GEOLOGY | THE GEOLOGICAL SOCIETY OF AMERICA®

https://doi.org/10.1130/G51255.1

Manuscript received 23 March 2023
Revised manuscript received 30 May 2023
Manuscript accepted 6 June 2023

Published online 28 June 2023

Faunal provinciality in the Late Cretaceous Western Interior Seaway using network modeling

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ABSTRACT

The Western Interior Seaway (WIS) was historically divided into latitudinal faunal provinces that were taxonomically distinct from the adjacent Gulf Coastal Plain (GCP) and that shifted in space due to sea-level changes. However, no rigorous quantitative analyses using recent taxonomic updates have reassessed these provinces and their associations. We used network modeling of macroinvertebrate WIS and GCP fauna to test whether biotic provinces existed and to examine their relationships with abiotic change. Results suggest a cohesive WIS unit existed across the Campanian, and distinct WIS and GCP provinces existed in the Maastrichtian. Sea-level changes coincided with changes in network metrics. These results indicate that, while the WIS did not contain subprovinces in the Late Cretaceous, environmental factors influenced faunal associations and their communication over time.

INTRODUCTION

The Western Interior Seaway (WIS) and Gulf Coastal Plain (GCP) are characterized by a dense fossil record of marine invertebrates in the latest Cretaceous (ca. 100–66 Ma; Caldwell, 1974; Slattery et al., 2013), spanning 45° latitude, which experienced a wide range of environmental shifts. Fluctuating sea levels (Fig. 1C), for example, modified basin geometry and water-mass distributions, impacting marine life (e.g., He et al., 2005; Kauffman, 1984; Lowery et al., 2018). A restricted connection between the WIS and the open ocean affected oceanic conditions relative to the GCP and may have influenced biotic provinces (Kauffman, 1984, and references therein; Lowery et al., 2018). Biotic provinces are geographic regions characterized by distinct ecological associations. Previous studies of biotic provinces using fossil materials have attributed them to major climatic regions (e.g., Kocsis et al., 2021), associated shifting provinces with sea-level fluctuations (e.g., Kauffman, 1984), compared spatiotemporal influences on taxonomic association patterns (e.g., Kiel, 2017), and observed changes in provinciality relative to taxonomic loss (e.g., Kocsis et al., 2018).

Quantification of biogeographic patterns can therefore shed light on macroecology over evolutionary time. Kauffman (1984) described three significant biotic incursions during transgressions based on changes to WIS subprovinces (Fig. 1A). These subprovinces, determined using percent endemism of mollusk records analyzed from 1960 to the 1980s, are the (1) Northern Interior, (2) Southern Interior, and (3) Central Interior subprovinces (Kauffman, 1984). Another identified faunal province was the Gulf and Atlantic Coastal Plain subprovince. However, delineation of these paleobiogeographic provinces and their changes through time was based on qualitative assemblages limited by the available fossil data (Kauffman, 1984, and references therein). Analysis of WIS provinciality using current fossil data will improve the validity of these interpretations.

Network modeling analysis of faunal provinces is a novel approach (Kiel, 2016, 2017) to quantifying faunal similarity across spatiotemporal units. Using a well-vetted database of over 33,000 fossil occurrences from the WIS and the GCP, we used this approach to reevaluate WIS provinciality in the Campanian and Maastrichtian Stages of the Late Cretaceous. While previous studies have used network analysis to explore provincialism in fossil taxa (Kiel, 2016, 2017; Rojas et al., 2021; Muscente et al., 2018; Kocsis et al., 2018, 2021), none has applied the technique to a geochemically unique, restricted ocean system characterized by over 100 yr of dedicated sampling. This research may also inform general patterns of Earth-life interaction over long time scales (e.g., the nature of faunal variation through time and space) and serve as a foundation for future WIS/GCP investigations.

