Summer 6-26-2018

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Recommended Citation

Carrier, Agathe E.. "Investigation of molluscan survivorship across the Cenomanian-Turonian Boundary Event using ecological niche modeling." (2018). https://digitalrepository.unm.edu/eps_etds/233

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BY

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THESIS

Submitted in Partial Fulfillment of the
Requirements for the Degree of

Master of Science

Earth and Planetary Sciences

The University of New Mexico
Albuquerque, New Mexico

July 2018

Acknowledgements

I would like to thank my thesis advisor, Dr. Corinne Myers, for the great introduction to all things paleobiology, the guidance through graduate school, and the endless advice on life after Master’s. I would also like to thank Dr. Maya Elrick and Dr. Jason Moore, both of whom served on my thesis committee and provided guidance and expert knowledge during my graduate work. All three are not only dedicated scientists but also wonderful teachers, and I have learned so much from them during my time at UNM.

INVESTIGATION OF MOLLUSCAN SURVIVORSHIP ACROSS THE CENOMANIAN-TURONIAN BOUNDARY EVENT USING ECOLOGICAL NICHE MODELING

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ABSTRACT

In the beginning of the Late Cretaceous, the Western Interior Seaway experienced the effects of a global ocean anoxic event (OAE2, or the Bonarelli Event) across the Cenomanian-Turonian (C/T) boundary (~94 Ma). This event resulted in major environmental and biological disturbances creating significant biotic turnover, with recent research suggesting near mass extinction levels in some clades. In this study we utilize a paleobiological application of a modern ecological modeling technique (PaleoENM), to test whether changes in species' survivorship and distribution patterns across this event relate to changes in their predicted suitable habitat area and abiotic niche dimensions.

Results suggest that survivorship across the C/T is not strongly correlated with available suitable habitat. Additionally, a quarter of the taxa demonstrate significant abiotic niche stability across the C/T. These findings are consistent irrespective of higher taxonomic groups (i.e., genera), which suggests taxon-specific responses to environmental changes at the macroevolutionary scale of this study. This research supports the importance of biogeography in understanding and predicting species longevity and the maintenance of biodiversity. Application of the general principles described here to modern biological systems perturbed by human-induced anoxia may positively inform conservation efforts and predictions of modern extinction dynamics.

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1. Introduction

Mounting evidence supports an emerging global biodiversity crisis, with some suggesting an impending sixth mass extinction (Wake and Vredenburg 2008; Barnosky et al. 2011; Ceballos et al. 2015). Due to increasing human population size, habitat destruction and fragmentation, and the global spread of invasive taxa, many native species are losing large areas of available suitable habitat. This has led to a surge in rates of extinction that far exceed constant background rates (Nott et al. 1995; McCallum 2007; Barnosky et al. 2011; Ceballos et al. 2015). Already, there have been 800+ species extinctions since 1500 AD (IUCN Red List 2017). Further, over 5000 modern species are designated critically endangered with another 20,000+ either endangered or vulnerable (IUCN Red List 2018). Although much of the current crisis can be attributed to human predation and pollution, the long-term threats to global biodiversity are quite similar to those faced by species in the past – e.g., increased temperature, oceanic anoxia, ocean acidification, and habitat destruction and fragmentation.

Faced with this biodiversity crisis, research in the past few decades has turned to novel ways of predicting species' extinction potential in the near future (e.g., Miller and Botkin 1974; McDonald and Brown 1992). Ecological niche modeling (ENM) is a commonly used technique in modern biodiversity research that estimates species' abiotic niche requirements and applies these estimations to predict species' responses to future environmental changes. This technique relies on modern species distributions and assumes abiotic niche stability (i.e., no adaptation or other change in abiotic niche dimensions) through time (Peterson 2011; Stigall 2011; Veloz et al. 2012). However, investigation of biotic responses to changing environments can be difficult for several reasons. First, modern species distributions may not incorporate the full range of environmental conditions in which a species may thrive. That is, the current distribution reflects the "existing niche" of Peterson et al. (2011), which may only characterize a small portion of the "fundamental niche" of the species (*sensu* Hutchinson 1957; Peterson et al. 2011; Myers et al. 2012). Second, these studies are often biased because both laboratory and field experiments occur at much smaller spatiotemporal scales (decades) than evolutionary responses (Kyrs to Myrs) (Hönisch et al. 2012; Lima-Ribeiro et al. 2017). As a result, it is unclear whether or under what conditions species show niche stability over long time scales (Myers and Saupe 2013). For example, research in the fossil record suggests that patterns of niche stability may be different if the species is facing environmental change alone versus changes in biotic interactions via species invasions (Stigall 2014). Thus, paleobiological research that incorporates the full spatial and temporal distribution of species has the potential to uncover general principles surrounding how species respond to environmental change, which may improve upon future predictions based on the modern record.

ENM is a multivariate statistical modeling technique used to estimate a species' fundamental niche (*sensu* Hutchinson 1957), defined as the collection of resources and environmental conditions that allow a species to survive and reproduce (Soberón and Peterson 2005; Soberon and Nakamura 2009; Peterson et al. 2011). More recently, ENM has been applied to the fossil record to test hypotheses of survivorship, distribution change, and niche stability in deep time (see Nogués-Bravo 2009; Saupe et al. 2014 for examples of ENM application into the recent past via climate models; Stigall 2012; Brame and Stigall 2014; Myers et al. 2015 for deep time ENM application via sedimentary proxies). PaleoENM is the application of ENM methods to the deep time fossil record using sedimentological and geochemical proxies for environmental conditions (Myers et al 2015). This differs from other applications of ENM in the more recent fossil record, which use available climate models to apply traditional ENM analysis (Braconnot et al. 2007; Nogués-Bravo 2009; Haywood et al. 2011; Saupe et al. 2014; Lima-Ribeiro et al. 2015). In this study, we utilize PaleoENM methods to test molluscan responses to an environmental perturbation in the Western Interior Seaway (WIS) during the Late Cretaceous. Our goal is to test whether availability of suitable abiotic habitat influences species' survivorship.

The Cenomanian-Turonian (C/T) boundary is marked by a global period of ocean anoxia (OAE2). Here we test how changes in abiotic habitat before and after OAE2 affected mollusks' specific and generic niche dynamics. We test three hypotheses: (1) taxa that go extinct across the boundary experience significant reduction of predicted suitable habitat area, whereas surviving taxa experience no change or expansion of predicted suitable habitat area; (2) surviving taxa demonstrate niche stability (no change in abiotic niche dimensions) across the environmental perturbation of OAE2; and (3) genus-level abiotic niches are reasonable proxies for the abiotic niche dimensions of their constituent species.

The first hypothesis tests whether extinct taxa experienced substantial reduction or elimination of suitable habitat. This is supported by a substantial body of literature demonstrating that large geographic range (~suitable habitat area) increases the chance of survival in species and genera across periods of environmental change (Jablonski 1986, 1987; Harnik 2012; Orzechowski et al. 2015; Foote et al. 2016; see Myers et al. 2013 for an alternative view). Previous work has also shown that taxa most susceptible to extinction experience a decrease in continuity of suitable habitat (Thomas 1994; Hanski 1999; Gu et al. 2002; Maguire and Stigall 2009; Gil-Lopez et al. 2017; Crooks et al. 2017) as well as significant migration of suitable habitat at a rate beyond the capacity of taxon dispersal (Thomas et al. 2004; Reinhardt et al. 2005). Both habitat fragmentation and movement may contribute to population destabilization, eventually leading to a higher extinction potential at the species or clade level (Holt 1985; Gonzales et al. 2011).

The second hypothesis tests the assumption of niche stability within species and genera across the C/T boundary. Previous work has found niche stability during times of gradual abiotic change in the Ordovician (Malizia and Stigall 2011; Stigall 2012; Saupe et al. 2014). In this scenario, taxa demonstrate “habitat tracking” wherein the specific or generic distribution migrates to follow suitable environmental conditions as they move through space and time (Renaud and Schmidt 2003; Brett et al. 2007; Dudei and Stigall 2010; Walls and Stigall 2011). Habitat tracking is dependent on suitable habitat remaining accessible (e.g., not obstructed by geographic barriers), and environmental change keeping pace with the taxon’s dispersal ability (Pinsky et al. 2013). Therefore, if C/T patterns of survivorship were largely driven by abiotic change (i.e., those associated with OAE2), then taxon niche dimensions should remain stable across the boundary. This does not preclude changes in suitable habitat area, which could be modified in shape or size over the time interval.

The final hypothesis tested here addresses the long-standing debate about whether higher taxa (e.g., genera or families) are good ecological proxies for species. Arguments in favor of higher-level proxies include: easy identification of genera compared to species in the fossil record (e.g., Foote 1997; Jablonski and Finarelli 2009); vagaries of species taxonomy (e.g., Foote 1997; Jablonski 2008); and correspondence between diversity patterns of genera and constituent species (Sepkoski et al. 1981; Raup and Boyajian 1988; Roy et al. 1996). Conversely, several authors argue that the use of higher taxa as a proxy for species is inaccurate (e.g., Adrain and Westrop 2000; Hendricks et al 2014). Proponents here cite the arbitrary and potentially polyphyletic designation of higher taxa (Smith and Patterson 1988; Smith 1994) and the composite nature that leads to a false “smoothing out” of ecological traits at the higher taxa level (Jablonski and Hunt 2006; Roy et al. 2009; Harnik 2011; Myers et al. 2013; for more discussion, see Hendricks et al. 2014). This question is significant because genera are composed of many more occurrences than species; therefore, ecological models of genera have greater statistical power. However, if genera cannot be proxies of species-level behavior, then they are not beneficial in understanding paleoecology. To our knowledge, this is the first study to explicitly test the utility of higher taxa as ecological proxies through PaleoENM.

2. Geologic and Environmental Background

The Late Cretaceous was a time of extreme greenhouse conditions brought on by elevated atmospheric carbon dioxide levels (Ladant and Donnadieu 2015). During this time, global temperatures were much higher than today, with sea surface temperature possibly exceeding 32°C (Bice et al. 2003; Forster et al. 2007; O’Brien et al. 2017), eustatic sea level was at its highest of the Mesozoic at 240-250 m above present day mean sea level (Haq 2014), polar ice sheets were ephemeral or absent, and the latitudinal temperature gradient was significantly reduced (Huber et al. 1995; Hay 2008). High atmospheric carbon dioxide levels (varying between 500 and 7,500 ppm in the mid-Cretaceous; Bice and Norris 2002) coincide with an increase in oceanic crust production caused by enhanced seafloor spreading (Muller et al. 2008) and warming due to submarine volcanism (Sinton and Duncan 1997; Du Vivier et al. 2014). Both the increase in seafloor spreading and submarine volcanism likely contributed to the drastic rise in sea level and a positive shift in the carbon isotope curve (+2‰).

Owing to higher global temperatures, increased weathering and nutrient input, and a subsequent decline in available subsurface oxygen content, global oceans at this time underwent a series of ocean anoxic events (OAEs). One of the most substantial of these events is the Ocean Anoxic Event II (OAE2), occurring at the Cenomanian-Turonian (C/T) stage boundary (94.9-93.7 Ma; Eldrett et al. 2017). The OAE2 corresponds with global deposition of organic carbon-rich marine sediments (Wilson and Norris 2001) due to increased preservation of organic matter under anoxic conditions (Schlanger and Jenkyns 1976). In addition to a sudden positive carbon isotope excursion, the boundary is also typically characterized by short-lived (~800 Kyr; Sageman et al. 2006; Freymueller et al., in review) black shale deposits, an increase in the amount of total organic carbon (TOC) associated with the surge in organic carbon burial (Pratt and Threlkeld 1984; Bowman and Bralower 2005; Sageman et al. 2006), and an increase in redox-sensitive elements, such as manganese and molybdenum, in anoxic marine sediments around the globe (Pratt et al. 1989; Turgeon and Brumsack 2006).

The Cenomanian-Turonian stage boundary is also marked by heightened global extinction rates attributed to OAE2 (Elder 1985; Bambach et al. 2006; Kaiho et al. 2014; Freymueller et al., in review). The Cenomanian-Turonian Boundary Event is labeled one of the ten most substantial extinctions in Earth history (Raup and Sepkoski 1986; Bambach 2006), with proportion of extinction for marine genera at the end Cenomanian reaching 25% (Bambach 2006). Researchers have observed globally high levels of biotic turnover at this boundary across several disparate clades including Brachiopoda (Harries and Little 1999; Bambach 2006), Foraminifera (Eicher 1969; Leckie 1985; Xan et al. 2003; Kaiho et al. 2014; Lowery et al. 2014), Chordata (Bambach 2006), Radiolaria (Bragina 2016), Ammonoidea (Elder 1985; Elder 1989; Ifrim 2015), Dinoflagellata (Tocher and Jarvis 1995), and Bivalvia (Elder 1989; Harries and Little 1999; Walaszczyk et al. 2016). Among mollusks, a recent analysis has suggested as much as 36% of genera and 85% of species went extinct across this boundary (Freymueller et al., in review).

Resulting from the combination of generally high eustatic sea level and foreland basin formation during the Sevier and Laramide Orogenies, throughout the majority of the Cretaceous (~130-70 Ma) North America was inundated by an epicontinental sea known as the Western Interior Seaway (WIS) (McCarthy 2012). During regional and global sea level highs the WIS connected the Boreal Sea north of west-central Canada and the Gulf of Mexico in the south (Kauffman 1984; Wright 1987; Kauffman and Caldwell 1993). Mixing of these two very different water bodies contributed to the generally dysoxic conditions of the seaway, especially during times of highstand and regression from partial stratification and reduced downwelling (Eldrett et al. 2017; Lowery et al. 2018). The WIS spanned an estimated 4800-km length, with a maximum width of 1620 km (Kauffman 1984). Generally, the stratigraphy of the seaway is characterized by high subsidence and coarse clastic sedimentation to the west resulting from the Sevier orogeny (Rice and Shurr 1983, Elder et al. 1994). The eastern shoreline is a passive margin with very little clastic sedimentation and significant carbonate deposition (Kauffman 1984, Elder et al. 1994). These conditions facilitated the preservation of an extensive sequence of mollusks, foraminifera, and other marine fauna in offshore sediments; detailed study of WIS deposits over the past 100+ years has resulted in a well-sampled and well-characterized geological, paleobiological, and high resolution biostratigraphic record (e.g., see Kauffman et al. 1993, Walaszcyzyk et al. 2001, and Walaszczyk and Cobban 2016 for mollusks; Bralower 1988 and Kita et al. 2017 for nannofossils; Caldwell et al. 1993 for foraminifera).

The degree of oxygenation of WIS waters is still debated. Generally, the WIS experienced significant dysoxia during regional and eustatic sea level lows and more oxygenated, “normal marine” conditions during increasing sea level (Kauffman 1984, Arthur and Sageman 1994; Eldrett et al. 2017; Lowery et al. 2017). However, there is evidence of anoxic to dysoxic conditions in the Western Interior basin at the time of OAE2: organic-rich black shale deposits in the Hartland Shale Formation (Sageman 1985, 1989), a recorded spike in the amount of total organic carbon (TOC) (Mort et al.

2007; Zhou et al. 2015), and foraminiferal assemblages indicating oxygen deficient waters (Leckie et al. 1998; Corbett and Watkins 2013; Lowery et al. 2014) all reflect oxygen-poor conditions. Thus it is likely that marine taxa in the seaway responded to the global environmental perturbation of OAE2 (Hay 1995; Leckie et al. 1998). WIS strata from this time record 79% extinction across all macroinvertebrate fauna (Harries and Little 1999). Mollusks in particular show 13% generic extinction and 51% specific extinction in the WIS (Elder 1989, based on 61 genera and 84 species).

3. Methods

All ecological niche models require two sets of spatially and temporally explicit data: taxon occurrences and environmental parameters. Modern biologists have a range of free resources from which they can obtain environmental data for ENM (e.g., WorldClim; http://www.worldclim.org), and often carry out ecological niche modeling via climate models that are only available into the recent past (e.g., Martínez-Meyer and Peterson 2006; Nogués-Bravo 2009; Saupe et al. 2014). Deep time applications of ENM (i.e., PaleoENM *sensu* Myers et al. 2015), however, do not have access to GCM-derived environmental data, let alone direct measurements (although see Waterson et al. 2016 for GCM-based ENM analyses reaching back into the latest Cretaceous). To make up for the absence of direct measurements for environmental factors such as sea surface temperature or salinity in the fossil record, we reconstruct paleoenvironmental layers at the stage level through the use of sedimentological and geochemical proxies from outcrop-level analysis. These data are part of an ongoing effort to create a database for spatiotemporally explicit paleoenvironmental proxies

Environmental layers and occurrence data are then used to estimate a taxon's abiotic niche dimensions and, when projected onto geography, the taxon's suitable habitat area. The Maxent ENM algorithm (Maximum Entropy density estimation; Phillips et al. 2004, 2006; Phillips and Dudik 2008) was used to estimate niches, and the Ecospat package in R was used to compare niche dimensions through time (Broenniman et al. 2012; Di Cola et al. 2017). Ecological niche models work in a multidimensional environmental space (e-space of Myers and Saupe 2013), where the number of dimensions is equal to the number of environmental layers. Species distributions are reconstructed by projecting e-space predictions onto geography (g-space). Projections may be done across space, time, or both to test hypotheses of the influence of environmental change on biogeographic and macroevolutionary patterns.

3.1. Data collection

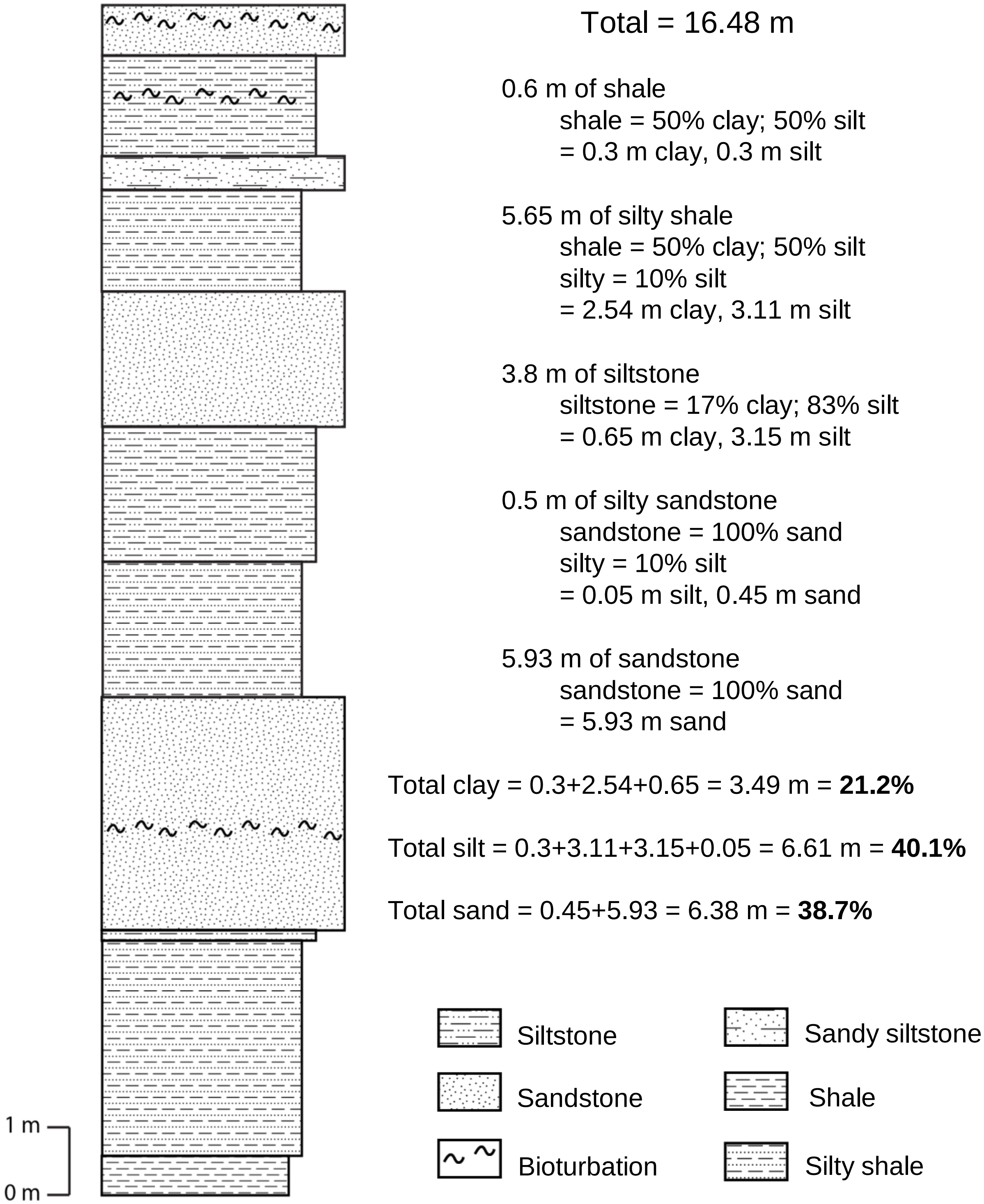
In this study we reconstructed 7 paleoenvironmental layers from field work and literature review throughout North American WIS strata (Appendix 1): percent clay; percent silt; percent sand; total percent siliciclastic rock; water depth; depositional environment; and bedding thickness. All layers were reconstructed using the best practices outlined in Myers et al. (2015). Percentages of clay, silt, sand, and total siliciclastic rock were calculated as the proportional contribution of each grain size or rock type to a given stratigraphic column. For example, if shale is 50% silt and 50% clay, then the total length of shale found in an outcrop will be halved into silt and clay components (see Figure 1). Water depth spans from “0,” or subaerial (above the tide line), to “4,” or offshore. Water depth categories are based on inferred wave energy (i.e., above, at, or below normal wave base or storm wave base). Bedding thickness spans from “1,” or less than cm-thick beds, to “4,” or m-thick beds. Depositional environment spans from “1,” or estuarine, to “6,” or basin, and is based on sediment type and grain size, amount of reworking or bioturbation, and other indicators of distance from shore.

Abiotic information collected primarily from benthic environments will best reflect presence-only benthic marine occurrence data (Myers et al. 2015); therefore, the layers chosen here best reflect the environmental conditions in WIS that may impact the distribution of molluscan taxa. Following test model runs, percent silt demonstrated percent values in the Turonian that were completely outside the Cenomanian range of values. This environmental layer was deemed a “non-analog” environment that would make environmental comparison between the stages difficult, and was thus removed from all models.

Molluscan taxon occurrence data (Table 1) were obtained from online museum databases, museum collections, field work, and peer-reviewed literature, with supplemental material from the Paleobiology Database (downloaded November 15, 2017, from https://paleobiodb.org/). Mollusks were chosen due to their quality of preservation, abundances, diversity of life strategies, and prevalence in the fossil record.

Taxa with less than 4 occurrence points in either stage were not used for modeling, because lower occurrence number often leads to poorer models (Pearson et al. 2007). Models were run at both the species and genus level to test the utility of both as eco-evolutionary units. In total, there were 1369 genus occurrences (656 Cenomanian, with an average of 29 points per taxon, and 713 Turonian, with an average of 36 per taxon), and 289 species occurrences (212 Cenomanian, averaged 19 per taxon, and 77 Turonian, averaged 15 per taxon).

The spatial extent of our PaleoENM analyses spanned the extent of WIS outcrops during the Cenomanian and Turonian stages, with a spatial resolution of 1°x1°. The 1°x1° grid was clipped to available outcrop area unique to each time period in order to minimize biases associated with incomplete sampling of fossil taxa. ArcMap (version 10.5.1; ESRI 2018) was then used to cull the occurrence data to a single taxon occurrence per 1°x1° grid cell for modeling; this reduces model bias in re-sampling grid cells with multiple taxon occurrences.



Total = 16.48 m

0.6 m of shale
shale = 50% clay; 50% silt
= 0.3 m clay, 0.3 m silt

5.65 m of silty shale
shale = 50% clay; 50% silt
silty = 10% silt
= 2.54 m clay, 3.11 m silt

3.8 m of siltstone
siltstone = 17% clay; 83% silt
= 0.65 m clay, 3.15 m silt

0.5 m of silty sandstone
sandstone = 100% sand
silty = 10% silt
= 0.05 m silt, 0.45 m sand

5.93 m of sandstone
sandstone = 100% sand
= 5.93 m sand

Total clay = 0.3+2.54+0.65 = 3.49 m = **21.2%**

Total silt = 0.3+3.11+3.15+0.05 = 6.61 m = **40.1%**

Total sand = 0.45+5.93 = 6.38 m = **38.7%**

Figure 1. Method for extracting sediment percentages from outcrop. Example taken from an outcrop in Fall River County, SD. Citations for environmental layer coding and percentages of each rock type (e.g., siltstone, sandstone, etc.) can be found in Myers et al. 2015.

CLASS	FAMILY	GENUS	SPECIES	CEN #	TUR #
Cephalopoda	Acanthoceratidae	*Acanthoceras*	*Acanthoceras amphibolum+*	38	0
Cephalopoda	Baculitidae	*Baculites**		62	60
			Baculites yokoyamai+*	6	50
Cephalopoda	Acanthoceratidae	*Euomphaloceras*		34	4
			Euomphaloceras septemseriatum+	29	0
Cephalopoda	Vascoceratidae	*Fagesia**		40	10
			Fagesia catinus	4	4
Cephalopoda	Acanthoceratidae	*Mammites*+*		5	28
Cephalopoda	Placenticeratidae	*Placenticeras*+*		11	33
			Placenticeras cumminsi+	8	4
Cephalopoda	Baculitidae	*Sciponoceras*		47	36
Cephalopoda	Scaphitidae	*Scaphites*+*		15	72
Bivalvia	Mactridae	*Cymbophora*+*		22	37
Bivalvia	Gryphaeidae	*Exogyra**		43	27
			Exogyra trigeri+	7	0
Bivalvia	Gryphaeidae	*Gryphaeostraea+*		6	0
Bivalvia	Naticidae	*Gyrodes*+*		17	37
Bivalvia	Inoceramidae	*Inoceramus**		107	87
			Inoceramus prefragilis+	31	0
Bivalvia	Veneridae	*Legumen**		7	13
Bivalvia	Lucinidae	*Lucina-*		18	10
Bivalvia	Inoceramidae	*Mytiloides*+*		16	89
Bivalvia	Ostreidae	*Ostrea**		65	76
			*Ostrea soleniscus**	11	10
			Ostrea beloiti+	42	0
Bivalvia	Pteriidae	*Phelopteria**		24	22
			Placenticeras dalli+	5	0
Bivalvia	Gryphaeidae	*Pycnodonte**		43	12
			Pycnodonte newberryi+	31	9
Bivalvia	Tellinidae	*Tellina*+*		8	15
Gastropoda	Turritellidae	*Turritella**		27	24

Table 1. Genera and species used for test of suitable habitat area. Asterisk (*) denotes any taxon also used for Ecospat tests; (+) signifies removal due to possible occurrence point bias. Occurrence number of “0” signifies an extinction at the C/T boundary.

Environmental data from individual stratigraphic sections was also loaded into ArcMap to convert environmental “point” data into interpolated raster environmental layers for both the Cenomanian and Turonian using the Inverse Distance Weighted (IDW) interpolation method (Blanco et al. 2012; Myers et al. 2015) and a 1°x1° grid cell size. Environmental layers were then “clipped” to the outcrop grid unique to the Cenomanian and Turonian stages. Because total study area was limited to grid cells that included outcrop, the area for training regions varied slightly across the boundary. Therefore, all suitable habitat area comparisons were normalized to the size of the training region, providing a “percent occupancy” of the entire area.

Niche models were performed using the Maxent algorithm to estimate taxon abiotic niche dimensions and projected suitable habitat area over the study area. All Maxent models were run using the default modeling parameters (Phillips et al. 2004, 2006). Maxent estimates the distribution of suitable habitat area in e-space based on a multivariate statistical correlation between environmental layers and occurrence data (Phillips and Dudik 2008). E-space model predictions were then projected onto g-space under four scenarios: (1) CEN_{tr} – Cenomanian training region, in which Cenomanian occurrence data and Cenomanian environmental layers were used to predict Cenomanian suitable habitat; (2) TUR_{tr} – Turonian training region, in which Turonian occurrences and environmental data were used to predict Turonian suitable habitat; (3) CEN_{prj} – Cenomanian projection, in which the e-space niche estimates from the Cenomanian training region were projected onto Turonian geography and environments; and (4) TUR_{prj} – Turonian projection, in which the e-space niche estimates from the Turonian training region were projected onto Cenomanian geography and environments.

The output of all Maxent models is a continuous suitability surface where each pixel in the region (either training region or projected region) has a value from 0 to 1, with higher values being more suitable. Because each Maxent model is internally calibrated, the continuous raw outputs from Maxent are not comparable among taxa (Elith et al. 2011; Myers et al. 2015, supplemental text). Therefore, all models were thresholded – i.e. converted into a binary output of "suitable" vs. "unsuitable" – using the conservative least-training presence method (Pearson 2007; Franklin et al. 2009; Peterson et al. 2011; Donalisio and Peterson 2011; see Liu et al. 2013 for a broader discussion on thresholding methods).

PaleoENM model performance was measured using the threshold independent Area Under the Curve of the Receiver Operating Characteristic (ROC/AUC) method (Phillips et al. 2006; Peterson et al. 2007, 2011; Franklin et al. 2009). This method compares sensitivity vs. specificity of model output and assigns an AUC score from 0 to 1. An $AUC > 0.9$ indicates good model performance, $0.7 < AUC < 0.9$ indicates a moderate model, $0.5 < AUC < 0.7$ indicates a poor performing model, and an $AUC < 0.5$ indicates a model that performs no better than a random model (Elith et al. 2006; Franklin et al. 2009). Given that the ROC/AUC metric of model performance utilizes specificity data, presence-only PaleoENM Maxent results (as used in this study) are biased by the lack of absence data, artificially lowering AUC scores (Peterson et al. 2008; Peterson et al. 2011). Therefore, an $AUC \geq 0.7$ is considered adequate here (Elith et al. 2006; Stigall 2011; Waterson et al. 2016).

3.2 Comparison of suitable habitat area

The area of a taxon's suitable habitat area (SH) was calculated as the percent occupancy of thresholded models, that is, the proportion of predicted suitable habitat normalized to region size. Rather than a strictly calculated area, percent occupancy was used to account for change in study area size across the C/T boundary. SH was calculated for models in three of the four modeling scenarios: CEN_{tr}, CEN_{prj}, and TUR_{tr}. The first hypothesis tested here is the relationship between SH and survivorship. If a larger SH is expected to provide extinction resistance, then model-predicted SH for taxa surviving across the C/T should remain approximately the same or larger when comparing CEN_{tr} and TUR_{tr} models, as well as when comparing the CEN_{prj} and TUR_{tr} models. Comparison of Cenomanian projection with the Turonian training model also provides a qualitative assessment of changes in niche dimensions through time (e.g., $CEN_{prj} < TUR_{tr}$ indicates niche expansion, and vice versa). Maxent results were generated for five species that survived the C/T boundary, six species that went extinct, 20 surviving genera, and four genera that went extinct.

3.3 Niche similarity and equivalency tests

To test hypotheses of niche stability across the C/T boundary, abiotic niche dimensions for each taxon were compared in e-space using the methods of Broennimann et al. (2017; see also Di Cola et al. 2016). The Ecospat package in the R programming language compares abiotic niches in two different ways: (1) niche similarity tests for abiotic niches that are more similar than expected by chance; (2) niche equivalency tests whether abiotic niches are identical to each other (Broenniman et al. 2012, 2017; Di Cola et al. 2016). There is no guarantee that the fullness of a species' fundamental niche in e-space exists in geography at any given time. Thus, the projection of an ENM onto geography shows the "potential niche" (*sensu* Peterson et al. 2011). Ecospat avoids this bias by performing the environmental comparison in e-space, as opposed to geographic space (Broenniman et al. 2012), thereby estimating the species' full range of niche requirements. For both tests, Ecospat ran 100 model iterations to produce a null distribution of values. This random distribution was compared to the Schoener's *D* test statistic. The *D* metric is a niche overlap statistic that describes niche similarity from 0 (no similarity) to 1 (perfect similarity) (Warren et al. 2008). Statistical significance of calculated D metrics is compared to an alpha value of 0.05 for rejection of the null hypothesis, which states that the compared niches are non-similar or non-identical in the case of the similarity and equivalency tests, respectively. Thus, a D metric closer to 1 in either test in combination with statistical significance indicates that the niches being compared show overlap in their environmental dimensions that is more similar or more equivalent than expected by chance.

More specifically, niche equivalency determines whether the niches of two sets of occurrences in different locations (or, in this case, at different times) are identical (Broenniman et al. 2012; Di Cola et al. 2012). Niche equivalency is calculated as the niche overlap observed between the occurrence density grids of a taxon at two different times (i.e., Cenomanian and Turonian stages). This overlap is compared to a distribution of the overlap of two randomly generated niches, which use the pooled set of environments from both training regions.

Niche similarity assesses whether the two observed niches are more similar or different than if one of the observed niches was compared to a niche randomly generated in the other pool of environments (Broenniman et al. 2012). Like the niche equivalency test, niche similarity compares niche overlap between the two occurrence density grids taken from the two separate environmental pools (i.e., the *D* metric, representing overlap, will be the same for both tests). The niche similarity test is different in that it compares this overlap to the distribution of overlap for an occurrence density grid for one set of environments (e.g., Cenomanian) and a randomly generated niche in the other set of environments (e.g., Turonian).

