Journal of Biogeography **WILEY**

Predation as an explanation for a latitudinal gradient in arm number among featherstars

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Handling Editor: Marcelo Rivadaneira

Abstract

Aim: The role of biotic interactions in generating broad patterns in organismal phenotypes is a central question in macroecology. We investigate global patterns in feeding morphology among featherstars, a globally widespread group of suspension-feeding echinoderms whose evolutionary history has been demonstrably shaped by predators.

Location: World's oceans.

Taxon: Crinoidea.

Methods: We tested for global patterns in the featherstar suspension-feeding apparatus, a filter made up of 5–200 arms which is the main interface with predators. We investigate a geospatial dataset of 23,950 occurrences in 442 species using statistical analyses including quantile regression and a new permutation-based phylogenetic comparative approach appropriate for testing for a broad range of patterns in data with strange distributions.

Results: We find that featherstars exhibit a latitudinal gradient in arm number: arm number is both greater on average and more variable between species at lower latitudes. This pattern holds across depths and hemispheres and is not a spurious result of either the latitudinal diversity gradient or phylogenetic autocorrelation. Tropical featherstars that conceal themselves have fewer arms, and also appear to experience less intense predation.

Main conclusions: Temperature, primary productivity and substrate type do not adequately explain the latitudinal gradient in arm number. We attribute it instead to a corresponding gradient in predation intensity: many armed featherstars can withstand more intense arm loss to predators. Concealment and other alternate solutions to the problem of predation, along with reproductive costs associated with having many arms, explain why the trend is wedge-shaped rather than linear. Our findings constitute a latitudinal gradient in functional diversity, paralleling recent findings in other taxa. The gradient may be a consequence of shallow tropical reefs; inasmuch as reefs as centres of biotic interactions promote functional richness, changes in the distribution of reefs through deep time probably entailed shifts in the global deployment of ecological diversity.

KEYWORDS
Crinoidea, ecological diversity, functional morphology, latitude, macroecology, phylogenetic comparative methods

1 | INTRODUCTION

The role of biotic interactions in structuring macroecological patterns is of central interest to biologists. Despite the obvious importance of organism–organism interactions at the local scale, the broadest spatial and temporal phenomena in biology are typically attributed to abiotic causes like climate or continental configuration (Antell, Kiessling, Aberhan, & Saupe, 2020; Barnosky, 2001; Benton, 2009). Nevertheless, biotic interactions demonstrably leave some signals in global phenotypic patterns. For example, increased intensity of predation and biological disturbance of the shallow seafloor throughout the Phanerozoic appears to have non-randomly restricted some kinds of organisms to the deep sea (Bottjer & Jablonski, 1988), and driven others into the infauna (Thayer, 1983). There is also direct evidence for a latitudinal gradient in the intensity of predation in some systems (Klompmaker et al., 2019; Schemske, Mittelbach, Cornell, Sobel, & Roy, 2009; Vermeij, 1978), and anti-predatory adaptations are more common among tropical representatives of many groups: tropical molluscs are apparently more resistant to shell-crushing predators (Palmer, 1979; Vermeij, 1978), and toxicity/unpalatability is more common closer to the equator in marine worms, caterpillars and various plant groups (Levin, 1976; Schemske et al., 2009). Beyond constituting good explanations for natural phenomena like these, predation and other biotic interactions form the core of a general evolutionary principle, albeit a contentious one (Dietl & Vermeij, 2006; Madin et al., 2006): escalation, the hypothesis that some of the most conspicuous Phanerozoic evolutionary trends are the result of natural selection on organisms by their ecological 'enemies' (Vermeij, 1993, 2008). It is worthwhile to tease apart the degree to which evolution is driven by biotic interactions as opposed to abiotic factors, as these correspond to quite different histories of life on Earth.

Crinoids are a useful study system with which to consider the evolutionary role of biotic interactions because some of the major features of crinoid evolution appear to correlate with changes in the role of predators in marine ecosystems through time (Meyer & Macurda, 1977). Despite being some of the most diverse and conspicuous members of shallow marine ecosystems during much of the Palaeozoic and Mesozoic (Kammer & Ausich, 2006), these suspension-feeding echinoderms are today restricted to deep waters (Bottjer & Jablonski, 1988)—with one conspicuous exception. Featherstars, those crinoids in the order Comatulida that shed their entire stalk during development, make up most of modern crinoid diversity and are common in shallow and deep water (Messing, 1997). These stalkless forms have a number of features that have been interpreted as anti-predatory adaptations: they are more mobile than stalked crinoids (Meyer & Macurda, 1977), most can swim (Janevski & Baumiller, 2010), they regenerate arms rapidly (Baumiller & Stevenson, 2018) and many have toxic flesh (Meyer, 1985; Slattery, 2010). The restriction to deep water of stalked but not stalkless crinoids occurred synchronously with the radiation of crinoid predators in shallow water during the so-called Mesozoic Marine Revolution (Vermeij, 1977), and is thought to reflect the respective success and failure of stalkless and stalked crinoids to persist in spite of increased intensity of predation (Meyer & Macurda, 1977). Even before the Mesozoic, morphological features that enhanced resistance to predation and parasitism were common in crinoids (Syverson & Baumiller, 2014; Syverson, Brett, Gahn, & Baumiller, 2018). Regenerating arms, thought to result in most cases from predation (Meyer, 1985), are prevalent among extant featherstars and in some populations can be found on virtually every individual (Baumiller & Stevenson, 2018). They have even been identified in one fossil featherstar (Baumiller & Fordyce, 2018). Predation is therefore a plausible and compelling agent in crinoid evolution.

