Niche Evolution and Phylogenetic Community Paleoecology of Late Ordovician Crinoids

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Abstract: Fossil crinoids are exceptionally suited to deep-time studies of community paleoecology and niche partitioning. By merging ecomorphological trait and phylogenetic data, this study summarizes niche occupation and community paleoecology of crinoids from the Bromide fauna of Oklahoma (Sandbian, Upper Ordovician). Further, patterns of community structure and niche evolution are evaluated over a ~5 million-year period through comparison with the Brechin Lagerstätte (Katian, Upper Ordovician). We establish filtration fan density, food size selectivity, and body size as major axes defining niche differentiation, and niche occupation is strongly controlled by phylogeny. Ecological strategies (i.e., adaptive zones) were relatively static over the study interval at high taxonomic scales, but niche differentiation and specialization increased in most subclades. Changes in disparity and species richness indicate the transition between the early-middle Paleozoic Crinoid Evolutionary Faunas was already underway by the Katian due to ecological drivers and was not triggered by the Late Ordovician mass extinction.

1 Introduction

Ecological communities have changed dramatically over the course of geological history as a result of environmental change, biotic interactions, evolution of new higher taxa, and extinction. At the ecosystem scale, a variety of approaches have been used to evaluate broad patterns of resource utilization, functional diversity, and complexity through deep time using theoretical concepts and methodological approaches like tiering, ecospace filling, limiting components, ecosystem engineering, ecological clustering, network analysis, niche modeling, and abundance distributions (e.g., Ausich, 1983; Bambach, 1983; Ausich & Bottjer, 1986; Wagner et al., 2006; Bambach et al., 2007; Erwin, 2008; Novack-Gottshall, 2007; Stigall, 2012; Dineen et al., 2014; Muscente et al., 2018). Many of these methods have also been successfully applied to community-level investigations to evaluate various aspects of ecology or make comparisons between paleocommunities (e.g., Brame & Stigall, 2014; Darroch et al., 2018; Perera and Stigall, 2018; Whittle et al., 2019; Cole et al., 2020; Nanglu et al., 2020). However, other ecological aspects of paleocommunities relating to niche partitioning, assembly, and structure are not readily captured by these methods and have received far less attention in past studies, particularly for clades of fossil marine invertebrates.

Niches are complex and multidimensional, reflecting a wide range of traits, behaviors, and abiotic factors that dictate the functional position of organisms within their environment, biotic interactions, and resource partitioning within communities (Hutchinson, 1978). Because of their fundamental role in ecology, niches are a necessary component for fully understanding community structure and evolution through deep time. Characterizing species niches is challenging in the fossil record, in part because of difficulties in extracting relevant biological/ecological information from fossils. As a result, many studies have focused on characterizing niches using abiotic data that can be extracted from the rocks associated with specimen occurrences, such as water depth, substrate consistency, turbidity, and temperature (e.g., Holland & Zaffos, 2011; Stigall, 2012; Myers et al., 2015; Antell et al., 2021). Others have used one or more ecologically-significant traits like body size as proxies for niche partitioning at broad levels, especially for groups like vertebrates where relationships between size and other niche parameters are well understood (e.g., Andrews et al., 1979; Pineda-Munoz et al., 2016; Fraser & Lyons, 2020; Schroeder et al., 2021). Within marine invertebrate faunas, classic work by Bambach (1983) identified three major categories—feeding, motility, and tiering—that could be used to characterize ecospace utilization, and subsequent investigations have expanded upon this approach to encompass additional ecological components and methods (Novack-Gottshall, 2007; Villéger et al., 2011). Although these categorical elements have been used to describe functional diversity within groups (e.g., Schumm et al., 2019), they are typically too broad to capture the range of variation between ecologically similar species, and thus do not represent niche concepts at the species level (Bambach et al., 2007; see Hadly et al., 2009). As a result, ecospace approaches have generally focused on patterns of functional diversity of whole ecosystems rather than the structure and dynamics of species niches within communities.

Some fossil organisms readily preserve anatomical features that can be linked back to ecological functions, referred to as ecomorphological traits. When multiple ecomorphological traits are available for a study group, they can be used in multivariate analyses to evaluate the relative position of species in ecomorphospace. They can also function as a proxy for niche occupation if traits are thought to capture major components of niche differentiation (Ricklefs & Miles, 1994; Pianka, 2017). Analyses of ecomorphospace occupation have been conducted widely across fossil and living taxa as a means of quantifying ecological variation, typically with continuous and/or discrete characters, and either with or without direct inferences of niche occupation being made (e.g., Van Valkenburg, 1994; Weiser et al., 2006; Anderson, 2009; Fischer et al., 2017; Pianka, 2017; Walton & Korn, 2018; Cole et al., 2019; Mallon, 2019; Cole & Hopkins, 2021). Using ecomorphospace to characterize species niches in multidimensional trait space is a powerful approach for community-level studies because it operationalizes complex concepts like niche breadth and permits investigation of a wide range of hypotheses relating to community assembly, biotic interactions, and resource partitioning.

Incorporating phylogenetic perspectives into studies of species niches can provide further insight into community ecology and niche evolution. When integrated with community-level data, phylogenies can be used to recognize evolutionary changes in patterns of assembly, structure, and trait distributions within communities, in addition to the underlying processes responsible for generating observed patterns. Further, combining phylogenies with data on niche occupation can allow identification of phenomena like niche convergence, divergence, and niche conservatism. Although phylogenetic community ecology has been applied widely to studies of modern systems (for reviews see Webb et al., 2002; Cavender-Bares et al., 2009; Qian & Jiang, 2014), it is challenging to obtain both robust phylogenetic hypotheses and detailed ecomorphological data for many fossil taxa. Nevertheless, the merging of phylogenetic and paleoecological perspectives represents a promising area of paleontological research (Lamsdell et al., 2017; Cole et al., 2019), and case studies using these approaches are becoming increasingly widespread, especially for terrestrial vertebrate communities (Raia, 2010; Fraser et al., 2015; Polly et al., 2017, Fraser & Lyons, 2017, 2020. Although these methods are more rarely applied to invertebrate fossil groups (e.g., Cole et al., 2019; Chang & Skipwith, 2020), fossil crinoids are a particularly promising system because they preserve extensive ecological data and have a robust phylogenetic framework (Wright et al., 2017; Cole et al., 2019). As a result, they are the only fossil invertebrate group for which community-level niche dynamics have been studied in a phylogenetic context (Cole et al., 2019; Cole et al., 2020), and have the potential to provide deep-time perspectives on niche evolution, niche dynamics, and community ecology.

1.2 Crinoid Paleoecology and Niche Partitioning

Among fossil marine invertebrates, it is often challenging to identify characters with unambiguous ecological functions, which can hinder quantitative investigations of niche evolution in deep time. Crinoids are ideally suited for questions that require knowledge of species ecology in deep time, because their skeletons preserve many features that directly correspond to ecological functions. This allows fossil crinoid niches to be quantitatively reconstructed with a high degree of fidelity. Notably, the ecology of both fossil and living crinoids has been studied extensively and cross-compared (Meyer, 1973, 1979; Macurda & Meyer, 1974; Ausich, 1980; Ausich & Bottjer, 1982; Baumiller, 1997; Brower, 2007, 2013; Kitazawa et al., 2007; Meyer et al., 2021; Messing et al, 2017). As passive suspension feeders, crinoids primarily partition niches through differences in feeding ecology, such as the differentiation of feeding structures (for example, the number, arrangement, and structure of arms and pinnules [Meyer, 1979;

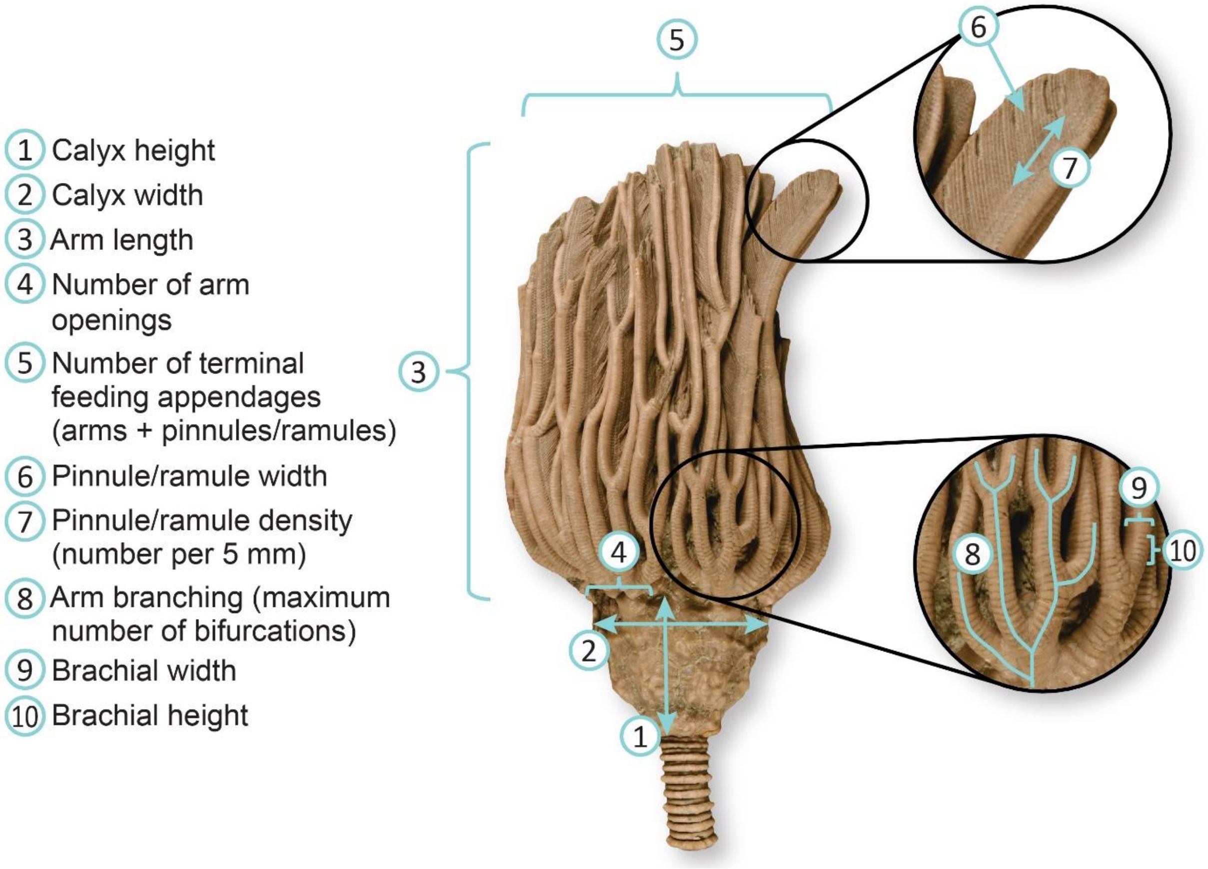

Figure 1. Collected measurements of ecomorphologic traits. Representative specimen shown is *Actinocrinites gibsoni* (Mississippian).