METHODS

Records of marine invertebrates from the Campanian and Maastrichtian intervals of the WIS and the GCP were compiled from digital databases, including the Paleobiology Database (25 August 2021 download) and iDigBio (30 August 2021 download), and from museum collections at the Black Hills Institute and U.S. Geological Survey–Denver (Cobban Collection), and from the Mackenzie (2007) thesis database (Table S1 in the Supplemental Material[1]). Taxa were binned into the early, middle, and late Campanian and the early and late Maastrichtian stages (Fig. 1B; Fig. S1). Localities were converted to paleocoordinates within a 60 km grid for analysis; nodes with fewer than three unique taxa were removed. The vetted database was analyzed prior to network modeling to determine fundamental sources of taxonomic and spatial bias that should be considered during network interpretations (Table S2; Figs. S2–S9).

Faunal provinces were delimited for substages individually and for the complete database (combined substages) using threshold weighted networks (Kiel, 2016) in the EDENetworks software (Table S3; Figs. S10–S20; Moalic et al., 2012; Kivelä et al., 2015; Kiel, 2016). Network components that were discon-

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[1]Supplemental Material. Taxonomic database, detailed methods and results, and references used for taxonomic vetting. Please visit https://doi.org/10.1130/GEOL.S.23519055 to access the supplemental material, and contact editing@geosociety.org with any questions.

CITATION: Purcell, C., Scuderi, L., and Myers, C., 2023, Faunal provinciality in the Late Cretaceous Western Interior Seaway using network modeling: Geology, v. 51, p. 839–844, https://doi.org/10.1130/G51255.1