We explored and attempted to explain global patterns in arm number among living featherstars. The feeding apparatus of extant crinoids consists of a system of particle-intercepting tube feet lining one side of a set of five (rarely 10) sets of arms that bifurcate to varying degrees and that bear unbranched 'pinnules' at regular intervals (Hess & Messing, 2011). Like other passive suspension feeders, crinoids do not create their own feeding currents, and the rate at which they encounter food-laden water is a function of local flow conditions and feeding morphology (Baumiller, 1997). In particular, crinoids with dense filtration fans can only feed effectively in fast-flowing water (Baumiller, 1993), and the most dense fans are found among the crinoids with the most arms (Kitazawa, Oji, & Sunamura, 2007). However, beyond simply reflecting fluid dynamic constraints, the crinoid feeding apparatus is also the animals' main interface with predators: the arms make up much of a typical crinoid's biovolume (most of it in featherstars; Janevski & Baumiller, 2010) and recorded predation events typically involve the arms (Baumiller & Gahn, 2013; Meyer, 1985). This study treats variation in arm number between featherstar species (Figure 1). Because the featherstar feeding apparatus is relatively stereotyped—all branching occurs near the base of the arms, and all species bear pinnules (Oji & Okamoto, 1994)—arm number captures the better part of its morphological variation, whereas across the crinoid tree of life, the feeding apparatus varies considerably in terms of the distribution of branching points along the arms, the thickness of the arms, the length and spacing of pinnules and tube feet and the presence or absence of pinnules (Baumiller, 1993; Cole, 2019; Kammer & Ausich, 1987). Variation in arm number within featherstar species is not sufficiently documented across taxa to be treated here but exceeds a factor of three in some species and seems to vary more in many-armed taxa (Clark, 1967). This within-species variability is worth investigating further, not least because it may correspond to differences in microhabitat: Messing (1994) reported that featherstars living in shallower water and exposed to more energetic flow regimes had more and shorter arms than their deeper water conspecifics, suggesting that crinoid feeding morphology exhibits phenotypic plasticity. Here, we investigate an apparent relationship between absolute latitude and arm number among featherstars, and explore predation and abiotic factors as possible causes.
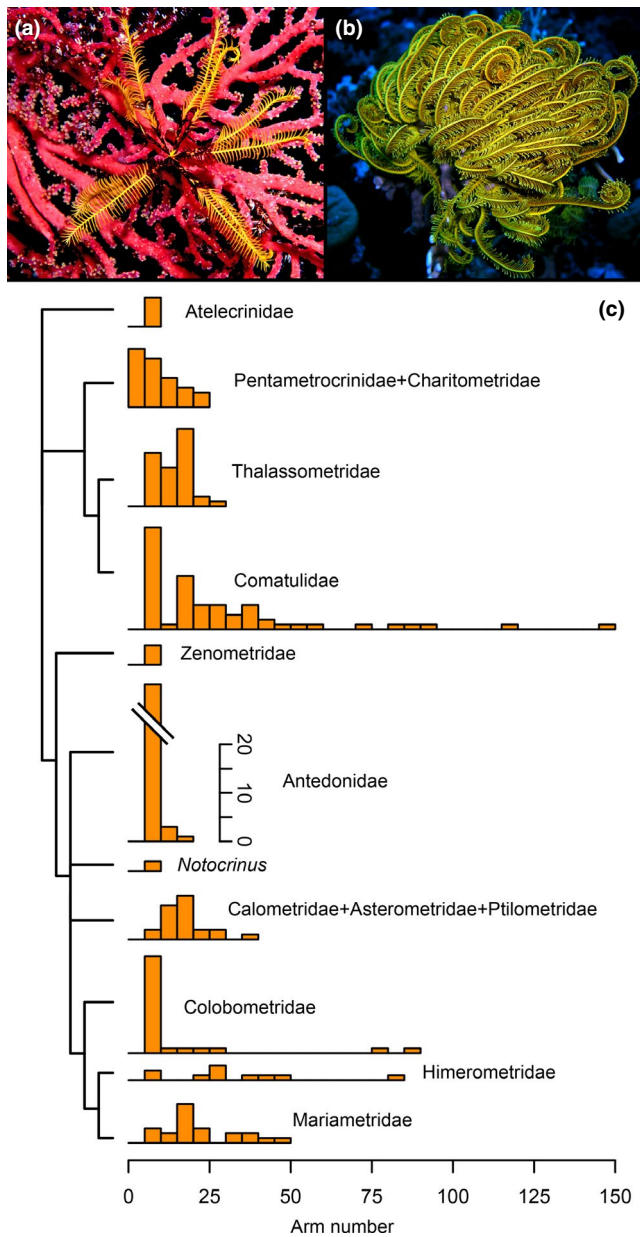
Bathycrinidae, Bourgueticrinidae, Guillecrinidae, Phrynocrinidae, Porphyrocrinidae and Septocrinidae) available from the Ocean Biogeographic Information System (OBIS) in August 2019 (OBIS, 2019). Although the stalkless featherstars have historically been identified with the order Comatulida, recent phylogenetic analyses have recovered several lineages of the stalked 'bourgueticrinids' within the Comatulida (Hemery, Roux, Ameziane, & Eleaume, 2013; Rouse et al., 2013). Importantly, our study relies on featherstars sharing some basic ecological similarities, but not on their monophyly. Forty-five 'rogue' terrestrial data points were removed from the dataset, resulting in 23,853 total occurrences. Depth data were available for 14,844 (62%) of these. Depth ranges for each species were supplemented with ranges recorded in the World Register of Marine Species (WoRMS). Our dataset includes 442 species of featherstar, encompassing 79% of the 556 species recorded in WoRMS. Many 'nodes' around the world contribute to OBIS and the geographic and bathymetric data vary in precision and accuracy. We recorded the latitudinal midpoint of each species, and tested for two potential features of the dataset that would make the use of midpoints problematic: geographic biases in sampling intensity, and a relationship between latitudinal range size and arm number (see Section 3).

2.2 | Arm number and habit

We gathered arm number data from the literature for 435 species of featherstar (Supplementary Information). For species with variable arm number—the case for most many-armed species—we recorded arm number as the midpoint between the maximum and minimum number reported. Arm number varies by a factor of over 30 and is strongly right skewed, with a clear mode at 10 (Figure 1). All Jurassic and Cretaceous featherstars that preserve the crown have 5 or 10 arms (Hess & Messing, 2011), so the few armed state is probably primitive in this group. Arm number varies substantially between species in many featherstar clades, and the many-armed condition appears to have been derived many times (Figure 1).

As an attempt to understand arm number in the context of other putative antipredatory adaptations, we combined our dataset with habit data from Schneider (1988), who scored 30 tropical featherstar species as feeding either diurnally or nocturnally and as feeding while fully exposed or while fully or partly cryptic. These modes of concealment are thought to be adaptations for avoiding predators (Meyer, 1985; Slattery, 2010). Schneider (1988) also assembled data on the frequency of arm regeneration among 406 featherstar populations in the same 30 species, which we coded into four variables: (a) the mean number of regenerating arms per individual, (b) the mean proportion of regenerating arms per individual (the number of regenerating arms divided by the number of arms checked by the investigator for each individual, averaged across the population), (c) the proportion of individuals in a population with at least one regenerating arm and (d) the number of individuals examined.

FIGURE 1 Arm number among featherstars. (a) An unidentified 10-armed featherstar perched on an octocoral. Photo © Paul Humann. (b) The large, many-armed (average: 55 arms) featherstar *Comaster schlegelii* (Comatulidae). Photo © James A. Maragos. (c) Phylogeny of featherstars and the distribution of arm number within major clades. Phylogeny shown is a summary of the relationships recovered by Hemery et al. (2013), with nodes without support values collapsed into polytomies. There are no featherstars with between 0 and 4 arms, or between 6 and 9 arms. There are 109 10-armed antedonid featherstars in the dataset (although 'Antedonidae' is non-monophyletic; Hemery et al., 2013)

2 | MATERIALS AND METHODS

2.1 | Occurrence data

We downloaded all available species-level occurrences of featherstars (order Comatulida minus the 'bourgueticrinid' families

The proportion of regenerating arms in a population does contain information on the rate of arm-loss events, but this information is indirect. A fully regenerated arm is typically indistinguishable from one that was never lost in the first place; individuals that fully regenerate lost arms more rapidly will therefore exhibit fewer apparent injuries, and an investigator might spuriously infer that those individuals encountered fewer predators (Baumiller, 2013). To our knowledge, only a few studies have attempted to use information on both regeneration rate and the proportion of regenerating arms to estimate predator encounter rate; we combined their findings ('Predator encounter rates.xlsx', Supplementary files) with our dataset.

