (D) or concealed horizontal (E)), the substratum type (live coral (LC), dead coral skeleton (DC), macro-algae (MA), coral rubble (RB) sand (SD), turf covered reef matrix (TR)), and the number of bites taken from the respective microhabitat were recorded. In addition, the extent to which an individual penetrated the substratum was measured using Vernier callipers. The average number of observations per species was 49.8 ± 1.3 (s.e.; details in reference [45]).

(d) Microhabitat availability

The abundance of different microhabitats was also estimated during April/May 2013, using 20 10-m chain intercept transects laid parallel to the reef crest (following reference [52]). A transect tape was laid conforming to the reef benthos to include concealed microhabitats. The underlying microhabitat was

recorded every 20 cm, using Vernier callipers to measure the depth of crevices and depressions. Measurements were taken perpendicular to the substratum. To match the foraging microhabitat observations, microhabitat characteristics included the surface orientation and exposure (A–E), substratum type (live coral, dead coral, rubble, etc.), and depth of interstices and crevices.

(e) Statistical procedures

In terms of morphological specialization, analyses were performed at the species level. Morphological data (traits averaged for each species) were analysed using a principal coordinate analysis (PCoA) based on the Gower's dissimilarity matrix. Distances were calculated among species based on the average trait measurements for each species. Using the coordinates for each species in the first two dimensions, we calculated the distance from the centroid of the ordination for each species as a proxy for morphological specialization (following reference [27]).

While this quantification is dependent on the relative proportions of species morphotypes used, the species were selected to broadly reflect the relative proportions of surgeonfish types in GBR assemblages.

We used an individual-based multidimensional framework for the calculation of behavioural niche spaces yielding quantitative, continuous estimates of niche space occupation for both dietary and microhabitat selection data based on interindividual variation for each species. First, we calculated the pairwise distances between all individuals of all species using Gower's distance metric. Following this, a PCoA was performed using Cailliez' correction for negative eigenvalues [53], yielding a distribution of all individuals in a synthetic dietary/microhabitat niche space. Subsequently, we computed species niche space occupation for diet and microhabitat utilization in the same fashion, based on individuals with the most extreme coordinates using convex hulls [54,55]. To account for unequal sample sizes in both datasets (i.e. different numbers of observations among species, which may lead to biased estimates of niche volumes as a matter of chance) and to decrease the effect of few extreme individuals on the overall volume for each species, we performed randomized permutations ($n = 999$) with a constant subsample of individuals for each species and calculated the mean niche space occupation for each species for further analyses (i.e. for each species, 999 volumes were calculated from subsamples of individuals). Thus, our measure of species' degree of specialization was a function of interindividual variability within populations, a common metric of species' ecological niches [1,56]. Owing to restrictions in the dimensionality of the data and because we did not directly compare dietary and microhabitat specialization, dietary niche space occupation was computed on two dimensions, whereas microhabitat niche space occupation was conducted on both two- and three-dimensional space to maximize extraction of information.

For foraging microhabitat specialization, we also computed Manly's χ^2 log-likelihood statistic ($\chi_{L^2}^2$) [57], which quantifies a population's selectivity for a given resource based on availability within the ecosystem. We used model design I with sampling protocol A [57], which measures resource selection on the population level, to calculate selection ratios for each species (used/available). High ratio values indicate high levels of specialization, whereas low ratio values suggest a generalist strategy.

We investigated the relationships between morphological specialization (as measured by the distance from the centroid in morphospace), dietary specialization, microhabitat specialization (both of the latter quantified as the dietary/microhabitat niche space occupied by individuals within a species, i.e. interindividual variability across time and space), and microhabitat selectivity (Manly's χ^2 log-likelihood statistic ($\chi_{L^2}^2$)) using Bayesian linear models with morphology as a fixed effect and the respective behavioural variable as response. Uninformative default priors were used on the fixed effect estimates (0 on intercept and regression coefficient, variance of 100 000 000 for both parameters [58]). For the residual variance, we specified uninformative inverse Wishart priors with $V = 1$ and $\nu = 0.002$. Models were run for 2 000 000 iterations with a burn-in of 50 000 and a thinning interval of 1000. Chain convergence was validated using trace chain plots.

(f) Phylogenetic correction and evaluation of assumed relationships

To account for biases owing to shared ancestry, we used a phylogenetically corrected principal component analysis (PCA) on the morphological data using phylogenetic distances from a pruned tree (electronic supplementary material, S2) based on Sorensen *et al.* [59–61]. In this ordination, evolutionary independence is achieved by incorporating estimated ancestral states for

each character into the analysis, therefore reducing phylogenetic correlation among scores on each axis to zero. Subsequently, we examined the relationship between morphological and dietary/microhabitat specialization using phylogenetic Bayesian mixed models (BMMs). Again, phylogenetic relatedness was determined from a pruned tree [61] and fitted as a random factor under a Brownian motion model of evolution in the BMM [58]. In order to evaluate whether phylogenetic correction altered the results from our previous models, and owing to the small sample size of only 10 species in three distinct phylogenetic groups, we specified informative priors using the parameter estimates obtained from the previous uncorrected models for each relationship. This was done as our prior belief in the respective relationships was based on the uncorrected model estimates. For both random and residual variance, we again specified uninformative inverse Wishart priors, and the number of iterations was specified as above. In addition, we performed a sensitivity analysis in order to assess the effect of the specified priors on the posterior estimates. Specifically, we specified three informative, but arbitrary, priors for each relationship, suggesting the relationship between morphology and the three behavioural variables to be either positive ($\mu = 1$, $V = 0.2$), non-existent ($\mu = 0$, $V = 0.2$) or negative ($\mu = -1$, $V = 0.2$). All analyses conducted in this paper were performed in the software R [62] using the packages *ape* [63], *MCMCglmm* [58], *phytools* [60], *geometry* [64], *rccd* [65], *cluster* [66], *adehabitat* [67] and *geiger* [68].