Ausich, 1980; Kitazawa et al., 2007]) and tiering (Ausich & Bottjer, 1982). The role these traits play in crinoid feeding ecology and niche partitioning have been extensively reviewed elsewhere (e.g., Baumiller, 2008; Cole et al., 2019: Figure 1).

Recent work established a series of continuous ecomorphological traits that could be used to capture niche differentiation in crinoids through variation in feeding structures and body size (Cole, 2017a, 2019). In a subsequent study, ecomorphological traits were combined with phylogenetic data to investigate niche occupation and community paleoecology of crinoids from the Upper Ordovician (Katian) Brechin Lagerstätte and test a wide range of hypotheses relating to community structure, niche partitioning, and niche conservatism within the fauna (Cole et al., 2019). Although this investigation primarily focused on a single fauna, it also looked at differences in filtration fan density between crinoids from the Ordovician-age Brechin Lagerstätte and the Mississippian-age Edwardsville Fauna, and found substantial shifts occurred through time, especially within subclass Pentacrinoidea (Cole et al., 2019). Notably, this study also provided a methodological proof-of-concept for phylogenetic investigations into the long-term evolution of crinoid niches and the structure of ecological communities through deep time.

Here, we apply a series of trait- and phylogeny-based analyses to crinoids from the Upper Ordovician (Sandbian) Bromide Formation of Oklahoma in order to characterize patterns of community assembly and niche space occupation. In addition, we compare the paleoecology of the Bromide fauna to that of the geologically younger Brechin Lagerstätte (Upper Ordovician, Katian) (Cole et al., 2019). We further characterize and compare aspects of crinoid functional ecology between the two faunas via application of disparity analyses to community-wide ecomorphological trait data. Through these comparisons, we evaluate niche partitioning, niche evolution, phylogenetic structure of niches, and changes in community structure over a ~5 million-year period. This work highlights the utility of integrating phylogenetic and trait-based methods for application to paleocommunities and provides a robust framework for future investigations of crinoid community evolution and changes in niche space through time.

2 Characteristics of the Bromide and Brechin Crinoid Faunas

The Upper Ordovician was a key interval in the early evolutionary history of crinoids. The earliest known crinoids are from the Lower Ordovician (Tremadocian) of Utah (Guensburg & Sprinkle, 2003), but crinoid taxonomic diversity remained relatively low until the Middle Ordovician (Peters & Ausich, 2008). During the Middle-Late Ordovician, rapid diversification of crinoids occurred as part of the Great Ordovician Biodiversification of marine invertebrate life (Webby et al., 2004; Wright & Toom, 2017). Peak genus-level diversity was reached during the Katian stage of the Upper Ordovician before it dropped precipitously during the Late Ordovician mass extinction across the Katian-Hirnantian boundary (Peters

& Ausich, 2008; Wright & Toom, 2017; Cole, 2018). The rapid increase in crinoid genus and species diversity led to greater morphological and ecological variation during Upper Ordovician (Foote, 1994, 1999; Deline & Ausich, 2011; Wright, 2017a; Deline et al., 2018, 2020; Cole & Hopkins, 2021) and increases in community complexity (Cole et al., 2020). As a result, the Upper Ordovician is dynamic interval of time in crinoid evolutionary history that is ideal for evaluating the evolution of niche occupation and community assembly in early crinoid communities. In terms of taxonomic richness, the two faunas compared here—the Bromide and the Brechin—have the highest known crinoid diversities from the Sandbian and Katian, respectively. As a result, both paleocommunities should be broadly representative of Laurentian crinoid faunas during these stages of the Upper Ordovician. For example, the relative proportions of major groups that make up the Brechin fauna are comparable to those of other Katian-age crinoid assemblages (Cole et al., 2017; Cole et al., 2020).

When making comparisons between fossil communities, it is important to account for potential biases that could generate spurious results, such as those relating to differences in taphonomy, depositional environment, and sampling intensity. The sections below summarize these aspects of the Bromide and Brechin crinoid faunas to highlight both strengths and limitations of the comparative study of these two crinoid paleocommunities.

2.1 Taxonomic Diversity

The Bromide Formation is the most diverse echinoderm fauna known from a single formation and is the most species-rich assemblage of Ordovician crinoids. As of 1982, More than 11,000 echinoderm specimens had been recovered from the Bromide Formation representing more than 60 genera across 13 classes (Sprinkle, 1982a). Echinoderms from the Bromide fauna, including a diverse crinoid assemblage, were described in detail in a 1982 monograph (Sprinkle, 1982a) that remains the most comprehensive treatment of Bromide echinoderms to date. Including subsequent studies describing new taxa, crinoid diversity from the Bromide Formation currently stands at 28 genera and 38 valid named species. However, specimens representing at least nine additional taxa have been figured in published literature but left indeterminate or questionably assigned because of poor preservation (e.g., Sprinkle 1982a), and other specimens representing new species or higher taxa are still awaiting formal description (e.g., Sprinkle et al., 2015, 2018). As a result, the total diversity of crinoids from the Bromide Formation is likely closer to 50 species.

The Brechin Lagerstätte is the second most diverse Ordovician crinoid fauna known. A description of the Brechin fauna, historically referred to as the "Kirkfield", was first published by Frank Springer in 1911, but the faunal list was incomplete. Subsequent collecting produced a large number of exceptionally preserved specimens that were used as the basis for a re-evaluation of the diversity of the fauna. These revisions of the fauna were covered in a series of recent publications that resulted in the recognition and description of 15 new species and 3 new genera, bringing the known diversity of Brechin crinoids to 27 genera and 39 nominal species (Cole et al., 2018, 2020; Ausich et al., 2018; Wright et al., 2019). Similar to the Bromide fauna, the Brechin also preserves a number of species belonging to other echinoderm classes (e.g., Sumrall & Gahn, 2006; Blake & Koniecki 2019, 2020), although most have not received comprehensive taxonomic assessment. In addition to echinoderms, both faunas preserve abundant fauna that are typical constituents of benthic Ordovician communities, such as trilobites, bryozoans, and brachiopods (Brett & Liddell, 1978).

2.2 Geology and Paleoenvironmental Setting

The Bromide Formation extends throughout a large portion of the Arbuckle Mountains and Criner Hills regions of south-central Oklahoma. Although the Bromide is over 100 m thick, echinoderm fossils have primarily been recovered from two zones in the middle Mountain Lake Member and a cluster of horizons in the overlying Pooleville Member. These fossil-bearing horizons are distributed over a ~75 m section of the Bromide Formation, and crinoids have been collected from numerous localities for each of these zones (Sprinkle, 1982b). Similar to the crinoid occurrences in the Bobcaygeon and Verulam formations, crinoid-bearing horizons in the Bromide Formation are predominantly shale beds interbedded with grainstones, packstones, and wackestones (Sprinkle, 1982b; Carlucci et al., 2014). During the interval of interest for this study, deposition of the Bromide Formation occurred along a carbonate-dominate ramp in a NW-SE trending trough (Carlucci et al., 2014). The fossiliferous horizons from which crinoids have been recovered are interpreted to have been deposited in shallow to deep shelf paleoenvironments (Longman, 1982; Carlucci et al., 2014). The Bromide Formation is thought to span the majority of the Sandbian stage (Carlucci et al., 2014), which is approximately 5.4 myr in length, concluding around 453 Ma (Goldman et al., 2020). However, fossil crinoids do not occur in the lower sandstone member (Sprinkle, 1982b), so the total age range spanned by crinoids from the Bromide is much shorter.

Crinoids from the Brechin Lagerstätte have been recovered from multiple quarries from the Lake Simcoe region of southern Ontario, Canada (Cole et al., 2018). These quarries are all located within ~6 km of the town of Brechin, Ontario, for which the fauna is named. Crinoid-bearing horizons are present throughout a ~20 m thick interval that spans the uppermost ~15 m of the Bobcaygeon Formation and ~5 m of the lowermost Verulam Formation (for further discussions of stratigraphic divisions, correlations, and nomenclature for the Upper Ordovician of southern Ontario, see Amstrong [2000], Cole et al. [2018], and Paton & Brett [2019]). The Bobcaygeon and overlying Verulam formations are composed of bioclastic grainstones, packstones, and wackestones that are interbedded with calcareous shales and siltstones. These strata are interpreted to have been deposited in a proximal carbonate shelf environment that varied in depth from shallow shelf in the Bobcaygeon to deep shelf in the Verulam (Armstrong, 2000), with gradual deepening moving upwards through the Bobcaygeon to Verulam (Liberty, 1969). Fossil horizons that make up the Brechin Lagerstätte span the lower portion of the Katian within the middle-upper Bobcaygeon and lower Verulam Formations. Although numerical ages for this interval are not tightly constrained, the Verulam-Bobcaygeon boundary should be approximately 451 Ma and the fauna should span an interval of roughly 2 million years or less (Sproat et al., 2015; Paton & Brett, 2019; Goldman et al., 2020). Thus, the estimated time between the latest fossiliferous horizons of the Bromide and the earliest fossiliferous horizons comprising the Brechin fauna is relatively short (~2 myr), and time elapsed between median ages for the faunas is <5 million years.