Lastly, colourful toxic secondary metabolites make some crinoids less palatable to potential predators (Slattery, 2010), and have made them the target of intense pharmacological research (Feng, Khokhar, & Davis, 2017). We combined our dataset with two recent experimental studies of the palatability of 16 featherstar species to their fish predators.

2.3 | Analysis 1

Arm number is visibly right skewed (nonparametric skew = 0.46; Figure 2), so we investigated its relationship with absolute latitude using rank correlation with Spearman's ρ. A biplot of arm number against absolute latitude is noticeably wedge-shaped (Figure 2); we used quantile regression to investigate this feature. Unlike least-squares linear regression, which estimates the mean of a response
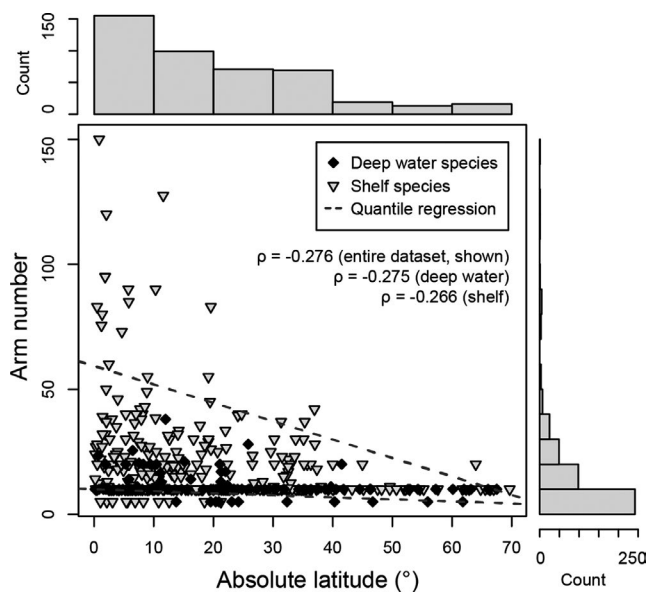

FIGURE 2 Arm numbers among extant featherstars show a wedge-shaped relationship with latitude. Absolute value of latitude against arm number, with Spearman rank correlations shown for the entire dataset and subsets including deep water (no occurrences above 200 m) and shelf taxa. All correlations shown are significant at the $p < 0.0005$ level. 5th and 95th conditional percentiles shown for the entire dataset. Marginal histograms for latitude (bin width = 10°) and arm number (bin width = 10) plotted at top and right respectively

variable conditional on one or more predictors, quantile regression estimates conditional quantiles—for example, the median—of a response variable by minimizing the sum of absolute distances between observations and the regression line, weighted to estimate the appropriate quantile (Koenker & Hallock, 2001). Quantile regression was implemented with the R package 'quantreg' v. 5.36 (Koenker et al., 2018). We also tested the latitude—arm number relationship for subsets of the dataset based on depth (species with or without occurrences above 200 m) and hemisphere (northern or southern). Quantile regression fits were assessed in an Akaike information criterion (AIC) framework: the likelihood of quantile regression conditional on absolute latitude was compared to that of unconditional quantile regression (i.e., a regression model without latitude as a variable), and the former was considered well supported if it had a lower AIC score. In other words, this test asks whether adding information on latitude improves estimates of upper or lower quantiles of arm number enough to justify the extra parameter.

An apparent latitudinal gradient in maximum arm number might appear spuriously as a result of the increase in species richness towards the equator, even if the underlying arm number distribution was uniform across latitude. To screen for this kind of bias, we re-evaluated the dataset after subsampling such that each 10° bin of absolute latitude had as many species as the least-sampled bin (50°–60°, $N = 13$).

We tested whether temperature, a close correlate of latitude, could explain geographic patterns in arm number better than latitude itself. Temperature and absolute latitude can be analytically pulled apart because they do not correspond perfectly: ocean gyres cause sea surface temperature (SST) at the same latitude to differ on the east and west sides of oceans, and mean annual SST changes nonlinearly with latitude, decreasing gradually from the equator to the tropics and then declining steeply in the higher latitudes (Webb, 2019). To generate comparable metrics of temperature and latitude, we randomly drew one occurrence above 100 m depth for each species with shallow-water occurrences, and matched these occurrences with SST using the *lookup_xy* function in the R package 'obistools' v.0.0.9 (Bosch, Provoost, & Appeltans, 2018). We assessed correlations between arm number and both absolute latitude and SST for these randomly drawn occurrences, and repeated the procedure many times.

2.4 | Analysis 2: Phylogenetic permutation

The previous section comprises 'equilibrium analyses' (Lauder, 1982): they assume there is no historical phylogenetic component to the variation in trait values, effectively treating each data point as independent and at equilibrium with its environment. We devised a new permutation-based approach to investigate the properties of a comparative dataset with respect to the phylogenetic history on which it evolved. We generated a timetree with penalized likelihood (Sanderson, 2002)—implemented with the program *treePL* (Smith & O'Meara, 2012)—using the molecular phylogeny inferred by Saulsbury and Zamora (2019). Two fossil calibrations were used to scale the tree to units of time (Appendix S1). Both absolute latitudinal midpoint

(Blomberg's K = 0.6355, $p < 0.001$) and arm number (K = 0.4673, p = 0.004) exhibit moderate, statistically significant phylogenetic signal with respect to the resulting timetree. The phylogeny and trait values were visualized simultaneously with the *phylomorphospace* function in the R package 'phytools' v. 0.6.99 (Revell, 2012).

The problem with interpreting comparative data at face value is that species share phylogenetic history, and the resulting phylogenetic autocorrelation among trait values may violate the assumptions of most standard tests. Phylogenetic comparative methods like independent contrasts (Felsenstein, 1985) and its generalization, phylogenetic generalized least squares (PGLS; Grafen, 1989), get around the problem of non-independence of species by considering trait differences at phylogenetic splits as independent observations. These approaches have proven to be quite powerful, but are inappropriate for our data for two reasons:

1. The 'shape' of our data thoroughly violates the assumptions of least-squares regression. Arm number is strongly right skewed, left-bounded and characterized by some features peculiar to crinoid biology—for example, about half of the species in the dataset have exactly 10 arms, and there are no species with 0–4 or 6–9 arms (Figure 2). The residuals in a PGLS regression of arm number on absolute latitude are right skewed and gappy even when arm number is singly or doubly log-transformed (Figure A9), violating the assumption of normally distributed residuals. Kolmogorov–Smirnov tests confirm that the residuals in PGLS regressions of arm number, log(arm number) and log(log(arm number)) on absolute latitude clearly depart from normality ($p < $ 1E-10 in all cases). No less problematic is the visible heteroscedasticity in our dataset (Figure 2): variance of arm number in the lowest bin of absolute latitude (0–10°, var = 479.1, N = 155) is roughly 60 times that in the highest bin (60–70°, var = 8.2, N = 16). A Bruesch–Pagan test for heteroscedasticity, which regresses the squared residuals of a response variable on a predictor, recovers statistically significant departures from homoscedasticity in the PGLS residuals of arm number and singly and doubly logged arm number on absolute latitude (α = 0.05; using a standard correction for non-normality; Koenker, 1981). The consequences of heteroscedasticity for the validity of PGLS are poorly understood, but potentially severe (Mundry, 2014).
2. PGLS, and least-squares regression more generally, are meant to detect a narrow subset of biologically interesting patterns—namely, relationships between one or more predictors and the conditional mean of a response variable. They therefore lack the flexibility to explore other features of datasets, including trends in variance, trends in quantiles of a response variable or other patterns in trait space occupation.