3. Results

We found marked differences in morphological and behavioural specialization patterns among surgeonfish species (figure 2). Morphologically, *Z. velifer*, *N. unicornis* and *Z. scopas* were most specialized, exhibiting the greatest distance from the centroid of the biplot (electronic supplementary material, S3a). The least specialized morphologies were found for *C. striatus*, *A. nigricauda*, *A. olivaceus* and *A. blochii*. In the dietary niche space, *A. blochii* occupied the greatest area, followed by *N. unicornis*. The smallest areas were occupied by *A. olivaceus* and *Z. scopas* (electronic supplementary material, S3b). In terms of microhabitat utilization (in three dimensions), *Z. scopas* exhibited the largest niche volume, followed by *A. nigrofuscus* and *Z. velifer*. The other members of the genus *Acanthurus* occupied the smaller niche volumes (electronic supplementary material, S3c). Patterns were similar when using only two dimensions. When accounting for the availability of different microhabitats by using Manly's χ^2 log-likelihood ratio, *Z. velifer* and *A. nigrofuscus* had the lowest specialization scores, whereas *A. blochii* and *A. nigricauda* had the highest scores, therefore suggesting the latter species to be most specialized (electronic supplementary material, S4). The most abundant microhabitat in terms of benthic cover was open horizontal rock substratum (29.2%), followed by live coral (16.5%). The most common concealed microhabitat was crevices in horizontal rocky substrata (7.1%). Overall, concealed microhabitats accounted for 24.6% of available foraging microhabitats, whereas open microhabitats accounted for 75.4%.

Morphological specialization had a markedly different relationship with dietary and microhabitat specialization (figure 2), respectively. There was virtually no relationship between morphological and dietary specialization (Bayesian linear model: posterior mean density estimate $\beta = -0.025$, 95% credible interval (CI) = -0.096 to 0.043). In contrast, morphological specialization showed a negative relationship with foraging microhabitat utilization specialization

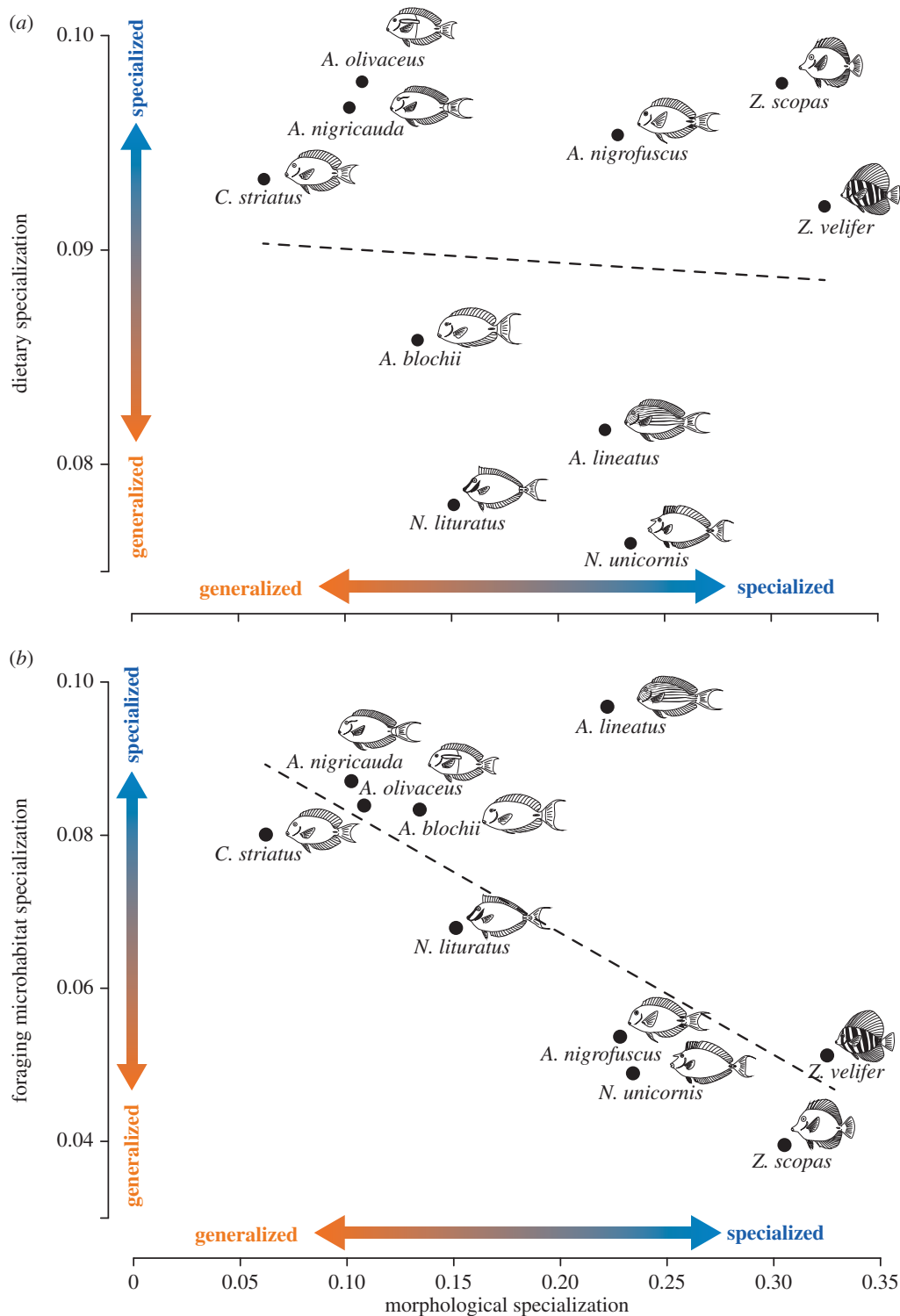


Figure 2. Relationships between morphological and behavioural specialization for (a) diet and (b) foraging microhabitat utilization. Morphological specialization and dietary niche space occupation showed no relationship, whereas there was a strong relationship between morphological specialization and microhabitat niche space occupation. For graphical purposes, behavioural specialization on the y-axis was inverted by subtracting the occupied niche space value from 0.1. (Online version in colour.)