3.4 Potential biases

PaleoENM analyses are dependent on the quality of environmental and taxon occurrence data. Biases in these data may be propagated through the modeling framework and result in poor model performance and/or spurious results. The most common biases include that of sampling and preservation of taxon occurrences, wherein suitable habitat area is contingent on the abundance of occurrence points. If this were the case, a small number of occurrence points for a species in the Cenomanian might result in an artificially small Cenomanian predicted suitable habitat area. This is because ENM algorithms treat environments lacking taxon occurrences as “low suitability” whether that taxon absence is real or the subject of sampling or preservation bias.

We explored this potential bias in two ways: first, CEN_{tr} and TUR_{prj} models were compared and vice versa (i.e., TUR_{tr} and CEN_{prj}). For taxa with more Cenomanian occurrences compared to Turonian occurrences, biased models would be expected to show $CEN_{tr} >> TUR_{prj}$ and $CEN_{prj} >> TUR_{tr}$ when comparing predicted suitable habitat. That is, Turonian model projections that significantly underestimate Cenomanian training region predictions, and Cenomanian model projections that significantly overestimate

Turonian training region predictions, may indicate a set of models biases by numbers of taxon occurrences. The converse would be expected for occurrence-biased models for taxa with many more Turonian compared to Cenomanian occurrences: Turonian projections overestimate when compared to Cenomanian training region ($TUR_{prj} >> CEN_{tr}$), and Cenomanian projections underestimate suitable habitat area when compared to Turonian training region ($CEN_{prj} << TUR_{tr}$). Taxa showing these patterns were removed from further interpretation.

It is important to note that the above test for bias is a qualitative criterion, and absence of this pattern does not mean that the model is not subject to occurrence biases. As a quantitative test for potential occurrence point bias, we calculated correlation between number of occurrences and area of predicted suitable habitat. Because the data are not normally distributed, a nonparametric Spearman rank correlation was used to compare data for Cenomanian species, Cenomanian genera, Turonian species, and Turonian genera. A positive, significant result ($p < 0.05$; $p < 0.013$ with Bonferroni correction to correct for multiple comparisons) would suggest possible occurrence point biases, wherein predicted suitable habitat area is potentially controlled more by number of occurrences than actual abiotic requirements of the taxa being modeled.

Other tests for bias include model performance. This was assessed with the ROC/AUC method discussed above. Only one model for genus *Mammites* produced an AUC less than 0.7; model performance was therefore not determined to have much effect on biased models. Another source of bias may be environmental layers that are not informative for the taxa being modeled. For example, sediment grain size or type may be expected to better reflect the environmental conditions required for benthic taxa (e.g., gastropods and bivalves) vs. nektonic taxa (e.g., cephalopods). If this were the case, model performance measures are expected to be correlated with specific ecological traits.

4. Results

Results of all 68 PaleoENM models and habitat continuity indices are presented in Table 3; Figures 2 and 3 illustrate example model outputs. Twenty-five out of 34 taxa survived the C/T boundary (five species and 20 genera) and nine taxa go extinct (six species and three genera). Model performance was overall good (AUC > 0.7 in all but one case), particularly given the use of presence-only data (Peterson et al. 2008). The single poorly performing model (*Mammites* $\mathrm{CEN}_{\mathrm{tr}}$; AUC = 0.57) performed well in other tests and therefore is retained for discussion, although interpretations should be taken cautiously.

4.1 Suitable habitat area

Increase or decrease in SH was characterized as a greater than 10% change between time periods. Out of the 25 surviving taxa 12 (one species and 11 genera) showed either no change or an increase in suitable habitat area between the Cenomanian and Turonian stages. The remaining 13 survivors (four species and nine genera) demonstrate a decrease in suitable habitat area between the two stages (Table 2). Further, no change or an increase in SH continuity across the C/T was the norm (four species and 11 genera demonstrate no change; 1 species and seven genera demonstrate an increase in continuity).

Of the nine extinct taxa, three genera (*Brachiodontes, Carycorbula,* and *Gryphaeostraea*) and two species (*Phelopteria dalli* and *Exogyra trigeri*) exhibit small or fragmented habitat in the Cenomanian. Overall, extinct taxa show a range of SH in the Cenomanian ($\mathrm{CEN}_{\mathrm{tr}}$) and little change in SH when the Cenomanian model is projected onto Turonian environments ($\mathrm{CEN}_{\mathrm{prj}}$*;* see Table 2). Further, although habitat continuity is generally

Table 2. Results from Maxent models. “N_{CEN}” is number of occurrence points in the Cenomanian. “SH_{CENtr}” is the percentage of suitable habitat area for that taxon in the Cenomanian training region. “$Cont_{CEN}$” is a continuity index for SH in the Cenomanian, with 1 = patchy and 3 = continuous. “ΔCont” is the change in continuity index from the CENtr → TURtr or CENtr → CENprj for extinct species. ΔCont > 1 is a positive change in continuity indicates decreased continuity of SH (greater patchiness) through time and vice versa for ΔCont < 1; ΔCont = 0 indicates no change in continuity. (*) indicates species that go extinct at the C/T boundary. Turonian continuity is recorded for surviving taxa (i.e., those with Turonian occurrence data). (+) denotes possible occurrence point bias.

Taxon	N_{CEN}	N_{TUR}	AUC $_{CEN}$	AUC $_{TUR}$	SH $_{CENtr}$	SH $_{TURtr}$	SH $_{CENprj}$	Cont $_{CENtr}$	Cont $_{CENprj/TUR}$	ΔCont
*Acanthoceras amphibolum**	38	0	0.825	N/A	78.8	N/A	69.5	3	3	0
Baculites	62	60	0.783	0.803	68.3	53.5	82.4	2	3	1
Baculites yokoyamai+	6	50	0.85	0.8	15.5	63.3	0	1	3	2
*Brachiodontes**	5	0	0.954	N/A	7.9	N/A	10.2	1	1	0
*Carycorbula**	7	0	0.866	N/A	57.9	N/A	59.4	1	2	1
Corbula	24	19	0.883	0.909	34.9	19.9	52.7	1	1	0
Cymbophora	22	37	0.879	0.862	38.5	41.8	41.8	1	3	2
Euomphaloceras	34	4	0.802	0.956	68.3	9	46.1	3	1	-2
*Euomphaloceras septemseriatum**	29	0	0.839	N/A	67.6	N/A	50.4	3	2	-1
Exogyra	43	27	0.802	0.824	73	70.7	88	3	3	0
*Exogyra trigeri**	7	0	0.97	N/A	4.7	N/A	5.9	1	1	0
Fagesia	40	10	0.817	0.815	68.7	43.8	69.9	2	2	0
Fagesia catinus	4	4	0.813	0.842	43.2	29.3	41.8	1	1	0
*Gryphaeostraea**	6	0	0.882	N/A	34.2	N/A	43.8	1	1	0
Gyrodes+	17	37	0.764	0.869	77	39.5	74.6	2	2	0

Taxon	N CEN	N TUR	AUC CEN	AUC TUR	SH CENtr	SH TURtr	SH CENprj	Cont CENtr	Cont CENprj/TUR	ΔCont
Inoceramus	107	87	0.732	0.733	83.8	84	91	3	3	0
*Inoceramus prefragilis**	31	0	0.795	N/A	69.1	N/A	87.1	3	3	0
Legumen	7	13	0.805	0.856	39.9	47.3	78.5	1	1	0
Lucina	18	10	0.871	0.744	36	51.2	5.9	2	1	-1
Mammites+	5	28	0.569	0.83	68.3	55.1	77.7	2	3	1
Mytiloides+	16	89	0.899	0.724	44.6	80.1	3.9	2	3	1
Ostrea	65	76	0.744	0.778	79.1	88.3	75.4	3	3	0
Ostrea soleniscus	11	10	0.869	0.936	46.8	15.6	71.5	1	1	0
*Ostrea beloiti**	42	0	0.84	N/A	74.5	N/A	81.9	3	3	0
Phelopteria	24	22	0.852	0.88	60.4	29.3	67.8	2	2	0
*Phelopteria dalli**	5	0	0.954	N/A	7.9	N/A	10.2	1	1	0
Placenticeras+	11	33	0.828	0.81	61.5	76.6	53.1	2	3	1
Placenticeras cumminsi+	8	4	0.848	0.887	28.1	17.6	1.2	1	1	0
Pycnodonte	43	12	0.848	0.851	69.8	40.2	77.3	2	2	0
Pycnodonte newberryi+	31	9	0.89	0.93	55.4	25	66	1	1	0
Scaphites+	15	72	0.766	0.769	73.4	43.8	99.6	3	3	0
Sciponoceras	47	36	0.804	0.812	77	68	73.8	3	3	0
Tellina+	8	15	0.884	0.821	18	45.3	99.6	1	2	1
Turritella	27	24	0.905	0.793	34.2	49.6	35.3	2	3	1

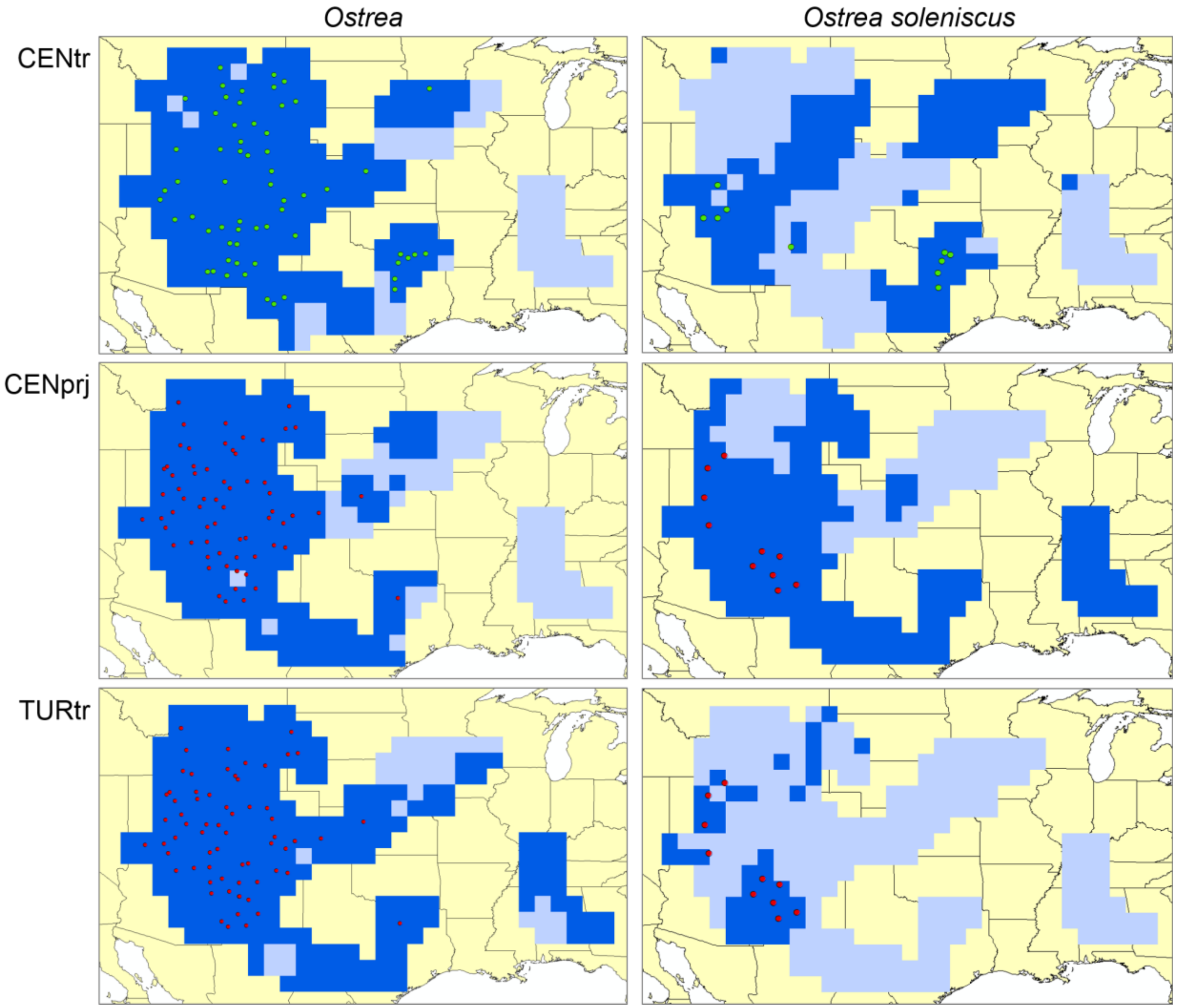


Figure 2: Surviving taxa. MaxEnt example results for the surviving genus *Ostrea* and species *Ostrea soleniscus.* Dark blue is suitable habitat, light blue unsuitable, green points are CEN occurrences, and red TUR. Top figures depict CENtr based on Cenomanian occurrences and environments; bottom figures depict TURtr based on Turonian occurrences and environments; and middle figures are CENprj onto TUR.

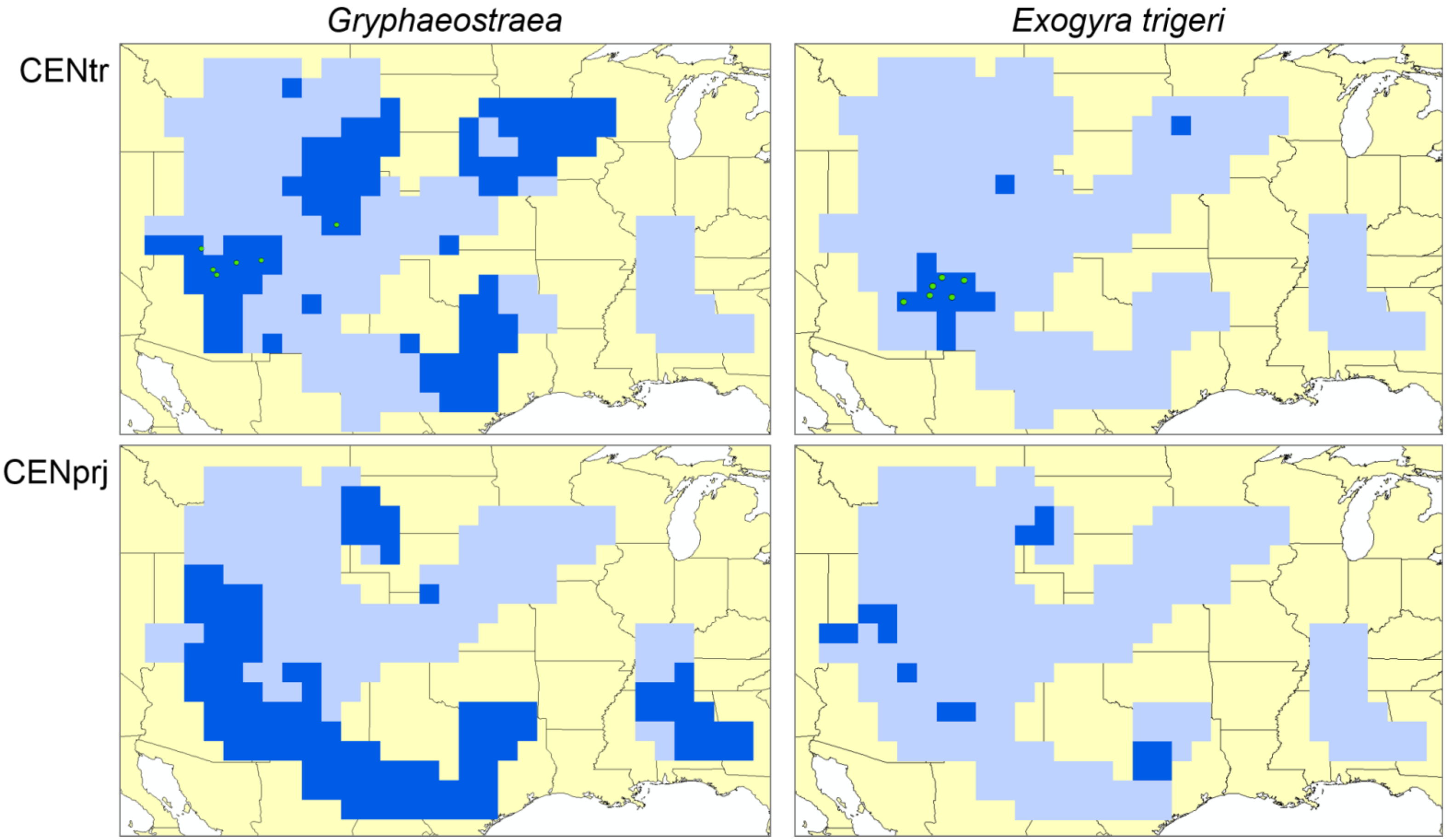


Figure 3: Extinct taxa. MaxEnt example results for the genus *Gryphaeostraea* and species *Exogyra trigeri*, both of which went extinct at the C/T boundary. Top figures depict Cenomanian training region based on Cenomanian occurrences and environments, and bottom figures depict projection of Cenomanian suitable habitat onto Turonian environments.

low for extinct taxa, there is very little change in this continuity index across the boundary, indicating a lack of association between extinctions and increased habitat fragmentation (see Table 2).

4.1.1 Correlation tests for potential biases

Spearman rank correlation between number of occurrence points and model-predicted SH area was used to investigate potential occurrence-point biases among models. The Spearman correlation test yield significant results (Table 3) and moderate to high correlation coefficients, indicating that occurrence number is directly correlated with available suitable habitat area for Cenomanian genera, Turonian genera, and Cenomanian species, but not for Turonian species. Correlations are depicted graphically in Figure 3. Lack of correlation between Turonian species' occurrences and suitable habitat could be attributed to lack of surviving species data in the Turonian.

Further, tests of potential occurrence point bias suggested that eight of the 25 surviving taxa examined here may produce biased PaleoENMs (*Baculites yokoyamai, Pycnodonte newberryi, Euomphaloceras, Gryphaeostraea, Mammites, Mytiloides, Placenticeras,* and *Scaphites*). It is important to note that the observation of either of these patterns does not conclusively determine sampling bias, since the positive relationship between abundance and geographic range has been well supported in both the modern and fossil literature (e.g., Venier and Fahrig 1996; Welters-Schultes and Williams 1999; Munday 2002; Paramo and Roa 2003). Removal of these eight taxa from analysis did not substantially change the results: nine genera show consistent or increased suitable habitat area across the C/T boundary, ranging from no change (*Inoceramus*) to 27% (*Tellina*) increase in SH occupancy.

	Number of taxa	*p*-value	rho
CEN genera	23	0.002433	0.6007925
TUR genera	20	0.00945	0.5649229
CEN species	11	0.0007614	0.8564942
TUR species	5	0.7406	0.2051957

Table 3. Spearman correlation test results show moderate to strong correlations (rho) between number of occurrence points and suitable habitat area for all groups but Turonian species. Significant *p*-values for all but Turonian species support the alternative hypothesis of correlation.

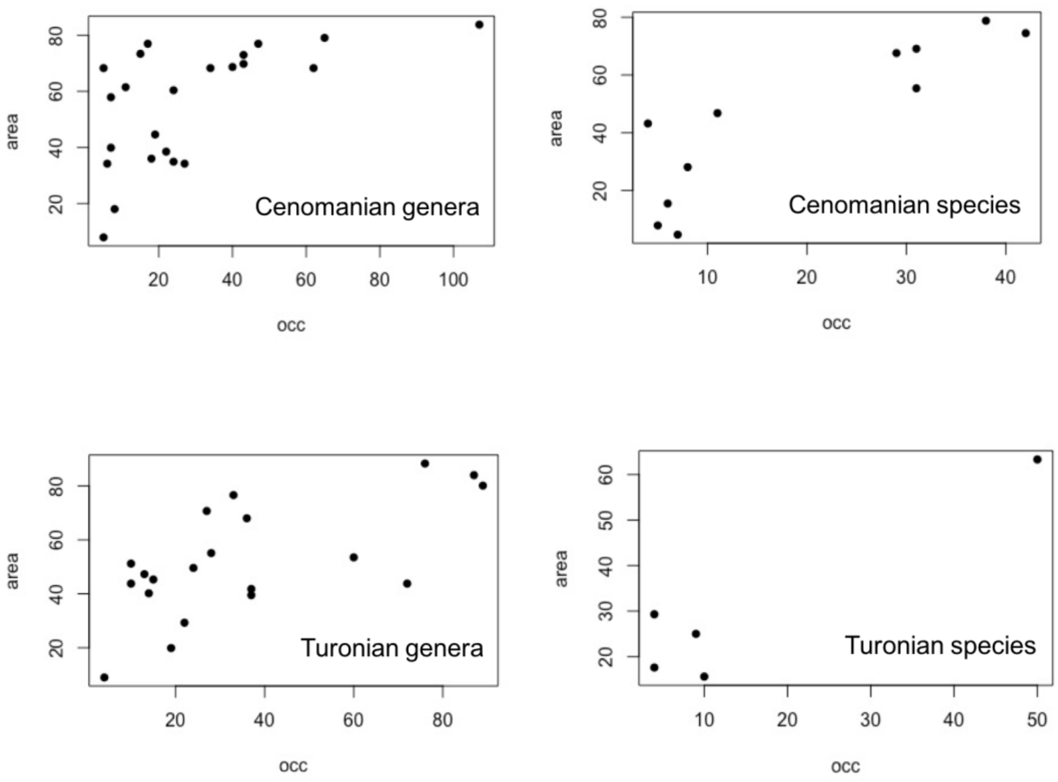


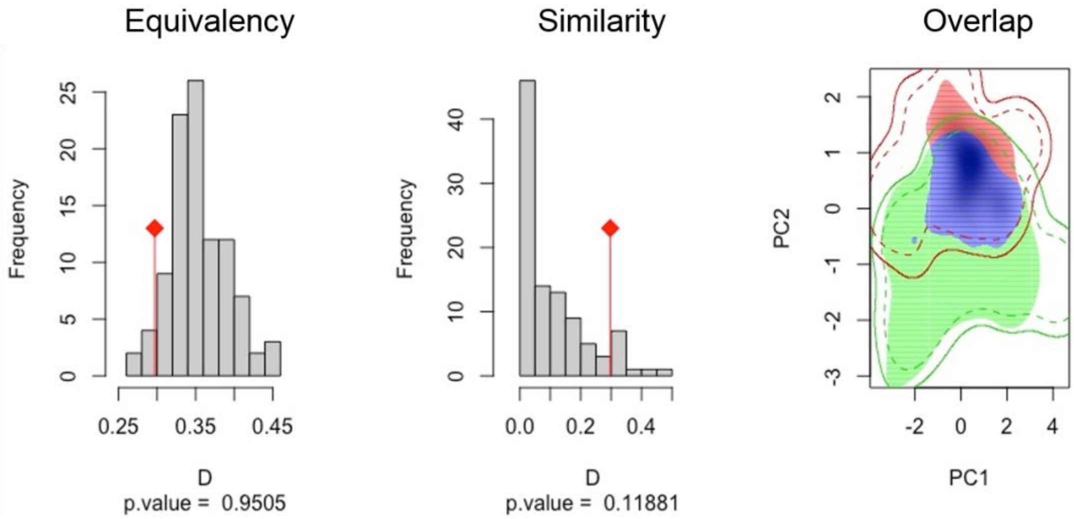
Figure 4. Correlations between occurrence points and suitable habitat area for Cenomanian genera (top left), Cenomanian species (top right), Turonian genera (bottom left), and Turonian species (bottom right).

The remaining eight taxa (three species and five genera) demonstrate a decrease in predicted SH across the C/T boundary, ranging from a decrease of 11% (*Placenticeras cumminsi*) to 59% (*Euomphaloceras*). Habitat continuity is also largely consistent after removing potentially biased taxa: 12 taxa show no change in continuity (three species and nine genera), four genera show increased continuity, and two genera show a decrease in continuity across the boundary.

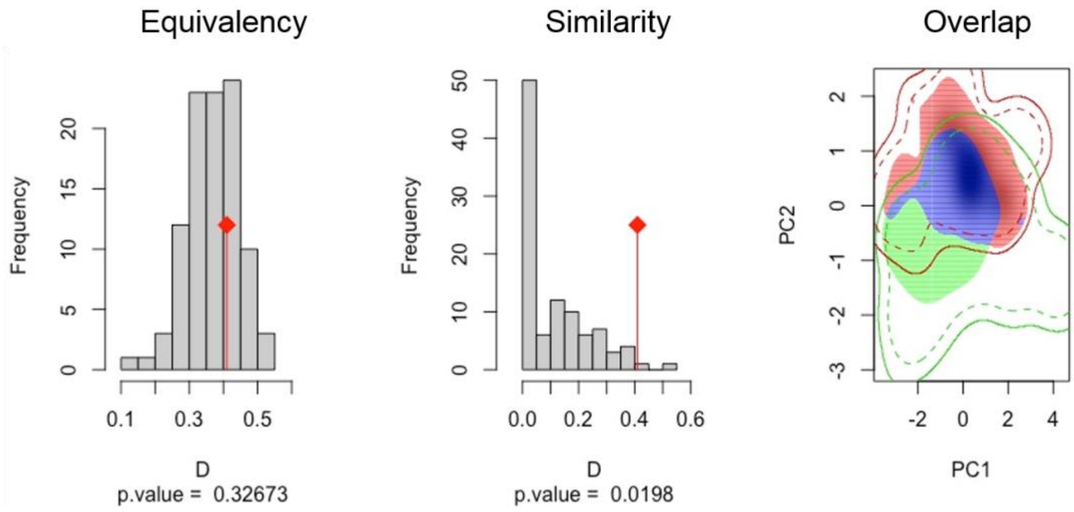
4.2 Niche similarity and equivalency

Genus	Species	*D*	Equivalency test *p*-value	Similarity test *p*-value
Baculites		0.27	1	0.11881
Baculites	*yokoyamai+*	0	1	1
Fagesia		0.38	0.07921	0.07921
Mammites+		0.39	0.07921	0.0396*
Placenticeras		0.05	1	0.31683
Scaphites+		0.4	0.32673	0.0198*
Sciponoceras		0.22	1	0.19802
Corbula		0.33	0.63366	0.05941
Cymbophora		0.46	0.05941	0.0198*
Exogyra		0.28	0.70297	0.12871
Gyrodes+		0.26	0.63366	0.10891
Inoceramus		0.35	0.55446	0.0495*
Legumen		0.08	0.86139	0.14851
Lucina		0	0.88119	0.11881
Mytiloides+		0.25	0.92079	0.15842
Ostrea		0.3	0.9505	0.11881
Ostrea	*soleniscus*	0	0.9901	0.08911
Phelopteria		0.24	0.9802	0.11881
Pycnodonte		0.31	0.67327	0.08911
Tellina		0.07	0.9703	0.18812
Turritella		0.35	0.23762	0.0495*

Table 4. Ecospat results for all assessed surviving genera and species. Schoener's *D*, a niche overlap metric, spans from 0 (no niche overlap) to 1.0 (100% niche overlap). Asterisks (*) denote significant *p*-values ($p < 0.05$) for similarity and equivalency tests. (+) denotes possible occurrence point bias.



(a) *Ostrea* demonstrates no niche similarity across the C/T boundary.



(b) *Scaphites* demonstrates niche similarity across the C/T boundary.

Figure 5. Examples of genera that demonstrate no significant (a) and significant (b) niche similarity across the C/T boundary. Left depicts niche equivalency and middle depicts similarity tests. The null distribution of random niches, based on 100 model iterations, is represented by grey bars, and the *D* metric by the red diamond. Right illustrates niche overlap in environmental space along the top two contributing PC axes. Green is Cenomanian niche space, red is Turonian, and blue is overlap.

Ecospat analyses for niche stability were performed on two surviving species and 19 surviving genera across the Cenomanian-Turonian boundary (remaining taxa did not meet the criterion of five or more occurrence points). Ecospat directly compares model output for the Cenomanian and Turonian training regions in environmental space (Broenniman et al. 2012). Results of all Ecospat tests are provided in Table 4. Examples of the output from niche equivalency and similarity tests are presented in Figures 5a and 5b. The two species tested showed mixed results with niche contraction observed in *Ostrea soleniscus*, and no real change in niche size (only movement of the niche in e-space) in *Baculites yokoyamai*. Of the 19 genera, nine also showed no major change in e-space niche dimensions (although some movement was observed in all), eight genera showed niche contraction, and two genera (*Mammites* and *Mytiloides*) showed niche expansion into the Turonian.

All tests for niche equivalency failed to reject the null hypothesis, indicating no evidence of identical niche dimensions in surviving taxa across the boundary. However, five genera (*Cymbophora, Inoceramus, Mammites, Scaphites,* and *Turritella*) demonstrate significant niche similarity across the C/T ($p < 0.05$) with D values greater than or equal to 0.35. The remaining 14 generic tests and both species-level tests were non-significant, indicating that the Cenomanian and Turonian niches were not more similar than expected when compared to a randomly generated niche.

4.3 Species vs. genera model comparison

Nine species-genus pairs were examined to test for the utility of genera as eco-evolutionary proxies for species in the Cenomanian and Turonian WIS. MaxEnt and Ecospat results were different when comparing species to their corresponding generic model. Species-level PaleoENMs tended to perform better than genus-level models (average AUC for Cenomanian models was 0.86 for species and 0.82 for genera; average AUC for Turonian models was 0.88 for species and 0.82 for genera). Estimated SH also varied as expected, with genera showing higher SH (average SH of 55.4% and 51.85% in the Cenomanian and Turonian respectively), than species (average SH of 44.7% and 30.2% in the Cenomanian and Turonian respectively).

Five out of the nine species-genus pairs included at least one surviving species. Three of these demonstrated a change in suitable habitat across the C/T that was inconsistent between taxonomic levels. The *Baculites* model was comprised of 8 constituent species and showed a 14.8% decrease in SH into the Turonian compared to 47.8% increase for the species *Baculites yokoyamai*. The *Ostrea* model included nine constituent species, with a 9.2% increase in SH compared to 31.2% decrease for *Ostrea soleniscus*. The *Placenticeras* model included three constituent species, with a 15.1% increase in SH compared to *Placenticeras cumminsi* with 10.5% decrease in suitable habitat area. The remaining two genera (*Fagesia* and *Pycnodonte*) did show comparable suitable habitat changes to that predicted for their constituent species (*F. catinus* and *P. newberryi*). The *Fagesia* model includes occurrences from seven constituent species, while the *Pycnodonte* model includes three constituent species. *Fagesia* and *Ostrea* are the only two unquestionably unbiased genera with unbiased constituent species, and both follow different trends, making generalized interpretations difficult.

Ecospat analysis of niche stability also yielded differences in species- vs. genus-level results. Both species assessed via Ecospat (*Ostrea soleniscus* and *Baculites yokoyamai*) have a *D* value of 0 (i.e., no overlap of Cenomanian and Turonian niches), corresponding to definitively insignificant *p*-values for both the equivalency and similarity tests (Table 4). Their corresponding genera, *Baculites* and *Ostrea*, have *D* values of 0.27 and 0.30, respectively, although again with insignificant *p*-values in the niche equivalency and similarity tests. By comparing generic niche overlap graphs (Appendix 5) with constituent species, substantially more overlap through time in genera is demonstrated (as expected). Niche contraction is observed across the C/T boundary for both *Ostrea* and *O. solensicus*; *Baculites* also shows niche contraction, but *B. yokoyamai* indicates substantial niche migration rather than contraction.

5. Discussion

5.1 Suitable habitat area change for surviving vs. extinct

The majority of surviving genera demonstrate a consistent or increased suitable habitat area across the C/T boundary. These taxa span all three major molluscan clades (i.e., 11 bivalves, three cephalopods, and one gastropod), and vary in ecological traits (e.g., motility, tiering, feeding, etc.). Out of the five surviving species, four demonstrate a decreased suitable habitat area (two bivalves and two cephalopods) and only one cephalopod (*Baculites yokoyamai*) increases in suitable habitat area. Similarly, taxa that go extinct at the C/T boundary span a range of evolutionary and ecological traits. The apparent decrease in SH in some groups cannot be attributed to poor occurrence data.

Altogether, these data suggest that changes in suitable habitat area and/or continuity of that habitat were not a driving force for extinctions across OAE2. This potentially supports anoxia as the primarily kill mechanism, as opposed to habitat loss or fragmentation. Papers that support anoxia as having a causal role in the C/T extinction cite stepwise extinctions during the OAE2 at the stage transition period, wherein extinction rates rise gradually as anoxia inflates and grows closer to the sea surface (Kaiho et al. 2014). On the other hand, there is evidence that anoxia was not the main causal role in extinction for some groups. For example, Monnet and Bucher (2007) demonstrates a decoupling of ammonite biodiversity trends and spreading anoxia, and the authors conclude that anoxia was not the reason for ammonite extinctions. Also, when comparing the global record, Monnet (2009) reports a lack of connection between anoxia and ammonoid biodiversity patterns, citing sea level and climate change as the more likely culprit of extinctions.

Moreover, the lack of consistency in model predictions at both taxonomic levels suggests taxon-specific responses to the environmental changes associated with OAE2. It has been found that during heightened extinction levels (i.e., mass and/or secondary extinctions), selectivity on ecological traits is lost in favor of selectivity patterns more closely associated with mass extinctions (Droser et al. 2000; McGhee et al. 2012; Freymueller et al., in review) such as geographic range size (Jablonski 1986, 2005). If this were the case during the OAE2, then one would expect selectivity more closely related with anoxia-driven extinctions.

Geographic range size is often cited as a good predictor of extinction resistance at both the genus- and species-levels (Kiessling and Baron-Szabo 2004; Jablonski 1986, 2005), particularly during mass or secondary extinction events like the C/T (Raup and Sepkoski 1984, 1986; Sepkoski 1990). However, our data do not fully support this theory, as five out of eight taxa that go extinct across the C/T demonstrate over 50% habitat occupancy of Cenomanian area (see Table 3) and survivors also show a large range of suitable habitat occupancy in the Cenomanian. Previous work has found a deviation from this hypothesis for mass extinctions other than the end-Cretaceous (Erwin 1996 for end-Permian; Foote et al. 2003 for end-Ordovician; Kiessling and Aberhan 2007 for Triassic-Jurassic; Myers et al. 2013 for Late Cretaceous stages). Kiessling and Aberhan (2007) hypothesize that this deviation may arise when global perturbations and selectivity overshadow regional changes. This may be the case for the C/T global OAE2 event.