2.3 Taphonomy and "Paleocommunities"

The Bromide and Brechin faunas are similar taphonomically, although there is greater taphonomic heterogeneity between fossil-bearing horizons in the Bromide Formation. A greater proportion of articulated cups and crowns are recovered from the Brechin than from the Bromide, but the sheer number of specimens recovered from the Bromide has resulted in a large sample of well-preserved specimens with arms intact. As a result, the two faunas are broadly comparable in terms of taphonomy and specimen-level sampling intensity of their constituent species .

Because crinoids disarticulate rapidly upon death, preservation of specimens with arms and/or stems intact signals rapid burial and little to no time-averaging or transport (Donovan, 1991; Brett et al., 1997; Ausich, 2001, 2021; Ausich & Baumiller, 2003). As a result, horizons of well-preserved crinoids, such as those recovered from the Bromide and Brechin faunas, should not be subject to spatial or temporal averaging. Individual horizons of well-preserved crinoids can be treated as ecological snapshots (Ausich, 2016), and this approach has been applied to hardground surfaces in the Brechin fauna (Taylor & Brett, 1996; Paton et al., 2019). However, here we combine all crinoid-bearing horizons from the Bromide and Brechin fauna in order to provide reasonable sample sizes. As a result, as they have been assembled here, the Bromide and Brechin datasets do not represent ecological snapshots *per se*. Instead, they reflect recurring species assemblages that are both temporally and spatially restricted (e.g., within a single basin), which is consistent with the traditional use of the term "paleocommunity" in paleoecological literature (e.g., Walker and Laporte, 1970; Ausich, 1980; Bennington & Bambach, 1996; Wagner et al., 2006;

Perera & Stigall, 2018; Lyons et al., 2019).

3 Methods

3.1 Collection and Vetting of Ecomorphologic Trait Data

We us the term “ecomorphologic traits” to describe morphological characters that directly correspond to or strongly correlate with ecological functions. Following the model of crinoid niche differentiation outlined by Cole (2017a) and later expanded upon by Cole et al. (2019), we collected data for ten ecomorphological traits and calculated an additional three composite characters (Figure 1). Measured characters include (1) calyx height, (2) calyx width, (3) arm length, (4) number of arm openings, (5) arm branching, (6) terminal feeding appendages (Ω), (7) brachial width, (8) brachial height, measured at the midpoint of the arms, (9) pinnule/ramule density, and (10) pinnule/ramule width. In addition, we calculated three composite characters that represent important aspects of crinoid morphology and ecology: (1) calyx volume (V), calculated using the standard equation for a cone, (2) Filtration fan area (f_A), calculated using the Ausich (1980) equation with modifications by Cole (2017), and (3) Filtration fan density (F_D), calculated by dividing the total number of terminal feeding appendages (Ω, quantitative trait 6) by the total area of the filtration fan (f_A). More detailed descriptions of trait measurements and calculation of composite characters are given in Cole et al. (2019: Figure 1) and the Supplemental Materials.

We collected ecomorphologic data from 95 specimens representing 37 species from the Bromide fauna. Specimens representing juveniles were not included in the study. *Cleiocrinus ornatus* Kolata 1982 was the only named species from the fauna for which data were not collected because it is known only from fragmentary material where fundamental measurements like calyx height and width could not be collected. Of the 37 species for which data were collected, 36 are currently valid named species and one is represented by an unidentified specimen belonging to the disparid family Cincinnaticrinidae (Sprinkle, 1982a). This specimen has not been assigned a genus or species name because it does not preserve the posterior interray, which is necessary for classification at finer taxonomic scales. However, it was suitable for inclusion in this study because it preserves a complete calyx and partial arms and unquestionably represents a unique taxon from the Bromide fauna.

Ecomorphological data were collected from Brechin Lagerstätte crinoids in a previous study by Cole et al. (2019) using the same methods that were here applied to the Bromide fauna. For this study, we added trait data for three additional Brechin species so that all known taxa were included. These species were *Grenprisia springeri*, based on a new well-preserved specimen (Wright et al., 2019), *Abludoglyptocirnus steinheimerae*, which was only recently described from the fauna (Cole et al. 2020), and *Cleiocirnus regius*, which did not have any specimens available for study in the original paleoecological investigation. The three composite characters—fan area, fan density, and calyx volume—were also calculated for each species from the Brechin Lagerstätte. In total, the Brechin dataset was compiled from measurements of 168 specimens across 38 species. For both the Bromide and Brechin datasets, mean values for measured and composite ecomorphological traits were calculated for each species and used for all subsequent analyses.

Some crinoid species in the study are only known from poorly preserved specimens and have extensive missing data. To evaluate the effect of this missing data, we conducted a series of sensitivity tests using four different thresholds for missing data (Supplemental Materials). Based on the results of these sensitivity tests, we determined that only taxa preserving at least partial arms should be included in the study. As a result, we simultaneously minimize the amount of missing data and maximize the number of species that could be reliably included (30 out of 37 Bromide species, 39 out of 39 Brechin species; Figure S1). Thus, all remaining analyses were conducted using the vetted datasets that excluded species without at least partial arms preserved (Figure S1, see Supplemental Materials for additional discussion of sensitivity tests).

3.2 Analyses

Analyses were conducted in R version 4.1.0 (R Core Team 2021). R packages used for analyses were cluster (Maechler, 2019), vegan (Oksanen, 2013), paleotree (Bapst, 2012), phytools (Revell, 2012), phangorn (Schliep et al., 2021), geiger (Harmon et al., 2008) and ape (Paradis et al., 2004). All R scripts and data needed reproduce analyses are provided in the online supplemental materials.

3.2.1 Ecomorphospace Occupation

The vetted datasets of 10 measured characters, which included all taxa with at least partial arms preserved, were combined for the Bromide and Brechin faunas, and a dissimilarity matrix for the dataset was calculated using Gower's coefficient. A principal coordinates analysis (PCO) was then conducted for the resulting dissimilarity matrix, and the major axes were plotted to visualize ecomorphospace occupation of the two faunas. To interpret major sources of variation from the PCO, Spearman's rank correlation tests were used to evaluate dominant associations between PCO scores and ecomorphologic traits, including both measured and calculated traits. To visualize shifts in ecomorphospace occupation between faunas, we used the PCO scores to calculate centroids and visualize their positions on ecomorphospace plots. Centroids were calculated for each fauna as a whole as well as for subclasses Camerata and Pentacrinoidea.

3.2.2 Disparity

Disparity, which captures the diversity of morphological forms, is a valuable tool for investigating evolutionary dynamics that has been widely applied to the crinoid fossil record (Deline, 2021). We conducted a series of disparity analyses to further evaluate (1) ecomorphological disparity of crinoids from the Bromide and (2) changes in disparity between the Bromide and Brechin faunas. Dissimilarity matrices and PCOs were calculated separately for each fauna and used to calculate three common disparity indices that capture different facets of morphological disparity: (1) sum of ranges (SOR), which reflects the total amount of morphospace occupied; (2) sum of variances (SOV), which provides a measure of dispersion of taxa around the centroid of the group, and (3) and mean pairwise dissimilarity, which summarizes the average distance between all possible taxon pairs and is typically very similar to SOV (Ciampaglio et al., 2001; Lloyd, 2016; Hopkins & Gerber, 2017). To investigate patterns of disparity at different taxonomic scales, we calculated the three disparity indices for each fauna as a whole and for major groups in each fauna. Groups evaluated were subclass Camerata and its constituent subtaxa (order Diplobathrida, order Monobathrida, and "stem" eucamerates) and subclass Pentacrinoida and its constituent major subtaxa (parvclass Disparida, magnorder Eucladida, suborder Porocrinoidea [porocrinids + hybocrinids], and suborder Flexibilia), based on the revised classification of Wright et al. (2017). Although the genus *Cleiocrinus* has long been classified as a diplobathrid camerates, this affinity has been questioned on the basis of many atypical features, including the absence of interray plates that are considered a synapomorphy of Camerata (Ubaghs, 1978; Cole, 2018). As a result, we included *Cleiocrinus* in measures of total faunal disparity, but excluded it when calculating disparity for diplobathrids. Because disparity indices can only be calculated from samples with two or more taxa, it was not possible to calculate disparity in the Bromide fauna for monobathrids (1 species), "stem" eucamerates (1 species), or flexibles (no species present).

To further evaluate changes in disparity between the Bromide and the Brechin faunas, we calculated relative disparity for all major groups by diving the disparity of the group of interest within a fauna by total disparity of the fauna. We also calculated change in relative disparity for all groups with at two taxa per fauna by subtracting the relative disparity of a group in the Brechin from the relative disparity of the same group in the Bromide. Statistical significance for (1) change in disparity between the Bromide and Brechin faunas and (1) change in relative disparity between groups was calculated for 1000 bootstrap replications, where taxa in the group of interest were resampled with replacement.

3.2.2 Ecological Clustering and Tree-based Analyses

Multivariate cluster and phylogeny-based analyses were conducted for the Bromide fauna using the same methods previously applied to the Brechin fauna (Cole et al., 2019). Recent work has resulted in relatively well-resolved phylogenies of Ordovician crinoids at the genus level (Ausich et al., 2015; Cole, 2017b, 2018; Wright, 2017a, 2017b; Wright et al., 2017; Ausich, 2018), and we used these existing phylogenetic hypotheses as a framework to construct an informal tree topology for crinoid genera in the Bromide fauna (Figure 2). Generic relationships that were ambiguous based on previous analyses were left as polytomies at the level of the least inclusive clade. Because species-level phylogenetic hypotheses do not exist for the taxa considered, species were appended onto the genus-level tree assuming monophyly of genera, with species collapsed into polytomies in instances where three or more species were present within a genus. To avoid conditioning results on a single tree topology and set of branch lengths (Soul and Wright, 2021), we used the *cal3* method in the R package paleotree to randomly resolve polytomies from the informal tree topology and produce a set of fully-resolved, time-scaled trees (Bapst 2012, 2013). This procedure uses an a posteriori probabilistic time-scaling approach that draws node ages from a probability distribution based on diversification and sampling rate estimates (Foote, 1997; see Cole et al., 2019 for additional details and R code). The procedure was repeated 500 times to produce a set of time-scaled trees that reflect uncertainty in both tree topologies and branch lengths that were used in subsequent tree-based analyses.