($\beta = -0.392$, CI = -0.679 to -0.106), with morphologically specialized species exhibiting the largest niche volumes, i.e. being the most behaviourally generalized species. There was a similar trend in the relationship between morphology and microhabitat selectivity (Manly's χ^2 log-likelihood statistic), although 95% CIs of the mean posterior estimate also extended beyond zero ($\beta = -1.020$, CI = -2.876 to 1.172).

Accounting for shared ancestry in a morphological PCA and in the phylogenetic BMMs did not change the overall result, although it slightly altered the effect sizes and CIs (figure 3). For the relationship between morphological and

dietary specialization, the mean posterior estimate for the fixed effect was centred around zero (figure 3a; phylogenetic BMM: $\beta = -0.020$, CI = -0.081 to 0.039), with both the 95% and 50% CIs intersecting zero. The relationship between morphological specialization and microhabitat specialization (based on species' niche volumes) was less diffuse (figure 3b) with consistently negative estimates for the mean ($\beta = -0.294$, CI = -0.527 to -0.084) despite a slight shift towards zero compared with the uncorrected model. When regressing morphological specialization against Manly's χ^2 log-likelihood statistic of resource specialization (figure 3c), the relationship

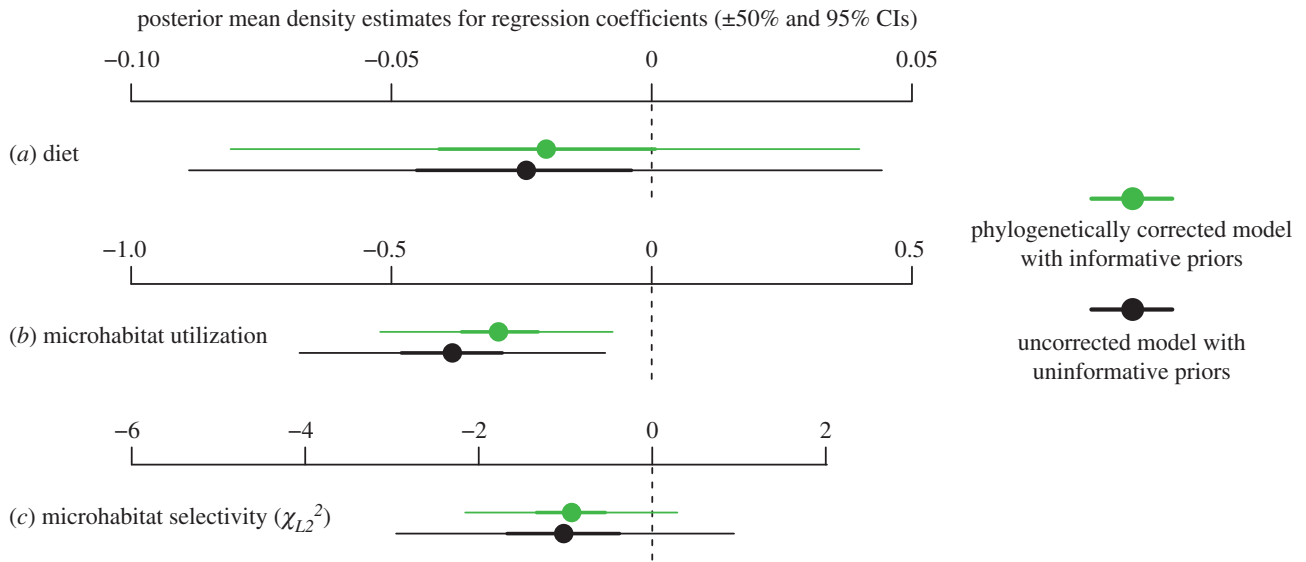


Figure 3. Comparisons of models estimating the relationship between morphological specialization and (a) dietary specialization, (b) foraging microhabitat specialization and (c) microhabitat selectivity. Plots show the mean posterior density estimates of regression coefficients and their 50% and 95% CIs in phylogenetically corrected (green) and uncorrected models (black). Relationships between morphological and behavioural specialization were consistent after phylogenetic corrections, with no relationship between morphological and dietary specialization (a). In contrast, a clear negative relationship is seen between morphological and microhabitat utilization specialization, regardless of phylogenetic correction (b). A possible negative relationship is seen between morphological specialization and microhabitat selectivity; however, 95% CIs extend beyond zero (c). (Online version in colour.)

also showed a negative trend but 95% CIs did intersect zero ($\beta = -0.929$, CI = -2.117 to 0.326).