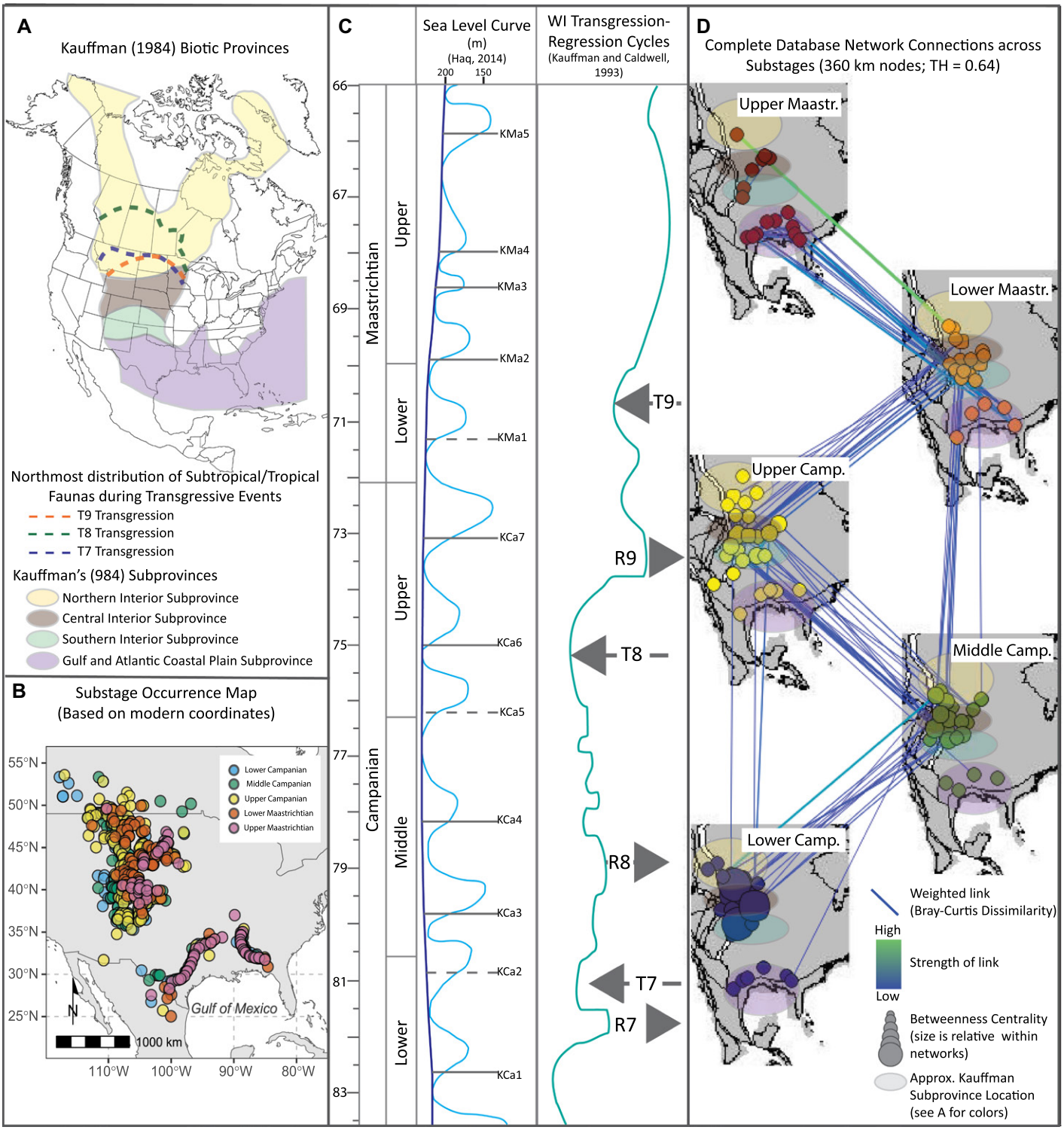

Figure 1. (A) Previously defined subprovinces and northernmost extent of tropical/subtropical faunas during transgressions, modified from Kauffman (1984). (B) Occurrence map of data from this study. (C) Global and regional sea-level curves with major transgressive-regressive (T-R) events. (D) Complete database for 360 km network with Kauffman's subprovinces indicated. Modified version of this figure with additional biostratigraphic and isotopic data is available as Figure S30 (see text footnote 1). Camp.—Campanian; Maastr.—Maastrichtian; TH—threshold.

nected at and below a network-specific threshold identified by EDENetworks, known as the percolation point, were interpreted as representing distinct "community" groups (Newman, 2012) or faunal provinces. General patterns in network connections across all substages together were assessed using coarser spatial aggregations of the data, and minor network components were assessed for spatiotemporal consistency (Figs. S21–S23).

Average network clustering coefficient (CC) values, indicative of network organization ranging from 0 (no cluster) to 1 (fully connected cluster), were compared with a null model of randomized networks to determine if the topology was more or less clustered than a random distribution (Table S4; Kiel, 2016). Link weights, or the degree of dissimilarity between