Here, we introduce a nonparametric phylogenetic comparative approach to evaluate the possibility that the statistics associated with our dataset could have been generated if the traits under consideration were independent, given the phylogenetic structure underlying the dataset. This method generates a set of nulls that can be used to understand how the phylogenetic signal in the data affects the range of patterns the data can potentially generate given no relationship, and how those patterns compare with the empirical signal.

An investigator could generate a set of phylogenetically informed nulls using either simulations or permutations. A simulation approach would be straightforward to implement for normally distributed data, as Mahler, Ingram, Revell, and Losos (2013) did in their study of convergence in *Anolis*, but the features of our data already described would make simulating comparable data difficult. Instead, we generate a set of nulls using a phylogenetically informed permutation approach: empirical patterns are compared to the subset of permuted datasets in which the phylogenetic signal of the permuted data on the empirical tree matches the phylogenetic signal in the empirical data. In practice, one phylogenetic permutation of a single trait is generated by shuffling the species labels on the data and then iteratively swapping pairs of observations via a simple hill-climbing algorithm until a specified metric of phylogenetic signal (in our case, Blomberg's K or Pagel's λ) is within a specified tolerance (for this study, 0.01) of the empirical signal (Figure 3a,b; Appendix S1). Note that this hill-climbing approach was taken for the sake of expediency only; phylogenetic permutations could also be obtained by permuting many times and only considering those permutations whose phylogenetic signal was within the specified tolerance, though this could be far more computationally intensive. Statistics associated with the set of phylogenetic permutations are then compared with empirical statistics, and can yield a p-value in the same way as an ordinary permutation test. The distribution of phylogenetic permutations can also be compared to that of ordinary permutations to understand the effect of the phylogeny on the range of possible patterns. This approach is distinct from the 'phylogenetic permutations' approach introduced by Lapointe and Garland (2001). This simple frequentist test has two chief virtues. First, like all permutation tests, it is nonparametric and therefore appropriate for highly non-normal datasets like ours. Second, it can be used to explore the phylogenetic component of any statistics applied to a comparative dataset as such, rather than using transformations that may remove information and limit the range of patterns that can be considered. Phylogenetic permutation successfully rejects apparent trait associations induced solely by shared phylogenetic history: it yields a non-significant result for Felsenstein's (1985) 'worst case' scenario in which a spurious correlation appears between two traits that evolved independently on a tree of two polytomous clades separated by a long span of evolutionary time (Appendix S1). Importantly, the phylogenetic permutation approach is similar to the restricted permutation test (Anderson, 2001), in which shuffling only occurs within sets of exchangeable data points. In fact, in the case of Felsenstein's worst case, phylogenetic permutation is nearly equivalent to a restricted permutation test in which exchanges only occur within the two polytomous clades.

We analysed our dataset using phylogenetic permutation, considering Spearman's ρ and the slopes of the 90th and 95th conditional percentiles. We generate phylogenetic permutations with Blomberg's K, but our results are statistically indistinguishable from those obtained with Pagel's λ (Appendix S1). The distribution of
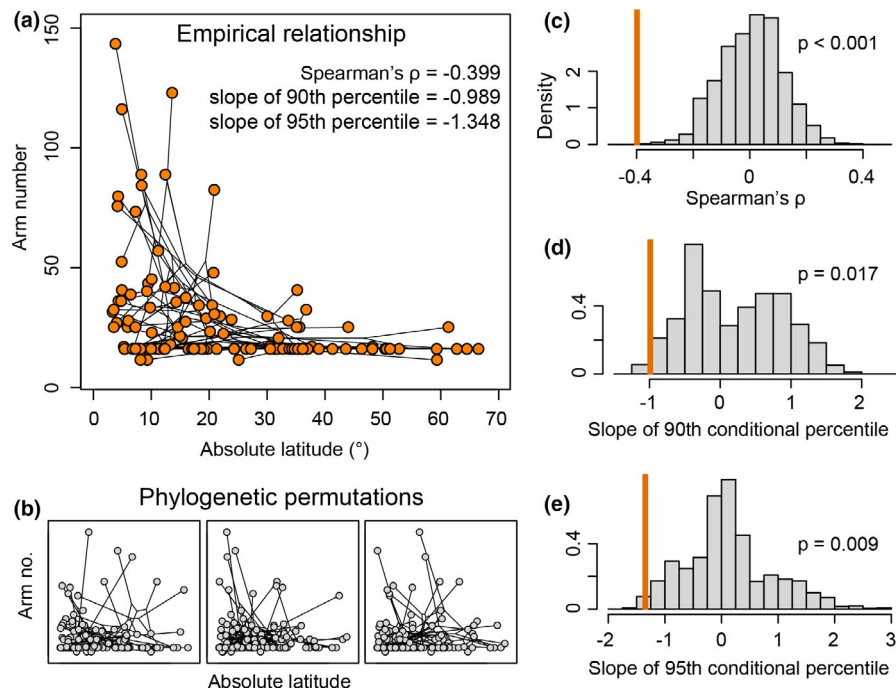
FIGURE 3 Comparing empirical relationships with a set of 1,000 phylogenetic permutations in which both the predictor and response variable have been randomly rearranged such that their phylogenetic signal (here, Blomberg's *K*) on the phylogeny is approximately equal to that of the observed data. (a) Arm number against absolute latitude for the 122 species represented in the phylogeny, with the phylogeny connecting tip values with ancestral state estimations for internal nodes. (b) Three sets of phylogenetic permutations. (c–e) Histograms of summary statistics of phylogenetic permutations, with empirical statistics plotted as an orange bar. One-sided *p*-value shown. (c) Spearman's *ρ*. (d) Slope of the conditional 90th percentile estimated with quantile regression. (e) Slope of the conditional 95th percentile

statistics for phylogenetic permutations differs slightly depending on whether the predictor, response variable or both are permuted. We present results in which both variables are permuted, but results are qualitatively identical for all three methods (Appendix S1).