While the results from the phylogenetically corrected BMMs indicate that substantial information for the posterior estimates came from the specified priors, the decrease of the CIs surrounding the posterior estimates in the phylogenetic BMMs suggests that the data did support the initial findings (figure 3). This is further supported by the results of the sensitivity analysis (electronic supplementary material, S5). For the relationship between morphological and dietary specialization, none of the models yielded a clear trend, regardless of the specified priors. In contrast, an unambiguous negative relationship between morphological specialization and microhabitat specialization was present in the models featuring the negative priors, whereas there was no clear relationship when neutral or positive priors were specified. The same pattern was present for the relationship between morphological specialization and Manly's χ^2 log-likelihood statistic of resource specialization, with a clear relationship only found when a negative prior was used. Thus, although the data did not override the neutral/positive priors, for both aspects of microhabitat specialization, the models with the negative priors resulted in a clear negative relationship in the posterior, suggesting that the data supported such negative relationship. Therefore, although small sample sizes may limit the strength of the support, the main suggestion of our analyses is that morphological specialization is negatively related to microhabitat utilization specialization, whereas dietary specialization shows no relationship with morphology.

4. Discussion

(a) Ecological specialization in surgeonfishes

Links between morphological specialization and dietary strategies are widespread, supporting the paradigm that specialized morphological features are related to dietary

specialization [4,10,17]. However, we found no such relationship in coral reef surgeonfishes, supporting a small number of similar studies in teleost fishes [24–27,30]. Basically, morphologically similar surgeonfish species showed marked differences in the range of food items ingested (e.g. *A. blochii* versus *A. nigricauda*), whereas morphologically disparate species shared a quantitatively similar dietary range (*A. olivaceus* versus *Z. scopas*). These results call for caution when identifying functional groups based solely on morphological similarity or phylogenetic relatedness: realized niches need to be examined carefully if we are to understand and monitor ecosystem functioning of coral reefs [69].

In contrast, we found an interesting, negative relationship between morphological specialization and foraging microhabitat preferences in surgeonfishes. While foraging microhabitat utilization has been identified as an important axis of niche partitioning in fishes [47], few ecomorphological studies have considered the relationship between microhabitat specialization and morphological specialization in a broad quantitative framework (but see [21]). For surgeonfishes, it has been proposed that certain morphological characteristics such as a small and deep body, large eyes, a truncate caudal fin or a concave forehead are linked to the exploitation of concealed resources and that these features enable species to use a broad range of resources [42,43]. This was supported by our results: morphologically specialized species are microhabitat generalists, whereas morphological generalists are foraging microhabitat specialists. Two extreme examples are *Z. scopas* and *A. nigricauda*. While *Z. scopas* exhibits a highly specialized morphology, distinguishing it from most other surgeonfish species, this species foraged over the widest range of microhabitats. In contrast, despite exhibiting the generalized *Acanthurus* morphology, *A. nigricauda* almost exclusively targeted flat and exposed rocky substrata.

Furthermore, these patterns seem consistent when the availability of microhabitats is accounted for. For example, the three closely related species *A. blochii*, *A. nigricauda*, and

A. olivaceus forage almost exclusively on flat horizontal surfaces and although these surfaces are readily available, their disproportional use of open sand, rubble and rock microhabitats results in a high level of selectivity. In contrast, species such as *Z. velifer* and *A. nigrofuscus* appear to distribute their foraging efforts relatively evenly across available microhabitats, resulting in low selectivity scores for these species. Such patterns of specific habitat or microhabitat use by specialized species has been reported previously in parrotfishes [70], but not to the extent seen in surgeonfishes.

The links between morphological and behavioural specialization in surgeonfishes are, in part, driven by phylogenetic relatedness. For example, the two species of *Zebrasoma* are closely related to each other, but phylogenetically distinct from most species within the *Acanthurus* clade [61]. It is therefore not surprising that the two *Zebrasoma* species exhibit a similar morphology and foraging strategies but differ markedly from most of the *Acanthurus* species. Despite this clear influence of shared ancestry, the phylogenetically corrected BMMs suggest that the observed relationships are robust and still supported when phylogeny is accounted for. Thus, there appears to be no relationship between morphological and dietary specialization, whereas the negative relationship between morphological and microhabitat specialization is consistent for the overall niche volume measures and, to a lesser extent, possibly for microhabitats selectivity (Manly's χ^2 log-likelihood ratio). However, given the small sample size of the phylogenetically corrected dataset and the influence of the used priors on the posterior estimates (revealed in the sensitivity analysis), the broader validity of these findings will have to be confirmed using a more extensive sampling protocol, ideally across a broader phylogenetic sample.

Interestingly, the described relationship between morphological and foraging microhabitat specialization is strikingly similar to patterns found in terrestrial plant–pollinator networks. In both arthropod and avian pollinator communities, species with ‘specialized’ morphologies such as long probosces or bills have been identified as generalists, feeding on a wide range of flower types, whereas species with shorter mouthparts are restricted to flowers with shallow tubes [71,72]. These ecological parallels may not be coincidental. Algal and detrital resources on coral reefs and nectar in plant–pollinator communities are both replenished at high rates [73,74] and form a highly diverse network of resources with varying accessibility [75]. Furthermore, similar to flowers with long tubes, which provide high rewards in terms of available nectar [76], inaccessible microhabitats appear to harbour richer algal resources [77], potentially offering higher rewards than flat microhabitats. Thus, although the two systems exhibit different consumer–producer relationships (mutualism versus prey–predator relationships; [78]), the ecological processes shaping both plant–pollinator and herbivore–benthos dynamics may be more similar than previously thought. This further suggests that the relationship between morphological and foraging microhabitat specialization present in both systems may be more broadly applicable.