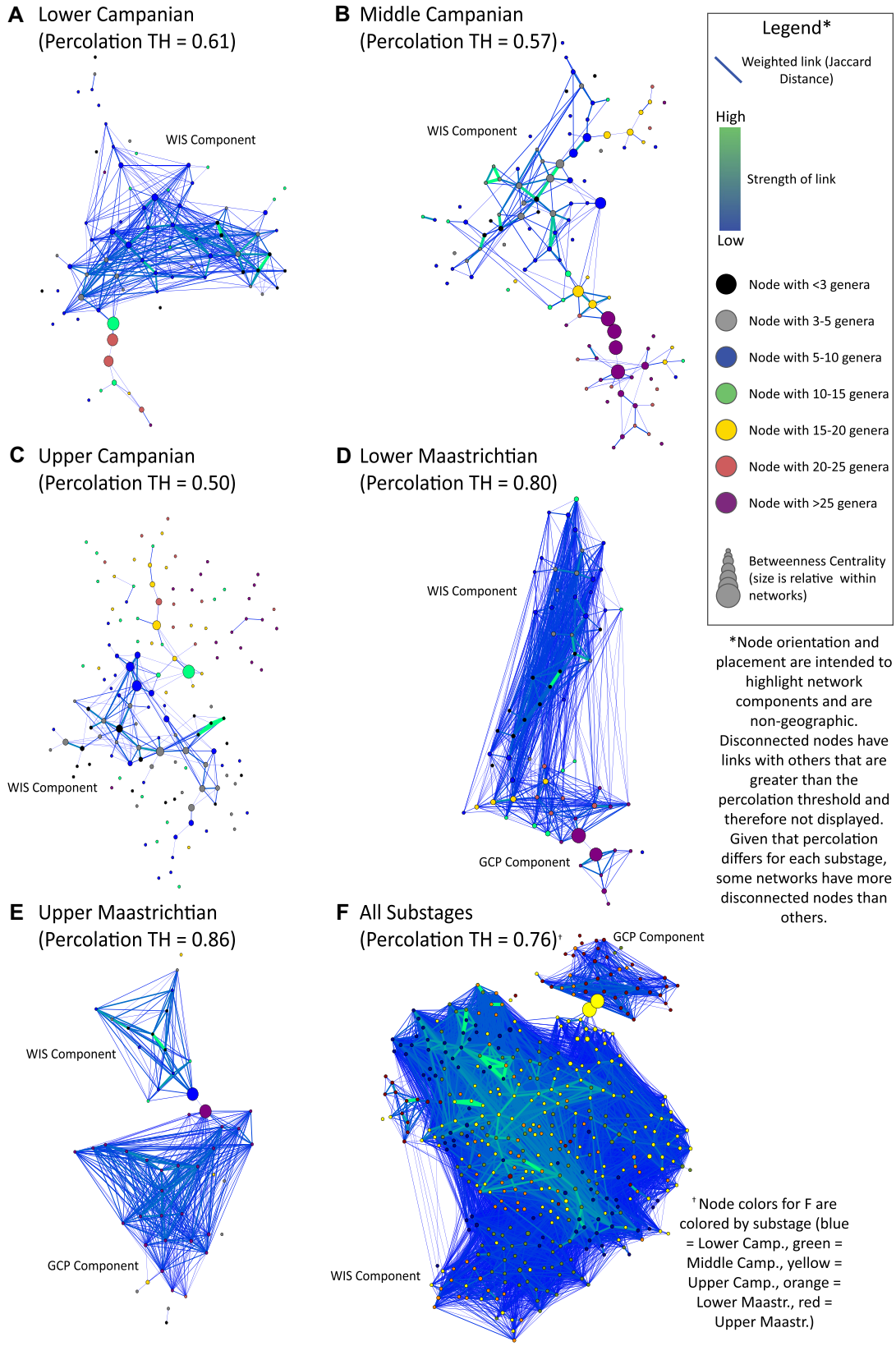

Figure 2. Substage and complete database networks at percolation points. WIS—Western Interior Seaway; GCP—Gulf Coastal Plain; Camp.—Campanian; Maastr.—Maastrichtian; TH—threshold.

nodes, and betweenness centrality (BC), a measure of the degree to which a node acts as a geographic connection between regions, were averaged by 5° paleolatitudinal bins for comparison (Figs. S24–S26). Link weights were also binned by geographic distance to test for correlation between faunal dissimilarity and distance (Table S5; Fig. S27). Given the latitudinal overlap between the WIS and GCP around 35°N, we separated the data by major components and evaluated link similarity between the two regions independently (Table S6; Fig. S28). Sampling bias influence on network communication was assessed by binning average betweenness centrality (BC_{ave}) by generic richness as a proxy for

sampling effort (Fig. S25) and using a minimum spanning tree (MST) algorithm (Fig. S29). Additional explanation of methods is provided in the Supplemental Material (see footnote 1).

RESULTS AND DISCUSSION

WIS versus GCP Provinces

The presence of a single faunal province in the WIS was supported by all network permutations and subsequent analysis (Fig. 2). This province was geographically consistent with the WIS (Fig. S21), was maintained at all threshold levels (Figs. S10–S15), did not contain spatiotemporally consistent minor components (Figs. S22–S23), and was faunally distinct from GCP grid cells (Fig. S21). For Maastrichtian substages, which contained more GCP fossil occurrences relative to the Campanian, a well-supported GCP faunal province was observed (Fig. 2; Figs. S16–S19). This distinct GCP province was supported by the full database network as well (Fig. S20). Network randomization comparisons demonstrated that these results were nonrandom and likely reflect biogeographic patterns (Table S4; average CC >3 standard deviations from mean). They did not result from sampling bias based on comparisons with spatial cluster analysis (Figs. S5–S9), BC comparisons (Fig. S25), and MST (Tables S7–S12). Thus, our quantitative analysis does not support the existence of WIS biotic subprovinces but does support a distinct GCP province in the Maastrichtian (Kauffman, 1984).