To evaluate ecological similarity among taxa, the vetted ecomorphological dataset that included all taxa with at least partial arms was subsetted to include only Bromide taxa and normalized by making the margin sum of squares equal to one (Oksanen, 2020). A dissimilarity matrix was calculated from the normalized trait data using Gower’s coefficient, and a cluster analysis was performed using the Ward

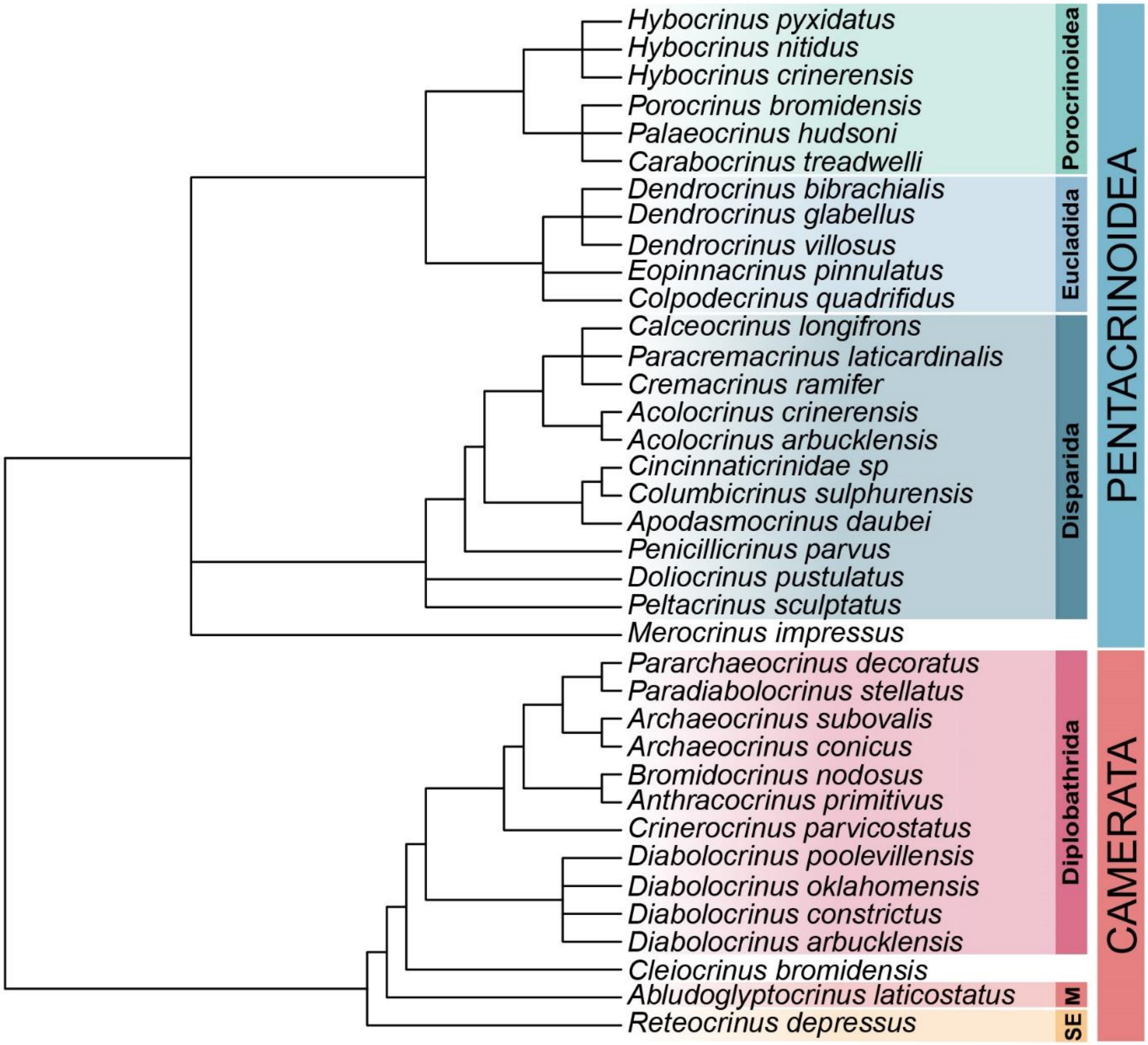

Figure 2. Phylogeny of crinoids from the Bromide fauna with major groups identified. The informal species-level tree topology was constructed using a framework of existing genus-level phylogenies for fossil crinoids (Ausich et al., 2015; Cole, 2017b, 2018; Wright, 2017a, 2017b; Wright et al., 2017; Ausich, 2018). SE = "stem eucamerates", M = Monobathrida.

method to produce a dendrogram that represents ecological similarity among Bromide crinoids. A co-phylogenetic plot, also known as a tanglegram, was then used to visualize the similarities between ecological clustering and the phylogeny of Bromide fauna crinoids. We employed a Monte Carlo procedure to evaluate whether mismatches between ecological clusters and the phylogeny were statistically different from random. The Robinson-Foulds (RF) distance (Robinson & Foulds, 1981), a measure of similarity between tree topologies, was calculated for empirical data from the Bromide fauna and compared with a null distribution of RF distances calculated from 10,000 simulated tree topologies (Cole et al., 2019). Because only tree topology is taken into account when calculating RF distances, only the unscaled tree topology (i.e., a cladogram) was used for calculating the observed RF value between ecological clusters and the phylogeny.

To evaluate the phylogenetic structure of ecological similarity, we calculated phylogenetic signal of major ecomorphological characters. Ecomorphological characters considered were filtration fan density (Ω/cm^2), filtration fan area (in cm^2), and body size (calyx volume in cm^3). Both Pagel's Lambda (λ; Pagel, 1999) and Blomberg's K (Blomberg et al., 2003) were calculated for the three ecomorphological characters over the set of 500 time-scaled phylogenies.

4 Results

4.1 Species Richness and Trait Distributions Within Clades

There are several notable differences between the Bromide and Brechin assemblages relating to overall faunal composition and species richness of major taxonomic groups (Figure 3). First, flexibles are absent from the Bromide fauna, but are represented by three species in the Brechin. In fact, the *Cupulocrinus*-Flexibilia lineage is by far the most numerically abundant group within the Brechin fauna due to the large number of *Cupulocrinus humilis* specimens (Brett & Taylor, 1999; Cole et al., 2020). Diplobathrids and disparids are the most species-rich groups in the Bromide formation with 12 and 11 species, respectively, but richness of both groups decreases by about half in the Brechin fauna (Figure 3). By contrast, monobathrid camerates are represented by only a single nominal species in the Bromide but increase to seven species in the Brechin. For stem eucamerates, eucladids, and porocrinoids, species richness is similar, or in some cases identical, between faunas (Figure 3).

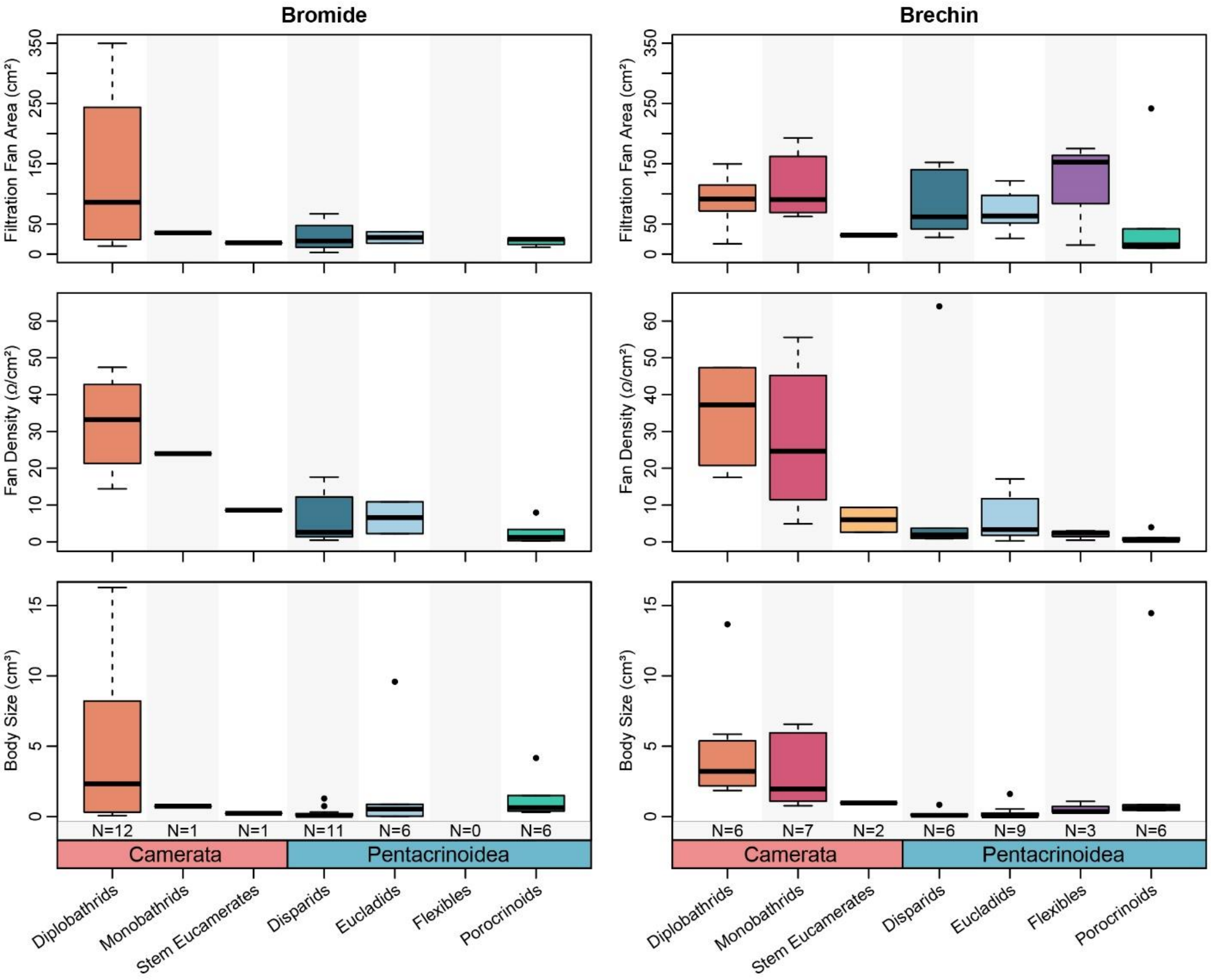

Figure 3. Boxplots comparing fan area, fan density, and body size for the Bromide fauna (left panels) and the Brechin fauna (right panels). Note that flexible crinoids are absent from the Bromide fauna. An outlier for Bromide diplobathrid body size is not show for plotting purposes (Body size = 27.57 cm^3). Known species diversity (N) of each group is given at the bottom of the panels.