(b) The role of microhabitat specialization for the evolution of coral reefs

The observed pattern in surgeonfishes is superficially consistent with a phenomenon termed Liem's paradox. While the

idea of Liem's paradox operating on coral reefs seems appealing in the light of the extraordinary diversity present in reef fishes, there are theoretical inconsistencies in the context of our findings. The most popular evolutionary framework for Liem's paradox posits that the basic strategy for every species is to forage on an easily exploitable resource, which is subsequently followed by ‘secondary’ specialization on less abundant or accessible resources [21]. In the Acanthuridae, however, specialized morphotypes similar to *Zebrasoma* or *Naso* are recorded from coral reefs in the Eocene 60 Ma [51], suggesting that microhabitat generalists have been present on reefs throughout most of their evolutionary history. Furthermore, although generalized morphs were also present in the Eocene [51], the expansion of morphological generalists specialized on flat microhabitats appears to have been a later trend (rapidly increasing species richness and relative abundance in the Miocene *ca* 25 Ma [51,61]), questioning the applicability of Liem's paradox in this case. Interestingly, reef parrotfishes which predominantly target open microhabitats [36,45], also appeared on scleractinian-dominated reefs around the same time as surgeonfishes of the genus *Acanthurus* [41], supporting the hypothesis that increased exploitation of open microhabitats occurred predominantly in the Miocene. It appears probable that morphological specialists added the exploitation of open microhabitats to their initial feeding repertoire and that the subsequent major radiations in surgeonfish lineages specialized on flat open microhabitats may be due to the increased availability of these foraging surfaces.

There are three non-exclusive hypotheses that may explain this trend: first, mirroring recent trends towards the loss of topographical complexity on coral reefs [79], coral reefs may have undergone a transition from complex, microtopographically intricate systems to flatter, less complex systems over the last 50 million years through increasing rates of external bioerosion [80], resulting in an increase in the proportion of planar surfaces with easily accessible resources for herbivorous/detritivorous fishes. Second, biotic or abiotic processes such as sea-level fluctuations or increasing calcification and accretion may have increased the extent of reef flats, a habitat that frequently supports the largest area of hard, open surfaces on modern coral reefs [81] in the most productive zone of primary production [82]. Finally, reef flats may have been available throughout the last 60 Ma, but the establishment of a nutritionally attractive epilithic algal matrix and its associated detrital resources may have only arisen once coral reef fishes increased grazing intensities throughout their radiation in the Miocene [83,84], leading to the evolution of specialized herbivores foraging exclusively on flat open surfaces. In all three cases, the expansion of specialized open-microhabitat foraging species appears to have been an essential step in the establishment of modern herbivorous coral reef fish assemblages.

(c) Significance, limitations and future perspectives

Ecomorphological assessments attempting to relate morphological specialization to dietary specialization have been invaluable for our understanding of the ecology and evolution in animals. However, there is increasing evidence that the relationship between morphological specialization and dietary preferences is multifaceted and often less clear and

linear than expected. We do not suggest that the link between morphological specialization and diet in reef fishes (or, more specifically, surgeonfishes) is absent; such a conclusion would be unwarranted given the potential for more detailed assessments of this relationship (such as a higher resolution classification of morphology or dietary items or the mapping of the latter onto different microhabitats). However, our study serves as a cautionary note, suggesting that there is a potential for more than one ecologically significant axis that one may find reflected in a species' morphology.

Our findings present an intriguing case for the exploration of foraging microhabitats as a potentially important niche axis in benthic feeding reef fishes. Although limited by the relatively small sample size of 10 species with shared ancestries within a large lineage, the results suggest that the identified pattern may persist if the assessment is expanded. Furthermore, the list of factors that may influence the foraging behaviour and microhabitat selection of reef fishes is long: exploring the range of dietary items present in various microhabitats and their rate of replenishment, a finer classification of dietary items or nutritional analyses of resources in different microhabitats and their post-ingestive utilization by both specialists and generalists would offer interesting avenues for future research and may help uncover more detail about the dynamics between benthic organisms and mobile consumer communities on coral reefs. Here, we are only scraping the surface of a largely untouched ecological niche axis. Nevertheless, our findings, particularly regarding the similarities between plant–pollinator communities and coral reef herbivores and the superficial parallels to Liem's paradox, are encouraging for future investigations of foraging microhabitat utilization on coral reefs.