The WIS and GCP provinces may have resulted from geochemical and bathymetric changes across the transcontinental arch (TA), which may have acted as a bathymetric high between the regions (He et al., 2005; Lowery et al., 2018, and references therein), rather than resulting from latitudinal factors (e.g., temperature). Geochemical studies have found evidence for nonnormal marine conditions in the WIS, including low salinity or brackish conditions (Cochran et al., 2003; Dennis et al., 2013; Fricke et al., 2010) and lower $\delta^{18}O$ values of seawater than in the open ocean (Fricke et al., 2010; Petersen et al., 2016). There is also evidence for stratification within the WIS during the Campanian and Maastrichtian, produced by mixing water masses (He et al., 2005; Lowery et al., 2018). These factors could have created a habitat barrier between the GCP and WIS, facilitating provincialism. The WIS fauna may have been more tolerant of nonnormal conditions, supported by a lack of abundant reef-building and reef-associated taxa (Gill and Cobban, 1966; Caldwell, 1968; Kauffman, 1984; Kauffman and Caldwell, 1993).

The lack of latitudinally defined provinces within the WIS is unsurprising given a flattened latitudinal temperature gradient in the Cretaceous greenhouse (Mannion et al., 2014; Super et al., 2018). However, evidence for different water-mass distributions and salinity/temperature gradients has long been associated with latitude and faunal gradients in the WIS (Fisher et al., 1994; Slingerland et al., 1996; Longman et al., 1998; Elderbak and Leckie, 2016; Lowery et al., 2018). During much of the study interval, a cool water mass circulated south through the WIS from the northern connection with Greenland and northern Europe, interacting with the northward-moving warm water mass from the Tethys Ocean, forming a counterclockwise gyre (Steel et al., 2012; Lowery et al., 2018). However, no evidence for provinces matching these water bodies was observed in our results. Instead, this gyre could have contributed to faunal homogenization despite ocean stratification or abiotic gradients. Further, the unique geochemical nature of the basin may have encouraged WIS incumbents and generalists to flourish over specialists or invaders. Data set differences, including improved sampling and the lack of foraminifera in this study, may have hindered observation of Kauffman's (1984) subprovinces, though this requires further investigation. Indeed, the potential for along-seaway variation within specific WIS faunas, as observed by previous authors (i.e., Sohl, 1971; Jeletzky, 1971, etc.), was not tested by this analysis, which tested for discrete clusters of faunal assemblages.

Decreasing Faunal Similarity and Sea-Level Fall

Network dissimilarity values increased through time (i.e., decreasing similarity), particularly in the WIS province, based on average link values per substage (Table 1); in contrast, the GCP province showed increasing similarity through the Maastrichtian (Table S6). Bathymetric and geochemical changes coincided with these shifts, suggesting a potential relationship. The WIS gyre may have promoted mixing of water masses, WIS dispersal, and mixing with the GCP (Fisher et al., 1994; Slingerland et al., 1996; Longman et al., 1998; Elderbak and Leckie, 2016). However, falling sea levels likely impacted circulation patterns, water-mass dynamics, and geochemical and environmental gradients (e.g., nonnormal salinity, nutrient load), which would have limited WIS migration and thereby insulated existing fauna from outside invasion (Cochran et al., 2003; He et al., 2005; Fricke et al., 2010; Petersen et al., 2016). Shallowing along the TA may also have created a geographic barrier between the WIS and GCP as early as the late Campanian (Lehman, 1987; Lowery et al., 2018, and references therein).

Dampened circulation and salinity gradients may have also caused declining faunal similarity within the WIS alone, as evidenced by lower average faunal similarity within each substage network across time (Table S6). Below $\sim$1000 km, faunal similarity comparisons showed weak correlation between distance and link weight (Fig. 3; Fig. S28), indicating only a slight decline in similarity over distance within a substage, despite decreasing similarity though time. Sedimentary evidence for tidal circulation influences through at least the middle and late Campanian (Steel et al., 2012) suggests continued circulation and mixing that could have promoted homogenization. Distance comparisons for the WIS and GCP components individually produced similar patterns (Fig. S28), indicating that these results were not basin specific. Additional study of WIS oceanography is needed to confidently assess the potential influence of late Campanian oceanographic changes.