Boxplots summarizing variation in filtration fan area, filtration fan density, and body size for clades within each fauna further highlight some substantial differences between faunas (Figure 3). Across all three of these measures in the Bromide fauna, diplobathrids consistently have the highest median values as well as the greatest range of variation. By contrast in the Brechin fauna, both monobathrids and flexibles surpass diplobathrids in terms median fan area, and many other groups also show notable increases in fan area. Although diplobathrids retain the highest median fan density and body size, both these measures expand dramatically in monobathrids and result in a range that exceeds that of diplobathrids (Figure 3).

4.3 Ecomorphospace Occupation

The first three PCO axes account for 36.36%, 17.28%, and 13.62% of variation in the dataset respectively, encompassing 67.26% of variation in total. Interpretations of PCO axes based on Spearman's rank correlations with traits are broadly comparable to those made of the Brechin fauna (Cole et al., 2019). The first PCO axis is significantly correlated with all but one trait (brachial width), suggesting PCO 1 strongly reflects aspects of both filtration fan density and size. The second PCO axis correlates almost exclusively with traits related to calyx and fan size, such as arm length, calyx volume, fan area. The third PCO axis is only significantly correlated with traits tied to feeding ecology, including the number of arm openings, arm branching, and traits tied to brachial and pinnule size. Notably, it is not significantly correlated with filtration fan density or total number of feeding appendages, which suggests PCO 3 reflects components of feeding ecology other than fan density, such as food size selectivity. Full results of correlations between traits and the first three PCOs are given in the supplemental materials (Figures S2-S4).

Taxa from the Bromide fauna fall into two distinct regions of ecomorphospace that are strongly divided along the first PCO axis and correspond to subclasses Camerata and Pentacrinoidea (Figure 4a). The only exception to this pattern is *Reteocrinus*, a member of a morphologically atypical camerate lineage, which plots within the pentacrinoid region of ecomorphospace. Within the regions occupied by subclasses, there is extensive overlap between subclades, especially for the pentacrinoids. The overall region of ecomorphospace occupation is also larger for pentacrinoids than for camerates.

Ecomorphospace occupation of the Bromide fauna is very similar to that of the Brechin fauna, in that camerates and pentacrinoids from the Brechin are divided into almost non-overlapping regions of

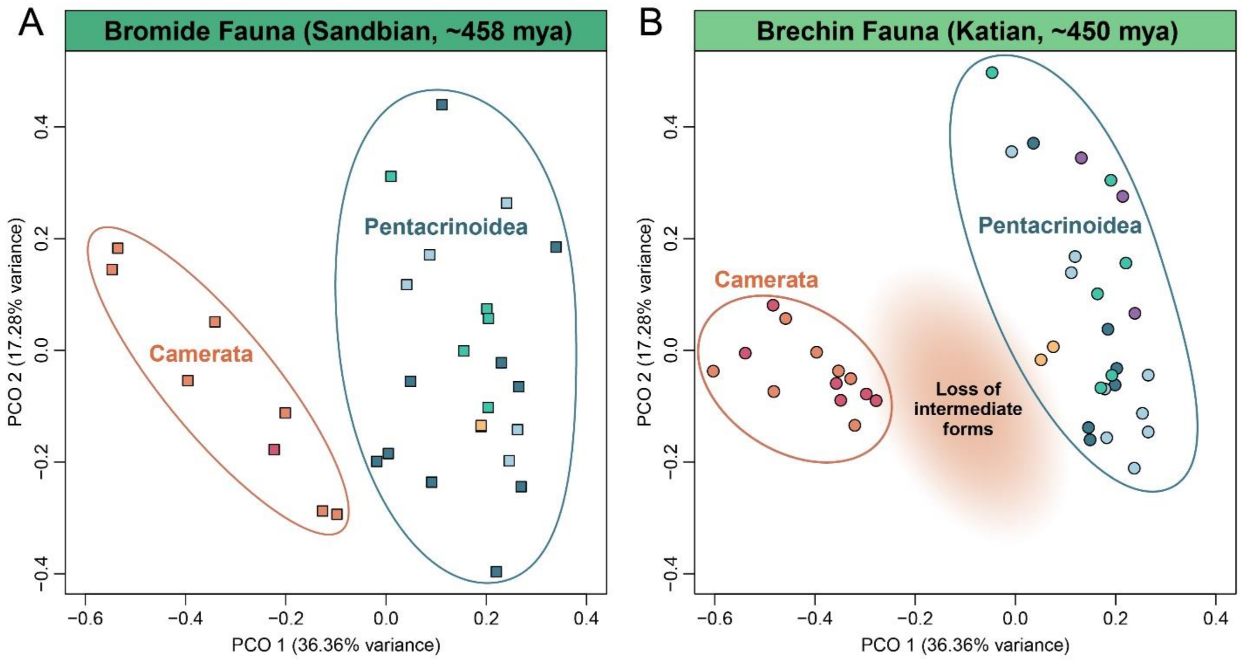

Figure 4. Ecomorphospace occupation of the Bromide (N=30) versus the Brechin (N=36) fauna including only taxa with at least partial arms. Colors correspond to groups in Figure 2.

ecomorphospace along the first PCO axis (Figure 4). Again, the only exceptions to this pattern are the stem eucamerate species belong to the genus *Reteocrinus*. Aside from the stem eucamerates, the separation between the camerate and pentacrinoid regions of ecomorphospace is much more pronounced in the Brechin fauna than in the Bromide, particularly along the first PCO axis (Figure 4). Further, both camerates and pentacrinoids from the Bromide occupy a large range of variation along the second PCO axis, whereas in the Brechin, camerates are restricted to a relatively narrow range along PCO 2 and pentacrinoids maintain a broad distribution along PCO 2.

Centroids for the Bromide at the scale of the whole fauna as well as for subclasses differ only marginally from those for the Brechin fauna (Figure 4). Between the Bromide and Brechin faunas, centroids for the faunas as a whole and for camerate and pentacrinoid subclasses shift slightly toward more negative values along PCO1, and shift toward more positive values along PCO2 (Fig 5a). Along PCO3, values increase very slightly for camerates, decrease slightly for pentacrinoids, but remain nearly identical between

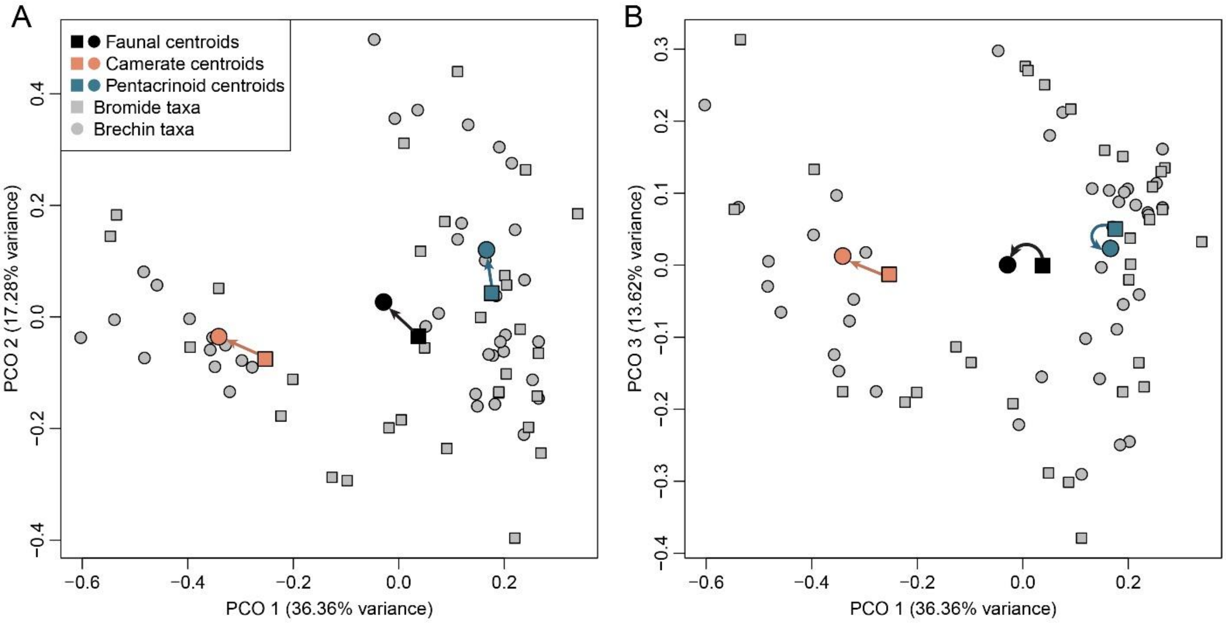

Figure 5. Change in centroid between the Bromide and Brechin faunas, as a whole and for subclasses Camerata and Pentacrinoidea across (A) PCO1 and PCO2, and (B) PCO1 and PCO3. Arrows show direction of centroid shifts from the Bromide (large squares) to the Brechin (large circles), and grey points give position of species from the Bromide fauna (squares) and Brechin fauna (circles).

faunas as a whole (Figure 5).

4.4 Disparity

Generally, disparity is greater among clades in the Bromide fauna than in the Brechin (Table 1). Porocrinoids are the only group that consistently goes against this trend, with all three disparity indices increasing from the Bromide to the Brechin. Disparity for all other subclades is consistently lower in the Brechin than the Bromide, regardless of the disparity index considered. For the two faunas as a whole, MPD increases slightly in the Brechin, presumably as a result of the major increase in porocrinoid disparity (Table 1). However, neither the increase in MPD between faunas, nor the decreases in SOV or SOR are statistically significant (*p*=0.54, 0.48, and 0.2, respectively; Figure S5).