References

- Whittaker RH, Levin SA, Root RB. 1973 Niche, habitat, and ecotope. *Am. Nat.* **107**, 321–338. (doi:10.1086/282837)
- Futuyma DJ, Moreno G. 1988 The evolution of ecological specialization. *Annu. Rev. Ecol. Syst.* **19**, 207–233. (doi:10.1146/annurev.es.19.110188.001231)
- Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W, Venail P, Villeger S, Mouquet N. 2010 Defining and measuring ecological specialization. *J. Appl. Ecol.* **47**, 15–25. (doi:10.1111/j.1365-2664.2009.01744.x)
- Forister M, Dyer L, Singer M, Stireman JIII, Lill J. 2012 Revisiting the evolution of ecological specialization, with emphasis on insect–plant interactions. *Ecology* **93**, 981–991. (doi:10.1890/11-0650.1)
- Schluter D. 2000 *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press.
- Emery NC, Forrester EJ, Jui G, Park MS, Baldwin BG, Ackerly DD. 2012 Niche evolution across spatial scales: climate and habitat specialization in California *Lasthenia* (Asteraceae). *Ecology* **93**, 151–166. (doi:10.1890/11-0504.1)
- Clavel J, Julliard R, Devictor V. 2010 Worldwide decline of specialist species: toward a global functional homogenization? *Front. Ecol. Environ.* **9**, 222–228. (doi:10.1890/080216)
- Bolnick DI, Svanbäck 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)
- Poisot T, Bever JD, Nemri A, Thrall PH, Hochberg ME. 2011 A conceptual framework for the evolution of ecological specialisation. *Ecol. Lett.* **14**, 841–851. (doi:10.1111/j.1461-0248.2011.01645.x)
- Ferry-Graham LA, Bolnick DI, Wainwright PC. 2002 Using functional morphology to examine the ecology and evolution of specialization. *Integr. Comp. Biol.* **42**, 265–277. (doi:10.1093/icb/42.2.265)
- Grant BR, Grant PR. 1996 High survival of Darwin's finch hybrids: effects of beak morphology and diets. *Ecology* **77**, 500–509. (doi:10.2307/2265625)
- Henderson RW, Pauers MJ, Colston TJ. 2013 On the congruence of morphology, trophic ecology, and phylogeny in Neotropical treeboas (Squamata: Boidae: Corallus). *Biol. J. Linn. Soc.* **109**, 466–475. (doi:10.1111/bij.12052)
- Huckins CJF. 1997 Functional linkages among morphology, feeding performance, diet, and competitive ability in molluscivorous sunfish. *Ecology* **78**, 2401–2414. (doi:10.1890/0012-9658)
- Aguirre LF, Herrel A, van Damme R, Matthyssen E. 2002 Ecomorphological analysis of trophic niche partitioning in a tropical savannah bat community. *Proc. R. Soc. Lond. B* **269**, 1271–1278. (doi:10.1098/rspb.2002.2011)
- Wainwright PC, Reilly SM. 1994 *Ecological morphology*. Chicago, IL: University of Chicago Press.
- Wainwright PC. 1988 Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. *Ecology* **69**, 635–645. (doi:10.2307/1941012)
- Douglas ME, Matthews WJ. 1992 Does morphology predict ecology? Hypothesis testing within a freshwater stream fish assemblage. *Oikos* **65**, 213–224. (doi:10.2307/3545012)
- Wainwright PC, Bellwood DR. 2002 Ecomorphology of feeding in coral reef fishes. In *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. PE Sale), pp. 33–55. San Diego, CA: Academic Press.
- Wainwright PC. 1996 Ecological explanation through functional morphology: the feeding biology of sunfishes. *Ecology* **77**, 1336–1343. (doi:10.2307/2265531)

5. Conclusion

Our study shows that morphological specialization and its behavioural correlates are not as easily inferred as frequently assumed. We demonstrate that there is no evidence for a correlation between morphological specialization and dietary specialization, but reveal a potential link between morphological specialization and foraging microhabitat specialization. However, this relationship is inverted: species with specialized morphologies are foraging microhabitat generalists, whereas generalized morphotypes are behaviourally specialized on exposed microhabitats. These results suggest that we may need to look beyond the most commonly investigated links between species' morphological and behavioural niches and that on coral reefs, morphological specialization may be tightly intertwined with foraging microhabitat utilization. Consequently, the use of different microhabitats may be an important ecological axis to understand the past, present and future of coral reefs.

Ethics. The study was performed under ethics approval nos. A503, A504 and A1641.

Data accessibility. Raw data are deposited in Dryad at <http://dx.doi.org/10.5061/dryad.634n8>.

Authors' contributions. S.J.B. and D.R.B. designed the study; S.J.B. and W.D.R. collected the data; S.J.B. performed the analyses; S.J.B., D.R.B. and W.D.R. wrote and edited the paper.

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Competing interests. We declare we have no competing interests.