While faunal connectivity within the WIS and between the WIS and GCP decreased over time, Maastrichtian average link weights showed that GCP faunal similarity increased (Table S6; Fig. S21). As a longitudinally broad, open ocean–facing province, the GCP would have experienced normal marine conditions, less latitudinal variation, and the potential for long-distance dispersal, potentially supporting faunal similarity across the Maastrichtian by reducing the endemism. Within the WIS province, from the early Campanian to the early Maastrichtian, network connections remained strong between substages across time, indicating weak faunal turnover in the region even as faunal similarity decreased, until the late Maastrichtian, when

TABLE 1. AVERAGE/MEDIAN LINK WEIGHTS WITHIN SUBSTAGES AND BETWEEN DIFFERENT SUBSTAGES

Substage link weights (mean ± 95% CI/median)	Substages link weight comparisons (mean ± 95% CI/median)				
	Lower Camp.	Middle Camp.	Upper Camp.	Lower Maastr.	Upper Maastr.
Lower Camp. (0.78 ± 0.004/0.80)	–	0.83 ± 0.002/0.84	0.85 ± 0.002/0.86	0.87 ± 0.003/0.88	0.96 ± 0.001/0.98
Middle Camp. (0.79 ± 0.002/0.82)	–	–	0.83 ± 0.001/0.85	0.86 ± 0.002/0.88	0.95 ± 0.001/0.96
Upper Camp. (0.82 ± 0.002/0.84)	–	–	–	0.86 ± 0.002/0.88	0.95 ± 0.001/0.96
Lower Maastr. (0.83 ± 0.004/0.86)	–	–	–	–	0.93 ± 0.003/0.95
Upper Maastr. (0.85 ± 0.006/0.95)	–	–	–	–	–

Note: 95% confidence intervals (CI) of the mean are indicated. Camp—Campanian; Maastr—Maastrichtian.

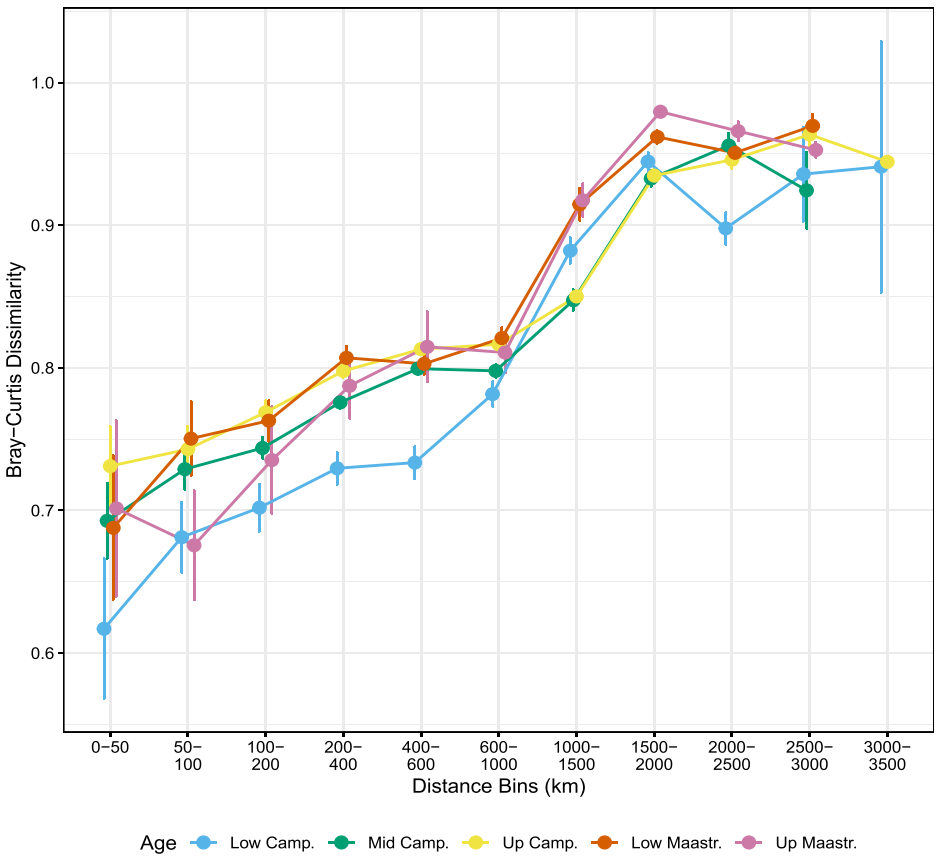

Figure 3. Plots of average link weights within geographic distance bins (World Geodetic System 1984 [WGS84] ellipsoid). Bars indicate 95% confidence intervals. Camp.—Campanian; Maastr.—Maastrichtian.