Disparity patterns of major crinoid groups are further reinforced by evaluation of relative disparity

Table 1. Summary of disparity in the Bromide and Brechin faunas across three different disparity indices. Note that monobathrids and stem eucamerates are represented by a single taxon each in the Bromide fauna, and thus disparity indices cannot be calculated for these groups; flexibles are entirely absent from the Bromide fauna. Abbreviations: Subcl.=Subclass, O.=Order, Gr.=Grade, Parv.=Parvclass, Mag.=Magnorder, S.o.=Superorder.

	SOV	**SOR**	**MPD**
Bromide (whole fauna)	0.2091	4.6183	0.2263
Subcl. Camerata	0.1787	3.2023	0.1947
O. Diplobathrida	0.1768	2.8603	0.1881
O. Monobathrida	NA	NA	NA
Gr. Stem eucamerates	NA	NA	NA
Subcl. Pentacrinoidea	0.1690	3.9878	0.1902
Parv. Disparida	0.2057	3.8593	0.2129
Mag. Eucladida	0.1503	2.4120	0.1819
S.o. Porocrinoidea	0.0885	1.8334	0.1360
S.o. Flexibilia	NA	NA	NA
Brechin (whole fauna)	0.1818	4.2056	0.2323
Subcl. Camerata	0.0964	2.6141	0.1657
O. Diplobathrida	0.0908	2.0350	0.1499
O. Monobathrida	0.0436	1.3432	0.1306
Gr. Stem eucamerates	0.0074	0.2886	0.0296
Subcl. Pentacrinoidea	0.1299	3.4897	0.1772
Parv. Disparida	0.1140	2.2266	0.1708
Mag. Eucladida	0.0926	2.1379	0.1465
S.o. Porocrinoidea	0.1264	2.4521	0.1679
S.o. Flexibilia	0.0670	1.1796	0.1222

Table 2. Summary *p*-values for change in relative disparity between the Bromide and Brechin faunas. Statistically significant changes ($p < 0.05$) are denoted by asterisks. Clade abbreviations as for Table 1.

	SOV	**SOR**	**MPD**
Subcl. Camerata	0.131	0.245	0.178
O. Diplobathrida	*0.005	*0.001	*0.000
Subcl. Pentacrinoidea	0.350	0.251	0.068
Parv. Disparida	0.089	*0.003	0.051
Mag. Eucladida	0.206	0.654	0.383
S.o. Porocrinoidea	*<0.000	*<0.000	*0.014

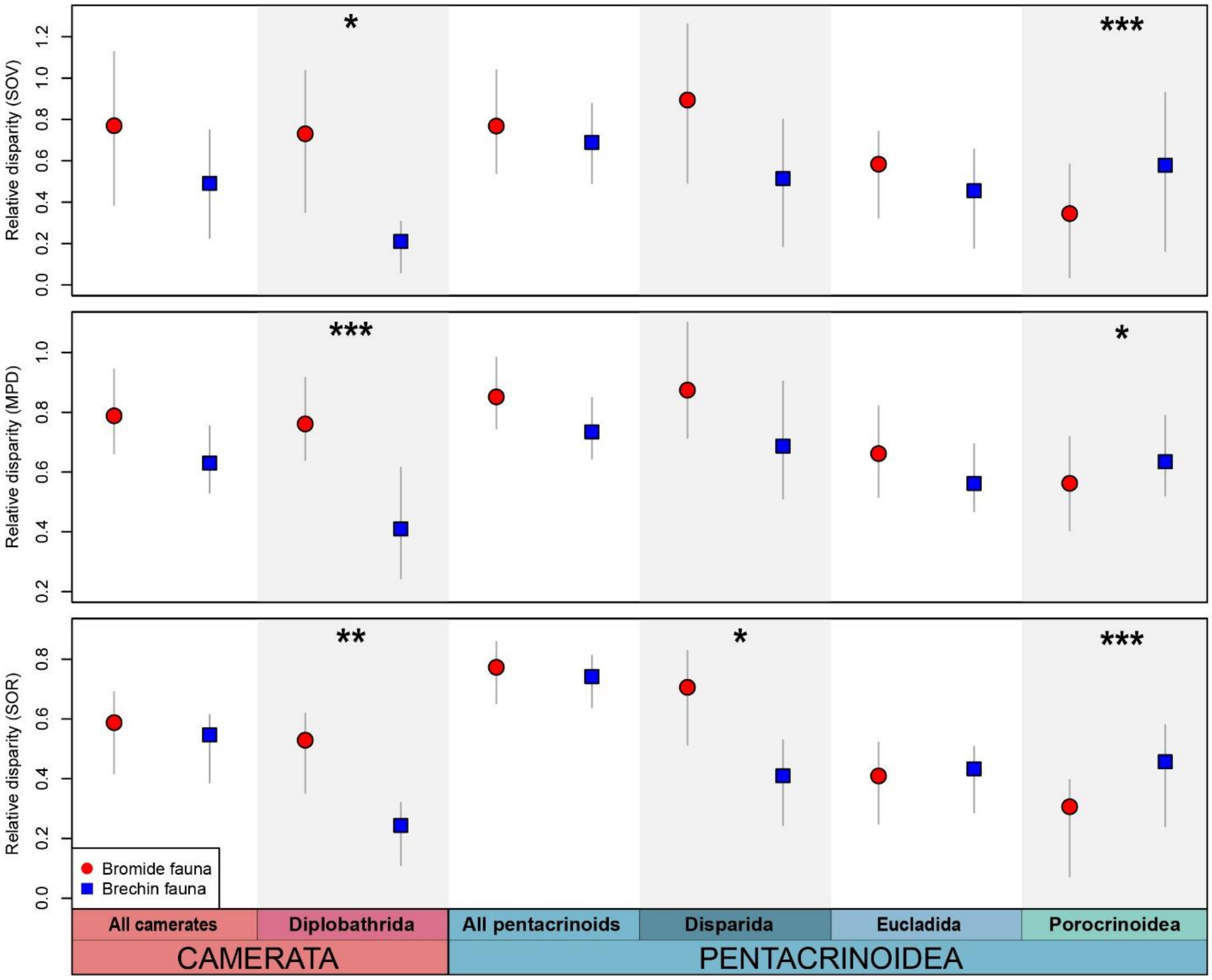

Figure 6. Relative disparity in the Bromide versus Brechin faunas. Relative disparity is calculated by dividing disparity of subgroups in each fauna by the total disparity of the fauna. Plotted points are means from 1000 bootstrap replications, and error bars reflect the 95% confidence intervals generated from bootstrap results. Disparity indices calculated are sum of variances (SOV), mean pairwise dissimilarity (MPD), and sum of ranges (SOR). Asterisks indicate groups for which changes in disparity between the Bromide and Brechin faunas are statistically significant (*$p < 0.05$, ** $p < 0.01$, ***$p < 0.001$).

patterns among subclades but also reveal additional dynamics that are masked at higher taxonomic levels (Figures 6-7). As with raw disparity measures, relative disparity decreases across all groups except for porocrinoids. Within the camerate subclass, the decrease is not significant for camerates as a whole but is statistically significant for diplobathrids across all three disparity indices (Table 2). Likewise, disparity decreases in the pentacrinoid subclass are not statistically significant for pentacrinoids as a whole or for eucladids. In disparids, the decrease in the SOR disparity index is statistically significant, but changes in

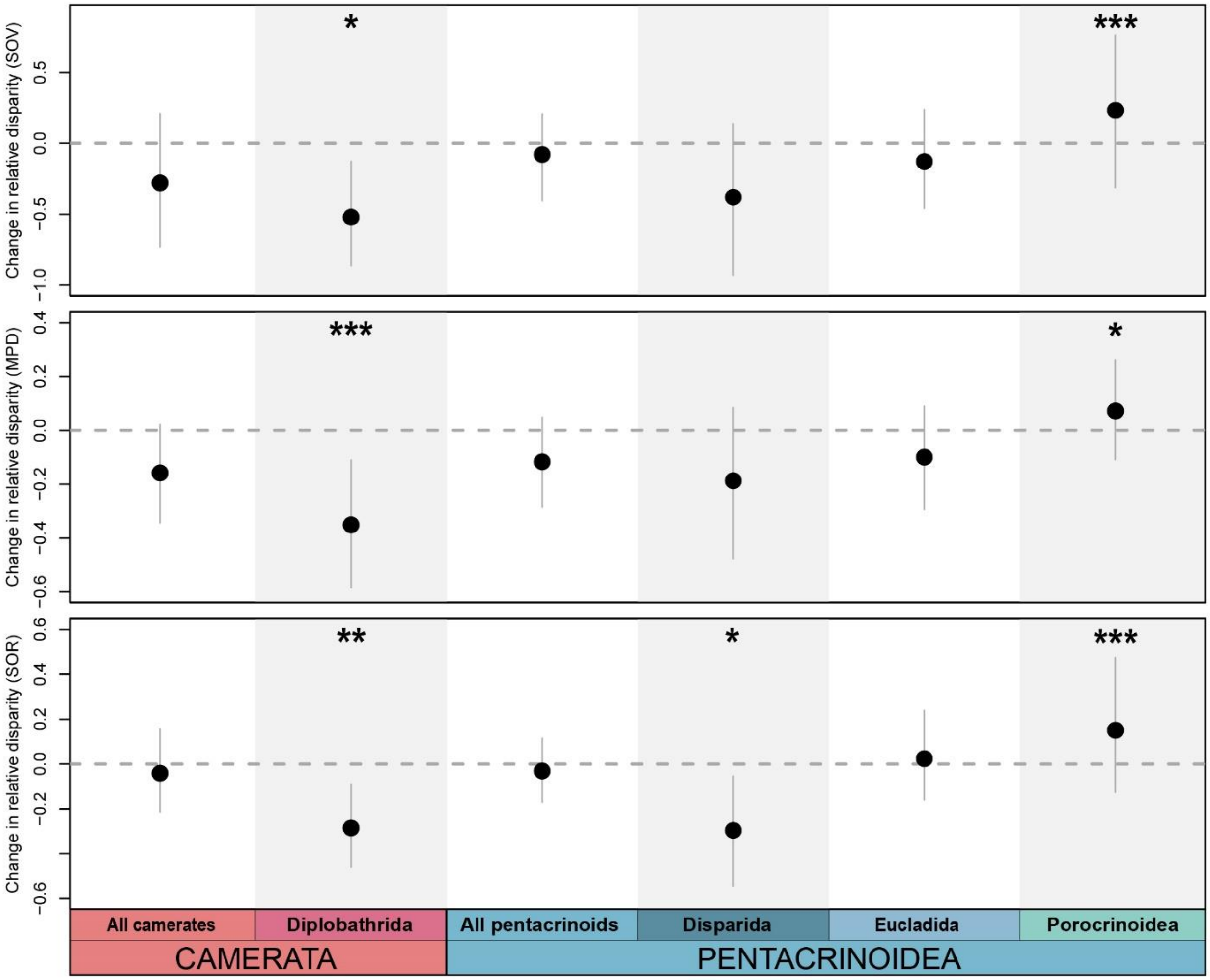

Figure 7. Change in relative disparity between the Bromide and Brechin faunas. Change in relative disparity is calculated by subtracting relative Bromide disparity from relative Brechin disparity (see Fig. 6 for relative disparity of each fauna). Values falling above zero (horizontal line) indicate increasing relative disparity through time, whereas those falling below zero indicate decreasing relative disparity. Asterisks indicating statistical significance of changes in relative disparity are as for Fig. 6.