Among the 17 taxa that were not removed due to potential bias (three species and 14 genera), eight genera demonstrated consistent or increased suitable habitat across the boundary, and nine taxa (including all three species) demonstrated decreased suitable habitat. Both groups (i.e., consistent/increased SH *vs*. decreased SH) are composed of different clades, life habits, and occurrence numbers. Our strictly unbiased PaleoENM data therefore show no consistent trend that could explain suitable habitat change across the C/T. The only pattern worth noting is that all cephalopods display decreased SH across the boundary. This is in line with prior research indicating lower extinction rates and weak anoxia closer to the sea surface and ammonoid habitat (Kaiho et al. 2014). In summary, because only cephalopods show a strong pattern toward a decrease suitable habitat, the unbiased data does not support habitat loss or fragmentation as the major driving factor in the C/T extinction. Moreover, the lack of expected ecological selectivity in the remaining data once again suggests that the OAE2 was such a powerful environmental perturbation that background extinction selectivity patterns ceased in favor of those associated with more major extinction events.

The lack of consistent or increased SH in cephalopods could also be in support of the possible environmental parameter bias: environmental layers compiled from proxies primarily reflecting seafloor conditions may not adequately capture important aspects of pelagic environments. However, all unbiased cephalopod taxa examined here are nektobenthic (Landman and Geyssant 1993; Tsujita and Westermann 1999), which suggests that benthic environmental proxies would be relevant for predicting distribution patterns. Further, all but one models have high AUC scores indicating that the models are discerning; that is occurrences of these taxa can be assigned to specific portions of environmental space with confidence.

Low spatiotemporal resolution may also play a role in biasing our model results by decreasing the signal-to-noise ratio and thus obscuring the impact of habitat fragmentation and continuity on survivorship. Poor stratigraphic and occurrence data resolutions may lead to low spatial resolution, which may bias assessment of ENMs in geographic space (Waltari et al. 2007). Low temporal resolution is the result of averaging environmental conditions over geologic stages, which usually span a few Myrs each. This was done in order to match the lowest common denominator of temporal resolution in species and genus occurrence data (i.e., to preserve more occurrences and reduce occurrence-based model bias). However, macroecological questions on evolutionary timescales necessarily take a broad spatiotemporal view (Brown and Maurer 1989; Brown 1999); thus, the time resolution for this study is standard in practice.

Additionally, to our knowledge there have been no explicit sensitivity analyses to understand the appropriate temporal resolution for PaleoENM studies. Species usually live for several million years, and genera tens of millions of years, which suggests that species-level models may be more sensitive to low temporal resolution biases. Therefore, even if a species went extinct “naturally” (i.e., not associated with C/T boundary conditions) in less than the span of the Cenomanian stage, it is worth noting that the species models here still performed better (i.e., were more discerning) than the genus-level models.

5.2 Niche stability in survivors

Tests for niche stability also did not recover patterns consistent across taxonomic levels, clade, or ecological traits. Niche equivalency was never observed across the C/T boundary. This result is not surprising. Equivalency tests compare actual niche overlap with the overlap of two niches randomly generated in the environmental parameters of each time period or location being studied. If the actual niche overlap is greater than the overlap of 100 randomly generated niches, then the observed niches are determined equivalent. This framework makes the equivalency test a very strict test of niche conservatism, akin to testing for identicality in niche dimensions (Peterson et al. 1999; Warren et al. 2008; Stigall 2012), and difficult to ever demonstrate. The results presented here are thus in line with previous work (Graham et al. 2004; Warren et al. 2008; Pyron and Burbrink 2009; Debandi et al. 2011; Zhu et al. 2013).

Niche similarity was only recovered among five genera. The predominant pattern was contraction in abiotic niche dimensions in concert with a shift of the niche in environmental space. The majority of taxa that demonstrate niche contraction across the C/T do so because they are limiting their niche dimensions to accommodate for changes and/or disappearance of preferred environment. Previous research has also found niche contraction into a subset of a taxon's previously observed niche space (Brame and Stigall 2014; Stigall 2014) and that this is often accompanied by a decrease in niche similarity (as seen here; Stigall 2014). Further, the two genera that demonstrated niche expansion across the C/T (*Mammites* and *Mytiloides*) do not unequivocally support niche evolution. Both *Mammites* and *Mytiloides* Turonian niches expand further outside of the original Cenomanian realm of available environments. Any observation of niche expansion could indicate evolution in environmental tolerances or utilization of environmental space that was always within the taxon's fundamental niche, but simply did not exist on geography in the preceding time period. Life habit for both genera are very different; therefore, the results do not suggest a certain life habit beneficial to the environmental changes across the C/T and OAE2.

Notably, *Baculites yokoyamai* is the only taxon that displays complete lack of niche equivalency or similarity (i.e., *p*-values of 1) and $D = 0$ for niche overlap. Further, it displays no niche contraction, in contrast from the majority of the models, but rather demonstrates substantial niche migration. This may be due to specimen misidentification: it is possible that *Baculites yokoyamai* occurrence data is the false accumulation of two different *Baculites* species with varying niche requirements. It can often be difficult to identify species and rely on them as true evolutionary units in the fossil record, especially if the traits used to separate species in the modern are not well-preserved from the past (Hendricks et al. 2015; also see Saupe and Selden 2011 for a more in-depth example). Incorrect identification of a taxon for ENM purposes can result in both false negative and false positive errors (Stigall 2014). Others argue that this does not pose a huge problem in ENM studies, as correct identification in the fossil record can be very difficult (Stigall 2014) and often underprediction is a much more common issue than overprediction (Walls and Stigall 2012).

In part this analysis was hampered by low numbers of occurrences among the sampled taxa, particularly at the species level. This limited the number of taxa that could be used to effectively compare results at the species and genus levels. Additionally, and as with the Maxent results, pelagic environments are much less likely to be recorded in bottom-accumulating environmental data. Further, e-space ENMs can often experience the same issues as those in g-space; these include model overfitting due to sampling biases (Boria et al. 2014, Varela et al. 2014).

5.3 Species and genera comparison

Macroevolutionary and macroecologial studies often employ genera as ecological proxies for species (Raup and Boyajian 1988; Sepkoski and Kendrick 1993; Foote 1996; Sepkoski 1998; see also Hendricks et al. 2014) without explicit analysis of their fidelity. Here we explicitly compared species- and genus-level patterns because the way that genera are defined in practice, and clades in theory, are unconvincing for the use of higher level taxa as ecological proxies of species. Theoretically, generic distributions may be dominated by a single species with a large range (that dampens smaller ranged species signals), be composed of a composite of non- or partially-overlapping species ranges, or be composed of all species with overlapping ranges. This first scenario would result in a genus-level model biased toward that one dominant species; the second would result in a potentially informative clade-level model that does not inform species-level patterns. Both of these scenarios results in genus-level distributions that are not good proxies for species-levels biogeographical patterns. On the other hand, the third scenario (niche overlap among all species within a genus) would be the only situation in which genus-level models are appropriate species proxies.

In general, the species datasets performed better than their generic counterparts. Three out of five species-genus pairs showed inconsistencies in suitable habitat predictions between taxonomic levels. These results do not clearly support genera as reliable proxies for biogeographic patterns of species on evolutionary timescales. Based on the figures illustrating suitable habitat in the Cenomanian and Turonian stages (Appendix 4), it is possible that multiple species within a genus, when compiled, show a composite suitable habitat area matching that of the genus. For example, the bivalve genus *Ostrea* has two constituent species: *Ostrea congesta* and *Ostrea beloiti*. The two species' Cenomanian compiled suitable habitat suggest a composite generic-level niche. This is not ideal and suggests that genera cannot be used as ecological proxies for species. Further comparison of Ecospat models demonstrate species with patterns of niche change that are different from their genera. It is possible that these genera would show the same composite pattern as *Ostrea*, but further investigation into additional component species is needed.

We conclude that species and generic-level models, in most cases, will depict different ecological results. It is understandable that genera are more convenient for paleoecological studies, as they have more data which can provide clearer and more robust statistical models. However, if one cannot interpret those models in a rigorous biological context, then it is difficult to accurately interpret what the models. Because this study only investigated nine pairs of species- and genus-level models, there is not enough data to make a definitive argument in this debate. Nevertheless, the data presented here does not support genera as an ecological proxy for species, and until further evidence accumulates, it may be best to use species for ENMs and other paleoecological tests, and simply tailor the study question to the resolution of species-level data.

6. Conclusion

This contribution tested three hypotheses surrounding the influence of biogeography on survivorship across the environmental perturbation of OAE2 at the Cenomanian-Turonian boundary: (1) Taxa that survive across an environmental perturbation show a consistent or increased suitable habitat, while taxa that go extinct show habitat loss or fragmentation; (2) taxa demonstrate niche stability across the C/T; and (3) genera can be used as paleoecological proxies for their constituent species. We show that survivorship across the OAE2 is not strongly correlated with available suitable habitat nor its continuity. This supports taxon-specific responses to environmental changes at the macroevolutionary scale of this study. Additionally, only about a quarter of taxa demonstrated significant abiotic niche stability (similarity) from the Cenomanian into the Turonian, which also supports the taxon-specific observations from niche models. Thus, in contrast to more recent analyses (e.g., Saupe et al 2015), but in agreement with other deep time studies (e.g., Stigall 2014), this data suggests that the assumption of niche stability on evolutionary timescales may be erroneous. Finally, species and genera were not found to show similar patterns in suitable habitat area and environmental space niche dimensions. Although this does not represent an exhaustive test of genera as paleoecological proxies for species, these results suggest that genera are not reliable proxies for species-level biogeography without further investigation.

The OAE2 is analogous with today’s rising greenhouse temperatures, ocean anoxia, and habitat destruction and fragmentation. These similarities make this study applicable to the growing biodiversity crisis. If C/T biota demonstrate taxon-specific responses during the OAE2, then we are likely to see the same pattern in the modern.

This may have implications for current and future conservation efforts, as it may not be beneficial to make widespread conservation decisions if all taxa respond differently to climate change.

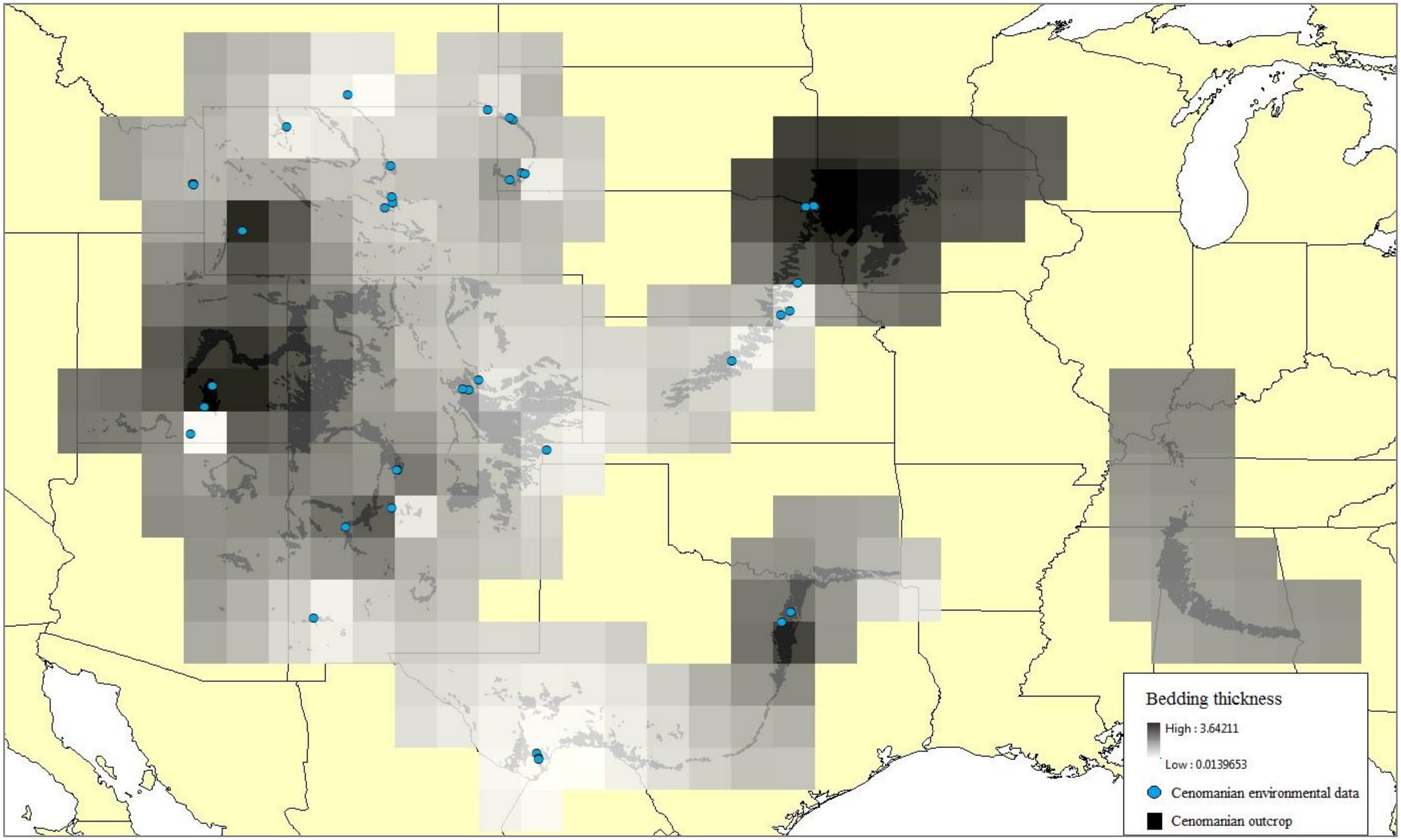
Appendices

Appendix 1 – Table of environmental layer references for Cenomanian and Turonian by US state.

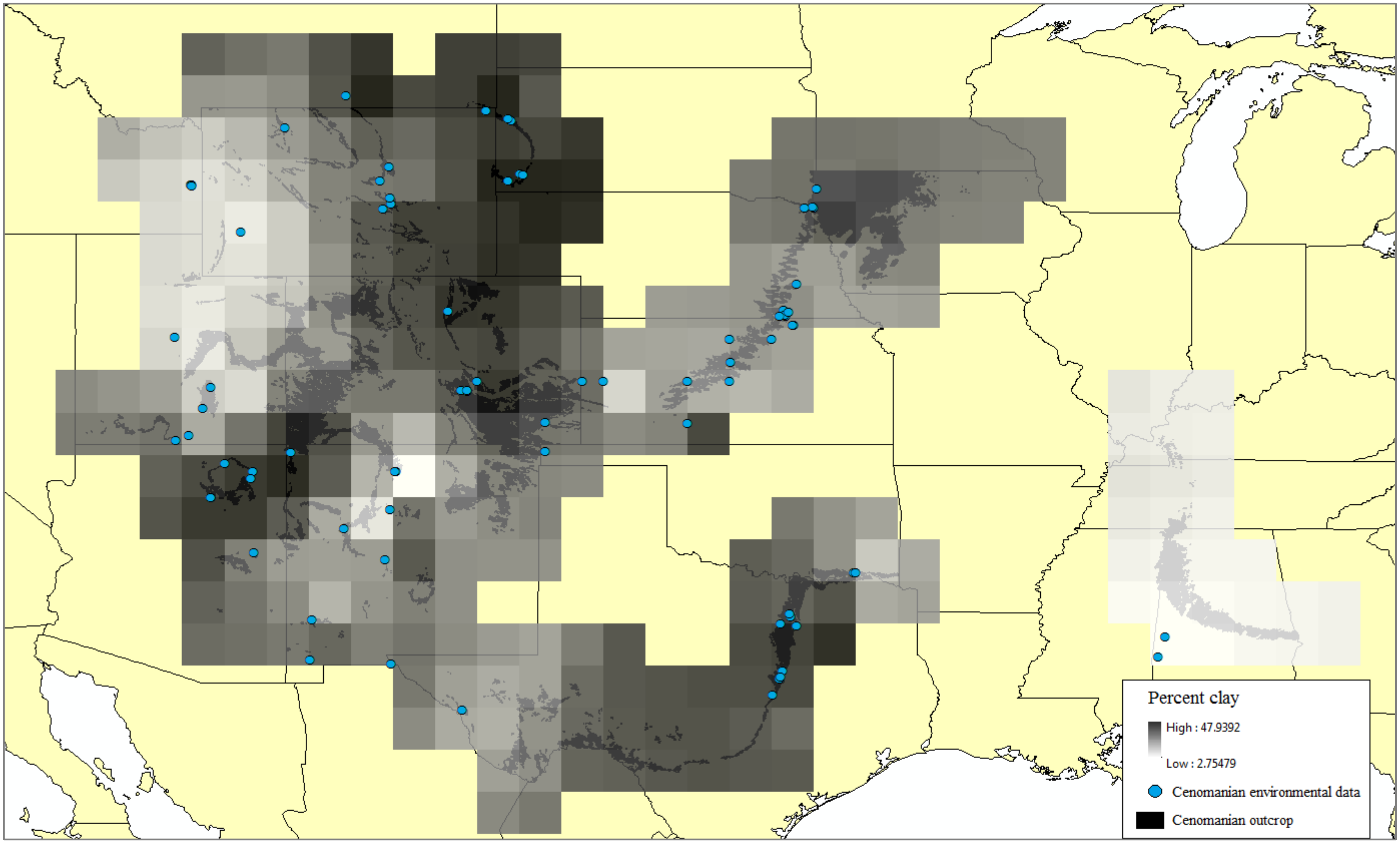
State	CEN environmental references	TUR environmental references
Texas	Christopher 1982; Clark 2009 (M.Sc. Thesis); Huffman 1960 (M.Sc. Thesis); Powell 1965; Ambrose et al. 2009; Hancock 2004; McArthur et al. 1994; Main 2005 (M.Sc. Thesis); Tiedemann 2010 (M.Sc. Thesis); Reaser and Dawson 1995; Denison et al. 2003	Powell 1965; Christopher 1982; Clark 2009 (M.Sc. Thesis)
Colorado	Hancock 2004; McArthur et al. 1994; Simmons et al. 2001; Elder 1985; Keller and Pardo 2004; Keller et al. 2004; Cobban and Scott 1972 (informed by Elder and Kirkland 1985)	Cobban and Scott 1972; Elder 1985; Glenister and Kauffman 1985; Keller and Pardo 2004; Keller et al. 2004; Merewether et al. 2006; Lewis 2013 (M.Sc. Thesis)
South Dakota	Ryan 1964; Hancock 2004; Desmares et al. 2007; Cicimurri 2001; Kennedy et al. 1998	McArthur et al. 1994; Harris et al. 2003; Cappetta 1973
New Mexico	McArthur et al. 1994; Chafetz 1982; Hook and Cobban 2007; Lucas and Lawton 2005; Lucas and Reinhart 2009; Owen et al. 2005; Lucas et al. 2010; Simons et al. 2001; Curiale 1994 (vol. 22); Nummedal et al. 1993; Coates and Kauffman 1973; Elder 1985	Dane et al. 1957, 1966, 1968; Coates and Kauffman 1973; Hook 1983; Elder 1985; Nummedal et al. 1993; McArthur et al. 1994; Curiale 1994; Simons et al. 2001; and Cobban 2011
Utah	McArthur et al. 1994; Titus et al. 2005; Alright et al. 2007; Harris et al. 2003; Tibert et al. 2003; Antia and Fielding 2011	Kauffman 1985 (SEPM Field Guide 3); White 1999 (Ph.D. Dissertation); Titus et al. 2005; Albright et al. 2007; Tibert et al. 2003
Wyoming	Myers 1977; McArthur et al. 1994; Bhattacharya and Willis 2001; Merewether and Gautier 2000; Merewether and Cobban 1986; Eicher 1967	McArthur et al. 1994; Tillman and Almon 1979; Winn 1989; Haun 1958; Merewether and Cobban 1986
Arizona	Kirland 1982; Elder 1985; Elder 1991; Kirkland 1991; Olson 1991	Elder 1985; Elder 1991; Kirkland 1991; Olson 1991; Puckett 2003; Mancini et al. 2008
Alabama	Mancini and Payton 1987; Puckett 2003; Mancini et al. 1987, 2008	Puckett 2003; Mancini et al. 2008
Oklahoma	Huffman et al. 1975; Kauffman et al. 1977	Kauffman et al. 1977
Nebraska	Koch 2007 (M.Sc. Thesis; Koch et al. 2009; Pabian and Lawton 1987 (GSA Centennial Field Guide); Pratt and Threlkeld 1984; Joeckel 1987; Koch and Brenner 2009	Arratia and Chorn 1998; Pratt and Threlkeld 2009
Iowa	Witzke et al. 1983; Witzke and Ludvigson 1987; Elderbak et al. 2014	Witzke et al. 1983; Witzke and Ludvigson 1987 (GSA Centennial Field Guide); Elderback et al. 2014; White and Arthur 2006
Kansas	Hattin 1965, 1969, 1975; Scott et al. 1998; Koch 2007 (M.Sc. Thesis); Koch et al. 2009; Hattin and Twiss 1988 (GSA Centennial Field Guide); Simons et al. 2001; Elder 1985	Hattin 1962, 1966, 1975; Elder 1985; Hattin and Twiss 1988 (GSA Centennial Field Guide); Scott et al. 1998 (SEPM Sed/Paleo No. 6)
Montana	Lang and McGugan 1987; Mudge and Sheppard 1968; Cobban et al. 1976	Gautier 1985; McArthur et al. 1994; Lang and McGugan 1987; Mudge and Sheppard 1968; Young 1951; Nielsen et al. 2008; Cobban et al. 1976
Idaho	Krumenacker 2010	

Appendix 2 – Interpolated environmental layers, in which lighter colors are less suitable habitat and darker colors are more suitable for that taxon. Blue dots denote areas where environmental data was collected (i.e., outcrop location). Outcrop for Cenomanian or Turonian is also displayed.