the province became disconnected from previous iterations (Fig. 1D). The late Maastrichtian disconnect with previous iterations matches expectations of oceanic changes that would have decreased dispersal and habitat homogenization for WIS taxa (Elderbak and Leckie, 2016; Steel et al., 2012; Fisher et al., 1994; Longman et al., 1998; Slingerland et al., 1996).

Latitudinal Patterns

Results do not support latitude-based faunal provinces, despite changes in network metrics across latitudes (Fig. 2). However, the region of highest average faunal similarity (HFS) shifted 5° north from the 40°N–45°N bin to the 45°N–50°N bin across the R9 regressive event at the end of the middle Campanian (Fig. 1C; Kauffman and Caldwell, 1993). Prior to the R9 regression, sea levels were more stable, and the HFS region was fixed (Fig. S26). This HFS shift appears to reflect biogeographic patterns and is unlikely to be a product of data distributions given that faunal similarity compared to geodesic distance remained relatively stable over <1000 km (Fig. 3). The geodesic distance covered by a 5° latitudinal bin in this region is ~555 km, and the distance covered by two bins is ~1110 km. Thus, similarity begins to strongly decrease over distances greater than 10° latitude. This suggests a regional control on network metrics. If faunal similarity only depended on distance, then similarity would show a uniform pattern across latitude rather than the observed peaks and dips (Fig. S25). Therefore, an HFS region that shifts parallel to sea level likely represents a distinct biogeographical component influenced by oceanographic changes.

Similarly, although the region of highest BC_{ave} (indicating highest faunal communication between regions) primarily occupied northern latitudes (40°N–60°N), it shifted south from the middle to late Campanian (Fig. S25). This region of highest communication may indicate intermediate habitat (Kiel, 2016), uniformity of conditions (i.e., water depth), or currents that transported taxa long distances (Lowery et al., 2018). The latter would support larval migration of marine taxa, especially those with long planktonic larval stages (Nickols et al., 2015). However, more specific bathymetric, geochemical, and sedimentological evidence for habitat conditions is sorely needed, but is outside the scope of this analysis. The region of highest BC_{ave} may also correspond to Kauffman's (1984) mixing zone. Despite the shifts in highest BC_{ave}, all networks showed a minor or major peak in the central WIS (45°N–50°N; Fig. S25) corresponding with a region of mixing water masses (Lowery et al., 2018). This supports oceanographic or habitat controls on fauna in the WIS.

CONCLUSIONS

Network analysis of the Late Cretaceous WIS and GCP regions supports a single biogeographic province throughout the Campanian and an independent GCP province in the Maastrichtian with decreasing faunal connectivity through time. This contrasts with Kauffman's (1984) original division of the region into four "subprovinces." Decreasing faunal similarity over the study interval is consistent with oceanographic and geochemical changes that restricted the WIS and exacerbated nonnormal marine conditions. Though no overarching relationship between faunal associations and latitude was observed, regional movement of the HFS and highest BC_{ave} values suggest that environmental changes (i.e., falling sea levels and associated effects) were the primary control on biogeographic connections. This study also provides further evidence for the utility of network modeling to quantitatively characterize paleobiogeographic trends on evolutionary time scales relative to major environmental shifts, representing an important analytical tool in modern tests of marine biogeographic change under predicted global change.

ACKNOWLEDGMENTS

Thanks to Timothy Nagle-McNaughton, Steffen Kiel, and Xi Gong for helpful discussions and assistance with methods and visualization. Thanks also go to Steve Holland and two anonymous reviewers, whose comments improved this manuscript. C. Purcell acknowledges support from National Science Foundation (NSF) grant 2021744; C. Myers acknowledges support from NSF grant 1924807.

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Printed in the USA