3 | RESULTS

We detect a pervasive latitudinal gradient in the mean and spread of arm number (Figure 2). Arm number among featherstars decreases from the equator to the poles ($\rho = -0.276$), even when analysing northern ($\rho = -0.183$) and southern ($\rho = -0.349$) hemispheres or deep ($\rho = -0.275$) and shallow-water ($\rho = -0.266$) species separately. All correlations are statistically significant (or statistically clear, after Dushoff, Kain, & Bolker, 2019) at the $p < 0.01$ level. The relationship between absolute latitude and arm number is visibly wedge-shaped, and this is borne out by quantile regression: the 5th and 10th conditional percentiles had slopes near zero (−0.08 and −7.9E-18 respectively), and neither had a better (lower) AIC score than the corresponding unconditional quantile. Conversely, the 90th and 95th conditional percentiles had quite negative slopes (−0.49 and −0.74 respectively) and received overwhelming AIC support, with ΔAIC values in excess of 70 in both cases. In other words, information about latitude improves estimates of upper but not lower quantiles of arm number. The latitudinal gradient in arm number therefore

reflects an increased maximum arm number towards the equator without corresponding changes in the minimum. Arm number also declines steeply with depth ($\rho = -0.360$; Figure 2; Figure A3), and the variance among species with shallow-water occurrences (<200 m) is 15 times greater than for deep-water species.

The negative relationship between absolute latitude and arm number is apparent even when the dataset is randomly subset such that each 10° bin has the same number of species. Arm number was significantly negatively correlated with absolute latitude in all 10,000 subsets (median $p = 4.8E-8$), with a median effect size of $\rho = -0.358$. Likewise, regression fits of the 95th quantile had comparable slopes (median slope = −0.579) to quantile regression fits for the raw dataset, and AIC tests favoured them in all but three of 10,000 replicates (median ΔAIC = 42.6). Thus, the latitudinal gradient in arm number is not a spurious result of the greater diversity of featherstars in the tropics.

Midpoints are a convenient summary statistic for latitudinal ranges, but there are important caveats to interpreting them at face value (Colwell & Hurtt, 1994), two of which we deal with here. First, geographically biased sampling could systematically shift midpoints. For example, if marine biological research was more intense in the northern hemisphere, it could 'pull' latitudinal midpoints north. However, we recover no such northern hemisphere bias in our occurrence dataset (sample size, northern hemisphere = 10,803 [45%]; sample size, southern hemisphere = 13,050 [55%]). A plot of per-species sampling intensity across latitude (Figure A7) exhibits no clear
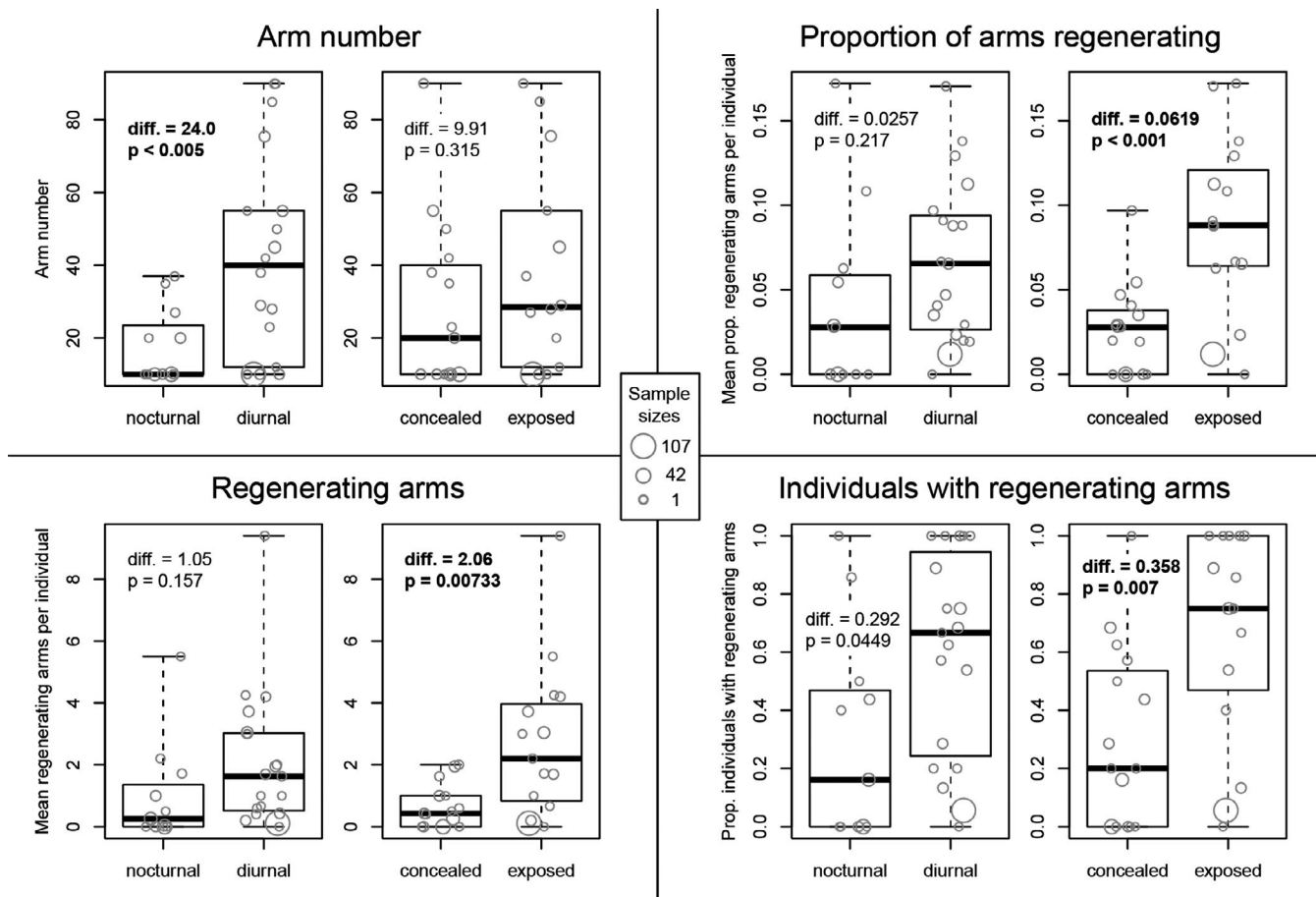
FIGURE 4 Arm loss and arm number in populations of tropical shallow-water featherstar species with differing habits. Differences in means are shown, along with p-values for Welch's unequal variances *t*-tests. Jittered points are species; larger points represent greater sample sizes. Statistically significant differences (controlling for a false discovery rate of 0.05 following Benjamini & Yekutieli, 2001) shown in bold. See text for habit details. Nineteen species are diurnal and 11 are nocturnal; 15 species are scored as concealed and 15 exposed

latitudinal trends, and the number of samples per species in each 5° latitudinal bin is not correlated with either latitude (Pearson's $r = 0.0853$, $p = 0.637$) or absolute latitude ($r = 0.276$, $p = 0.12$) As such, geographic bias in sampling intensity probably does not pose a serious problem for the use of latitudinal midpoints. Second, if many-armed featherstars had greater latitudinal ranges, it would tend to pull their latitudinal midpoints towards the equator, potentially engendering a spurious relationship between latitudinal midpoint and arm number. We do detect a weak but statistically perceptible relationship of this kind (Spearman's $\rho = 0.168$, $p = 4.326E-4$), so it is necessary to demonstrate that this alone does not cause the latitudinal gradient in arm number that we observe. For each species, we drew one latitude from a uniform distribution bounded by the observed latitudinal range limits of that species. We then calculated the correlation between arm number and those randomly drawn latitudes, and repeated this procedure many times. Absolute latitude was significantly correlated with arm number in all 1,000 replicates (median $\rho = -0.220$, median $p = 3.40E-6$), indicating that the use of latitudinal midpoints does not induce a gradient in arm number where none truly exists. This finding is corroborated by a plot of arm number against the observed latitudinal range of each species

(Figure A1) and a boxplot of arm number for all species in each 10° bin of absolute latitude (Figure A2).