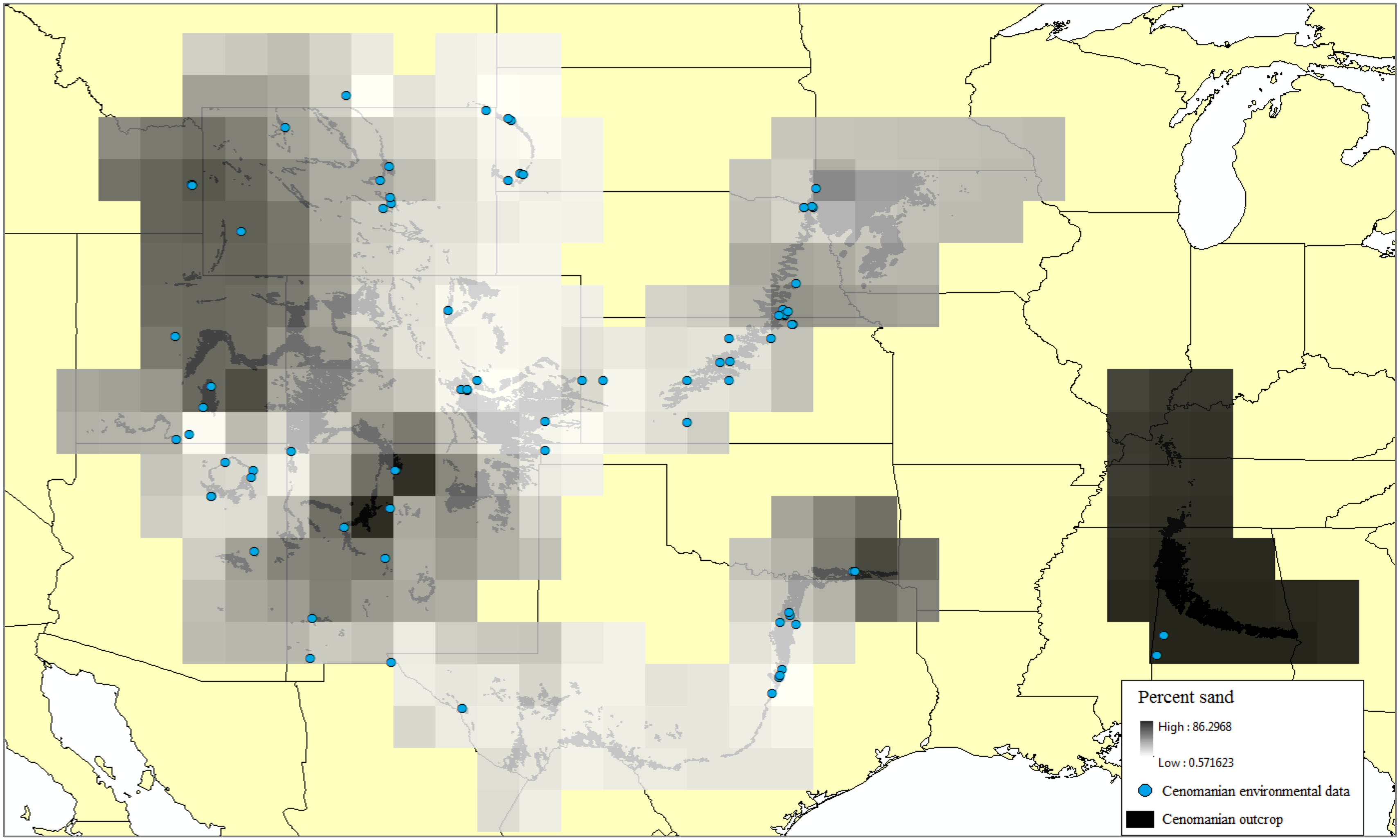
Cenomanian: Bedding thickness



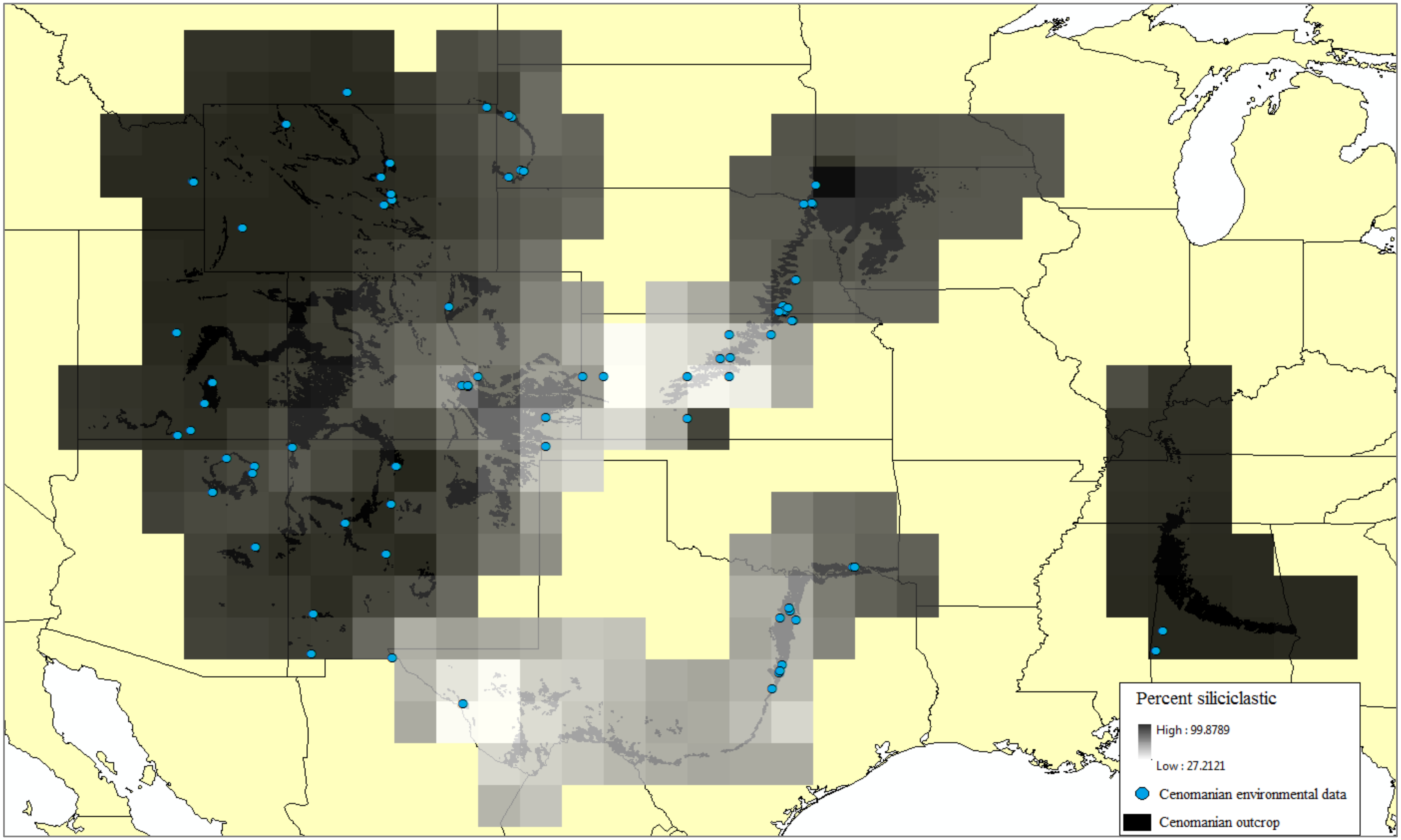
Cenomanian: Percent clay



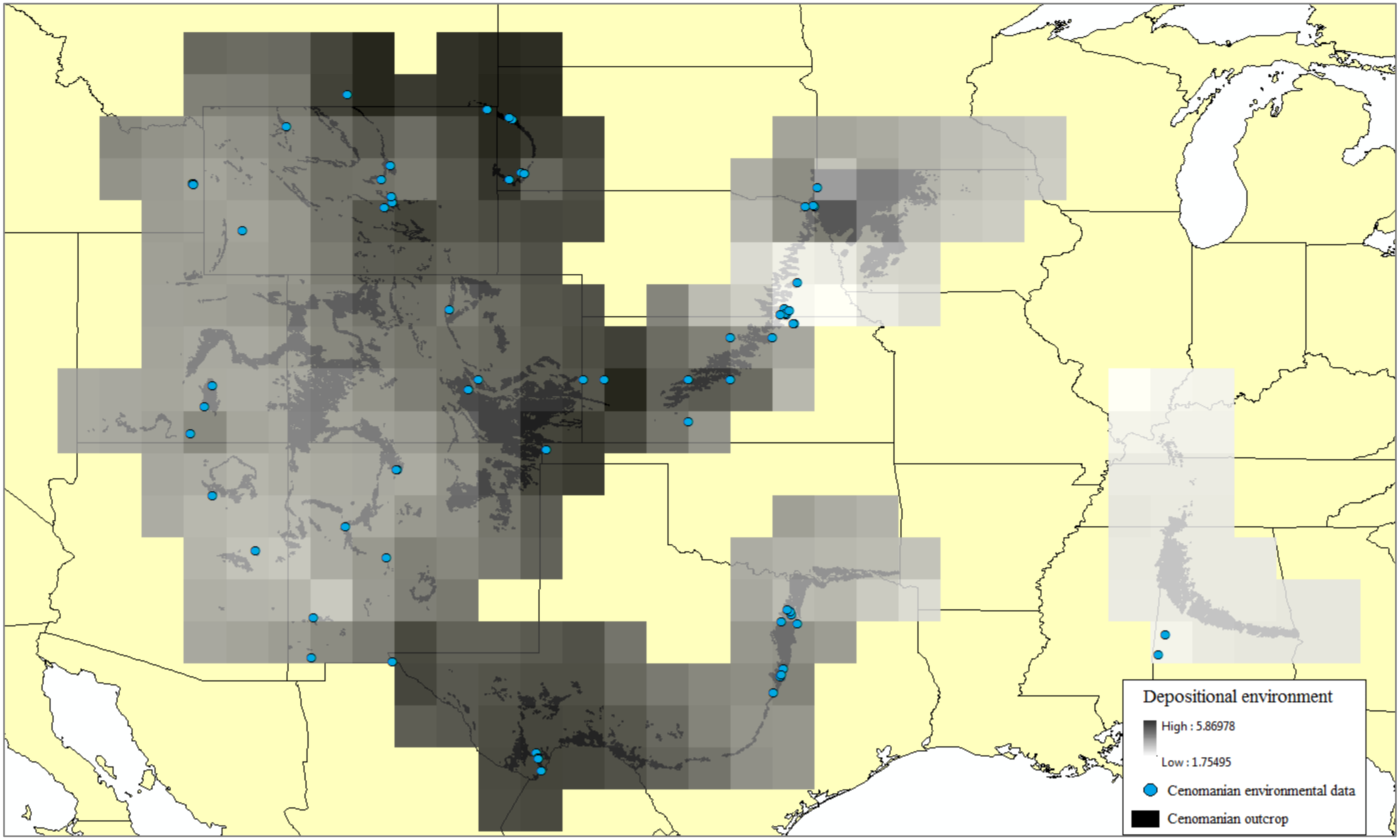
Cenomanian: Percent sand



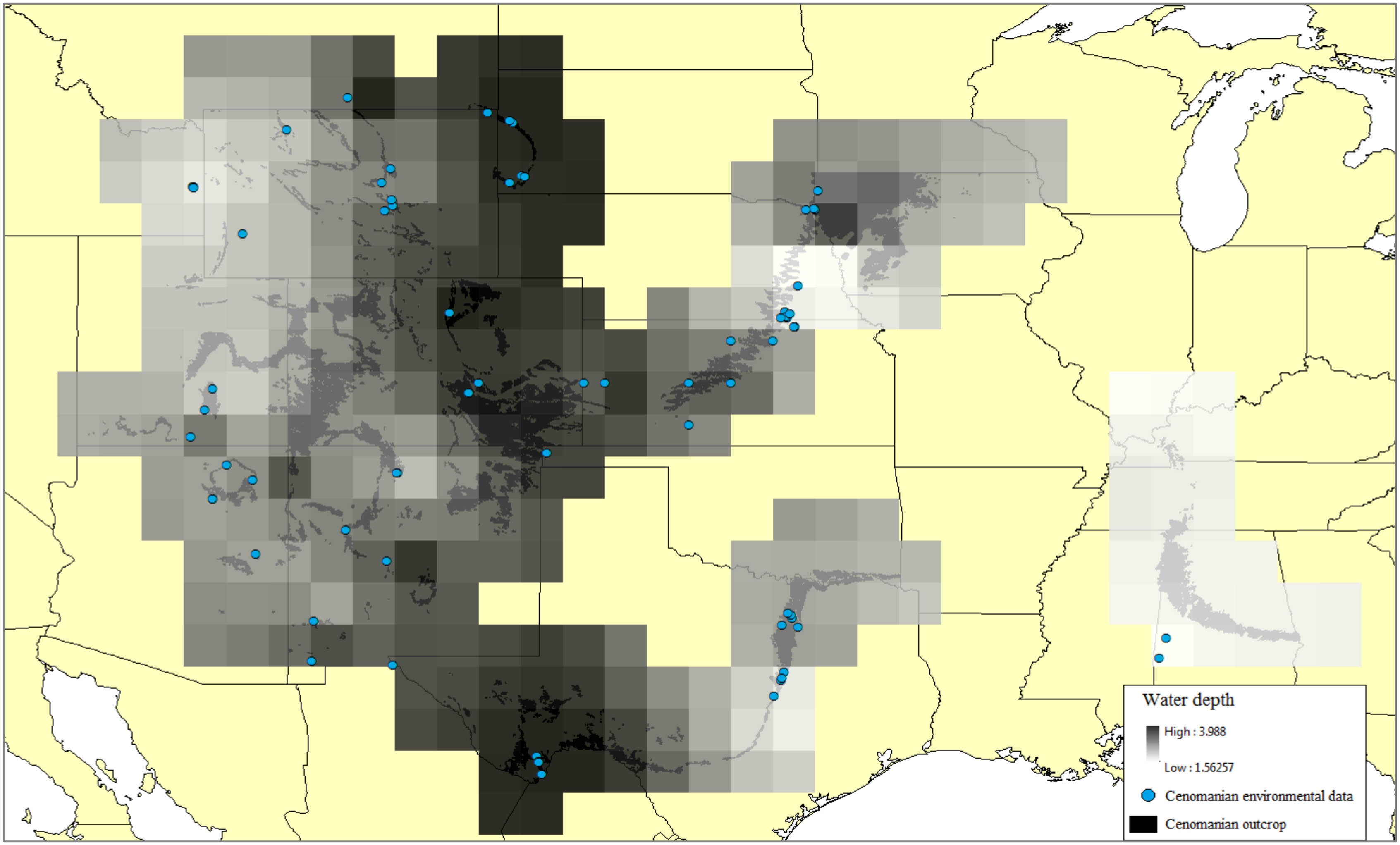
Cenomanian: Percent total siliciclastic



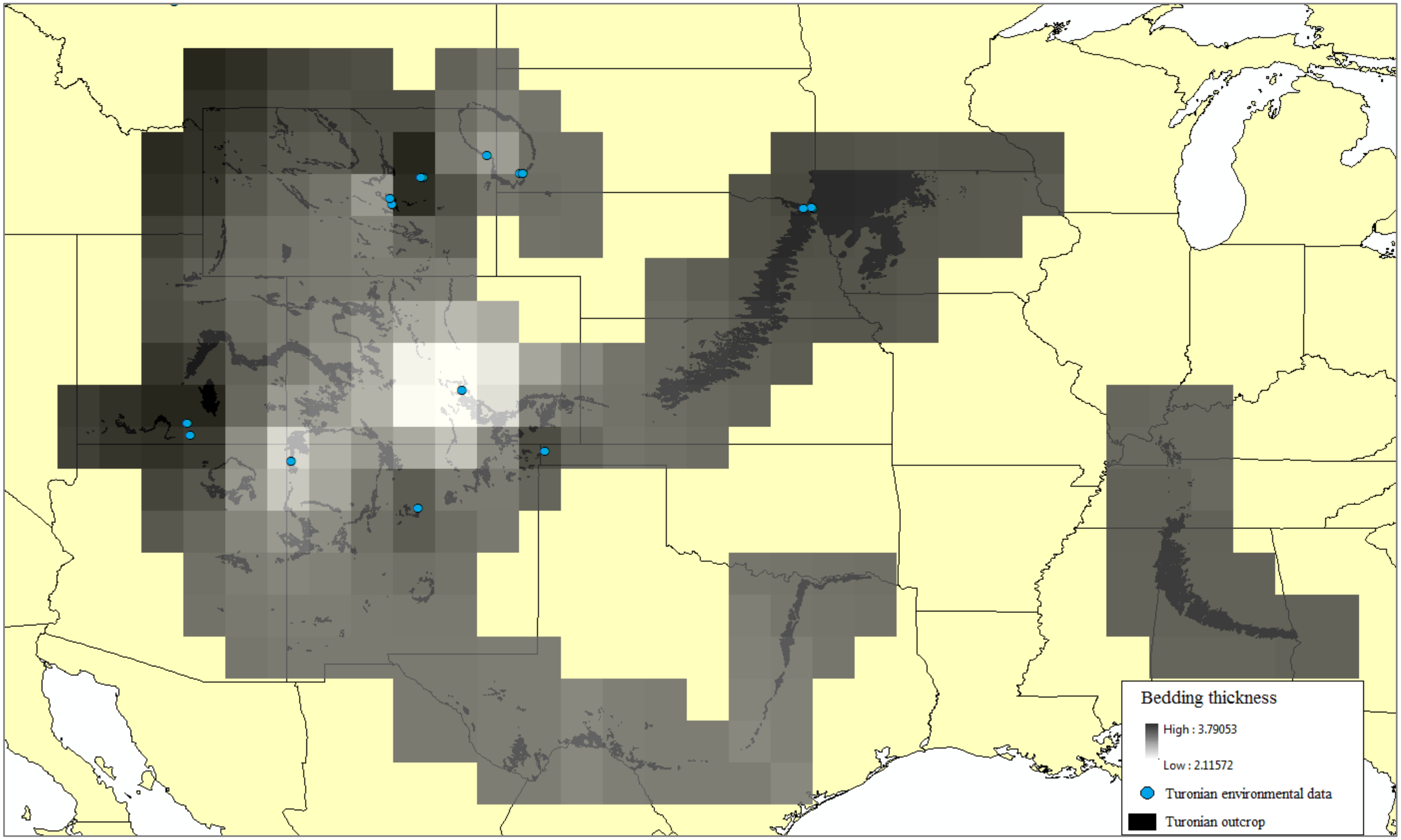
Cenomanian: Depositional environment



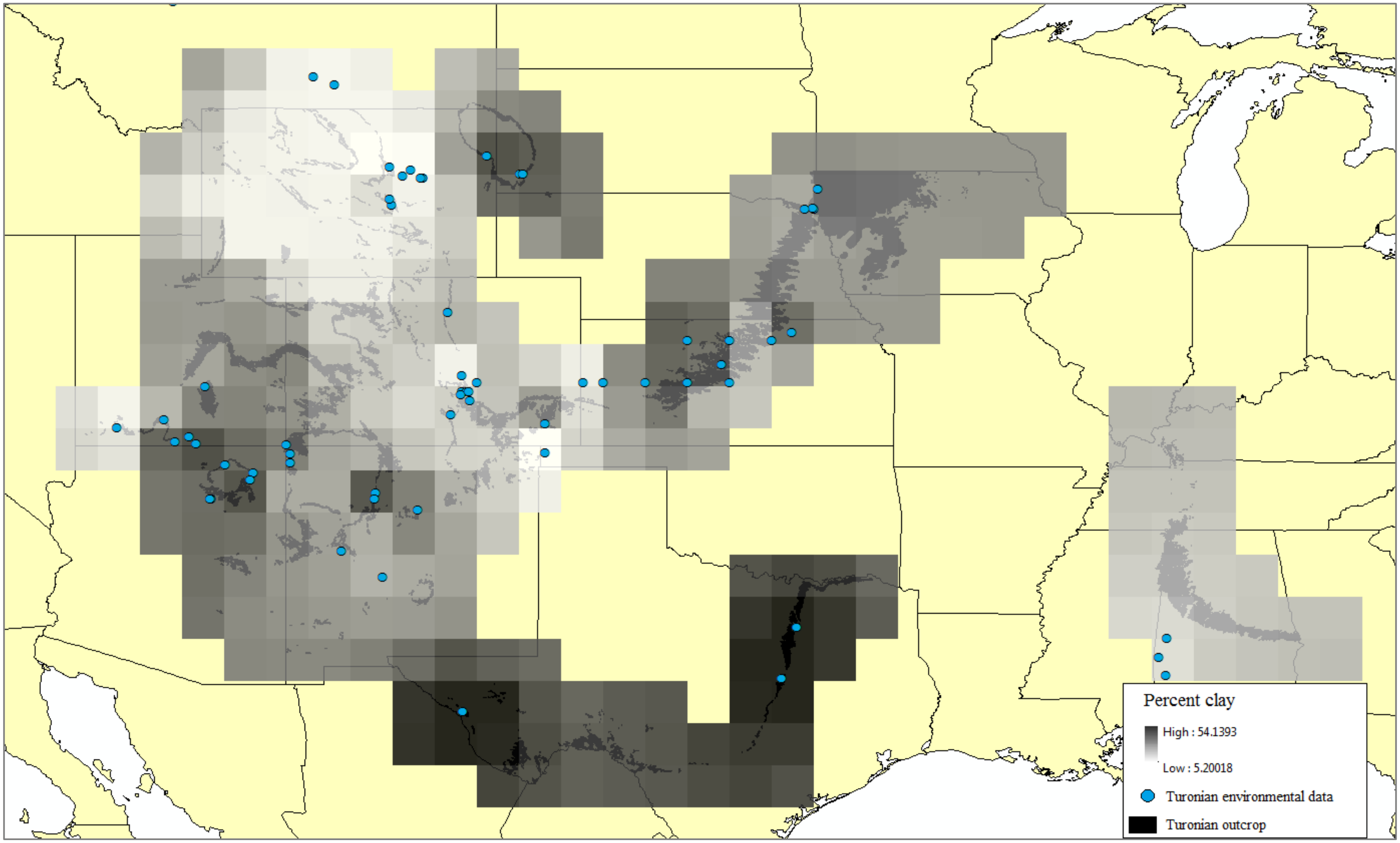
Cenomanian: Inferred water depth



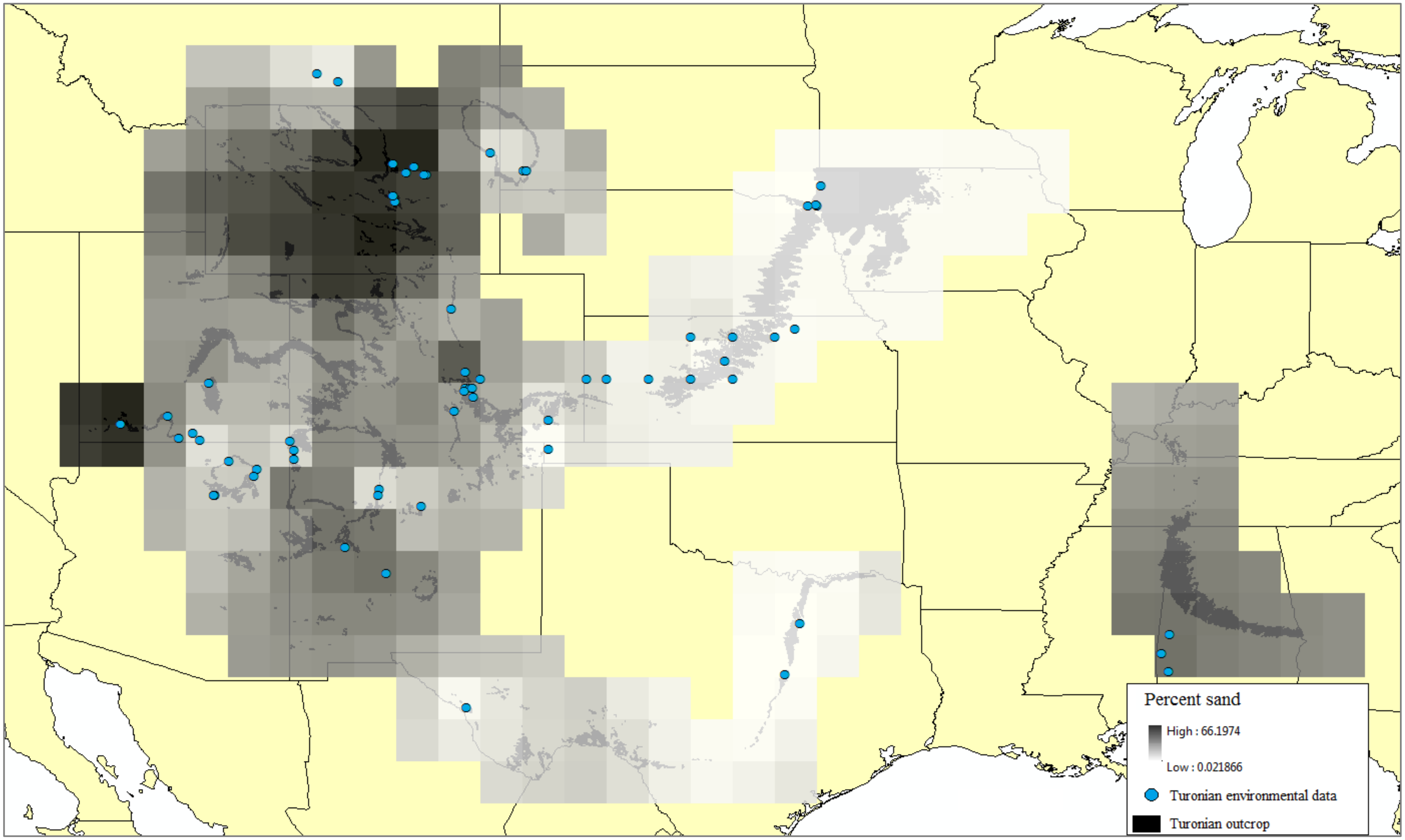
Turonian: Bedding thickness



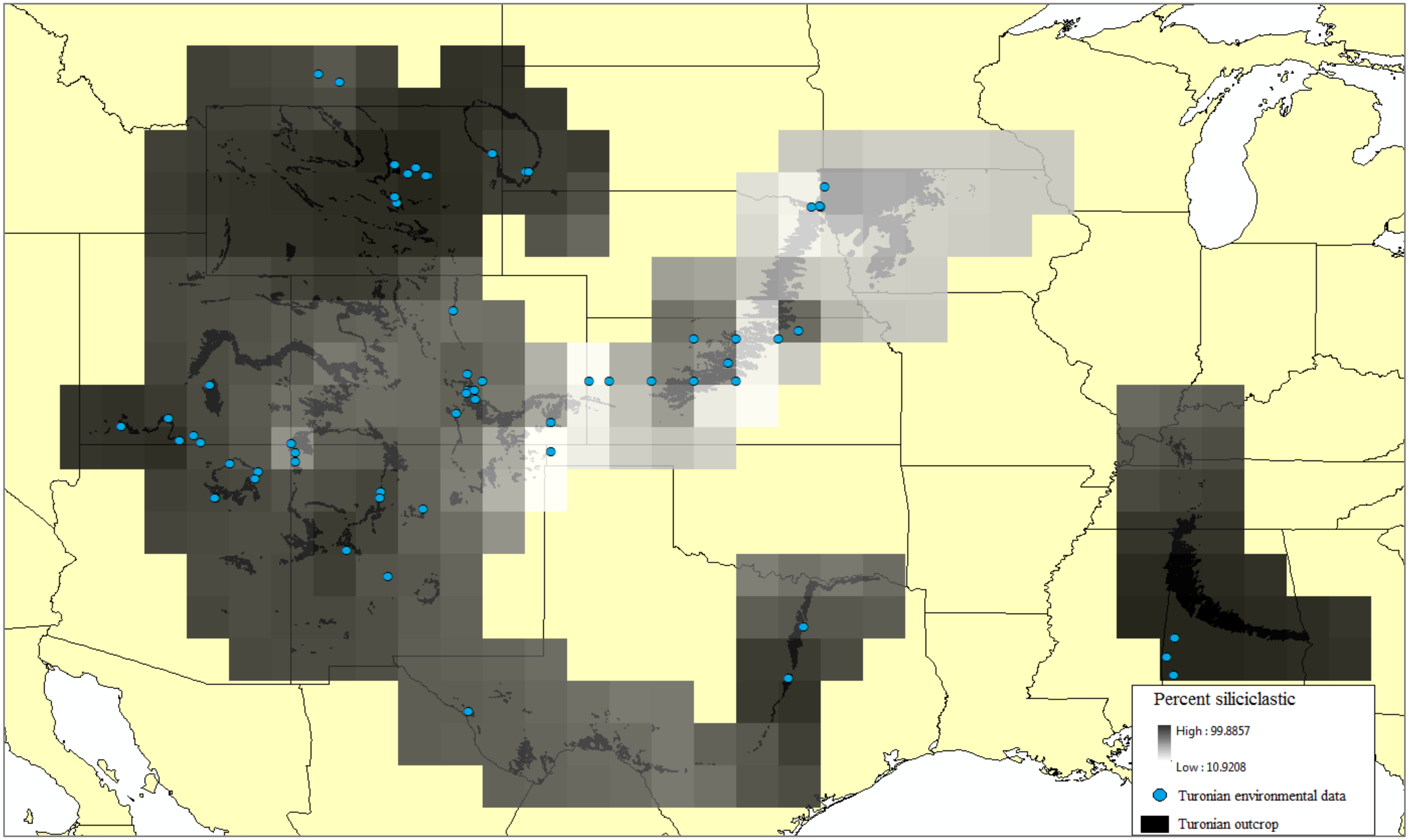
Turonian: Percent clay



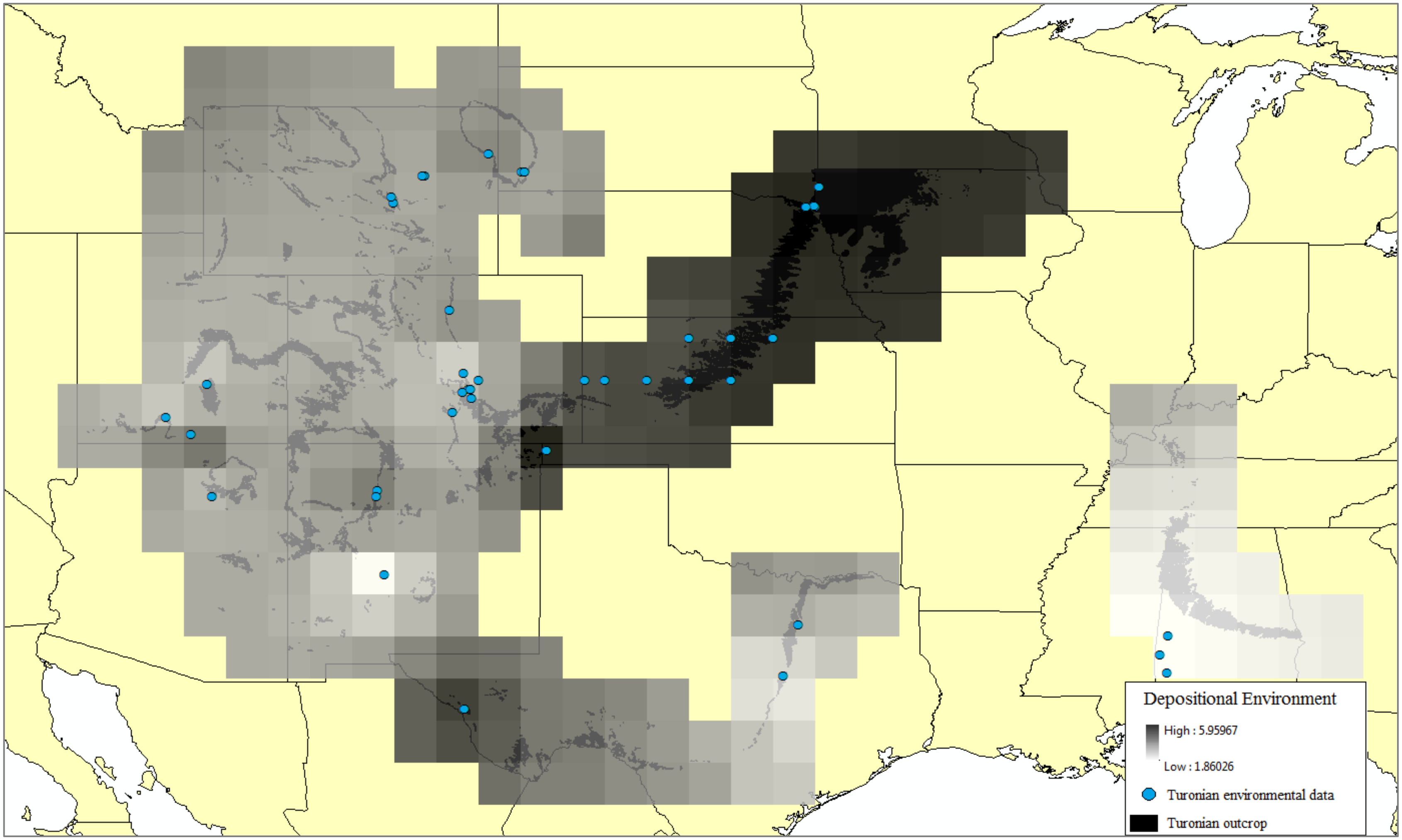
Turonian: Percent sand



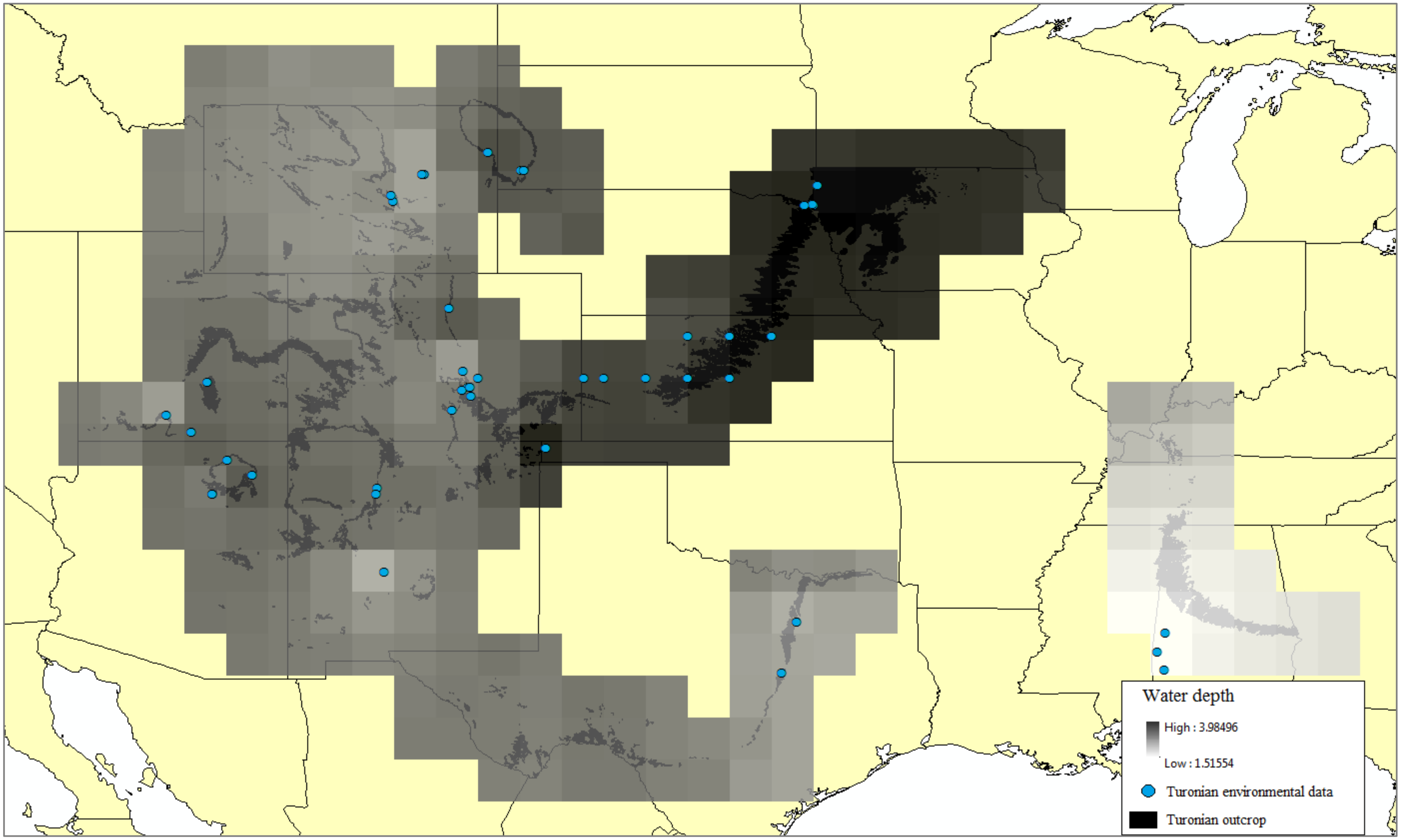
Turonian: Percent total siliciclastic



Turonian: Depositional environment



Turonian: Inferred water depth



Appendix 3 – Information on the environmental layers collected from various publications. Table includes publication, latitude and longitude, state and county, formation and member (if available), and the environmental layers used in this study (% clay, % silt, % sand, % total siliciclastic, bedding style or thickness, inferred water depth, and depositional environment).

Appendix 3.1 Cenomanian environmental data

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Christopher 1982	32.6956	-96.9044	TX	Dallas	Eagle Ford Group		61.6	25	0.5	87.1		3.30	4.26
Clark 2009 MS THESIS	32.7516	-97.2755	TX	Tarrant	Mainstreet Limestone		1	1	0	2	4	3	3.5
Clark 2009 MS THESIS	31.6114	-97.2289	TX	McLennan	Grayson Marl		58.2	38.4	0	96.6		2.5	4
Clark 2009 MS THESIS	31.4221	-97.3145	TX	McLennan	Grayson Marl		58.2	38.4	0	96.6		2.5	4
Clark 2009 MS THESIS	31.0558	-97.4642	TX	Bell	Buda Limestone		0	0	0	0			2.5
Clark 2009 MS THESIS	31.4850	-97.2713	TX	McLennan	Pepper Shale		50	50	0	100	1	3.5	5
Huffman 1960 MS THESIS			TX		Boquillas								
Powell 1965	30.6820	-104.8402	TX	Jeff Davis	Chispas Summit Formation & Buda Limestone		17.4	17.4	3.5	38.3			
Ambrose et al. 2009	32.1581	-94.9496	TX	Rusk	Woodbine Group		17.1	34	48.9	100	2.02	2.13	1.68
Ambrose et al. 2009	32.3843	-94.9088	TX	Gregg	Buda Limestone & Woodbine Group	Maness Shale	18.1	45.4	34.6	98.1		2	1.74
Hancock 2004	32.8983	-97.0402	TX	Dallas / Tarrant	Woodbine Group & basal Eagle Ford	Lewisville unit	68.2	0	0	68.2		1.63	2
Hancock 2004	38.2683	-104.7244	CO	Pueblo	Graneros Shale / Thatcher Limestone		38.1	46.9	0	85	0.85	3.85	4
Hancock 2004	43.3997	-103.3950	SD	Fall River	Belle Fourche Shale		44.6	43.2	10.5	98.3	1.1	3.80	4

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
McArthur et al. 1994	38.277	-104.7326	CO	Pueblo	Grnhrn Limestone								
McArthur et al. 1994	33.6267	-136.0108	TX	Grayson	Woodbine Formation								
McArthur et al. 1994	44.15958	-106.77783	WY	Johnson	Frontier Formation								
McArthur et al. 1994	33.2147	-97.1331	TX	Denton	Grayson Marl								
Main 2005 MS THESIS	32.9848	-97.0684	TX	line btwn Denton & Tarrant	Woodbine Formation	Lewisville Mbr	17.6	21.8	59.3	98.7	1	2.75	1.82
Tiedemann 2010 MS THESIS	29.6232	-103.1111	TX	Brewster	Buda Limestone						0	4	4.5
Tiedemann 2010 MS THESIS	29.4938	-103.0581	TX	Brewster	Buda Limestone						2.33	4	4.5
Tiedemann 2010 MS THESIS	29.4910	-103.0639	TX	Brewster	Buda Limestone & Boquillas Formation						0.75	4	5
Tiedemann 2010 MS THESIS	29.2021	-102.9878	TX	Brewster	Buda Limestone							4	4.5
Reaser and Dawson 1995	33.0210	-97.1478	TX	Denton	Buda Limestone							2.5	3
Denison et al. 2003	32.7660	-97.1850	TX	Tarrant	Grayson Marl								
Denison et al. 2003	32.7420	-97.1800	TX	Tarrant	Grayson Marl								
Denison et al. 2003	32.7690	-97.2150	TX	Tarrant	Grayson Marl								
Denison et al. 2003	30.2930	-97.7240	TX	Travis	Buda Limestone								
Denison et al. 2003	33.0460	-97.1860	TX	Denton	Buda Limestone & Grayson Marl								
Denison et al. 2003	33.0190	-97.1520	TX	Denton	Buda Lmst								
Chafetz 1982	32.8441	-108.4157	NM	Grant	Beartooth Quartzite & lower CO Shale		13.2	32.1	54.7	100	2.81	2.36	2.32
Hook and Cobban 2007	34.2626	-106.6793	NM	Socorro	Dakota Sandstone & Mancos Shale		36.3	36.3	27.4	100		3.86	3.73

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Lucas and Lawton 2005	31.8727	-108.4642	NM	Grant	Mancos Shale		39.2	47.9	5.8	92.9		4	4
Lucas and Reinhart 2009; Owen et al. 2005	36.3573	-106.4283	NM	Rio Arriba	Dakota Sandstone	Oak Canyon & Cubero SS Tongue Mbrs	3.1	15.1	81.1	99.3	4	2.46	3.21
Lucas and Reinhart 2009; Owen et al. 2005	36.3573	-106.4462	NM	Rio Arriba	Dakota Sandstone & Mancos Shale	Encinal, Oak Canyon, & Cubero SS	5.1	18.2	76.7	100	3.38	2.19	2.92
Lucas et al. 2010	31.7965	-106.5478	NM	Dona Ana	Del Rio, Buda, Mancos Shale	"Boquillas Fm" of Mancos Sh	30.6	29.3	0.2	60.1		3.5	4.86
Nummedal et al. 1993	35.0071	-107.6532	NM	Cibola	Dakota Sandstone	Twowells SS Tongue	0	0	100	100	3	3	3
Coates and Kauffman 1973	35.4635	-160.5633	NM	Santa Fe	Graneros Shale & Greenhorn Limestone	Bridge Creek Lmst equiv in Grnhrn	32.4	34.5	25.5	92.4	1.37		
Kirkland 1982	34.4376	-109.8047	AZ	Apache			17	27.1	55.9	100		2.5	2.5
Olsen 1991	35.7397	-110.8217	AZ	Coconino	Dakota Sandstone & Mancos Shale		52.3	36.3	3.1	91.7		2.36	2.71
Elder 1985	35.7300	-110.8183	AZ	Coconino			39.5	39.6	5.8	84.9			
Elder 1985	36.3483	-109.8183	AZ	Apache			42.6	44	0	86.6			
Elder 1985	36.8067	-108.9283	NM	San Juan			44.5	42.6	0	87.1			
Elder 1985	38.2817	-104.8680	CO	Pueblo	Greenhorn Limestone	Bridge Creek Lmst	24.5	18.4	0	42.9	2		
Elder 1985	37.5183	-102.8783	CO	Baca			32.1	31.8	0	63.9			
Elder 1985	38.9217	-98.7067	KS	Russell			27.3	30.2	0	57.5			
Kirkland 1991	35.7397	-110.8217	AZ	Coconino	Dakota Sandstone & Mancos Shale		56.5	33.2	3.5	93.2		3.40	2.38

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Kirkland 1991	36.5526	-110.4845	AZ	Navajo	Dakota Sandstone & Mancos Shale		36.6	35.8	22.7	95.1		2.54	2.21
Kirkland 1991	36.1836	-109.8800	AZ	Apache	Dakota Sandstone & Mancos Shale		48.3	32.9	2.1	83.3		3.97	2.49
Elder 1991	35.7397	-110.8217	AZ	Coconino						0			
Mancini et al 1987; Mancini/Pay.on 1981	31.2500	-87.8607	AL	Clarke	Lower Tuscaloosa	Pilot Sand unit & Marine Sh	15.3	5.2	76.9	97.4		2.5	3
Mancini et al. 2008 (including info from Mancini/Puckett 2003a)	30.7726	-88.1853	AL	Mobile	Lower Tuscaloosa Group and lowest Middle Tuscaloosa	Massive Sand, Marine Tuscaloosa	3.4	16.6	80	100		1.8	2.1
Mancini et al. 2008 (including info from Mancini/Puckett 2003a)	31.0468	-88.2853	AL	Mobile	Lower Tuscaloosa Group and lowest Middle Tuscaloosa	Massive Sand, Marine Tuscaloosa	2.1	10.4	87.5	100		1.5	1.88
Mancini et al. 2008 (including info from Mancini/Puckett 2003a)	31.5509	-88.1447	AL	Washington	Lower Tuscaloosa Group and lowest Middle Tuscaloosa	Massive Sand, Marine Tuscaloosa	1.2	5.9	92.9	100		1.28	1.71
Mancini et al. 2008 (including info from Mancini/Puckett 2003a)	31.9658	-88.3192	AL	Choctaw	Lower Tuscaloosa Group and lowest Middle Tuscaloosa	Massive Sand, Marine Tuscaloosa	1	4.8	94.2	100		1.24	1.68
Mancini et al. 2008 (including info from Mancini/Puckett 2003a)	32.4197	-88.1350	AL	Sumter	Lower Tuscaloosa Group and lowest Middle Tuscaloosa	Massive Sand, Marine Tuscaloosa	3.9	18.8	77.3	100		1.90	2.18