the other two indices are not. Finally, the disparity increase recovered for porocrinoids is statistically significant across all three indices (Figures 6-7, Table 2).

4.5 Ecological Clustering and Phylogenetic Structure of the Bromide Fauna

Comparison of the phylogeny of the Bromide fauna (Figure 2) with the dendrogram resulting from the cluster analysis reveals many similarities between the two when visualized as a tanglegram (Figure 8).

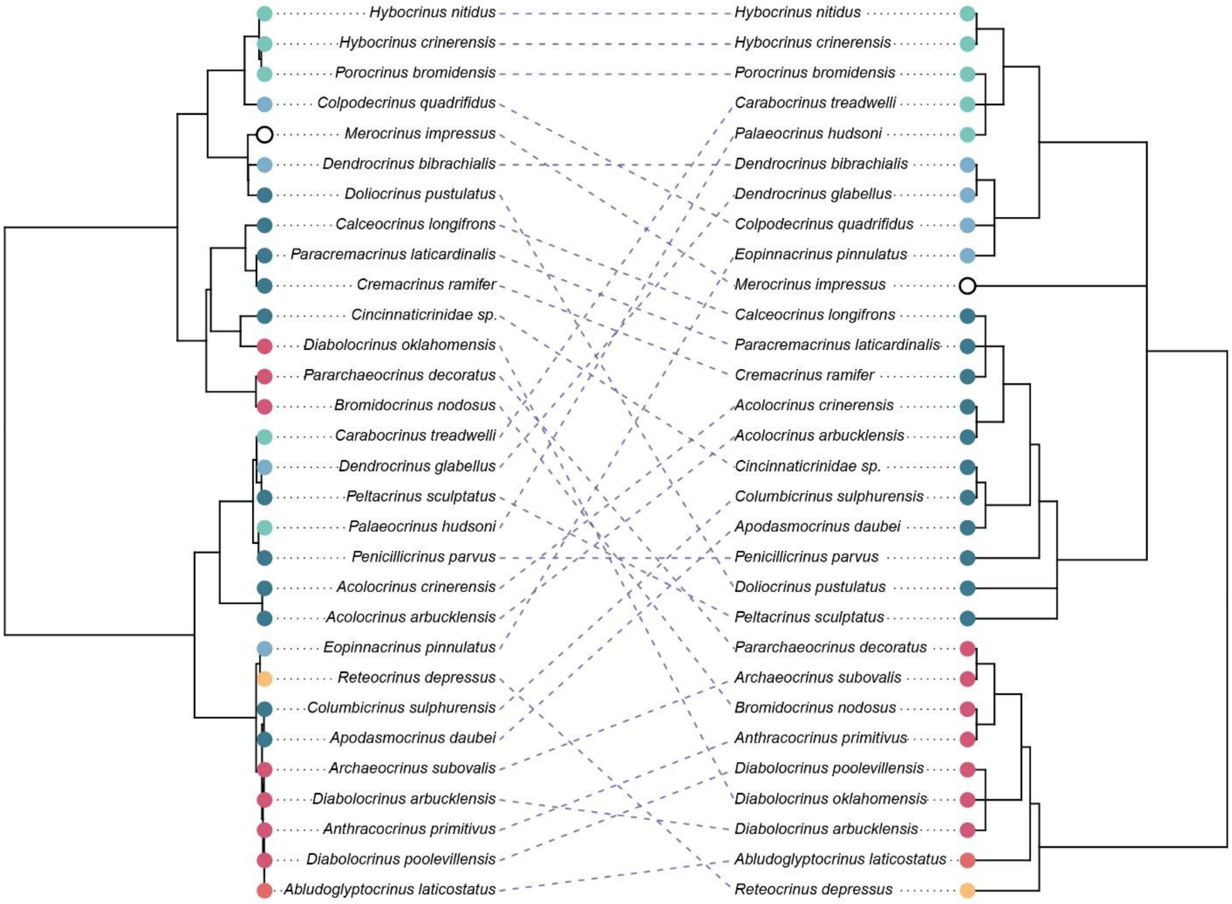

Figure 8. Tanglegram comparing ecological groupings (left) with the inferred phylogeny (right) of Bromide crinoids.

The Robinson-Foulds distance between the cluster analysis and the phylogeny was significantly shorter (p=0.043) than the distances calculated between the cluster analysis and a distribution of 10,000 random trees (Figure S6), indicating the ecological structure of the Bromide fauna is more similar to the underlying phylogeny that would be expected by chance. A similar pattern was previously recovered in the Brechin fauna (Cole et al., 2019).

The two phylogenetic signal measures, Pagel’s λ and Blomberg’s K, both produced similar results when calculated over a distribution of 500 time-scaled trees (Table 3, Figure S7). Significant phylogenetic signal was not recovered for body size or fan area using either of the phylogenetic signal measures, with

Table 3. Phylogenetic signal summary statistics calculated over a distribution of trees.

	Fan density	**Fan area**	**Body size**
Pagel's λ			
Mean λ	0.978	0.002	0.449
Mean *p*-value	$\mathbf{2.4x10^{-3}}$	0.991	0.089
% *p*-value <0.05	100%	0%	23%
Blomberg's *K*			
Mean *K*	1.259	0.442	0.591
Mean *p*-value	$\mathbf{1.8x10^{-3}}$	0.717	0.106
% p-value <0.05	100%	0%	40%

distributions centered well below 1 in all cases. By contrast, fan density had significant phylogenetic signal for both Pagel's λ and Blomberg's *K*, with significant *p*-values recovered for 100% of the trees (Table 3). These results differ somewhat from those previously recovered for the Brechin fauna, where both fan density and body size were found to express significant phylogenetic signal, but fan area did not (Cole et al., 2019). As a result, the main difference in phylogenetic structuring of these traits between faunas relates to body size, which occurs in the Brechin but not the Bromide.

5 Discussion

5.1 Niche Occupation in Upper Ordovician Crinoid Faunas

Overall, crinoid niche occupation is very similar between the Bromide and Brechin faunas. Although the present study combines the two assemblages for multivariate analyses, patterns of niche occupation recovered for the Brechin fauna are consistent with those from a previous investigation that considered the Brechin in isolation (Cole et al., 2019: Figure 4), indicating the same major axes of niche differentiation are being recovered in this study. These axes predominantly correspond to traits that are tied to many aspects of food particle capture like filtration fan density and food size selectivity (Ausich, 1980; Kitazawa et al., 2007) as well as body size. Within the Bromide fauna, the subclasses Pentacrinoidea and Camerata are clearly divided into two regions of ecomorphospace along the first PCO axis (Figure 4a); this division of ecomorphospace is also observed for the Brechin fauna (Figure 4b). The one exception to this division between camerates and pentacrinoids is *Reteocrinus*, which plots within the pentacrinoid region of ecomorphospace for both faunas. *Reteocrinus* is a morphologically divergent camerate that belongs to the “stem eucamerate” group (sensu Cole, 2017b) that is phylogenetically basal to orders Monobathrid and Diplobathrid. From an ecomorphological perspective, other camerates are united by the presence of pinnulate arms that results in high filtration fan density. By contrast, *Reteocrinus* has apinnulate arms, which is atypical for camerate crinoids and makes the ecomorphology of this genus more similar to that of certain pentacrinoid taxa (i.e., lower filtration fan density). Thus, its affinity within the pentacrinoid region of niche space is unique among camerate crinoids but predictable given its filtration fan morphology.

The strong division of ecomorphospace occupation at the subclass level indicates clade membership plays an important role in niche differentiation. Further, tree-based analyses of Bromide crinoids reveal ecological clusters are significantly correlated with phylogeny (p=0.04, Figures 8, S6). A similar result was previously recovered for Brechin crinoids (Cole et al., 2019), which indicates phylogenetic control on niche occupation is a recurring pattern among Upper Ordovician crinoid communities. Significant phylogenetic signal in terms of both Pagel’s λ and Blomberg’s K is recovered for filtration fan density of Bromide crinoids, but not for fan area or body size (Table 3, Figure S7). Additionally, the mean Blomberg’s K value for fan density is greater than 1, indicating fan density exhibits niche retention in addition to phylogenetic signal. Niche retention is a type of phylogenetic niche conservatism where traits of closely related species are more similar than would be expected given evolutionary models of diffusion through morphospace, which can suggest the trait(s) in question are subject to constraints or stabilizing selection (Blomberg et al., 2003; Cooper et al., 2010). By comparison, in the Brechin fauna evidence for niche retention was recovered for both filtration fan density and body size, but fan area did not exhibit phylogenetic signal. Combined, these results indicate that among Upper Ordovician crinoid communities, (1) filtration fan density consistently exhibits niche retention, (2) phylogenetic structuring of body size is variable, and (3) fan area is not controlled by phylogeny.