Temperature and latitude at one randomly selected occurrence per species were compared as predictors of arm number (see Section 2). Arm number exhibited a stronger relationship with latitude (median $\rho = 0.152$) than with temperature (median $\rho = 0.110$) in 494/500 replicates, with a median difference in rhos of 0.0411 (Figure A8).

With the phylogenetic comparative approach adopted here, we show that Spearman's ρ ($p < 0.001$) and the slope of the 90th ($p = 0.017$) and 95th ($p = 0.009$) conditional percentiles are more negative for the empirical dataset than in nearly all phylogenetic permutations (Figure 3). The distributions of statistics for phylogenetically permuted datasets are visually similar to those associated with ordinary permutations, but have greater variance in all three cases (e.g., the ratio of variances for ρ is 1.46; Appendix S1). Thus, phylogenetic autocorrelation does give the dataset a tendency to produce stronger correlations, but not enough to explain the strongly negative relationships we observe.

Arm number is greater on average among diurnal versus nocturnal featherstars (difference in means = 24.01; Welch's *t*-test, $p < 0.005$; Figure 4) and among exposed versus cryptic and semicryptic forms

(difference = 9.9; *p* = 0.315), although only the former is statistically significant. No nocturnal species has over 37 arms, whereas 10 of 19 of diurnal species have between 38 and 90 arms. Among the 21 of 30 species in the concealment dataset with phylogenetic information, the difference in arm number between diurnal and nocturnal species is not clearly distinguishable from the set of phylogenetic permutations (two-tailed test; *p* = 0.166). However, this is also true for the set of ordinary permutations (*p* = 0.1904), and therefore probably results from reduced sample size.

All three measures of the prevalence of regenerating arms were lower on average for cryptic and semi-cryptic or nocturnal species (Figure 4). Individuals of exposed species were found regenerating significantly more arms on average (difference in means = 2.06) than cryptic and semi-cryptic forms (controlling for a false discovery rate of 0.05 following Benjamini & Yekutieli, 2001). Exposed forms were also regenerating a significantly greater proportion of their arms (difference = 0.0619), and a significantly greater proportion of individuals were regenerating at least one arm (difference = 0.358). Diurnal species also had higher values of all three metrics than nocturnal species, but no differences were statistically significant. Significance was basically identical when tested with ordinary and phylogenetic permutations: the difference in all three regeneration metrics between exposed and concealed species was significantly greater than in sets of 1,000 phylogenetic permutations (number of regenerating arms per individual, *p* = 0.003; proportion of regenerating arms per individual, *p* = 0.001; proportion of individuals with at least one regenerating arm, *p* = 0.034).

The rate at which featherstars lose arms to predators decreases towards the poles among five shallow-water populations spanning 40° of latitude in the northern hemisphere (Figure A14). All individuals in a population of *Cenometra bella* in the Philippines were found regenerating at least one arm and were estimated to suffer an attack from a predator every 9 days, whereas individuals in two mid- to high-latitude populations of *Florometra serratissima* encounter predators at about one-sixth that rate. No statistical significance is associated with this finding.

Among five featherstars from the Great Barrier Reef that feed in exposed positions, species with more arms are apparently less palatable to the reef fish *Chaetodon* and *Canthigaster* (Figure A4; Slattery, 2010). However, another experimental study of eight shallow-water tropical featherstars from Southern Vietnam recovered the greatest palatability to the sergeant-fish *Abudefduf* among the two species with at least 95 arms (Tinkova, Kasumyan, Dgebuadze, Oanh, & Britaev, 2014). Importantly, palatability within species appears to be quite variable, either between fish or between localities: palability as measured by Slattery (2010) is inversely related to palatability as measured by Tinkova et al. (2014) among the three species considered in both studies.

4 | DISCUSSION

4.1 | Predation

We demonstrate a latitudinal gradient in the mean and spread of arm number that appears in shallow and deep water and on either side of the equator, and that cannot be plausibly attributed to the effects of phylogenetic autocorrelation (e.g., the coincidental diversification of one or a few clades of many-armed featherstars at low latitudes). We take the increase in maximum arm number towards the equator as the most biologically interesting feature of our dataset. As such, we attempt to explain why many-armed featherstars are restricted to the tropics, but few armed featherstars are everywhere.

We argue that predation is the most plausible explanation for the latitudinal and bathymetric trends in arm number described here. All else being equal, a crinoid with more arms will be able to encounter more predators without losing too many arms to feed effectively. Predation would therefore constitute a selective agent with a consistent latitudinal signal if tropical featherstars encounter predators more frequently. Predators are not universally more ecologically important or prevalent towards the equator (Klompmaker et al., 2019; Schemske et al., 2009), but this does seem to be the case for marine durophages (Vermeij, 1978). Moreover, the teleost fish and echinoid predators that matter most to crinoids (Baumiller et al., 2010; Meyer, 1985) have their greatest region-scale diversity and (at least for fishes) abundance in the tropics (Edgar et al., 2017; Stuart-Smith et al., 2013). The estimated waiting times between predator encounters decreases monotonically towards the equator among five featherstar populations (Figure A14), corroborating the existence of a latitudinal gradient in predation intensity. More ecological studies are needed to definitively establish this pattern. Importantly, the predation hypothesis predicts both 'first-order' spatial patterns in feeding morphology: the decrease in maximum arm number towards the poles and with depth. There is good evidence for a decrease in the intensity of predation on crinoids with depth (Baumiller, 2013; Oji, 1996); the relationship between latitude and predation intensity should be investigated further.

If arm number has evolved as a result of predation, it is not the only aspect of crinoid morphology to do so. Both the configuration of arm branching and the spacing of articulations specialized for autotomy in the arms of featherstars match theoretical predictions for a predator-resistant feeding apparatus (Oji & Okamoto, 1994). Featherstar arms branch close to the base, minimizing arm loss in the event of an attack but covering the filtration area less efficiently. Conversely, branching points are distributed more evenly along the arms of isocrinids—exclusively deep-sea stalked crinoids that encounter fewer predators than shallow-water stalkless forms (Meyer & Macurda, 1977; Oji, 1996). The spacing of autotomy articulations along the arms in both stalked crinoids and featherstars very closely approximates an anti-predatory theoretical optimum, but the arms of featherstars have more autotomy articulations (Oji, 1996). The placement of crinoid gametes on arms and pinnules close to the centre of the body, or on arms concealed in the substrate, has also been cited as an anti-predatory adaptation (Vail, 1987). It therefore does not stretch the imagination to suggest that spatial patterns in arm number are the result of corresponding patterns in predation intensity.