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Huffman et al. 1975	33.9463	-95.5126	OK	Choctaw	Bennington Limestone & Woodbine Formation		5.7	0	51.4	57.1			
Huffman et al. 1975	33.9608	-95.5476	OK	Choctaw	Woodbine Formation		33.7	0	64.3	98			
Huffman et al. 1975	33.9462	-95.4952	OK	Choctaw	Woodbine Formation		0	0	100	100			
Kauffman et al. 1977	36.8210	-102.8773	OK	Cimarron	Graneros Shale & Greenhorn Limestone		21.6	23.1	1.9	46.6	2.5	3.76	5.1
Hattin 1969 (KGS Bull 194)	38.9586	-98.4739	KS	Lincoln	Graneros Shale & Greenhorn Limestone		7.6	7.6	0.6	15.8	2.5		
Hattin and Twiss 1988 (GSA Centennial Field Guide)	38.9223	-98.6961	KS	Russell	Graneros Shale & Greenhorn Limestone								
Pabian and Lawton 1987 (GSA Cenntennial Field Guide)	42.6032	-96.7116	NE	Dixon	Omadi Sandstone & Dakota Group, Graneros Shale, Grnhrn Limestone		14.1	60.4	2.5	77	3		
Witzke and Ludvigson 1987 (GSA Centennial Field Guide)	42.6124	-96.4988	IA	Plymouth	Dakota, Graneros		41.6	49.2	4.9	95.7	3	3.72	2.94
Koch 2007 MS THESIS; Koch et al. 2009	40.1834	-97.2077	NE	Jefferson	Dakota Sandstone		45	45	0	90		1.5	1
Koch 2007 MS THESIS; Koch et al. 2009	39.8207	-96.9848	KS	Washington	Dakota Sandstone		8.3	40.6	51.1	100		1.5	1
Koch 2007 MS THESIS; Koch et al. 2009	40.0528	-97.1701	NE	Jefferson	Dakota Sandstone		38.3	38.3	23.4	100		1.5	1

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Koch 2007 MS THESIS; Koch et al. 2009	39.8207	-97.0035	KS	Washington	Dakota Sandstone		8.2	40.2	51.6	100		1.5	1
Koch 2007 MS THESIS; Koch et al. 2009	40.0669	-97.1989	NE	Jefferson	Dakota Sandstone		0	0	100	100		1.5	1
Scott et al. 1998 (SEPM Sed/Paleo No6)	38.4873	-101.9839	KS	Greeley	Dakota, Graneros, Greenhorn		36	27.9	27.6	91.5		3.17	4.18
Witzke et al. 1983	43.0768	-96.4218	IA	Sioux	Dakota, Graneros, Greenhorn	Woodbury Mbr / Dakota	27.2	35.4	36.4	99		2.57	2.38
Hattin 1965 (KGS Bull 178); Hattin 1975 (KGS Bull 209)	39.5000	-97.5000	KS	Washington	Dakota, Graneros, Greenhorn	Lincon / Grnhrn, Hartland (part) / Grnhrn	23.4	25.9	8.1	57.4		3.28	4.25
Hattin 1965 (KGS Bull 178); Hattin 1962 (KGS Bull 156)	39.5000	-98.5000	KS	Osborne	Dakota, Graneros, Greenhorn	Lincoln (part) / Grnhrn	36	44.8	15.6	96.4		2.97	3.5
Hattin 1965 (KGS Bull 178); Hattin 1975 (KGS Bull 209)	38.5000	-98.5000	KS	Russell	Dakota, Graneros, Greenhorn	Lincoln / Grnhrn, Hartland / Grnhrn	16.7	19.8	12.7	49.2		3.32	4.3
Hattin 1965 (KGS Bull 178); Hattin 1975 (KGS Bull 209)	38.5000	-99.5000	KS	Ford & Hodgeman	Dakota, Graneros, Greenhorn	Lincoln / Grnhrn, Hartland / Grnhrn	16	17.8	8.8	42.6		3.43	4.49
Hattin 1965	37.5000	-99.5000	KS		Dakota, Graneros		39.9	39	20.4	99.3		2.87	3.3
Hattin 1975	38.5000	-101.5000	KS	Hamilton & Kearney	Greenhorn Limestone	Lincoln / Grnhrn, Hartland / Grnhrn, Bridge Crk / Grnhrn (part)	5.4	5.3	0	10.7		3.89	5.39

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Keller and Pardo 2004; Keller et al. 2004	38.2817	-104.7313	CO	Pueblo	Greenhorn Limestone	Harland Sh / Bridge Crk Lmst	42.7	42.7	0	85.4			
Cobban and Scott 1972 (informed by Elder and Kirkland 1985); Kauffman 1985	38.5000	-104.5000	CO	Pueblo	Graneros Shale & Greenhorn Limestone	Lincoln Lmst, Hartland Sh, Bridge Crk Lmst / Grnhrn	44.8	46.2	0	91	3.03	3.65	4.1
Kauffman 1985 - SEPM Field Guide 3	40.1636	-105.1867	CO	Boulder	Graneros Shale & Greenhorn Limestone	Lincoln Lmst, Hartland Sh, Bridge Crk Lmst / Grnhrn	40.6	46.5	3.2	90.3		4	3.72
Lang and McGugan 1987	48.3536556	-113.2917343	MT		Marias River Shale	Cone	45	45	0	90	4	4	5.5
Titus et al. 2005	37.0825	-111.6643	UT	Kane/ Garfield	Straight Cliffs		27.75	33.3	99.8				
Mudge and Sheppard 1968	47.5333	-111.7214	MT		Marias River Shale	Floweree Shale	45.85	49.15	5	100			
Elderbak et al. 2014	42.641087	-96.525303	IA	Plymouth	Graneros & Greenhorn Shale		16.82	36	82	4	3	4.5	
Albright et al. 2007	37.5	-111.4	UT		Dakota Formation, Tropic Shale		34.375	25	93.75	3.33	3.38	3.88	
Albright et al. 2007	37.5	-111.33	UT		Dakota Formation, Tropic Shale		40.9	18.2	0				
Desmares et al. 2007	43.4316	-103.4744	SD	Fall River			42.9	0	0	42.9	3.5	4	4.09
Harris et al. 2003	37.2149496	-111.3417587	UT		Mancos Shale		18.375	79.54	0	97.915	2.5	3.04	3.58
Pratt and Threlkeld 2009	42.6052	-96.7193	NE		Greenhorn		45	45	0	90	4	4	5.5
Hancock 2004	43.399722	-103.395556	SD	Fall River	Frontier Formation	Belle Fourche Shale	44.28	43.42	10.63	98.33	3.6	3.82	3.89
Joeckel 1987	40.8066688	-96.9012981	NE	Lancaster	Dakota & Graneros Shale		50.7	38.9	100	4	0	1	

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Cicimurri 2001	44.691271	-103.693088	SD	Butte	Belle Fourche Shale & some OLLM		43.3	0	89.3	3.5	4	5.07	
Ryan 1964	43.2604946	-103.7591508	SD		Frontier Formation	Belle Fourche Shale	50	50	0	100	4	4	6
Myers 1977	42.0545467	-110.119037	WY	Lincoln	Frontier Formation	Coalville Member	6.5	31.6	61.9	100	4	2.27	3.08
Bhattacharya and Willis 2001	43.2533413	-106.802034	WY	Natrona	Frontier Formation	Belle Fourche Member	14.55	14.55	70.9	100	4	2.23	3.15
Tibert et al. 2003	39.5554	-111.6777	UT	Sanpete	Dakota Formation		3.8	37.1	59.1	100			
Kennedy et al. 1996	44.7344278	-103.7504644	SD	Butte	Greenhorn Formation		56.74	0	67.67	3	4	5	
Merewether and Gautier 2000	43.5999321	-106.5754541	WY	Johnson	Frontier Formation	Belle Fourche (part)	27.13	68.52	4.27	99.92	3.43	2.8	3.23
Antia and Fielding 2011	37.85	-111.02	UT		Dakota Sandstone		7.27	29.38	63	99.65	4	2	3
Antia and Fielding 2011	38.36262	-110.81659	UT		Dakota Sandstone		2.39	4.05	93.12	99.56	4	2	3
Merewether and Cobban 1986	42.7120168	-106.5313928	WY	Natrona	Frontier Formation	Belle Fourche Member	39.99	48.09	5.07	93.15	3.32	3.66	4.53
Merewether and Cobban 1986	42.8563121	-106.5633978	WY	Natrona	Frontier Formation	Belle Fourche Member	35.43	40.04	19.57	95.04	3	3.32	4.12
Cobban et al. 1976	47.7495005	-110.9939544	MT		Marias River Shale	Floweree Member	30.04	60.3	7.8	98.14	3.4	2.72	4.03
Krumenacker 2010	43.1504471	-111.2934479	ID		Wayans Formation		10.85	21.91	66.16	98.92	3	1.8	3.25
Krumenacker 2010	43.1583795	-111.2842757	ID		Wayans Formation		10.16	15.98	72.85	98.99	3.43	1.76	3.13
Krumenacker 2010	43.1438706	-111.2644746	ID		Wayans Formation		8.13	42.08	48.23	98.45	3.17	2.12	3.13
Koch and Brenner 2009	40.0454022	-97.3125411	NE	Jefferson			9.81	9.81	80.38	100	3.33	2.13	3.28
Koch and Brenner 2009	40.1319019	-97.0862145	NE	Jefferson			34.39	65.61	0	10	3.5	2.83	3.33
Eicher 1967	44.5283456	-109.0680478	WY	Park	Frontier Formation		43.92	34.03	100	2.84	2.16	3.55	

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Eicher 1967	42.5825862	-106.7268328	WY	Natrona	Frontier Formation	Belle Fourche equivalent	48.13	9.68	100	3.2	3.57	5.36	
Eicher 1967	45.2678886	-107.6117471	NT	Big Horn	Cody Shale	Belle Fourche	49.31	49.31	0	98.63	3.4	4	6
Eicher 1967	44.917166	-104.2800427	WY	Crook	Frontier Formation	Belle Fourche	49.25	49.25	0	98.5	3.25	4	6

Appendix 3.2 Turonian environmental data

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Christopher 1982	32.6956	-96.9044	TX	Dallas	Eagle Ford Group	uppermost Britton & Arcadia Park	48.2	38.9	0	87.1		2.39	3.21
Clark 2009 MS THESIS	31.4850	-97.2713	TX	McLennan	Eagle Ford Group: S Bosque Formation		50	50	0	100		2.5	2
Coates and Kauffman 1973	35.4635	-105.8985	NM	Santa Fe	Grnhrn Formation / Carlile Shale	Bridge Creek equivalent; Blue Hill Shale	40.5	40.4	0.1	81	3.47		
Dane et al. 1957	34.4845722	-107.7076917	NM	Socorro	Gallup Sandstone & Mancos Shale	Gallego SS, Pescado Tongue, Tres Hermanos equiv	28.8	28.8	39.1	96.7			
Dane et al. 1966	35.8775	-106.9097	NM	Sandoval	Mancos Shale	Juana Lopez	45.1	45.9	0	91		3	4
Dane et al. 1968	35.7278	-106.9239	NM	Sandoval	Mancos Shle	Semilla Sandstone	2.5	13.7	81.6	97.8		3.5	4
Elder 1985	35.7300	-110.8183	AZ	Coconino			44.4	44.8	0	89.2			
Elder 1985	36.3483	-109.8183	AZ	Apache			43.5	44.9	0	88.4			
Elder 1985	38.2817	-104.8680	CO	Pueblo	Greenhorn Formation	Bridge Creek Limestone	35.6	27.6	0	63.2	2		
Elder 1985	37.5183	-102.8783	CO	Baca			37.1	37.1	0	74.2			
Elder 1985	38.9217	-98.7067	KS	Russell			37.3	37.3	0	74.6			
Elder 1985	36.8067	-108.9283	NM	San Juan			39.4	29.3	0	68.7			

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Hook and Cobban 2011 & Hook 1983	33.8883	-106.7316	NM	Socorro	Bridge Creek Limestone, Tres Hermanos, & Mancos Shale	Atarque SS, Carthage Member, & Fite Ranch Member of Tres Hermanos; lower D-cross Tongue of Mancos Shale	25.3	25.3	37.6	88.2		2.37	1.92
Kauffman et al. 1977	36.8207	-102.8771	OK	Cimarron	Graneros Shale / Greenhorn Limestone	Bridge Creek Limestone	4.2	4.2	0	8.4	3.5	4	6
Kirkland 1991	35.7397	-110.8217	AZ	Coconino	Mancos Shale / Toreva Formation		29.1	40.4	25	94.5		2.76	2.20
Kirkland 1991	36.5526	-110.4845	AZ	Navajo	Mancos Shale / Toreva Formation		41	33.6	13.5	88.1		2.98	2.20
Kirkland 1991	36.1836	-109.8800	AZ	Apache	Mancos Shale / Toreva Formation		42.4	34.4	15.8	92.6		3.32	2.65
Mancini et al. 2008 (including info from Mancini & Puckett 2003a)	30.7726	-88.1853	AL	Mobile	Middle and Upper Tuscaloosa Group	"Marine Tuscaloosa" = middle Tuscaloosa	32.9	46.5	20.6	100		2.18	2.39
Mancini et al. 2008 (including info from Mancini & Puckett 2003a)	31.0468	-88.2853	AL	Mobile	Middle and Upper Tuscaloosa Group	"Marine Tuscaloosa" = middle Tuscaloosa	28.7	45.7	25.6	100		2.27	2.02
Mancini et al. 2008 (including info from Mancini & Puckett 2003a)	31.5509	-88.1447	AL	Washington	Middle and Upper Tuscaloosa Group	"Marine Tuscaloosa" = middle Tuscaloosa	18.9	43.6	37.5	100		1.5	1.88
Mancini et al. 2008 (including info from Mancini & Puckett 2003a)	31.9658	-88.3192	AL	Choctaw	Middle and Upper Tuscaloosa Group	"Marine Tuscaloosa" = middle Tuscaloosa	13.2	42.5	44.3	100		1.22	1.67

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Mancini et al. 2008 (including info from Mancini & Puckett 2003a)	32.4197	-88.1350	AL	Sumter	Middle and Upper Tuscaloosa Group	"Marine Tuscaloosa " = middle Tuscaloosa	19.2	43.7	37.1	100		1.52	1.89
Nummedal et al. 1993	36.5891	-108.9241	NM		Gallup Sandstone		0.1	0.1	99.8	100	2.72		2
Olsen 1991	35.7397	-110.8217	AZ	Coconino	Manchos Shale / Toreva Formation	Hopi Sandy Member & Blue Point Tongue / Mancos Shale	32.2	44.4	19	95.6		2.91	3.02
Powell 1965	30.6820	-104.8402	TX	Jeff Davis	Chispas Summit Formation		54.7	29.6	1.2	85.5			5
Witzke and Ludvigson 1987 (GSA Centennial Field Guide)	42.6124	-96.4988	IA	Plymouth	Greenhorn Limestone		13.6	8.3	0	21.9	3	4	5.5
Arratia and Chorn 1998			NE	Dixon	Greenhorn Limestone							3.5	
Scott et al. 1998 (SEPM Sed/Paleo No6)	38.4873	-101.9839	KS	Greeley	Greenhorn Formation, Carlile Shale	Bridge Creek Limestone / Grnhrn, Fairport Chalk / Carlile, Blue Hill Shale / Carlile, Codell SS / Carlile	17.4	19.1	25.2	61.7		3.22	4.31
Witzke et al. 1983	43.0768	-96.4218	IA	Sioux	Greenhorn Formation/ Carlile Shale		39	41.7	0	80.7		3.15	4.48

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Hattin 1975 (KGS Bull 209)	39.5000	-97.5000	KS	Washington	Greenhorn Formation	Hartland Mbr / Grnhrn, Jetmore Mbr / Grnhrn, Pfeifer Mbr / Grnhrn	3.6	3.6	0	7.2		4	5.5
Hattin 1962 (KGS Bull 156)	39.5000	-98.5000	KS	Osborne	Carlile Shale	Fairport Chk, Blue Hill Sh, Codell SS / Carlile	44.1	39.8	10.4	94.3		3.32	4.66
Hattin 1975 (KGS Bull 209)	38.5000	-98.5000	KS	Russell	Greenhorn Formation	Jetmore Mbr / Grnhrn, Pfeifer Mbr / Grnhrn	3.6	3.6	0	7.2		4	5.5
Hattin 1962 (KGS Bull 156), Hattin 1975 (KGS Bull 209)	38.5000	-99.5000	KS	Hodgeman & Ellis	Greenhorn Formation, Carlile Shale	Hartland Mbr / Grnhrn, Jetmore Mbr / Grnhrn, Pfeifer Mbr / Grnhrn, Fairport Chk / Carlile, Blue Hill Sh / Carlile, Codell SS / Carlile	39.7	34.5	3.8	78		3.38	4.79
Hattin 1975	38.5000	-101.5000	KS	Hamilton	Greenhorn Limestone	Bridge Crk (Hartland equiv, Jetmore equiv, Pfeifer equiv) / Grnhrn	4	4	0	8		4	5.5

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Hattin 1962	38.5000	-100.5000	KS	Hodgeman & Finney	Carlile Shale	Fairport Chk, Blue Hill Sh / Carlile	47.2	43.6	0.6	91.4		3.3	4.7
Hattin 1962	39.5000	-99.5000	KS	Ellis	Carlile Shale	Fairport Chk, Blue Hill Sh, Codell SS / Carlile	45	42.1	6.3	93.4		3.25	4.49
Keller and Pardo 2004; Keller et al. 2004	38.2817	-104.7313	CO	Pueblo	Greenhorn Limestone	Bridge Crk Lmst	25.9	1.7	0	27.6			
Lewis 2013 - MS THESIS	38.6721	-104.8572	CO	El Paso	Carlile Shale	Codell SS, Juana Lopez	5.7	18.2	66.7	90.6		2.24	2.3
Lewis 2013 - MS THESIS	38.2825	-104.7465	CO	Pueblo	Carlile Shale	Bluehill Sh, Codell SS	24.1	49.2	26.7	100		2.99	2.99
Lewis 2013 - MS THESIS	38.2097	-104.8905	CO	Pueblo	Carlile Shale	Codell SS, Juana Lopez	6.5	28	62.6	97.1		2.27	2.29
Lewis 2013 - MS THESIS	38.2681	-104.6912	CO	Pueblo	Carlile Shale	Bluehill Sh, Codell SS	15.9	51.1	33	100		2.61	2.61
Lewis 2013 - MS THESIS	38.0638	-104.6709	CO	Pueblo	Carlile Shale	Bluehill Sh, Codell SS, Juana Lopez	26.6	66.3	5.6	98.5		3.58	3.62

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Lewis 2013 - MS THESIS	37.7257	-105.1106	CO	Huerfano	Carlile Shale	Codell SS, Juana Lopez	10	19.6	46.7	76.3		2.47	2.61
Cobban/Scott 1972 - Bridge Crk (informed by Elder/Kirkland 1985); Glenister/Kauffmann 1985 - Carlile Sh	38.5000	-104.5000	CO	Pueblo	Greenhorn Limestone, Carlile Shale	Bridge Ck Lmst / Grnhrn, Fairport Chk, Blue Hill Sh, Codell SS / Carlile Sh	35.7	39.5	15	90.2		3.78	3.94
Merewether et al. 2006	39.6758	-97.0410	CO	Delta	Mancos Shale	Blue Hill Mbr, Juana Lopez Mbr, Montezuma Valley Mbr	42.2	53.8	0	96			
White 1999 PhD DISS	37.609708	-111.9324	UT	Garfield	Mancos Shale & Straight Cliffs Formation	Tropic Sh/Mancos, Tibbet Canyon Mbr/Straight Cliffs	19	40.6	35.6	95.2		2.34	2.52
White 1999 PhD DISS	38.4072	-110.9415	UT	Wayne	Mancos Shale & Straight Cliffs Formation	Tununk Sh/Mancos, Ferron SS Mbr/Straight Cliffs	25	33.1	30.8	88.9		3.09	2.61
Kauffman 1985 - SEPM Field Guide 3	40.1636	-105.1867	CO	Boulder	Carlile Shale / Greenhorn Limestone	Bridge Crk Lmst / Grnhrn, Fairport Chk, Blue Hill Sh, Codell SS / Carlile	28	36.6	14.6	79.2		3.54	3.98

Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Lang and McGugan 1987	48.3536556	-113.2917343	MT		Marias River Shale	Cone	45	45	0	90	4	4	5.5
Titus et al. 2005	37.0825	-111.6643	UT	Kane/Garfield	Dakota Formation, Tropic Formation, Straight Cliffs	Tibbet Canyon and Smoky Hollow	40.465	22.87	36.67	100			
Mudge and Sheppard 1968	47.5333	-111.7214	MT		Marias River Shale	Cone and Ferdig	30.71	38.63	29.3	98.64	4	3.07	3.77
Elderbak et al. 2014	42.641087	-96.525303	IA	Plymouth	Graneros & Greenhorn Shale		46.6	30.7	0	77.3	4	4	5.7
Albright et al. 2007	37.5	-111.4	UT		Dakota Formation, Tropic Shale		50	50	0	100	4	4	4
Albright et al. 2007	37.5	-111.33	UT		Dakota Formation, Tropic Shale		50	50	0	100			
Desmares et al. 2007	43.4316	-103.4744	SD	Fall River			42.61	42.61	0	85.22	3	4	3.58
Harris et al. 2003	37.2149496	-111.3417587	UT		Mancos Shale		38.48	53.85	0	92.33	3.5	3.77	5.03
Pratt and Threlkeld 2009	42.6052	-96.7193	NE		Greenhorn		15	15	0	30	3.5	4	5.83
Cappetta 1973	43.4338752	-103.4018236	SD	Fall River	Carlile Shale & Niobrara		44.15	44.15	9.19	97.49	3.67	2.81	2.86
Young 1951	45.7401005	-108.3867564	MT		Frontier Formation		15	73	3	91			
Young 1951	45.5620209	-107.8847463	MT		Frontier Formation		14.3	69.6	0	83.9			
Tibert et al. 2003	37.4316456	-113.0477238	UT	Washington	Dakota Formation		1.5	7.8	89.7	99			
Tillman and Almon 1979	43.3517126	-105.7888901	WY	Converse	Frontier Formation & Carlile Shale		14.07	50.45	35.48	100	3.89	2.43	3.29
Tillman and Almon 1979	43.337345	-105.7889533	WY	Converse	Frontier Formation & Carlile Shale		13.69	33.54	52.77	100	3.93	2.44	3.18
Tillman and Almon 1979	43.3519676	-105.8284913	WY	Converse	Frontier Formation & Carlile Shale		23.76	53.75	22.49	100	3.83	2.41	3.32
Winn 1989	43.6070048	-106.5654764	WY		Frontier Formation	Wall Creek Member	12.17	12.17	75.66	100			

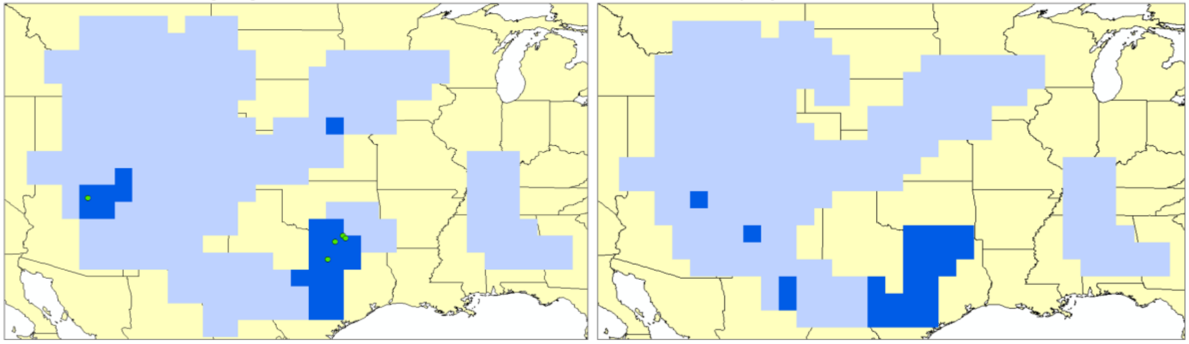
Publication	*LAT*	*LONG*	*State*	*County*	*Formation*	*Member*	*% Clay*	*% Silt*	*% Sand*	*% Total*	*Bed style*	*Water Depth*	*Dep. Environ.*
Winn 1989	43.4066517	-106.2624722	WY		Frontier Formation	Wall Creek Member	5	5	90	100			
Winn 1989	43.5381777	-106.0779753	WY		Frontier Formation	Wall Creek Member	5.98	5.98	88.04	100			
Haun 1958	43.8659664	-104.2676286	WY		Carlile Shale		45.35	50.47	0	95.81	2.77	3.49	4.42
Merewether and Cobban 1986	42.7120168	-106.5313928	WY	Natrona	Frontier Formation	Wall Creek Member	0	5.11	90.89	96	3	1.95	3
Merewether and Cobban 1986	42.8563121	-106.5633978	WY	Natrona	Frontier Formation	Wall Creek Member	33.5	38.89	25.43	97.83	3	3.24	3.68
Cobban et al. 1976	48.7835243	-111.861947	MT		Marias River Shale	Ferdig Member	48.33	44.92	3.05	96.3	3.43	2.83	3.83
Cobban et al. 1976	48.6606495	-111.676622	MT		Marias River Shale	Ferdig Member	34.58	43.62	1.01	79.21	3.48	2.55	3.48

Appendix 4 – Illustrated suitable habitat areas

Appendix 4.1 Extinct taxa

Illustrated suitable habitat area change for taxa that go extinct at the C/T boundary. On the right is Cenomanian training region, depicting suitable habitat in the Cenomanian based on Cenomanian occurrences and environment. On the right is a projection of Cenomanian suitable habitat onto Turonian environment. Green points are CEN occurrences; red points TUR occurrences; light blue is unsuitable habitat; dark blue suitable habitat.

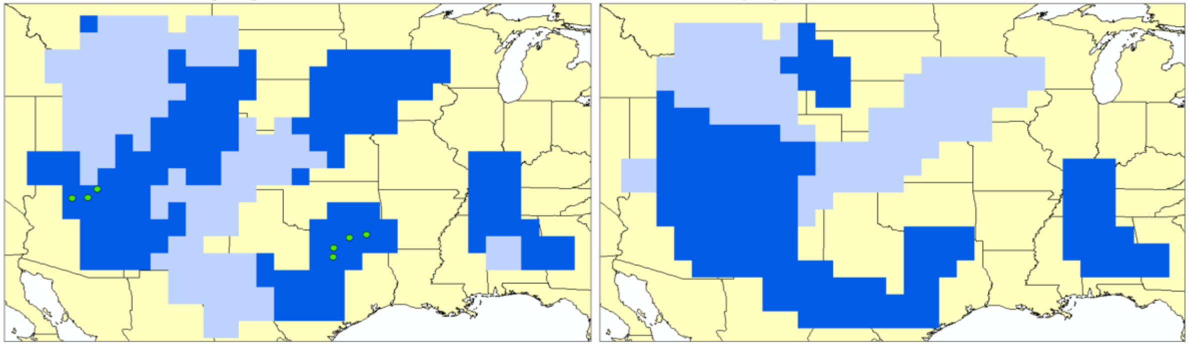
Brachiodontes



Cenomanian training region

Cenomanian projection onto Turonian environments

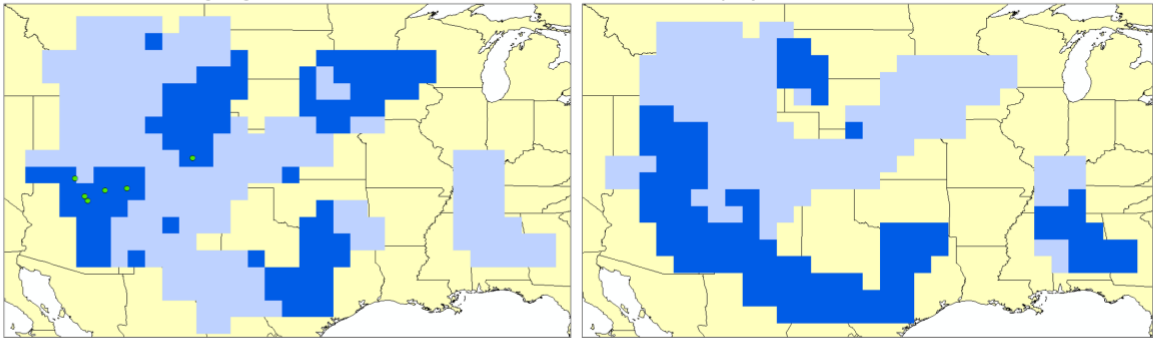
Carycorbula



Cenomanian training region

Cenomanian projection onto Turonian environments

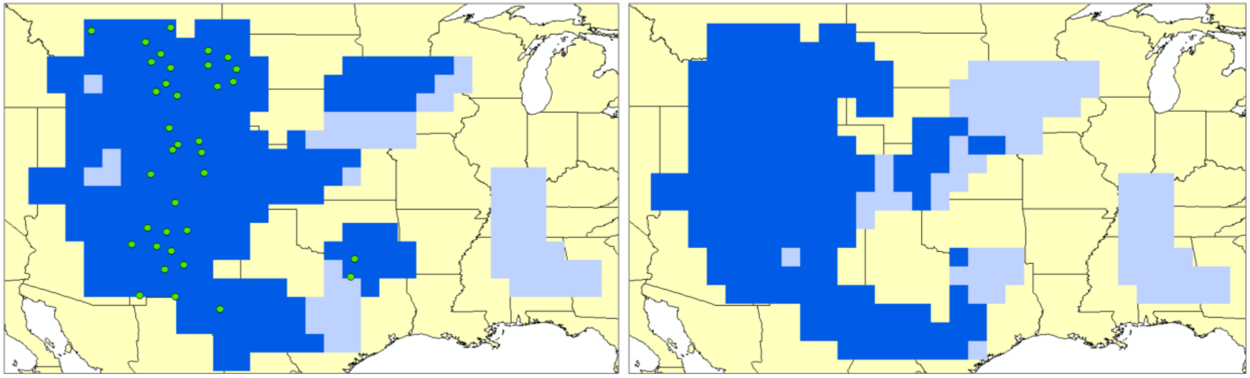
Gryphaeostraea



Cenomanian training region

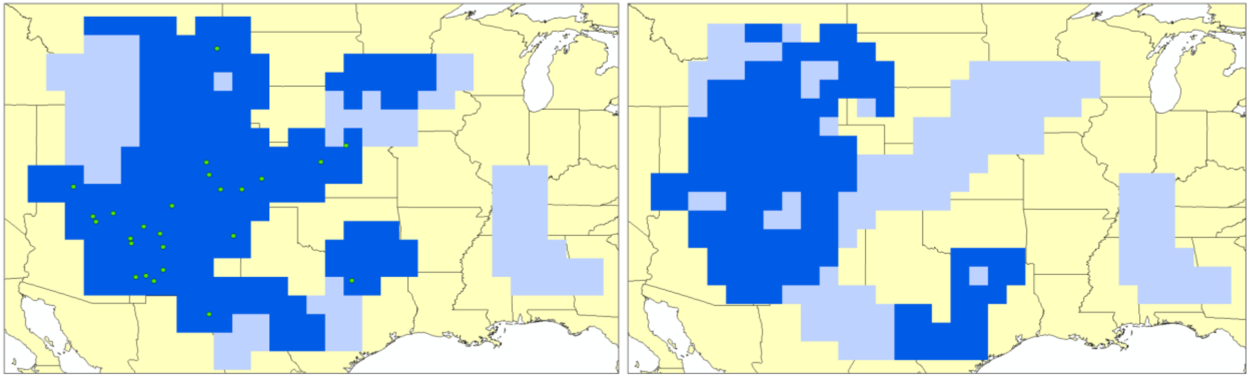
Cenomanian projection onto Turonian environments

Acanthoceras amphibolum


Cenomanian training region

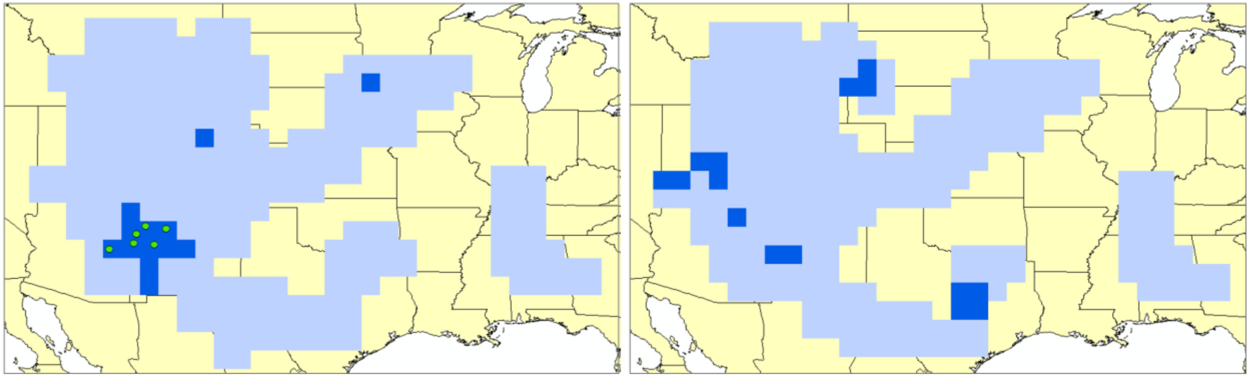
Cenomanian projection onto Turonian environments