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20. Pouilly M, Lino F, Bretenoux JG, Rosales C. 2003 Dietary–morphological relationships in a fish assemblage of the Bolivian Amazonian floodplain. *J. Fish. Biol.* **62**, 1137–1158. (doi:10.1046/j.1095-8649.2003.00108.x)
21. Snorrason SS, Skúlason S, Jonsson B, Malmquist HJ, Jónsson PM, Sandlund OT, Lindem T. 1994 Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological divergence and ontogenetic niche shifts. *Biol. J. Linn. Soc.* **52**, 1–18. (doi:10.1111/j.1095-8312.1994.tb00975.x)
22. Sturmhuber C, Mark W, Dallinger R. 1992 Ecophysiology of Aufwuchs-eating cichlids in Lake Tanganyika: niche separation by trophic specialization. *Environ. Biol. Fish.* **35**, 283–290. (doi:10.1007/BF00001895)
23. Hulsey CD, García de León F. 2005 Cichlid jaw mechanics: linking morphology to feeding specialization. *Funct. Ecol.* **19**, 487–494. (doi:10.1111/j.1365-2435.2005.00987.x)
24. Liem KF. 1980 Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Am. Zool.* **20**, 295–314. (doi:10.1093/icb/20.1.295)
25. Motta PJ, Clifton KB, Hernandez P, Eggold BT. 1995 Ecomorphological correlates in ten species of subtropical seagrass fishes: diet and microhabitat utilization. *Environ. Biol. Fish.* **44**, 37–60. (doi:10.1007/BF00005906)
26. Barnett A, Bellwood DR, Hoey AS. 2006 Trophic ecomorphology of cardinalfish. *Mar. Ecol. Prog. Ser.* **322**, 249–257. (doi:10.3354/meps322249)
27. Bellwood DR, Wainwright PC, Fulton CL, Hoey AS. 2006 Functional versatility supports coral reef biodiversity. *Proc. R. Soc. B* **273**, 101–107. (doi:10.1098/rspb.2005.3276)
28. Sanderson SL. 1990 Versatility and specialization in labrid fishes: ecomorphological implications. *Oecologia* **84**, 272–279. (doi:10.1007/BF00318284)
29. Alfaro ME, Bolnick DI, Wainwright PC. 2005 Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. *Am. Nat.* **165**, E140–E154. (doi:10.1086/429564)
30. Wainwright PC, Alfaro ME, Bolnick DI, Hulsey CD. 2005 Many-to-one mapping of form to function: a general principle in organismal design? *Integr. Comp. Biol.* **45**, 256–262. (doi:10.1093/icb/45.2.256)
31. Robinson BW, Wilson DS. 1998 Optimal foraging, specialization, and a solution to Liem's paradox. *Am. Nat.* **151**, 223–235. (doi:10.1086/286113)
32. Fontaine C, Collin CL, Dajoz I. 2008 Generalist foraging of pollinators: diet expansion at high density. *J. Ecol.* **96**, 1002–1010. (doi:10.1111/j.1365-2745.2008.01405.x)
33. Ungar PS, Grine FE, Teaford MF. 2008 Dental microwear and diet of the Plio-Pleistocene hominin *Paranthropus boisei*. *PLoS ONE* **3**, e2044. (doi:10.1371/journal.pone.0002044)
34. Bouton N, Os N, Witte F. 1998 Feeding performance of Lake Victoria rock cichlids: testing predictions from morphology. *J. Fish. Biol.* **53**, 118–127. (doi:10.1111/j.1095-8649.1998.tb01022.x)
35. Janovetz J. 2005 Functional morphology of feeding in the scale-eating specialist *Catopirion mento*. *J. Exp. Biol.* **208**, 4757–4768. (doi:10.1242/jeb.01938)
36. Price SA, Wainwright PC, Bellwood DR, Kazancioglu E, Collar DC, Near TJ. 2010 Functional innovations and morphological diversification in parrotfish. *Evolution* **64**, 3057–3068. (doi:10.1111/j.1558-5646.2010.01036.x)
37. Clements KD, Raubenheimer D, Choat JH. 2009 Nutritional ecology of marine herbivorous fishes: ten years on. *Funct. Ecol.* **23**, 79–92. (doi:10.1111/j.1365-2435.2008.01524.x)
38. Choat J, Clements K, Robbins W. 2002 The trophic status of herbivorous fishes on coral reefs. *Mar. Biol.* **140**, 613–623. (doi:10.1007/s00227-001-0715-3)
39. Hoey AS, Brandl SJ, Bellwood DR. 2013 Diet and cross-shelf distribution of rabbitfishes (f. Siganidae) on the northern Great Barrier Reef: implications for ecosystem function. *Coral Reefs* **32**, 973–984. (doi:10.1007/s00338-013-1043-z)
40. 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)
41. Choat J, Herwerden L, Robertson DR, Clements KD. 2012 Patterns and processes in the evolutionary history of parrotfishes (family Labridae). *Biol. J. Linn. Soc.* **107**, 529–557. (doi:10.1111/j.1095-8312.2012.01959.x)
42. Brandl S, Bellwood D. 2013 Morphology, sociality, and ecology: can morphology predict pairing behavior in coral reef fishes? *Coral Reefs* **32**, 835–846. (doi:10.1007/s00338-013-1042-0)
43. Robertson DR, Gaines SD. 1986 Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* **67**, 1372–1383. (doi:10.2307/1938693)
44. Robertson DR, Polunin NV, Leighton K. 1979 The behavioral ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon* and *Zebbrasoma scopas*): their feeding strategies, and social and mating systems. *Environ. Biol. Fish.* **4**, 125–170. (doi:10.1007/BF00005448)
45. Brandl SJ, Bellwood DR. 2014 Individual-based analyses reveal limited functional overlap in a coral reef fish community. *J. Anim. Ecol.* **83**, 661–670. (doi:10.1111/1365-2656.12171)
46. Fox RJ, Bellwood DR. 2013 Niche partitioning of feeding microhabitats produces a unique function for herbivorous rabbitfishes (Perciformes, Siganidae) on coral reefs. *Coral Reefs* **32**, 13–23. (doi:10.1007/s00338-012-0945-5)
47. Holbrook SJ, Schmitt RJ. 1992 Causes and consequences of dietary specialization in surfperches: patch choice and intraspecific competition. *Ecology* **73**, 402–412. (doi:10.2307/1940748)
48. Bellwood DR, Hoey AS, Hughes TP. 2012 Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. *Proc. R. Soc. B* **279**, 1621–1629. (doi:10.1098/rspb.2011.1906)
49. Edwards CB *et al.* 2014 Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. *Proc. R. Soc. B* **281**, 20131835. (doi:10.1098/rspb.2013.1835)
50. Cheal A, Emslie M, Miller I, Sweatman H. 2012 The distribution of herbivorous fishes on the Great Barrier Reef. *Mar. Biol.* **159**, 1143–1154. (doi:10.1007/s00227-012-1893-x)
51. Bellwood DR, Goatley CHR, Brandl SJ, Bellwood O. 2014 Fifty million years of herbivory on coral reefs: fossils, fish and functional innovations. *Proc. R. Soc. B* **281**, 20133046. (doi:10.1098/rspb.2013.3046)
52. Goatley CH, Bellwood DR. 2011 The roles of dimensionality, canopies and complexity in ecosystem monitoring. *PLoS ONE* **6**, e27307. (doi:10.1371/journal.pone.0027307)
53. Laliberté E, Legendre P. 2010 A distance-based framework for measuring functional diversity from multiple traits. *Ecology* **91**, 299–305. (doi:10.1890/08-2244.1)
54. Ackerly DD, Cornwell W. 2007 A trait-based approach to community assembly: partitioning of species trait values into within- and among-community components. *Ecol. Lett.* **10**, 135–145. (doi:10.1111/j.1461-0248.2006.01006.x)
55. Cornwell WK, Schilck DW, Ackerly DD. 2006 A trait-based test for habitat filtering: convex hull volume. *Ecology* **87**, 1465–1471. (doi:10.1890/0012-9658(2006)87[1465:ATTFHF]2.0.CO;2)
56. Colwell RK, Futuyma DJ. 1971 On the measurement of niche breadth and overlap. *Ecology* **52**, 567–576. (doi:10.2307/1934144)
57. Manly BF, McDonald L, Thomas D, McDonald TL, Erickson WP. 2002 *Resource selection by animals: statistical design and analysis for field studies*. Amsterdam, The Netherlands: Springer.
58. Hadfield JD. 2010 MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *J. Stat. Soft.* **33**, 1–22.
59. Martin CH, Wainwright PC. 2011 Trophic novelty is linked to exceptional rates of morphological diversification in two adaptive radiations of *Cyprinodon* pupfish. *Evolution* **65**, 2197–2212. (doi:10.1111/j.1558-5646.2011.01294.x)
60. Revell LJ. 2012 phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.* **3**, 217–223. (doi:10.1111/j.2041-210X.2011.00169.x)
61. Sorenson L, Santini F, Carnevale G, Alfaro ME. 2013 A multi-locus timetree of surgeonfishes (Acanthuridae, Percomorpha), with revised family taxonomy. *Mol. Phylogenet. Evol.* **68**, 150–160. (doi:10.1016/j.ympev.2013.03.014)
62. R Core Team. 2014 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
63. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)