If the latitudinal arm number gradient is caused by a corresponding gradient in the intensity of predation, then the few armed featherstars at low latitudes should have other ways of coping with predators. Two

such strategies have been documented extensively among featherstars: concealment (defined broadly here to include species nocturnal feeding and cryptic or semi-cryptic feeding positions) and toxicity. Our findings are consistent with concealment as an alternative to high arm number as an anti-predatory adaptation: featherstars that emerge to feed at night, when their predators are probably less active (Meyer & Macurda, 1977; Vail, 1987), have significantly fewer arms (Figure 4). Moreover, all metrics of the prevalence of regenerating arms are lower for both forms of concealment (though only with statistical significance for crypsis), corroborating their effectiveness as anti-predatory strategies. Results for palatability are less clear: Slattery (2010) found exposed species to be uniformly less palatable (more toxic) than cryptic ones, but the three most palatable species studied by Tinkova et al. (2014) were exposed. Combining the data from Slattery (2010) with our own, many-armed featherstars appear to be the least palatable, but the experimental results of Tinkova et al. (2014) support the opposite conclusion. Palatability of a single species can clearly be variable, but whether this is due to genuine within-species variability or to differences in taste among predators is not yet clear.

High arm number is probably just one among many solutions to the problem of intense predation at low latitudes. We are not aware of any tropical reef species without any of the solutions discussed in this paper— high arm number, toxicity or concealment—and we suggest more intense predation may favour a combination of these strategies, and perhaps others not mentioned here. Some strategies may not be available to members of some groups: for example, arm number appears exceptionally conserved within the Antedonidae (Figure A3). A survey of ecology across latitude among 10-armed featherstars would allow an investigator to isolate and study apparent anti-predatory adaptations besides arm number like concealment or toxicity, and would be a productive complement to this study.

If many-armed featherstars are better able to cope with intense predation, then why do few armed featherstars occur at all latitudes and constitute most of the extant species diversity (Figure 2)? The predominance of few armed featherstars would make sense if many-armed forms were at a relative disadvantage in terms of their ability to feed or reproduce, all else being equal. Featherstars typically increase arm number above 10 by autotomizing free arms close to the base and regenerating two in their place in a process known as augmentative regeneration, so growing more arms temporarily reduces food intake and sets an individual back the resources required to grow and maintain two new arms (Moore & Teichert, 1978; Shibata & Oji, 2003). However, featherstars with more arms can potentially harvest more food, so it is not clear how arm number ultimately affects feeding efficiency. Instead, growing many arms could push back the onset of sexual maturity. The 40-armed featherstar *Anneissia japonica* does not begin to augmentatively regenerate arms until roughly 8 months of age (Shibata, Sato, Oji, & Akasaka, 2008), and at a year old is still far from reaching its terminal arm number (Shibata & Oji, 2003). Although developmental data are excruciatingly scarce, the many-armed featherstars *Lamprometra klunzingeri* and *Anneissia japonica* reach sexual maturity later (1.5 and 2 years old respectively) than the few armed featherstars *Antedon bifida*

and *Florometra serratissima* (both 1 year; Holland, 1991; Shibata et al., 2008). Moreover, those many-armed featherstars appear to attain sexual maturity before reaching their adult arm number (Shibata et al., 2008), so further growth must involve wasting reproductive tissues. The cost of reproduction could therefore explain why many-armed phenotypes are rare in general, and are only present in the shallow and tropical waters where intense predation makes them necessary. The issue cannot be settled without more data on reproduction and development and should be treated as an open question.

If predation intensity on crinoids increases towards the equator, an interesting possibility is that phenotypic plasticity can account for some part of the latitudinal arm number gradient. Phenotypically plastic responses to predation (inducible defences) have not been documented in crinoids but are widespread in marine invertebrates, with six cases of inducible defences identified among non-crinoid echinoderms (Padilla & Savedo, 2013). Featherstars that repeatedly autotomize arms in response to predators might be induced to augmentatively regenerate more frequently. If hypothetically the ocean were suddenly made free of predators, a new generation of featherstars might exhibit a weaker latitudinal arm number gradient, even without any evolutionary change. The degree to which arm number exhibits a reaction norm controlled by predation intensity is not known, but could be tested with aquarium experiments in which the frequency of autotomy is manipulated by an investigator.

Although not considered in this study, stalked crinoids are thought to have been gradually excluded from shallow water by the ecological expansion of durophagous predators in the Mesozoic (Bottjer & Jablonski, 1988). We predict that predation on shallow-water stalked crinoids should exhibit predictable trends with both time and latitude, and that it became prohibitively intense in the tropics first and only later in higher latitudes. Such a prediction is consistent with recently described shallow-water stalked crinoids from Palaeogene and earliest Neogene localities across high southern latitudes (Whittle, Hunter, Cantrill, & McNamara, 2018), but could be more readily addressed by an attempt to comprehensively survey fossil occurrences across depth and latitude.

4.2 | Temperature, productivity and substrate

A latitudinal gradient in the intensity of predation on featherstars is a plausible explanation for the global phenotypic patterns documented here, and we have suggested several tests of this explanation in the preceding section, but the evidence is not conclusive. Here, we discuss three essentially abiotic correlates of latitude that could conceivably underlie the patterns in arm number: water temperature, food supply and coral reefs as a substrate.

Like mean and maximum arm number among featherstars, temperature increases towards the equator in shallow water and declines with depth. However, the mechanistic link between temperature and arm number is unclear. There is a well-documented relationship between sea-surface temperature and the frequency

of cyclones (Knutson et al., 2010), and the possibility that periodic intense tropical storms could select for more arms among exposed featherstars is worth exploring. Nevertheless, arm loss due to intense storms is apparently easy to distinguish anatomically from predator-induced arm loss: instead of being shed at articulations specially adapted for autotomy, arms are apparently broken off randomly by storms (Mizui & Kikuchi, 2013). Thus, studies of predation are unlikely to have been misled by damage from storms. Moreover, arm number is more weakly correlated with temperature than with latitude (Figure A8). We studied temperature as a predictor of arm number among shallow-water species, but the relationship is likely even weaker in deep water, where arm number increases towards the equator but temperature is nearly constant (Webb, 2019). The latitudinal temperature gradient may be causally 'upstream' of many hypothesized latitudinal patterns in biology, including the latitudinal diversity gradient (Willig, Kaufman, & Stevens, 2003) and the importance of predators at low latitudes (Schemske et al., 2009). Nevertheless, if global gradients in temperature have left an imprint in the distribution of arm numbers across the globe, they have probably done so indirectly.