Euomphaloceras septemseriatum


Cenomanian training region

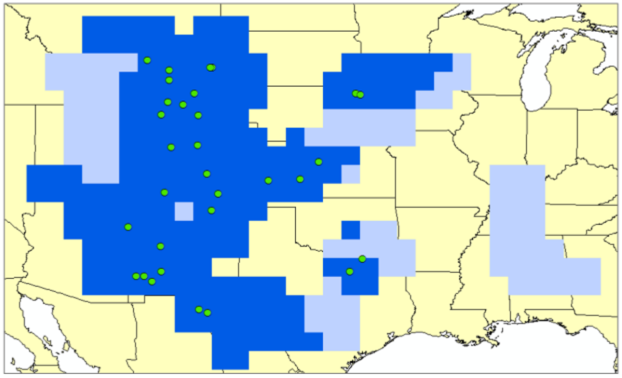
Cenomanian projection onto Turonian environments

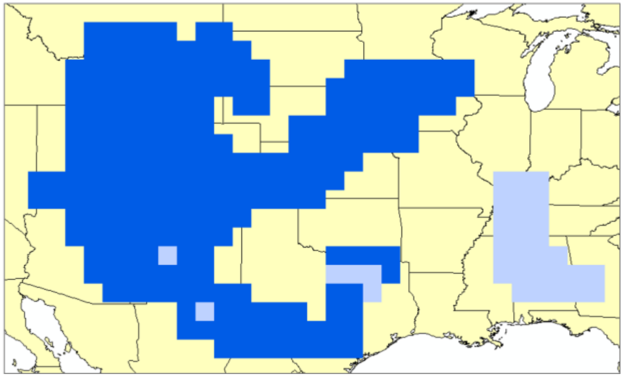
Exogyra trigeri


Cenomanian training region

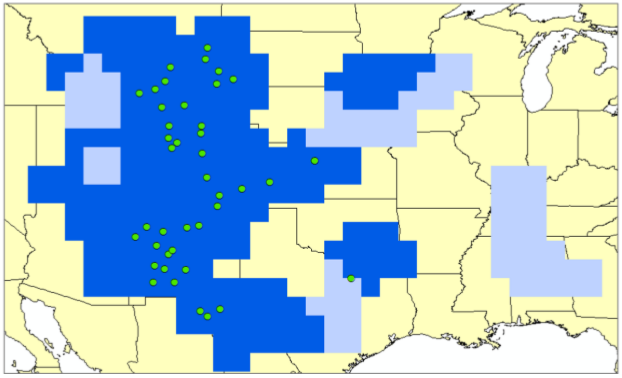
Cenomanian projection onto Turonian environments

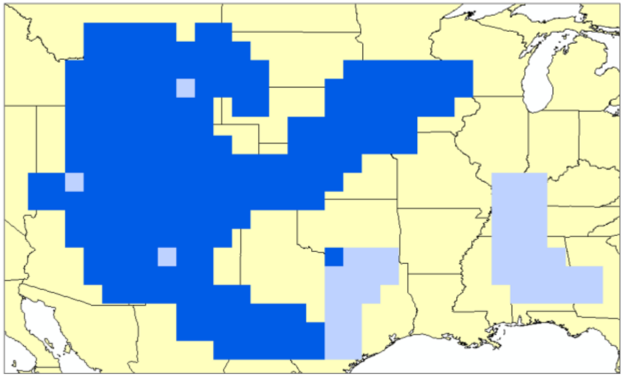
Inoceramus prefragilis


Cenomanian training region

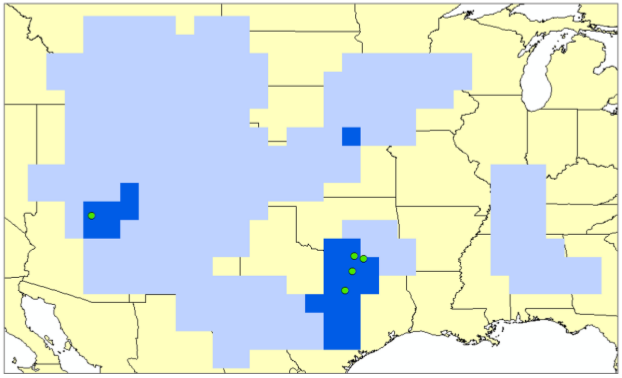

Cenomanian projection onto Turonian environments

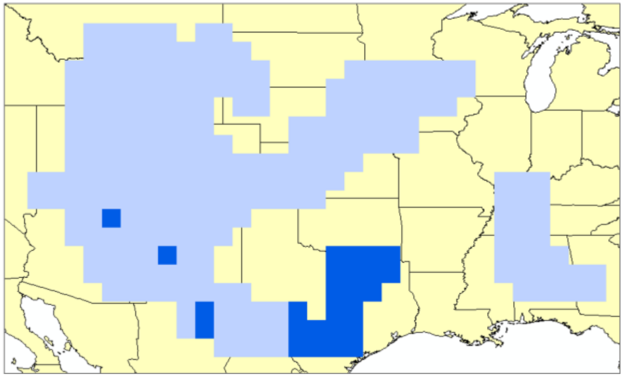
Ostrea beloiti


Cenomanian training region


Cenomanian projection onto Turonian environments

Phelopteria dalli

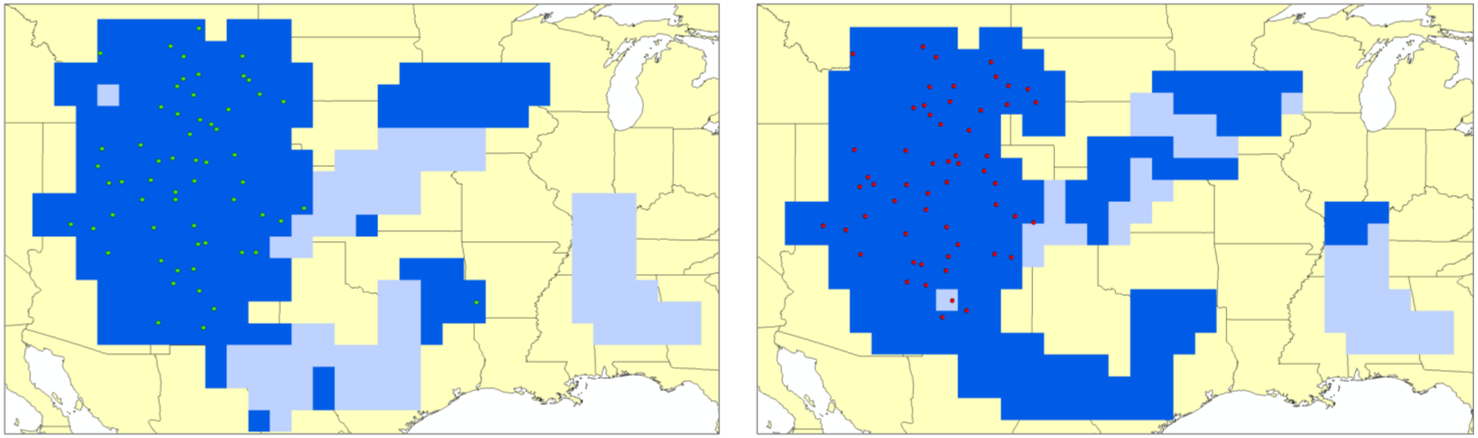

Cenomanian training region


Cenomanian projection onto Turonian environments

Appendix 4.2 Surviving taxa

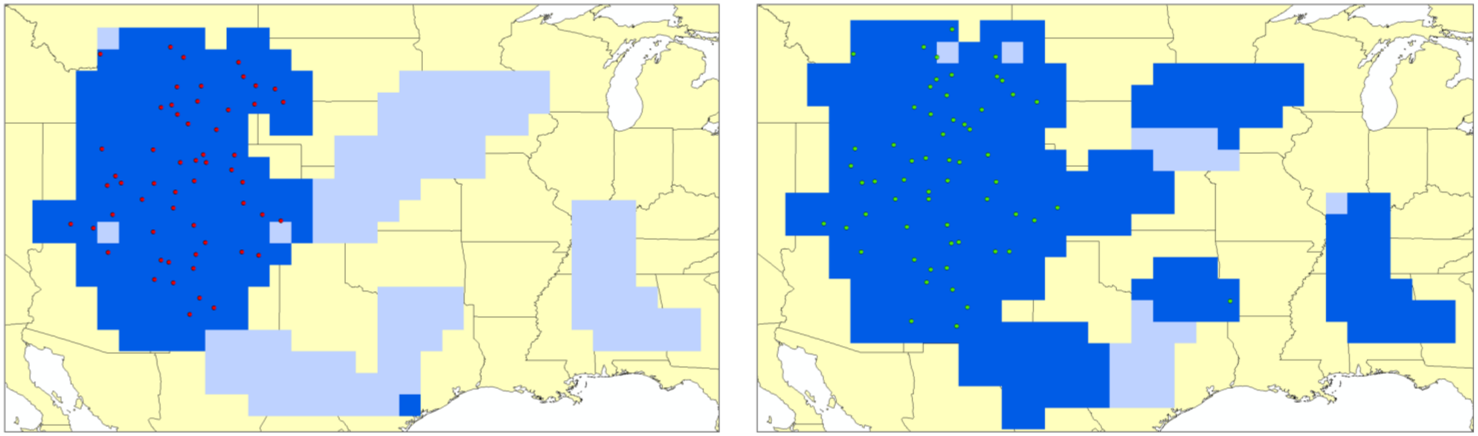
Illustrated suitable habitat area change for taxa that survive across the C/T boundary. On the right is Cenomanian and Turonian training regions are depicted on the left, and on the right are projections onto Turonian and Cenomanian environments, respectively. Green dots denote Cenomanian occurrences; red denote Turonian. Turonian occurrences (red) are shown in the CEN$_{prj}$ to demonstrate how accurately Cenomanian habitat predicts Turonian occurrences, and vice versa.

Baculites



Cenomanian training region

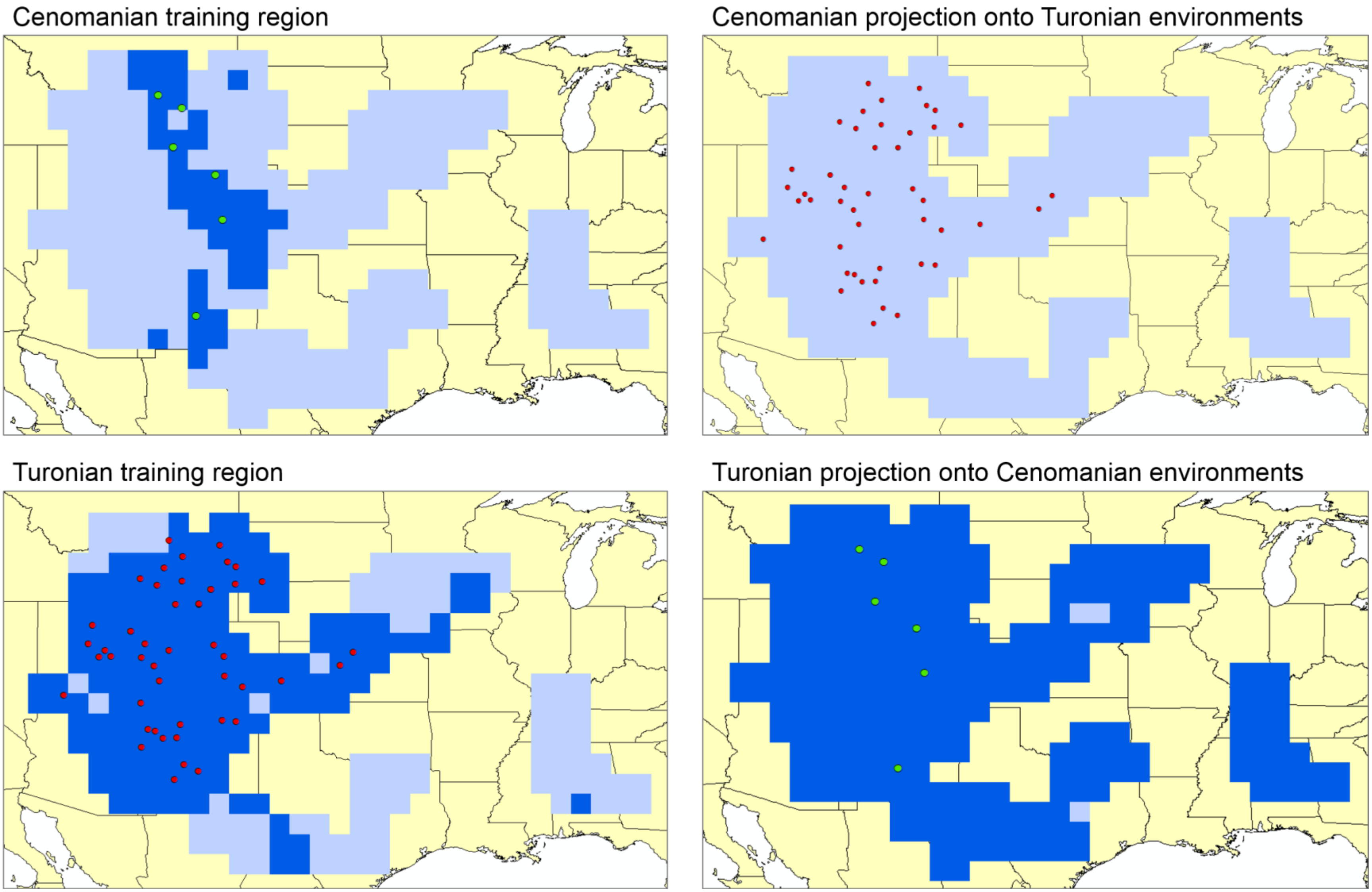
Cenomanian projection onto Turonian environments



Turonian training region

Turonian projection onto Cenomanian environments

Baculites yokoyamai



Cenomanian training region

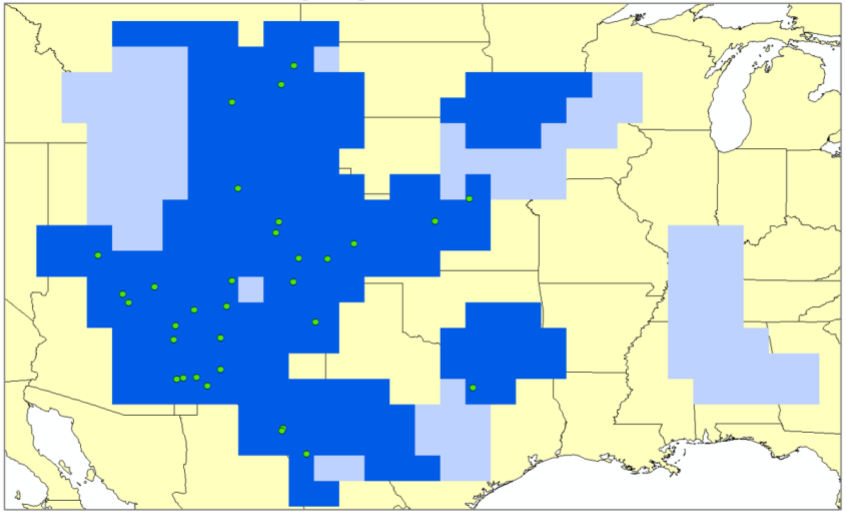
Cenomanian projection onto Turonian environments

Turonian training region

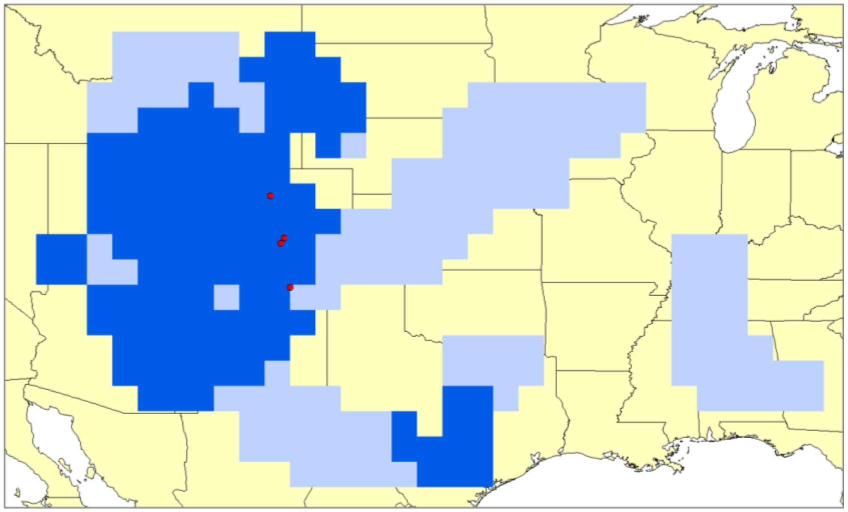
Turonian projection onto Cenomanian environments

Euomphaloceras

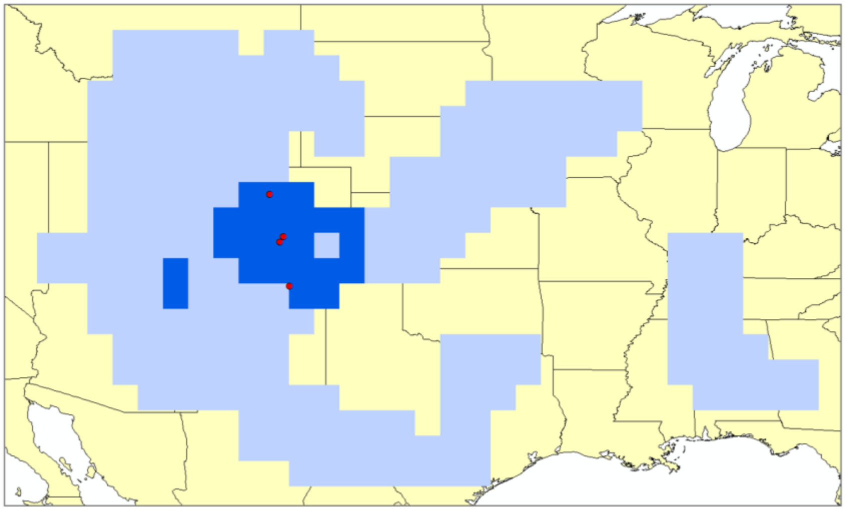
Cenomanian training region



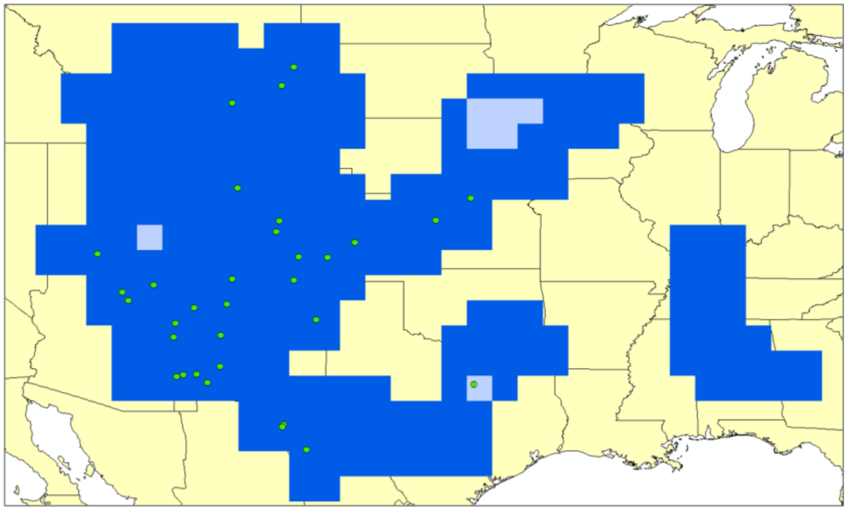
Cenomanian projection onto Turonian environments



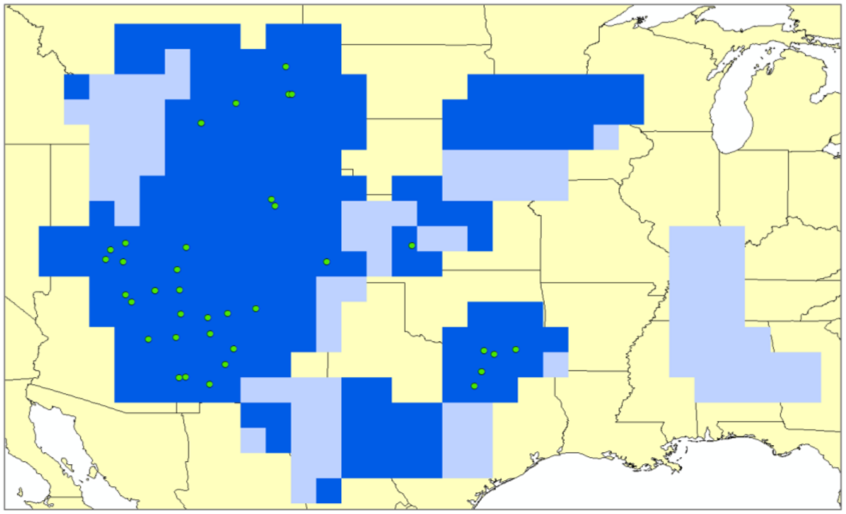
Turonian training region



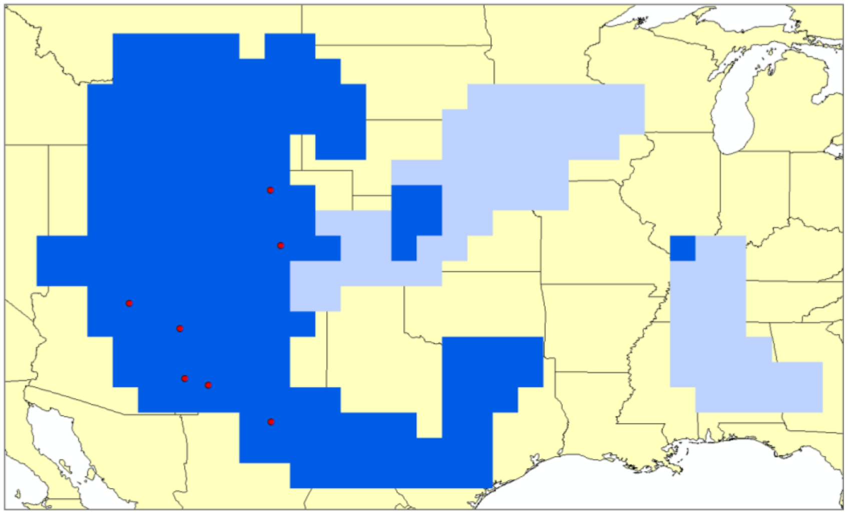
Turonian projection onto Cenomanian environments



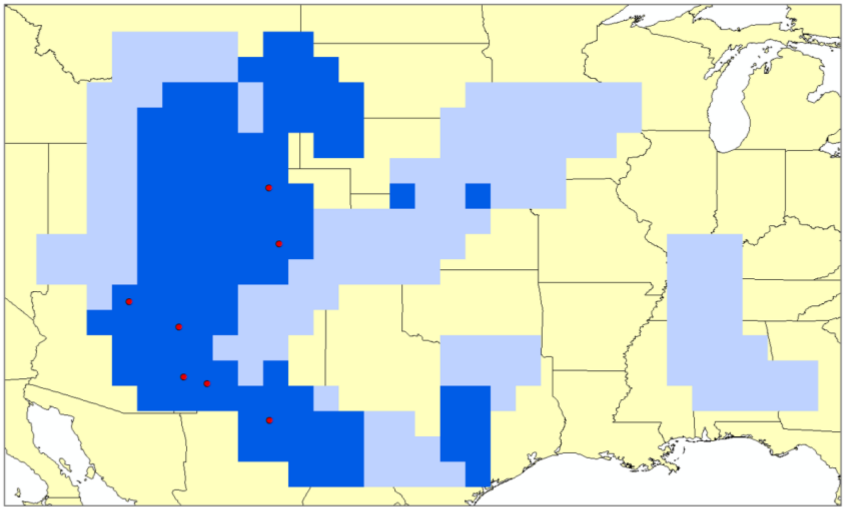
Fagesia



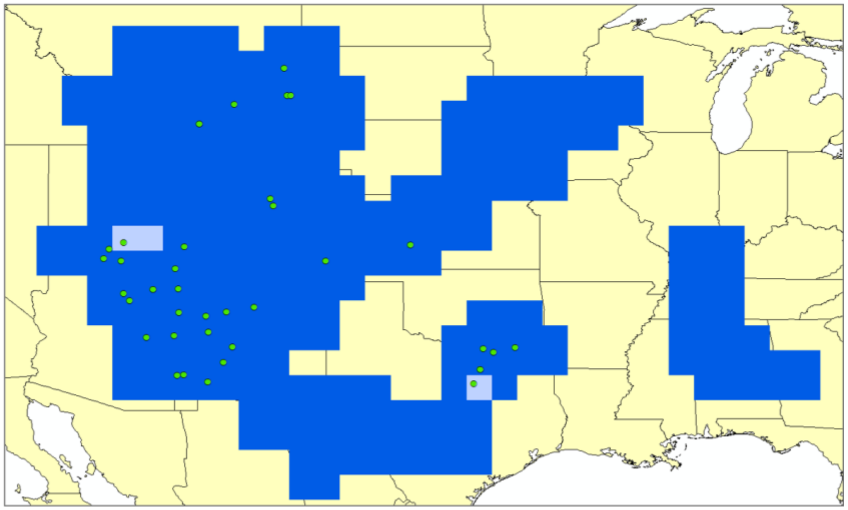
Cenomanian training region



Cenomanian projection onto Turonian environments



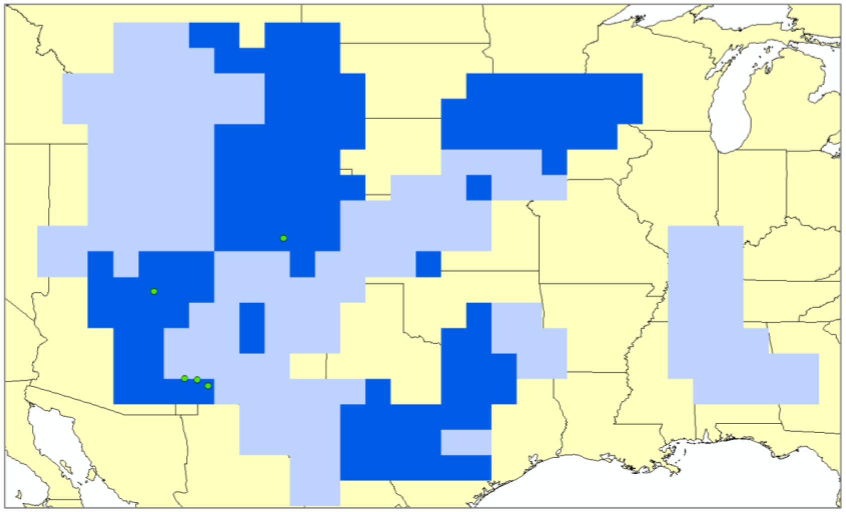
Turonian training region



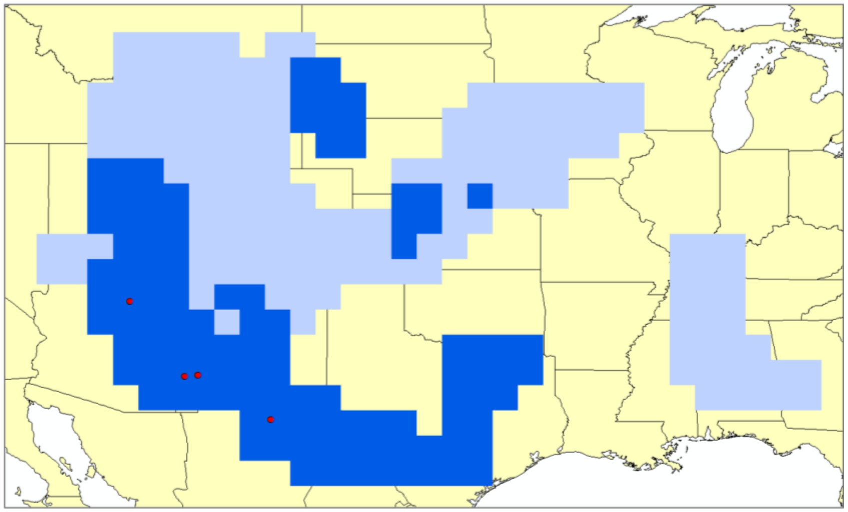
Turonian projection onto Cenomanian environments

Fagesia catinus

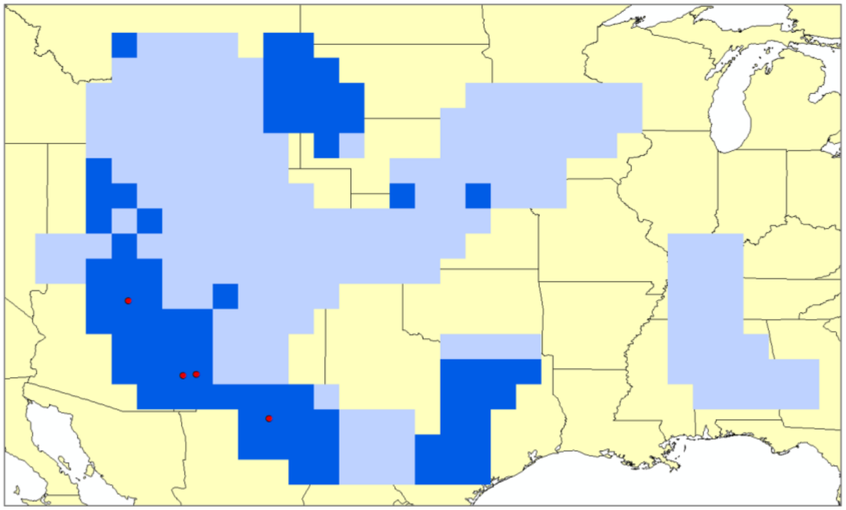
Cenomanian training region



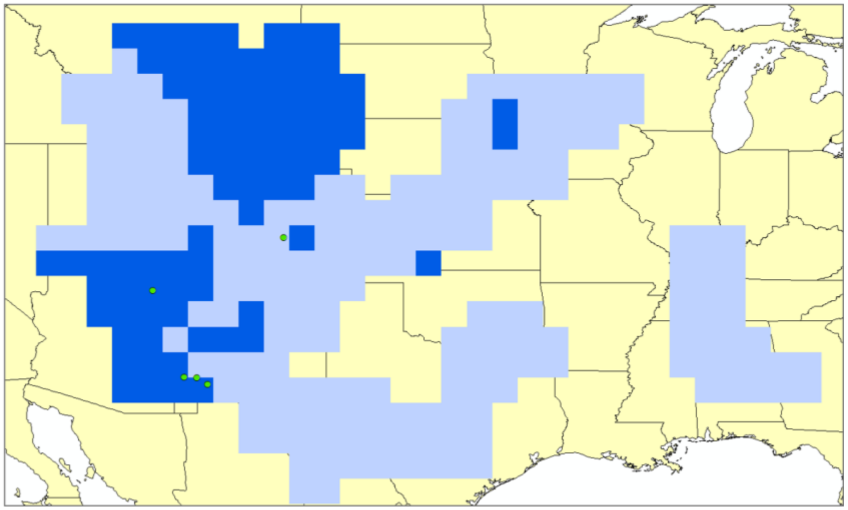
Cenomanian projection onto Turonian environments