64. Habel K, Grasman R, Stahel A, Sterratt C. 2014 *geometry: Mesh generation and surface tessellation. R package version 0.3–5*. See <http://CRAN.R-project.org/package=geometry>.
65. Geyer CJ, Meeden GD. 2014 *R package rccd (C Double Description for R). R package version 1.1–8*. See <http://CRAN.R-project.org/package=rccd>.
66. Maechler M, Rousseeuw P, Struyf A, Hubert M, Hornik K. 2015 *cluster: Cluster analysis basics and extensions. R package version 2.0.1*.
67. Calenge C. 2006 The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Model.* **197**, 516–519. (doi:10.1016/j.ecolmodel.2006.03.017)
68. Harmon LJ, Weir JT, Brock CD, Glor RE, Challenger W. 2008 GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**, 129–131. (doi:10.1093/bioinformatics/btm538)
69. Bellwood DR, Hughes TP, Folke C, Nystrom M. 2004 Confronting the coral reef crisis. *Nature* **429**, 827–833. (doi:10.1038/nature02691)
70. Bellwood DR, Choat JH. 1990 A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ. Biol. Fish.* **28**, 189–214. (doi:10.1007/BF00751035)
71. Borrell BJ. 2005 Long tongues and loose niches: evolution of euglossine bees and their nectar flowers. *Biotropica* **37**, 664–669. (doi:10.1111/j.1744-7429.2005.00084.x)
72. Temeles EJ, Koulouris CR, Sander SE, Kress WJ. 2009 Effect of flower shape and size on foraging performance and trade-offs in a tropical hummingbird. *Ecology* **90**, 1147–1161. (doi:10.1890/08-0695.1)
73. Thomson JD, McKenna MA, Cruzan MB. 1989 Temporal patterns of nectar and pollen production in *Aralia hispida*: implications for reproductive success. *Ecology* **70**, 1061–1068. (doi:10.2307/1941375)
74. Bonaldo RM, Bellwood DR. 2011 Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. *Coral Reefs* **30**, 381–390. (doi:10.1007/s00338-010-0704-4)
75. Jordano P, Bascompte J, Olesen JM. 2003 Invariant properties in coevolutionary networks of plant–animal interactions. *Ecol. Lett.* **1**, 69–81. (doi:10.1046/j.1461-0248.2003.00403.x)
76. Gómez JM, Bosch J, Perfectti F, Fernández J, Abdelaziz M, Camacho JPM. 2008 Spatial variation in selection on corolla shape in a generalist plant is promoted by the preference patterns of its local pollinators. *Proc. R. Soc. B* **275**, 2241–2249. (doi:10.1098/rspb.2008.0512)
77. Brandl SJ, Hoey AS, Bellwood DR. 2014 Microtopography mediates interactions between corals, algae, and herbivorous fishes on coral reefs. *Coral Reefs* **33**, 421–430. (doi:10.1007/s00338-013-1110-5)
78. Johnson SD, Steiner KE. 2000 Generalization versus specialization in plant pollination systems. *Trends Ecol. Evol.* **15**, 140–143. (doi:10.1016/S0169-5347(99)01811-X)
79. Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. 2009 Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. R. Soc. B* **281**, 20090339. (doi:10.1098/rspb.2009.0339)
80. Bonaldo RM, Hoey AS, Bellwood DR. 2014 The ecosystem roles of parrotfishes on tropical reefs. *Oceanogr. Mar. Biol. Ann. Rev.* **52**, 81–132. (doi:10.1201/b17143-3)
81. Bellwood DR, Wainwright PC. 2002 The history and biogeography of fishes on coral reefs. In *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. PE Sale), pp. 5–32. San Diego, CA: Academic Press.
82. Steneck R. 1988 Herbivory on coral reefs: a synthesis. In *Proc. 6th Int. Coral Reef Symp.* (eds JH Choat *et al.*), pp. 37–49. Townsville, Queensland: James Cook University.
83. Steneck RS. 1983 Escalating herbivory and resulting adaptive trends in calcareous algal crusts. *Paleobiology* **9**, 44–61.
84. Cowman PF, Bellwood DR. 2013 The historical biogeography of coral reef fishes: global patterns of origination and dispersal. *J. Biogeogr.* **40**, 209–224. (doi:10.1111/jbi.12003)