5.2 Crinoid Niche Evolution During the Upper Ordovician

Analyses characterizing patterns of niche occupation and phylogenetic structure reveal many similarities between the Bromide and Brechin faunas. However, further investigations of ecomorphospace occupation and ecological disparity at different taxonomic scales provide deeper insight into patterns of crinoid niche evolution during the Upper Ordovician. Although ecomorphospace occupation is broadly similar between the two faunas, separation between the pentacrinoid and camerate regions of morphospace increased in the Brechin paleocommunity, especially along the first PCO axis, due to an apparent loss of intermediate forms (Figure 4b). This left behind a noticeable gap in ecomorphospace and suggests increasing specialization and niche differentiation occurred within subclasses during this time. Despite the loss of these intermediate forms, shifts in centroid are relatively minor for the communities as a whole and for individual subclasses (Figure 5). In addition, the overall regions of niche space occupied by camerate and pentacrinoid subclasses both appear to shrink through time (Figure 4). This is further reflected by decreases in SOR, which here measures the total amount of trait space occupied over all PCO axes (Table 1). Other indices measuring different facets of ecological disparity (SOV, MPD) also decrease for both whole communities and subclasses, revealing that the dispersion of taxa around the centroid and the proximity of taxa to each other in niche space decrease through time as well, although these decreases are not statistically significant (Table 2, Figures 6-7). Combined, these results establish that ecological stasis is the dominant pattern apparent at high taxonomic scales over the study interval. In other words, the major ecological strategies were broadly conserved along clade membership lines. However, increasing separation of adaptive zones between subclasses (and within-group decreases in ecological disparity) suggest a trend of increasing niche differentiation across most major crinoid groups during the Late Ordovician, potentially driven by competition avoidance.

Although non-statistically significant decreases in ecological disparity are widespread at high taxonomic levels (e.g., whole communities and subclasses), they mask notable shifts occurring at lower taxonomic levels. In contrast to most groups that undergo only minor shifts in disparity, Porocrinoidea and Diplobathrida stand out as the only groups for which statistically significant changes in disparity occur through time across all disparity indices (Figures 6-7, Table 2). Porocrinoids are the only group for which a statistically significant *increase* in disparity through time is consistently recovered (Figures 6-7). This increase in porocrinoid disparity cannot be due to sample size alone, because equal numbers of porocrinoid taxa are sampled for both the Bromide and Brechin paleocommunities. Instead, the adaptive zone of porocrinoids appears to have expanded during this time, resulting in both a greater amount of occupied niche space and increased ecological distance between individual species. The most notable outlier responsible for the expansion of porocrinoid ecomorphospace is *Carabocrinus vancourtlandti*, which is particularly notable for its large body size. Diplobathrids are the only group for which a significant *decrease* in disparity through time is consistently recovered (Figures 6-7). Although diplobathrid richness decreases from twelve to six species in the communities compared, only seven of the Bromide species are included in disparity calculations due to preservational vetting, so richness/sample size alone is not sufficient to account for this significant drop in disparity. Additionally, the disparity of Brechin camerates as whole (monobathrids, diplobathrids, and stem eucamerates combined) is lower than that of Bromide diplobathrids, despite the fact that camerate species richness is far greater in the Brechin paleocommunity from the addition of many new monobathrid species. This suggests camerate niche occupation became increasingly constrained during the Upper Ordovician, with the ecology of newly evolved species deviating only minimally from that of ancestral forms. Further, it suggests diplobathrids were subjected to increasing ecological competition during the Upper Ordovician as monobathrids diversified within overlapping areas of niche space.

5.3 Transition Between the Early and Middle Crinoid Evolutionary Faunas

The evolutionary history of Paleozoic crinoids has been divided into the early, middle, and late Paleozoic Crinoid Evolutionary Faunas (CEFs), each of which were dominated by different groups of crinoids (Baumiller 1994; Ausich et al., 1994). The transition between the early and middle Paleozoic CEFs occurred around the close of the Ordovician and resulted in a shift from crinoid communities dominated by disparids, diplobathrid camerates, and hybocrinids to one characterized by monobathrid camerates, flexibles, and "primitive" cladids (Ausich & Deline, 2012). Traditionally, this major faunal transition is thought to be concomitant with the Late Ordovician mass extinction, an event that resulted in significant loss of crinoid genera at the end of the Katian stage due to glacially-induced, eustatic sea level fall (Peters & Ausich, 2008). As a result, the Late Ordovician mass extinction has been considered the trigger for this shift between evolutionary fauns, with heterogeneity in clades' extinction severity and post-extinction recovery leading to changes in dominance. However, there is also some evidence that faunal composition had begun to shift long before the end of the Katian (Ausich & Deline, 2012). Evaluation of trends in both richness and ecological disparity of Bromide and Brechin crinoid faunas provides further insight into ecological drivers of this transition during its early stages.

The taxonomic composition of the Bromide and Brechin faunas is broadly consistent with the expected early CEF makeup of abundant disparids, diplobathrid camerates, and hybocrinids. However, notable decreases in species richness of both diplobathrids and disparids occur over this interval, while both flexible and monobathrid crinoids—groups that define the middle CEF—increase in species richness (Figure 3). Similarly, the geologically younger Brechin fauna contains fewer hybocrinid species than the Bromide. Although smaller in magnitude, these patterns broadly parallel Late Ordovician to middle Silurian trends in increasing versus declining species richness that occur, especially within those crinoid groups that define the early and middle CEFs (Ausich & Deline, 2012). In addition, both diplobathrids and disparids experience statistically significant decreases in ecological disparity through time between the Bromide and Brechin faunas. This suggests decreases in overall ecological variation occurred within these groups, and niche evolution became increasingly constrained within shrinking adaptive zones.

Because ecological variation can serve as a major driver for speciation, it is possible that these decreases in ecological disparity reduced origination propensity within subclades , whereas the evolution and diversification of phylogenetically distant (but ecologically similar) groups may have increased competition. For example, diplobathrids and monobathrids experienced opposite diversification dynamics: diversity and ecological disparity both decreased in diplobathrids but increased in monobathrids. Because of the extensive overlap between monobathrid and diplobathrid niches, this likely resulted in increased competition pressure on diplobathrids. Overall, these changes in clade richness and ecological disparity between the Bromide and Brechin faunas provide evidence that the transition between CEFs may have begun during the Late Ordovician, well before the mass extinction event. Thus, instead of serving as the trigger of the early to middle CEF transition, the Late Ordovician mass extinction appears to have simply hastened and amplified a faunal transition that was already underway by the Katian (middle Late Ordovician). Large-scale faunal turnover in the absence of global-scale mass extinction is not unprecedented in the geological history of crinoids. Notably, the late Mississippian transition between the middle to late CEF did not coincide with a mass extinction, but instead was predominately driven by differences in rates of origination and extinction that were presumably caused by long-term ecological and environmental pressures (Kammer & Ausich, 2006; Sallan et al., 2011; Ausich & Kammer, 2013). Similarly, the Late Ordovician mass extinction may have acted to accelerate the long-term outcome of "background" turnover, at least for crinoids. These results suggest paleobiologists need not assume conflicts exist between tiers of ecological and evolutionary processes (Gould, 1985). Instead of investing in false dichotomies, comparisons between patterns at multiple taxonomic, temporal, and spatial scales may be used to determine when and how processes at acting at different hierarchical levels may hitchhike, reinforce, or obscure one another (Jablonski 2007). Only then can we build a more synthetic view of the evolution of clades and communities through time.

6 Conclusions

This study leverages the extensive amount of ecological data contained within the crinoid fossil record to evaluate patterns of community paleoecology, niche occupation, and niche evolution across the two most diverse and well-studied crinoid assemblages known from the Upper Ordovician: the Bromide fauna from the Sandbian of Oklahoma and the Brechin fauna from the Katian of Ontario. The same major axes of niche differentiation—fan density, food size selectivity, and body size—are recovered in the Bromide fauna as were previously recovered for the Brechin, suggesting these traits consistently delineated crinoid niches during the Upper Ordovician. Tree-based analyses of both the Bromide and Brechin faunas further reveal niche occupation was heavily influenced by phylogeny throughout the Upper Ordovician, with subclasses Camerata and Pentacrinoidea exhibiting almost non-overlapping adaptive zones. At a faunal-level scale, niche distributions did not change extensively over the study interval, indicating general ecological stasis over a time period of <5 million years. At the subclass level, however, crinoid niches became increasingly specialized and differentiated during this time, as revealed by increasing separation between regions of occupied niche space, decreases in total amount of niche space occupied, and increased species packing within occupied regions of ecomorphospace. Relatively minor decreases in ecological disparity also occurred at most higher taxonomic scales, suggesting a general trend of increased niche differentiation over the study interval. However, the patterns observed at higher taxonomic scales mask significant changes in disparity that occurred within porocrinoids, diplobathrids, and disparids, highlighting the importance of conducting these types of investigations at multiple scales in order to better capture dynamics occurring at different hierarchical levels.

Changes in both species richness and ecological disparity of major crinoid groups in the Bromide and Brechin faunas are consistent with the transition between the early and middle Paleozoic Crinoid Evolutionary Faunas. In particular, richness and disparity decreased in groups like diplobathrids and disparids but increased in groups like monobathrids and flexibles. These patterns reveal the shift between CEFs was underway by at least the Katian, well before the onset of the Late Ordovician mass extinction that has been considered the trigger of the early to middle CEF transition. Instead, these results indicate that the early to middle CEF transition initially began as a result of ecological drivers, and the Late Ordovician mass extinction served to intensify and/or speed up the timing of this transition. The role of ecological drivers in the generation and maintenance of macroevolutionary patterns are often obscured in the fossil record due to overprinting by environmental phenomena, such as mass extinction events. This study highlights the importance of using phylogenetic and other quantitative methods to study ecological phenomena in deep time, including identifying axes of niche differentiation, the control phylogeny exerts on niche occupation, time frames over which niches evolve versus remain static, and the role of ecology in major faunal transitions.

Acknowledgments

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Supporting Materials

Supplemental methods, figures, and all data and R scripts needed to reproduce analyses are available at: doi.org/xxxxxxx.

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