Turonian training region

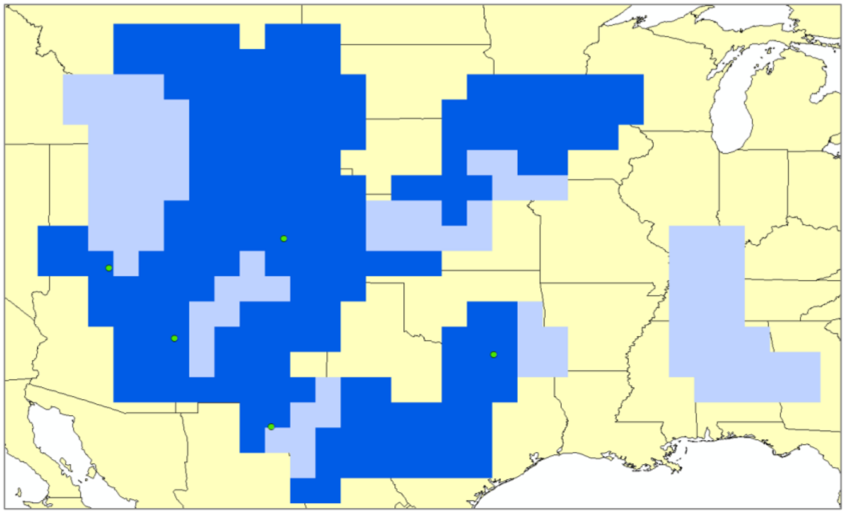


Turonian projection onto Cenomanian environments

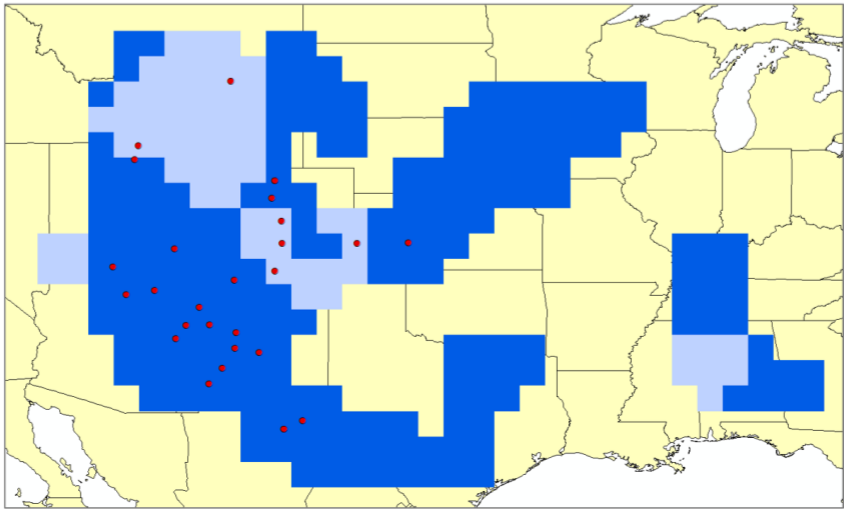


Mammites

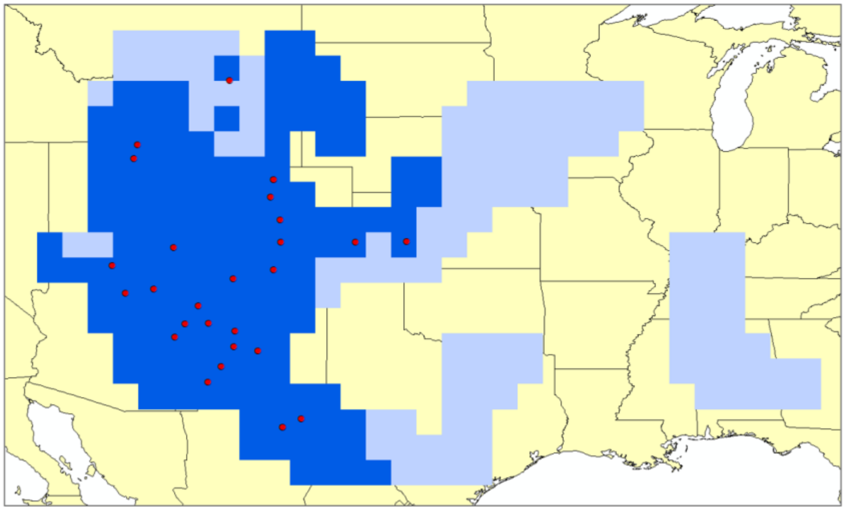
Cenomanian training region



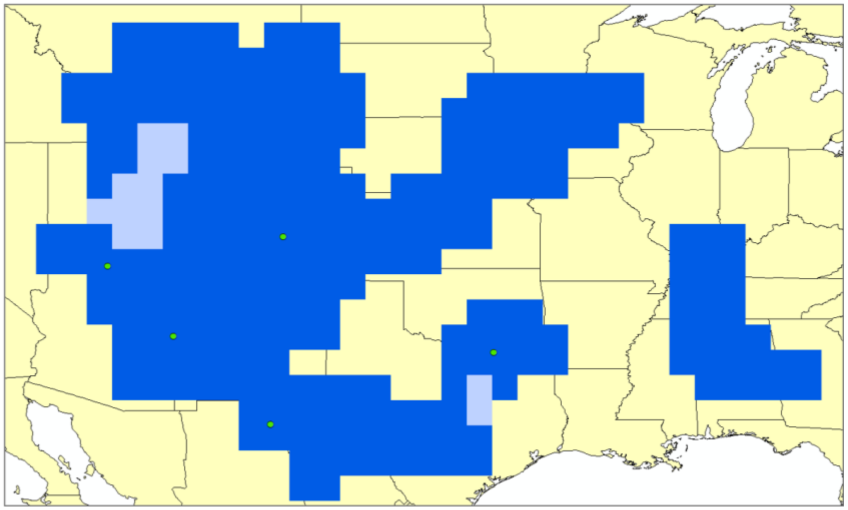
Cenomanian projection onto Turonian environments



Turonian training region

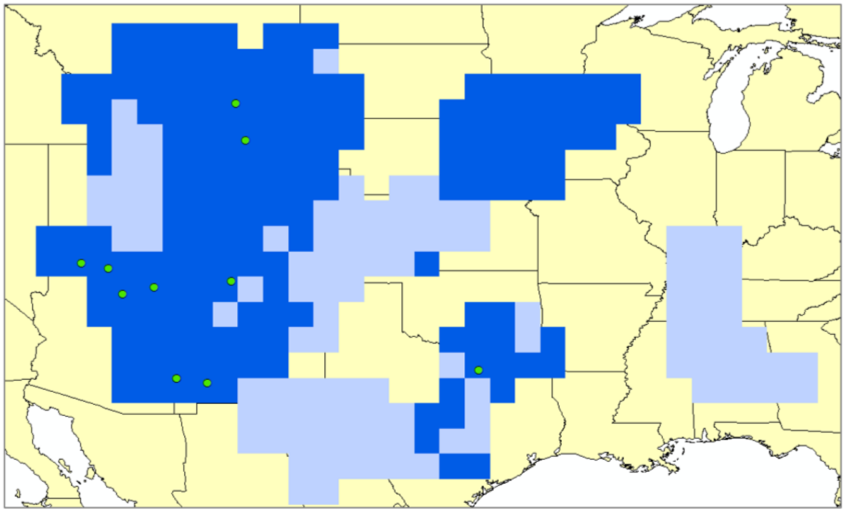


Turonian projection onto Cenomanian environments

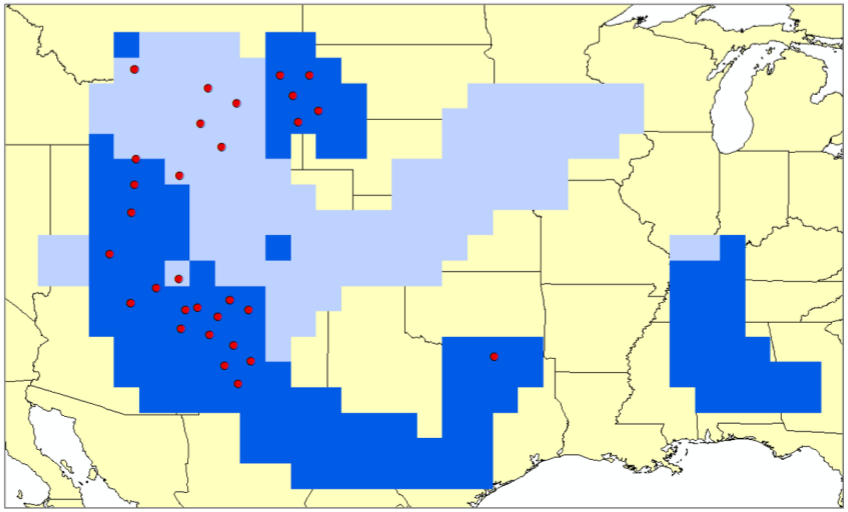


Placenticeras

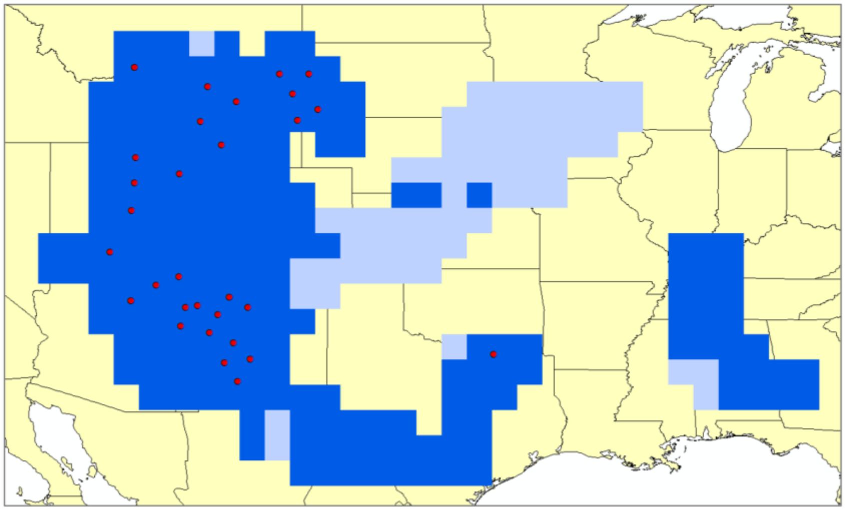
Cenomanian training region



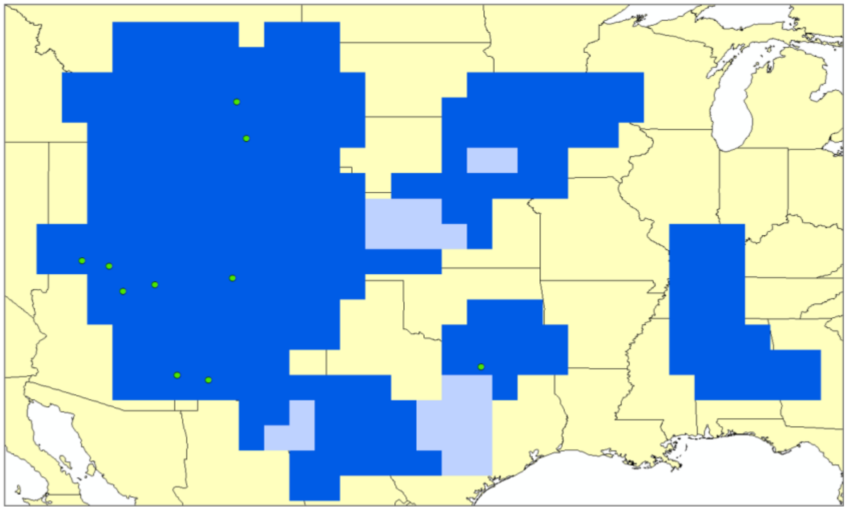
Cenomanian projection onto Turonian environments



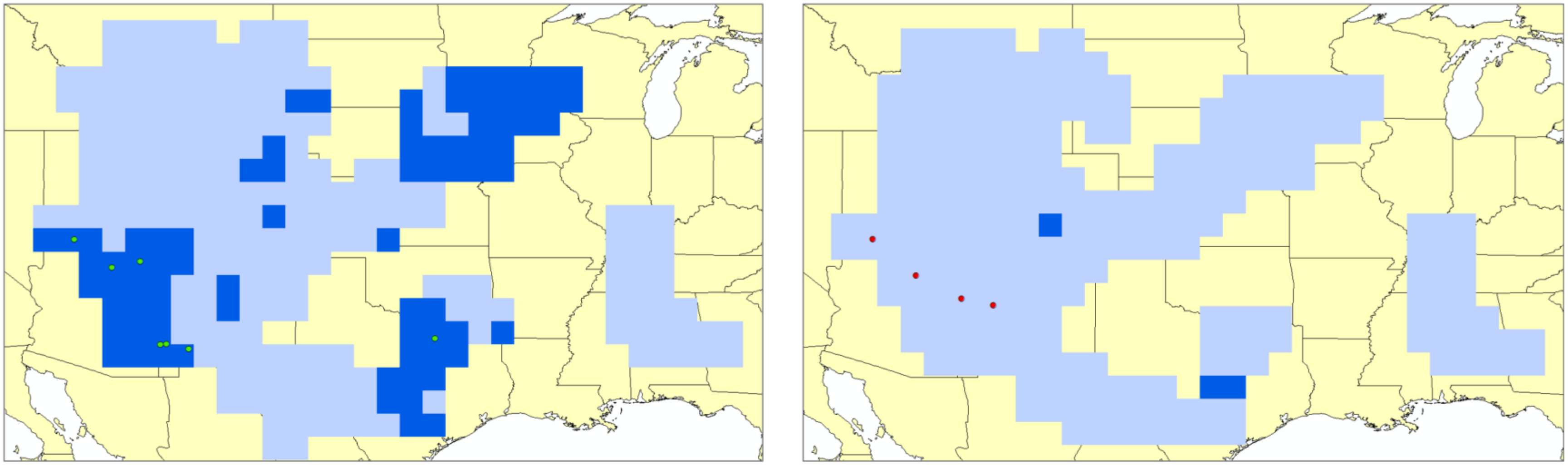
Turonian training region



Turonian projection onto Cenomanian environments

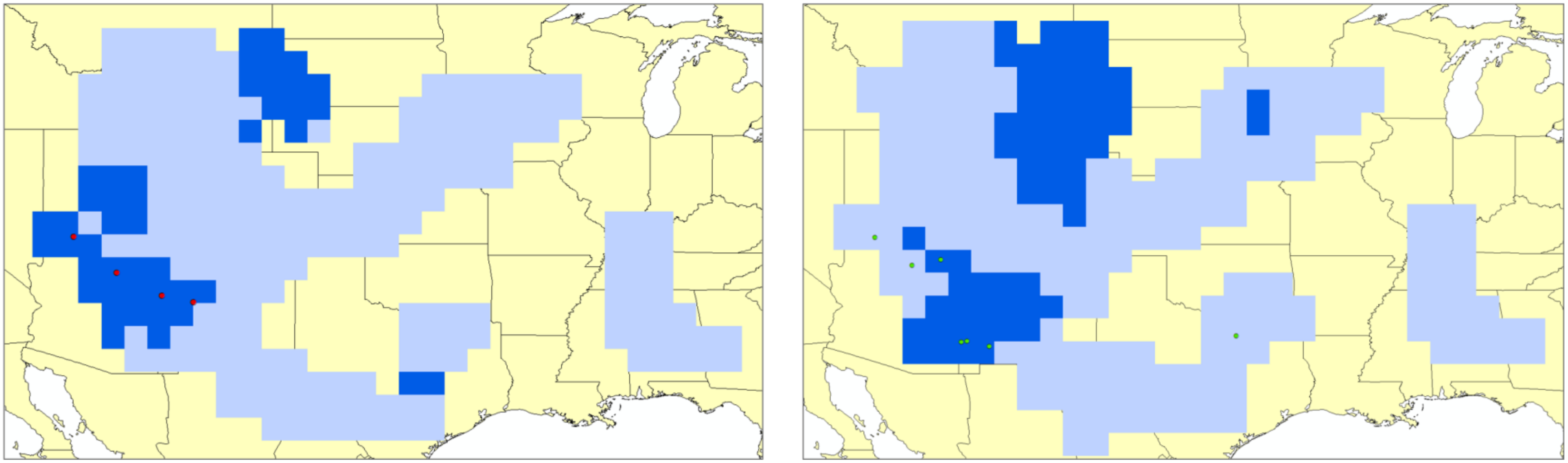


Placenticeras cumminsi



Cenomanian training region

Cenomanian projection onto Turonian environments

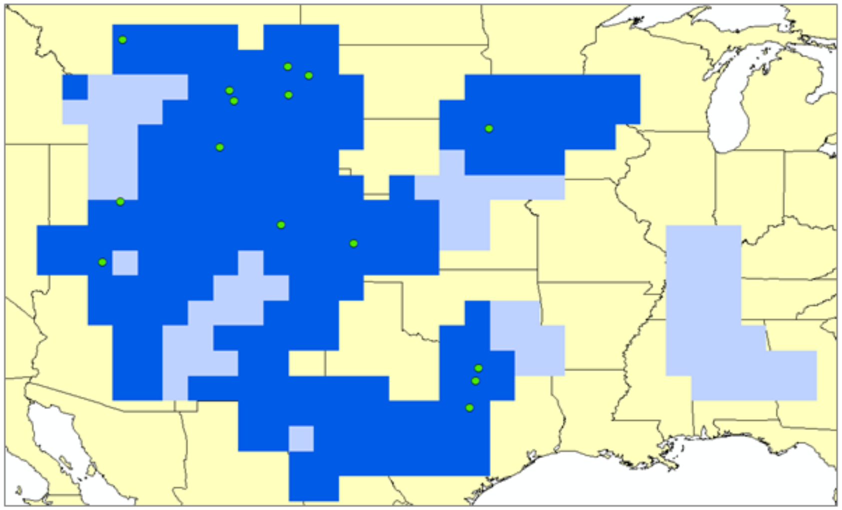


Turonian training region

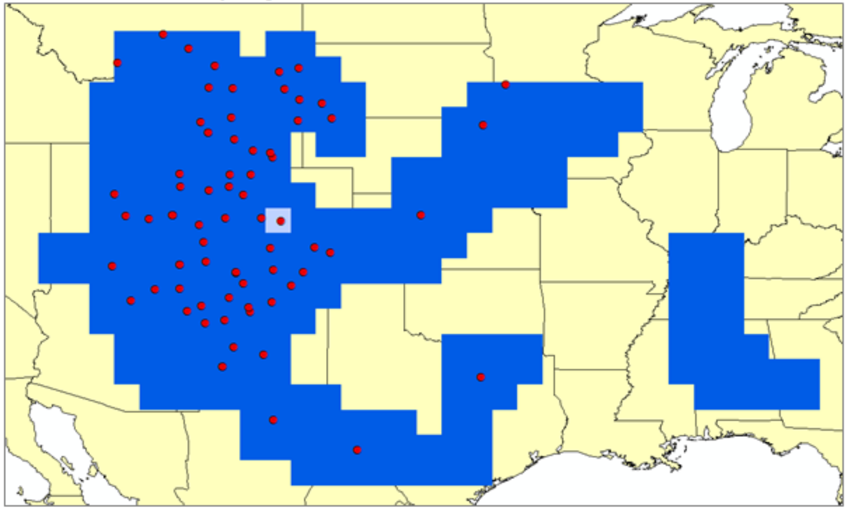
Turonian projection onto Cenomanian environments

Scaphites

Cenomanian training region



Cenomanian projection onto Turonian environments



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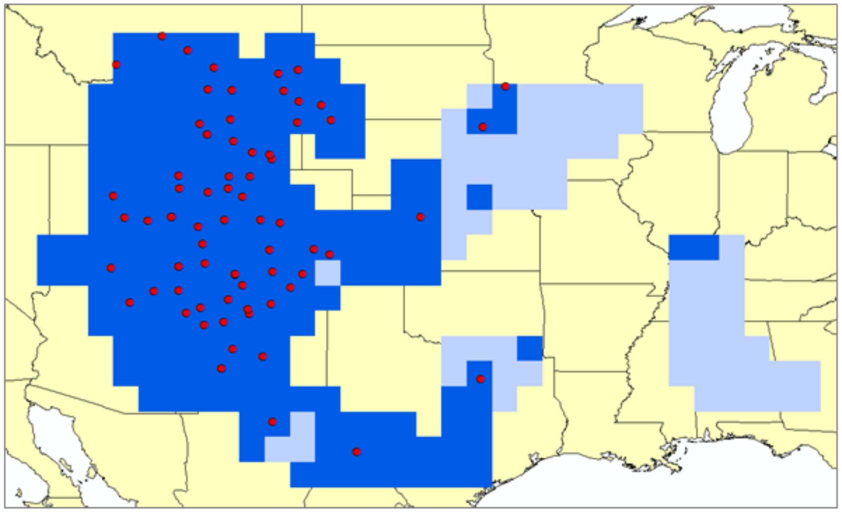
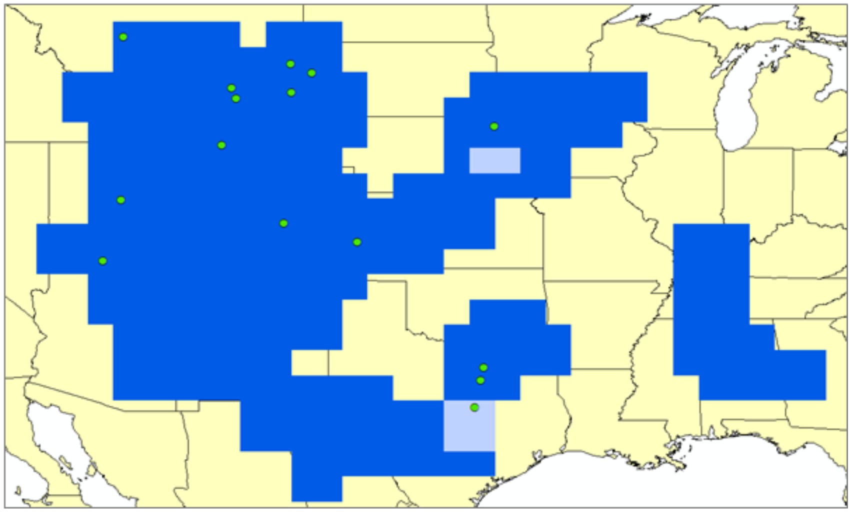
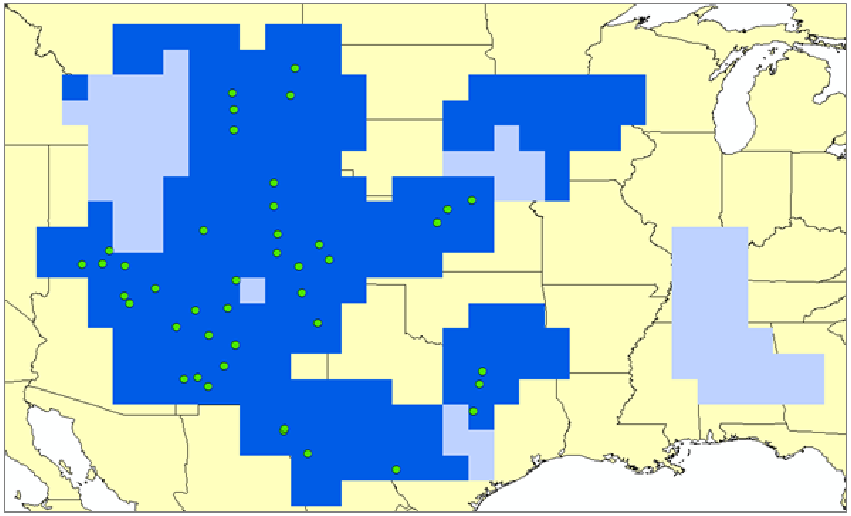


Turonian projection onto Cenomanian environments

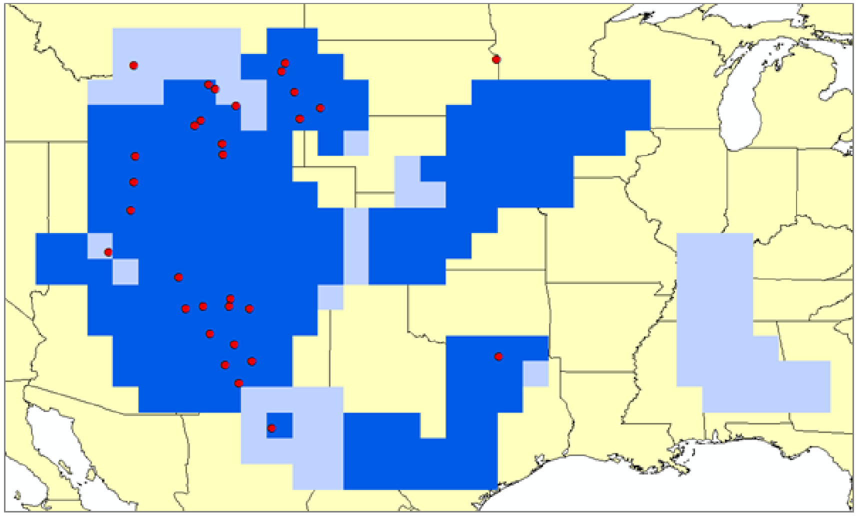


Sciponoceras

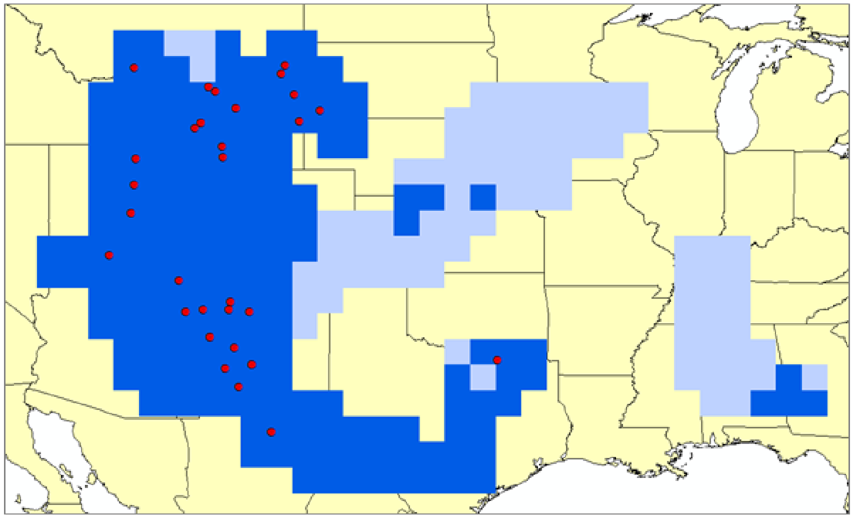
Cenomanian training region



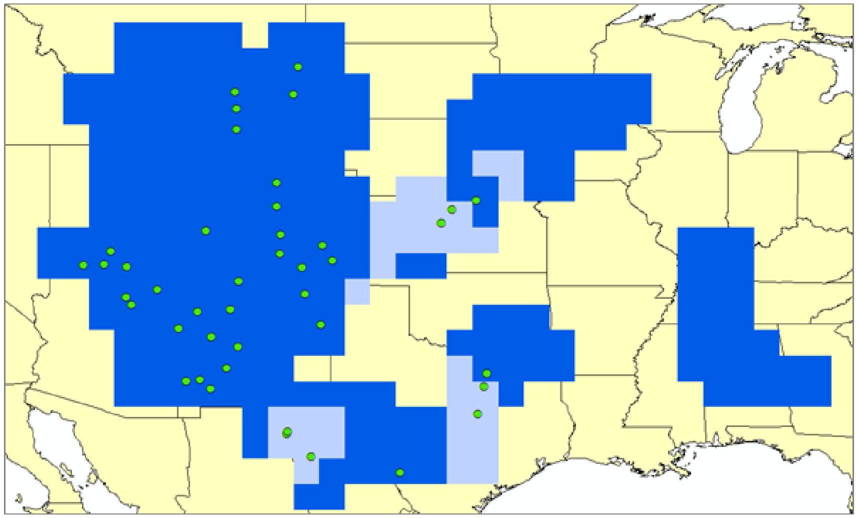
Cenomanian projection onto Turonian environments



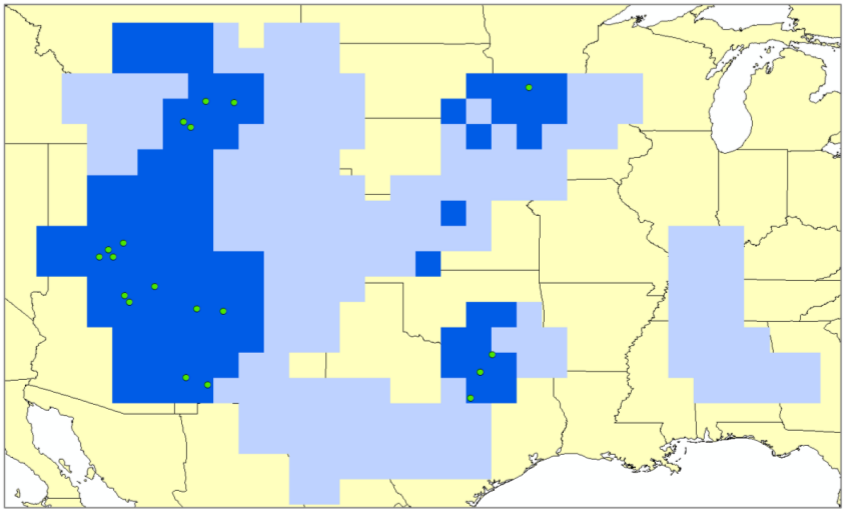
Turonian training region



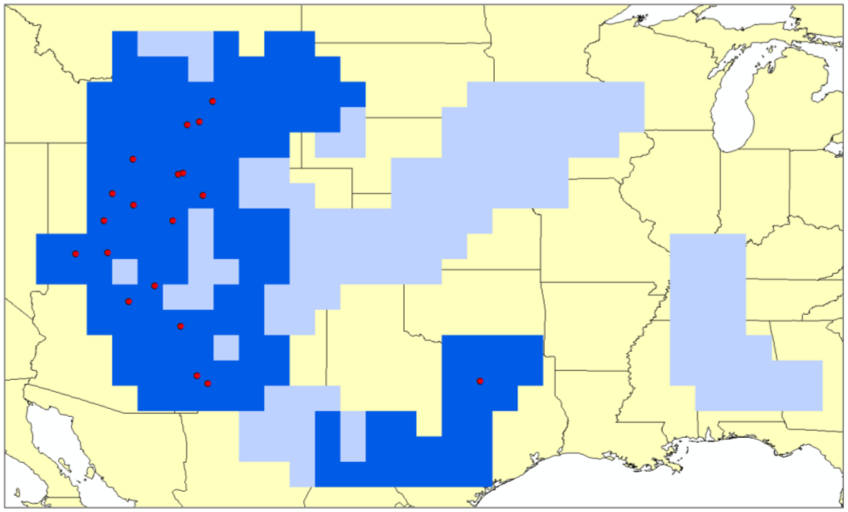
Turonian projection onto Cenomanian environments



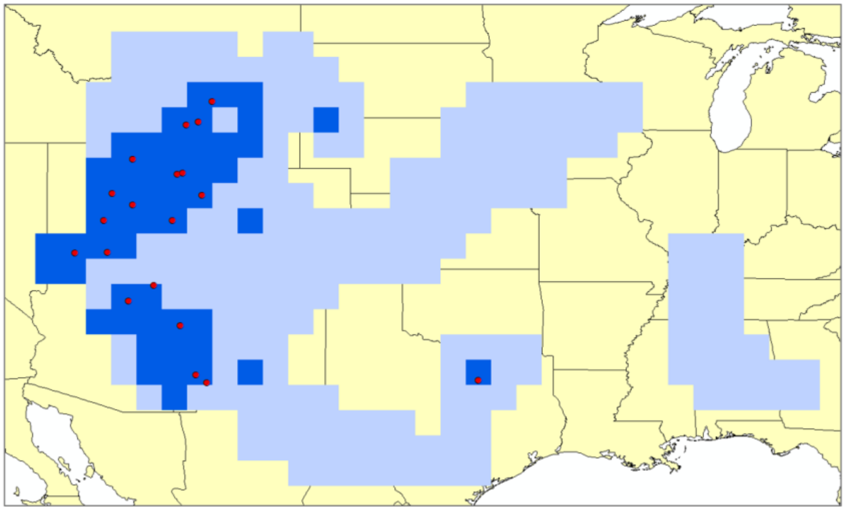
Corbula



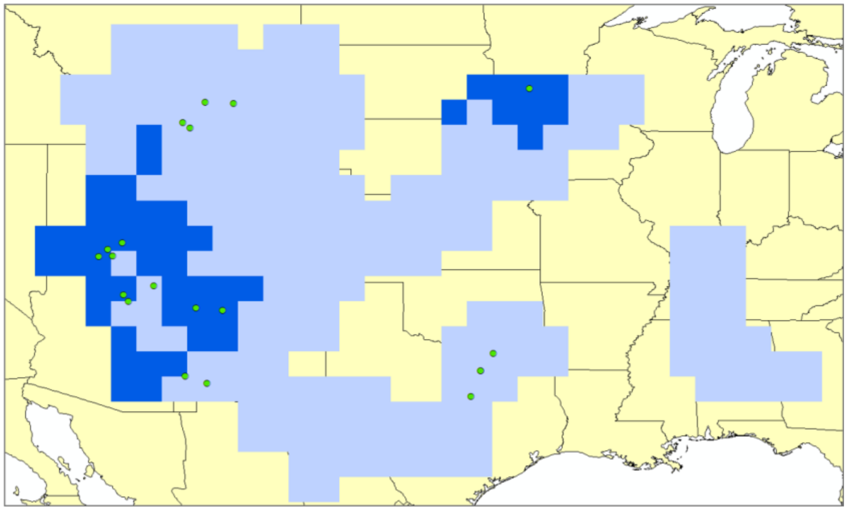
Cenomanian training region



Cenomanian projection onto Turonian environments



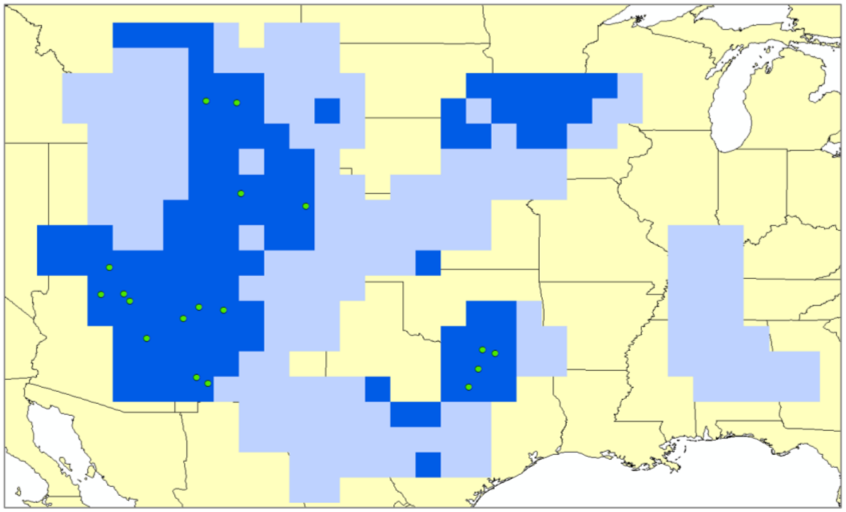
Turonian training region



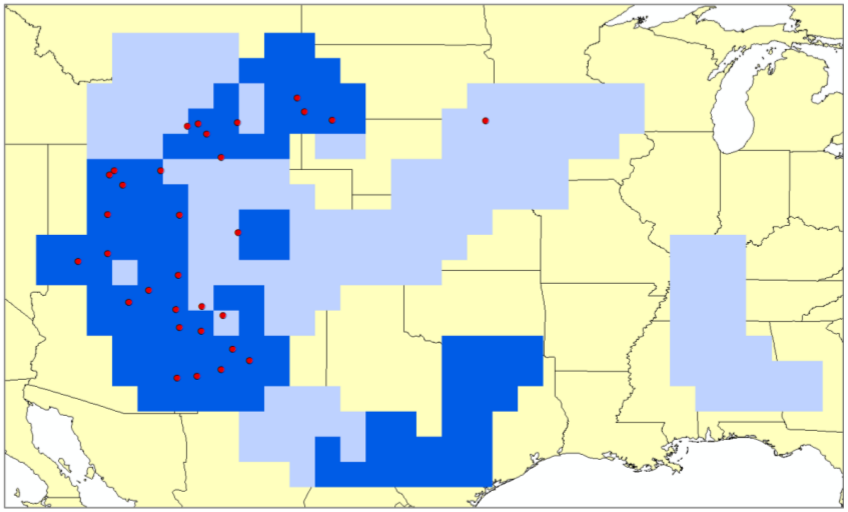
Turonian projection onto Cenomanian environments