Primary productivity also exhibits latitudinal trends, with peaks in high latitudes (Yoder, Keith Moore, & Swift, 2001), and could be implicated in latitudinal patterns of feeding morphology. Suspended phytoplankton makes up much of the crinoid diet, and the amount and kind of phytoplankton are surely important for crinoid feeding ecology (Kitazawa et al., 2007). However, the amount of particulate organic carbon that reaches the seafloor generally decreases towards the equator and with depth (Lampitt & Antia, 1997), whereas arm number increases towards the equator and decreases with depth (Figure 2; Figure A4). Moreover, phytoplankton abundance, and the availability of suspended particulate food more generally, is extremely heterogeneous geographically, and varies more across time and with terrestrial nutrient input than it does across latitude (Yoder et al., 2001). The correspondence between food supply and arm number is probably not analytically tractable with our dataset: the most consistent spatial correlate of particulate organic carbon supply is depth (e.g., the amount of particulate organic carbon reaching 2,000 m depth represents less than 1% of surface production; Lampitt & Antia, 1997), but we only have ready access to estimates of surface productivity. Most of the occurrences in our dataset are from deep water (e.g., 66% from below 100 m), where ocean colour estimates of surface productivity correspond only weakly with the amount of particulate organic carbon encountered by the benthos. Finally, neither a positive nor a negative relationship between arm number and food supply is predicted by crinoid biology: increased arm number and denser filtration fans are relatively well suited to fast-flowing water (Baumiller, 1993), but have no obvious implications for fitness in productive or unproductive waters. Increasing arm number should not only increase maximum food intake but also energy requirements (see previous paragraph). Global patterns in productivity can thus be safely rejected as causes of patterns in arm number on both pattern-based and mechanistic grounds.

The unique physical environment created by tropical coral reefs may facilitate the evolution of feeding morphologies not possible further towards the poles. High-flow microhabitats that can support featherstars with dense, many-armed filtration fans might be especially common on coral reefs. Local flow regime has clear consequences for the effectiveness of different crinoid feeding morphologies (Baumiller, 1993; Kitazawa et al., 2007; Leonard, Strickler, & Holland, 1988). A number of distinct microhabitats can be found across a coral reef (e.g., Zmarzly, 1984), and both crinoid-feeding postures (e.g., arcuate vs. parabolic vs. radial fan postures; Meyer & Macurda, 1980) and aspects of morphology (Meyer, 1973) seem to correspond to particular microhabitats. In theory, the role of coral reefs in facilitating the latitudinal gradient in arm number could be tested by comparing arm number among featherstars along the East Pacific and East Atlantic, where tropical reefs are rare to absent, with species along the reef-rich West Atlantic and Indo-West Pacific. However, while reef-poor continental margins do not exhibit latitudinal gradients in arm number (Figure A6), they are also extremely species-poor: the Tropical East Pacific marine province (following Spalding et al., 2007) and the tropical east Atlantic (the Western African Transition and Gulf of Guinea marine provinces) have occurrences from two and four featherstar species respectively. The question is therefore not amenable to a simple macroecological approach. Nevertheless, the physical properties of coral reef microhabitats are unlikely to directly account for the latitudinal arm number gradient alone. Arm number increases towards the tropics among shallow- and deep-water species alike (Figure 2), but zooxanthellate scleractinian reefs are exclusively found in shallow water. Moreover, although coral reefs present a unique physical environment, the high-energy flow regimes that favour many-armed filtration fans are not unique to the tropics: there are probably many habitats in temperate and polar regions in which many-armed featherstars could feed effectively. Lastly, some of the featherstars in our dataset with the greatest number of arms have been recorded living on soft bottoms (e.g., *Phanogenia multibrachiata*—150 arms, Mekhova & Britayev, 2012; *Zygometra microdiscus*—83 arms, Messing et al., 2006), indicating that coral reef substrates are not a prerequisite for the many-armed condition.

Physical factors and biotic interactions do not constitute mutually exclusive (or collectively exhaustive) explanations for the broad spatial patterns in functional morphology outlined here. A more holistic conception of the evolution of arm number is that intense predation in the shallow tropics promotes the relative success of many-armed featherstars, and the reefs that are there help facilitate their ecological disparification by creating unique microhabitats and flow regimes. Reefs also provide the deep infrastructure in which cryptic forms hide from predators (Meyer, 1985), and they recruit fish and echinoid predators (Baumiller & Stevenson, 2018). Thus, the greatest diversity of featherstar ecologies seems to be made possible by corals. Throughout the Phanerozoic, widespread reefs have not always been strictly tropical, made of photosymbiont-bearing coral or even present (Kiessling, Flügel, & Golonka, 1999). Inasmuch as reefs facilitate ecological disparification, changes in the global

assembly of reefs probably correspond with changes in the deployment of ecological diversity around the globe.

5 | CONCLUSIONS

We demonstrate a latitudinal gradient in mean and maximum arm number among featherstars that is symmetrical on either side of the equator, present in shallow and deep water and distinct from the latitudinal diversity gradient. Concurrently, we introduce a new nonparametric phylogenetic comparative approach appropriate for nonlinear trends in strangely distributed data, and use it to reject the possibility that the patterns we observe result solely from phylogenetic autocorrelation of arm number and latitude. We also present evidence against several plausible abiotic agents as causes of this gradient. Instead, consilient evidence from crinoid ecology and functional morphology indicates that a latitudinal gradient in the intensity of predation is a plausible and readily testable cause of the wedge-shaped relationship between arm number and absolute latitude. Many-armed featherstars are not only more predator-resistant but are also characterized by several unique ecologies, especially on tropical coral reefs. Crypsis and toxicity are additional ecologies that characterize the tropical reefs where predators make them necessary. Inasmuch as these ecomorphological roles are only or most viable in the face of intense predation, predators act as an 'enabling factor' sensu Vermeij (2020), expanding the range of viable ecologies. Conceptually, ecological diversity is typically linked with opportunity (e.g., unfilled niches), but we suggest that predation, typically thought of as a 'constraint', may just as readily promote functional innovation.

To the degree that arm number corresponds to feeding ecology, the wedge-shaped relationship between arm number and latitude implies a latitudinal gradient in functional richness (the number of unique ecologies) that is independent from the latitudinal diversity gradient. Similar patterns in functional richness have been reported in bats, birds, bivalves and shallow-water fish (Schumm et al., 2019; Stevens, Cox, Strauss, & Willig, 2003; Stuart-Smith et al., 2013). Notably, the proposed mechanisms for such a pattern in these taxa involve abiotic factors—for example, latitudinal gradients in temperature, with downstream effects on resource abundance/stability—whereas our explanation emphasizes predation as a causal/selective agent. Biotic interactions like competition have been incorporated by other authors into explanations for latitudinal gradients in species richness and evolutionary innovation (Schemske et al., 2009). Pianka (1966) implicated predation in the latitudinal diversity gradient, but to our knowledge, a model in which predation facilitates functional diversification is novel. The generality of latitudinal gradients in ecological diversity remains to be explored, but when they exist they need not be linked with ecological opportunity or resource availability.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.