Cymbophora

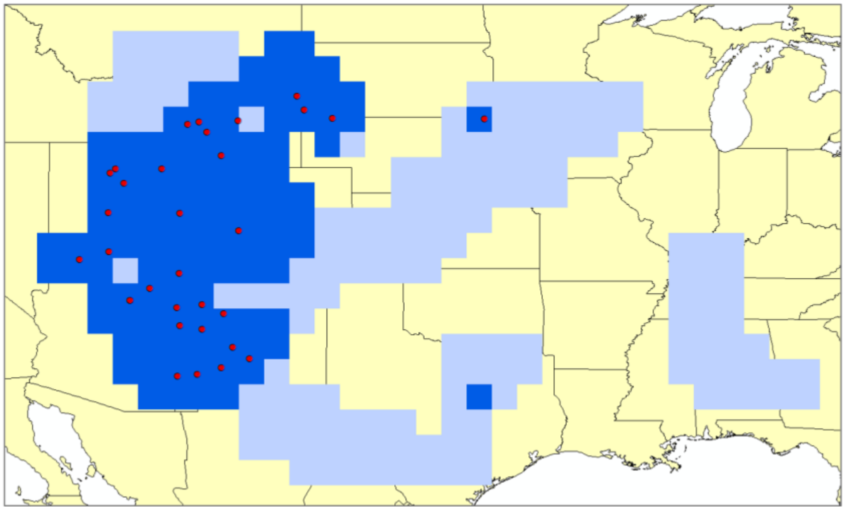
Cenomanian training region



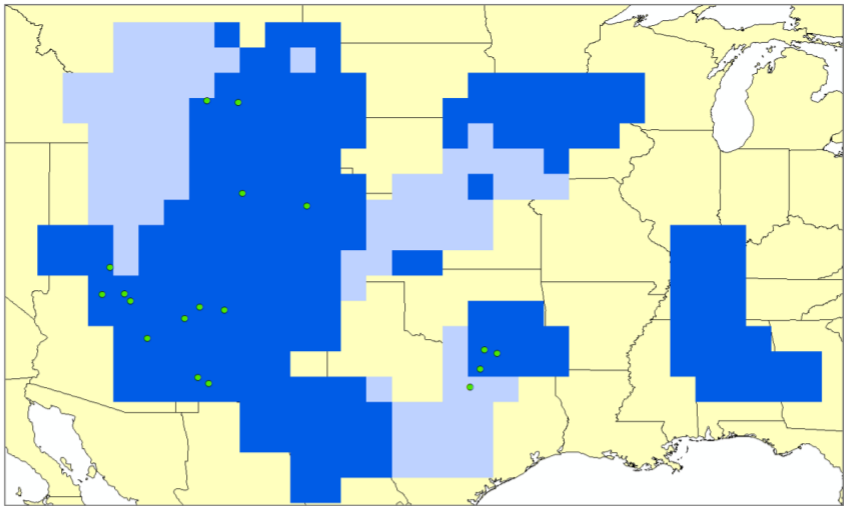
Cenomanian projection onto Turonian environments



Turonian training region

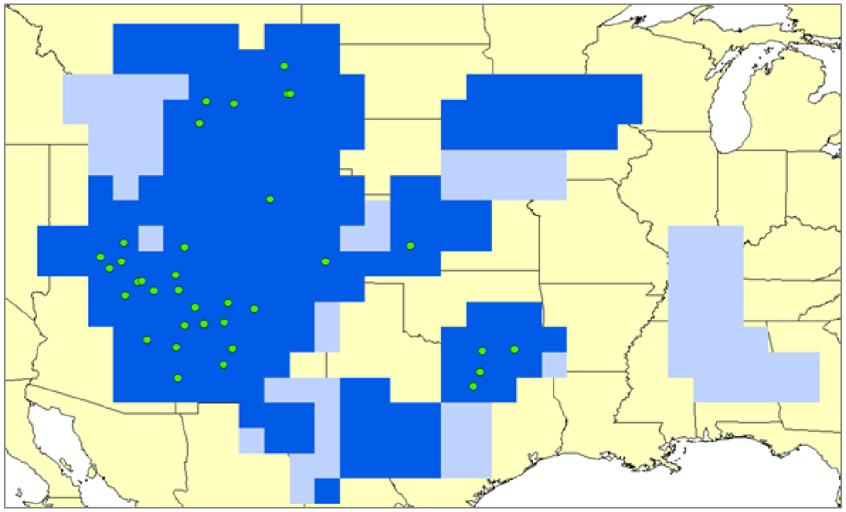


Turonian projection onto Cenomanian environments

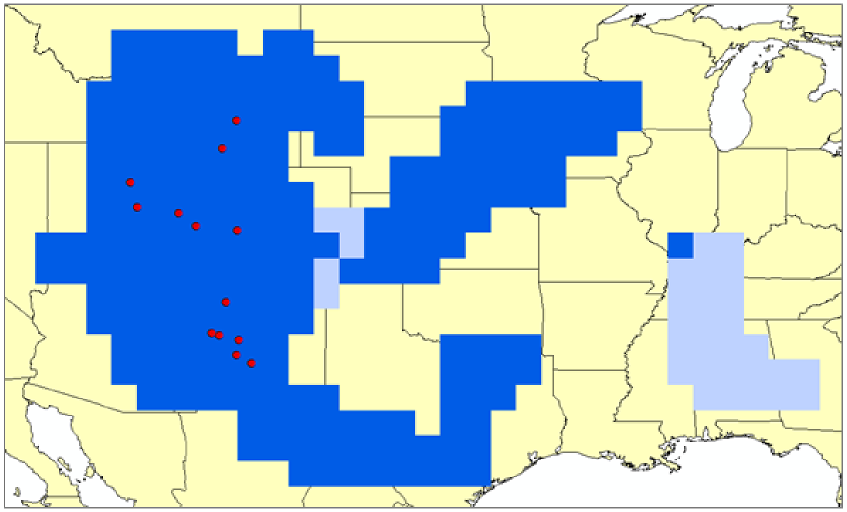


Exogyra

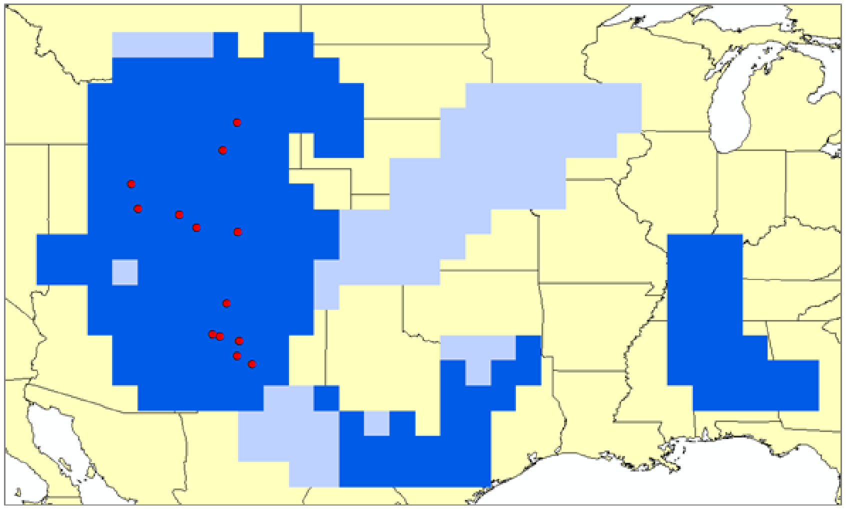
Cenomanian training region



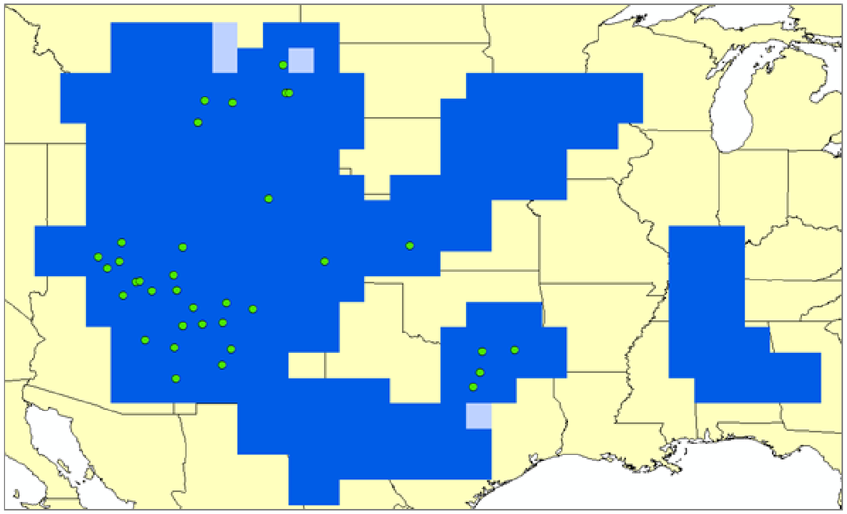
Cenomanian projection onto Turonian environments



Turonian training region

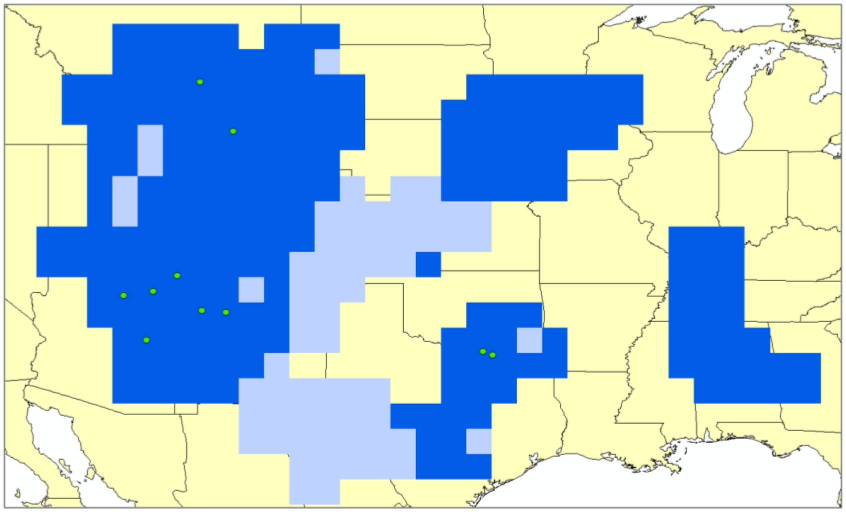


Turonian projection onto Cenomanian environments

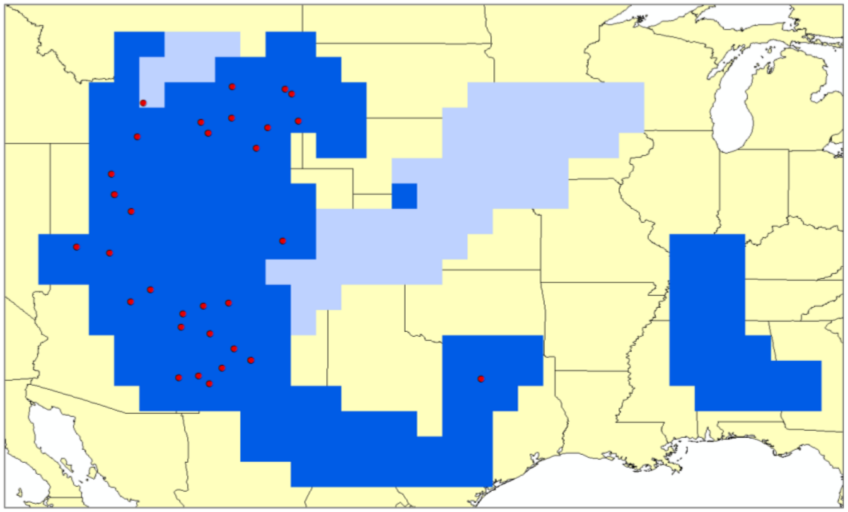


Gyrodes

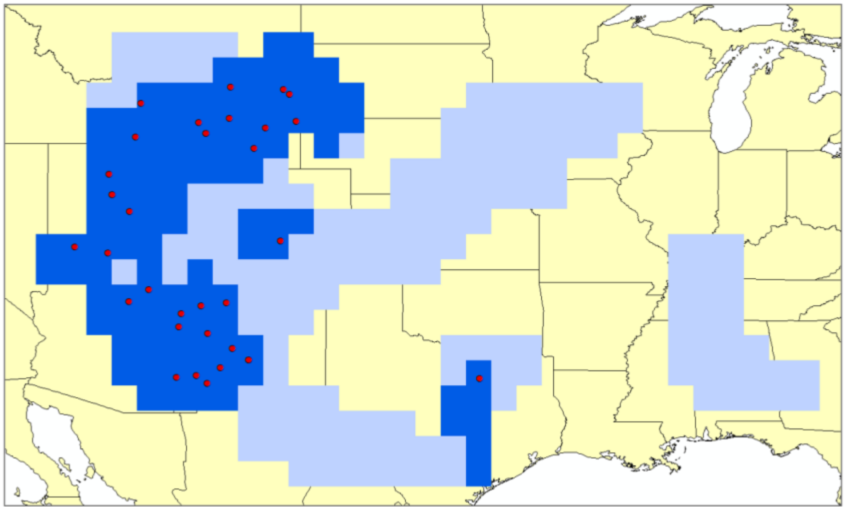
Cenomanian training region



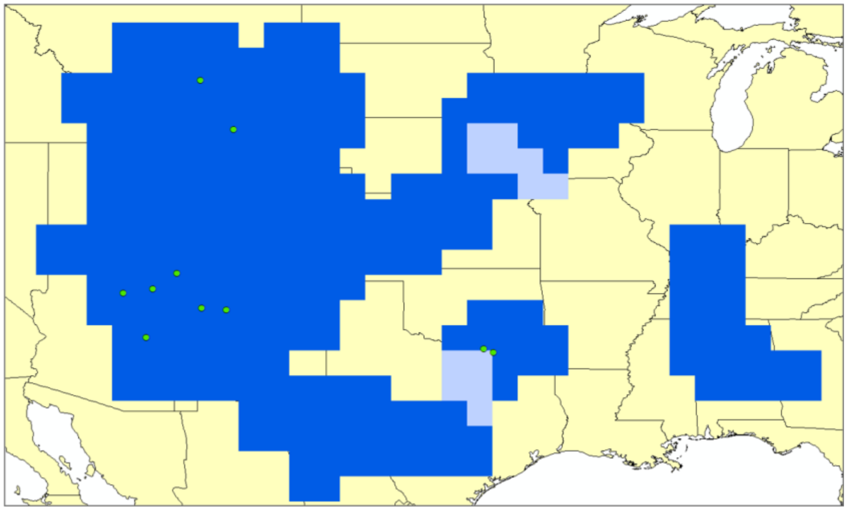
Cenomanian projection onto Turonian environments



Turonian training region

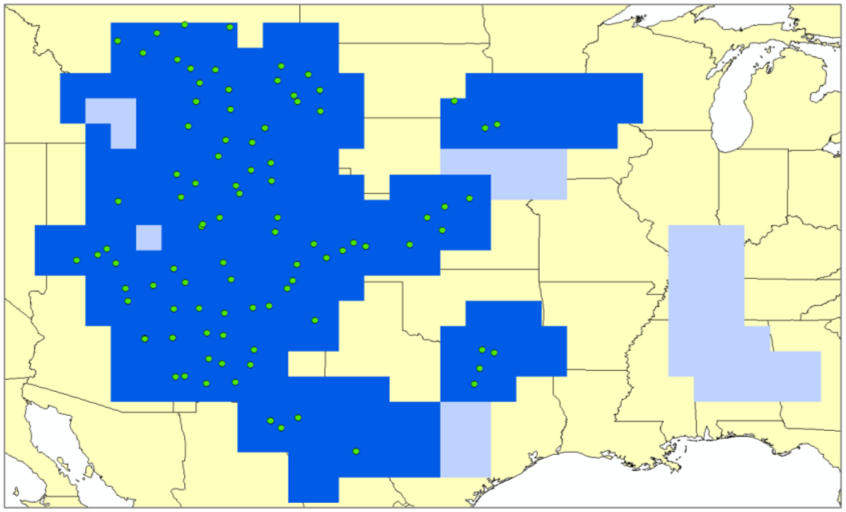


Turonian projection onto Cenomanian environments

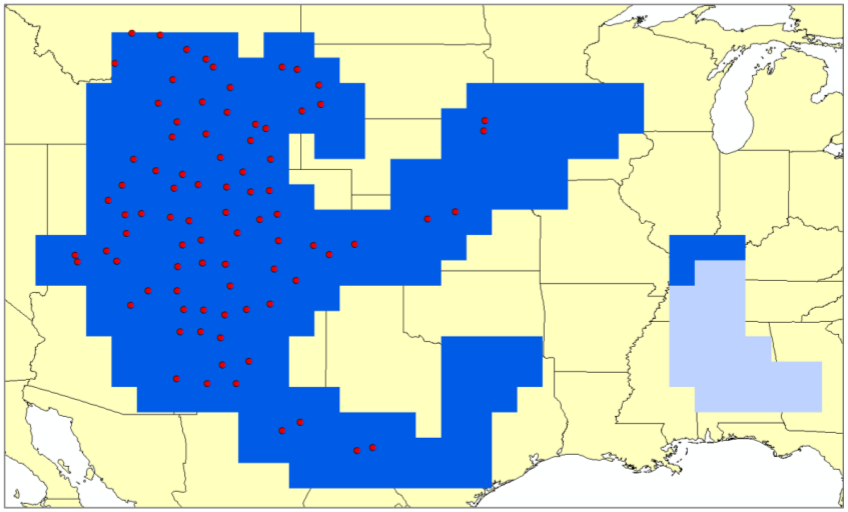


Inoceramus

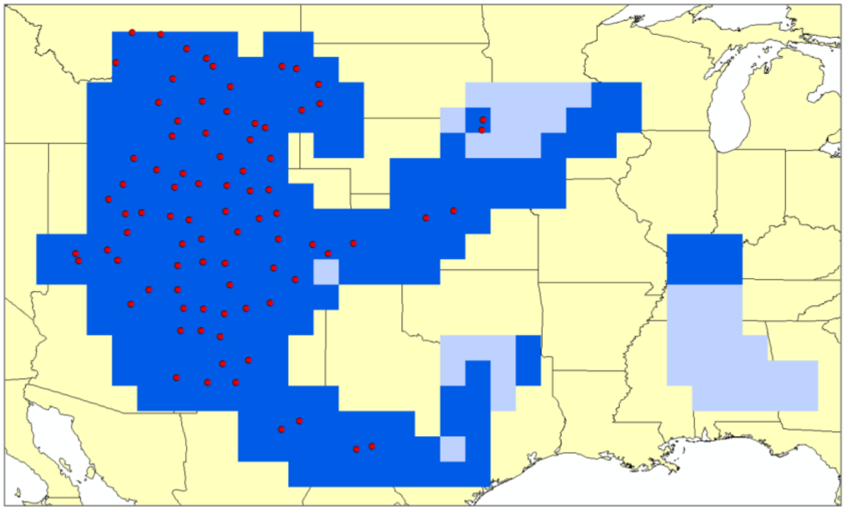
Cenomanian training region



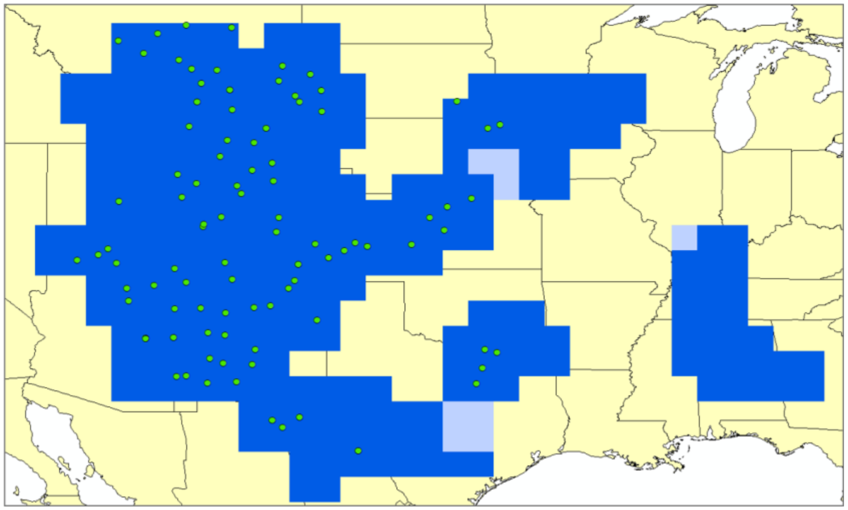
Cenomanian projection onto Turonian environments



Turonian training region

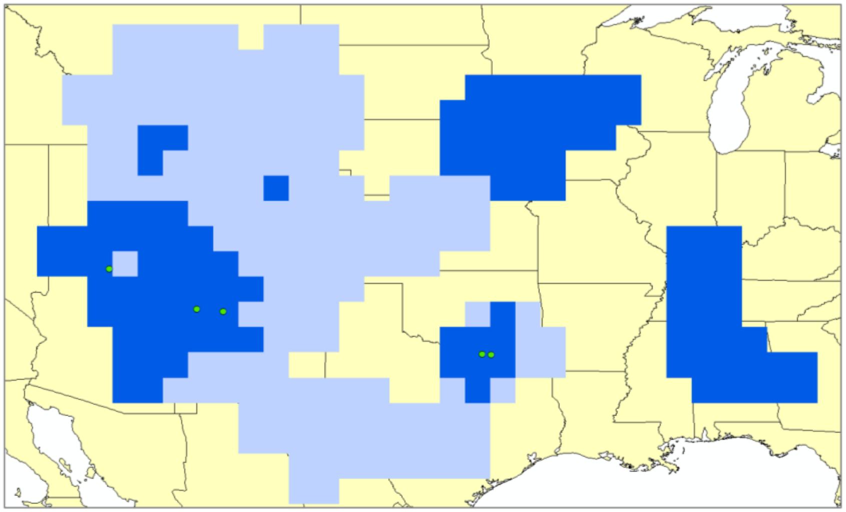


Turonian projection onto Cenomanian environments

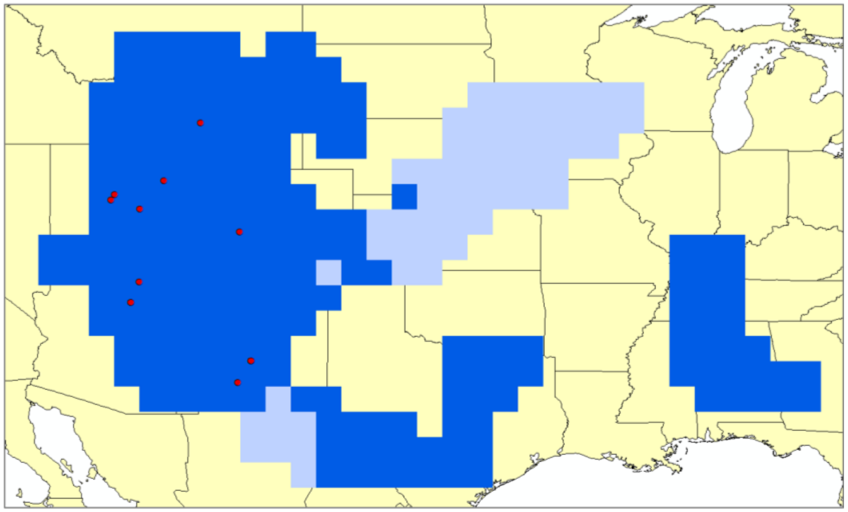


Legumen

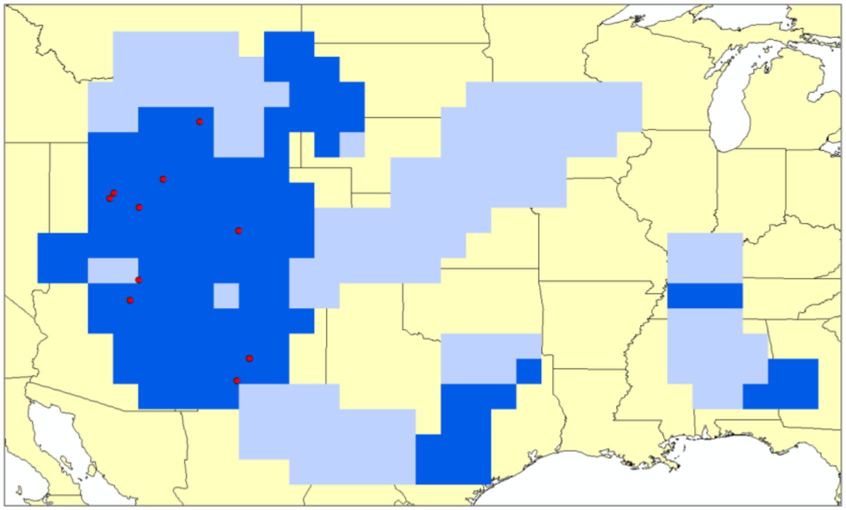
Cenomanian training region



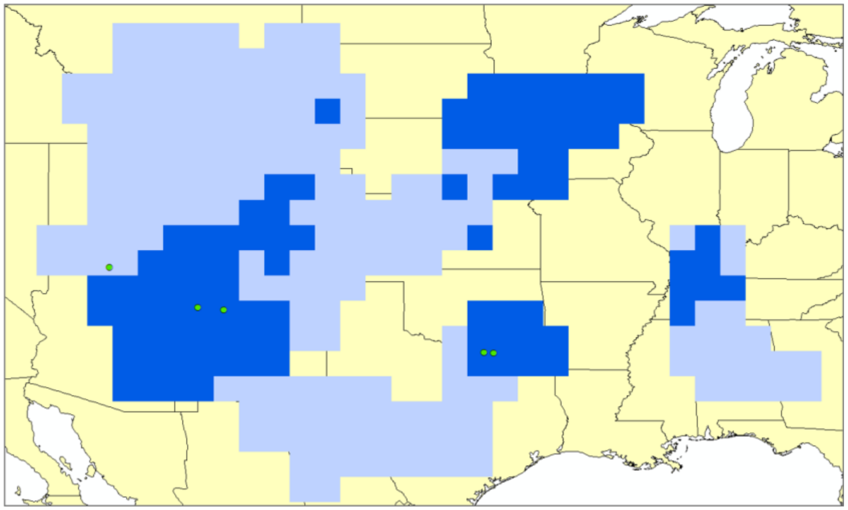
Cenomanian projection onto Turonian environments



Turonian training region

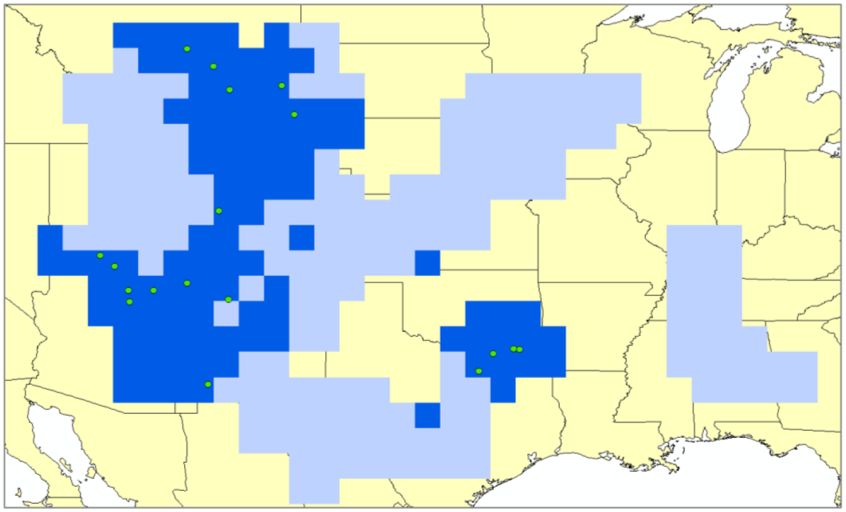


Turonian projection onto Cenomanian environments



Lucina

Cenomanian training region



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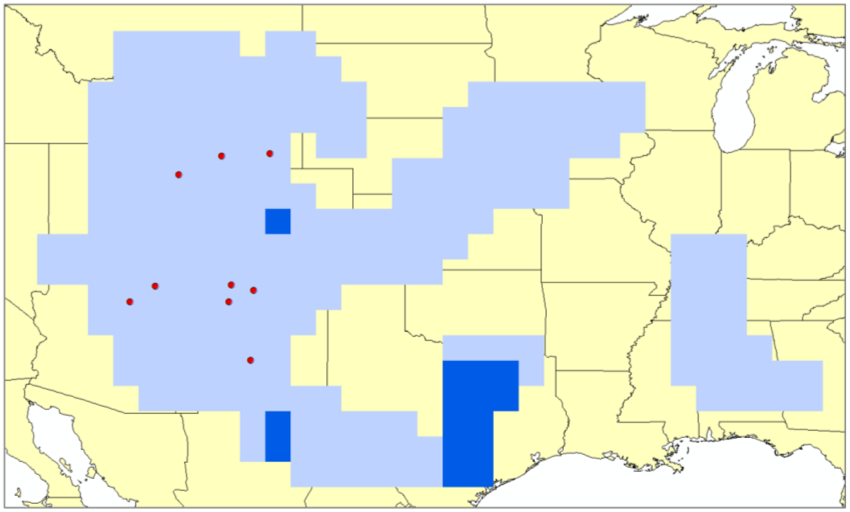

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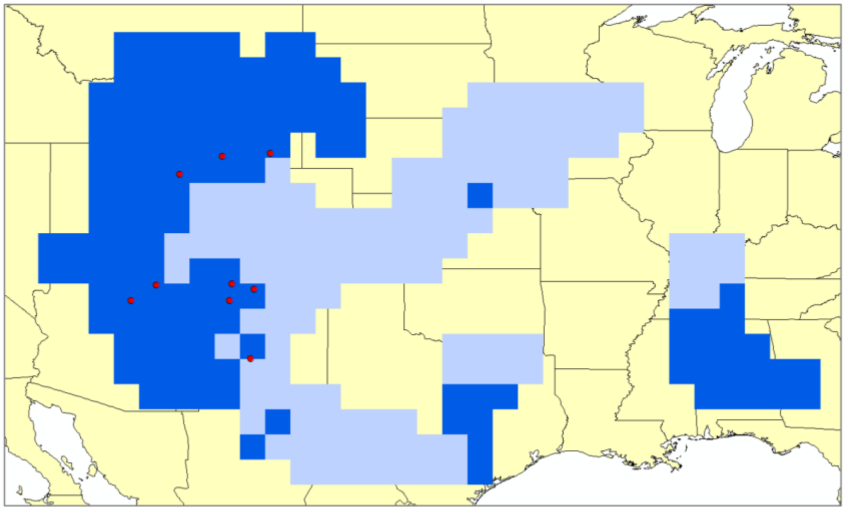
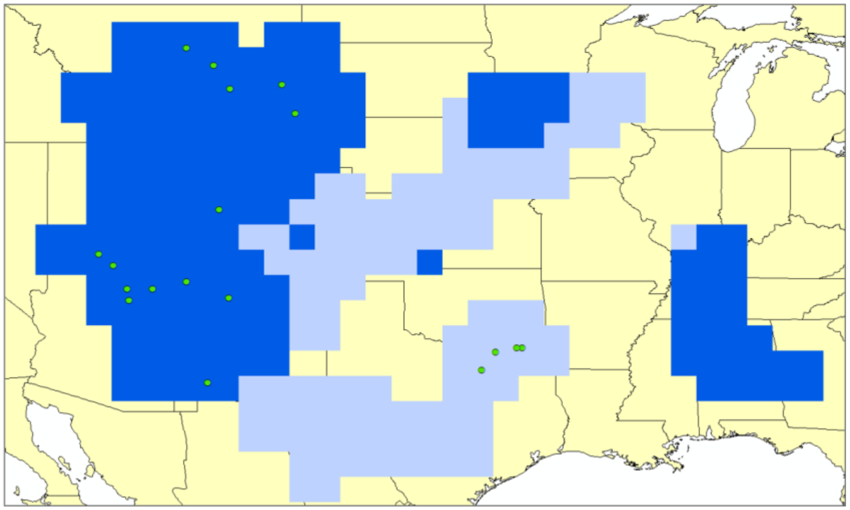
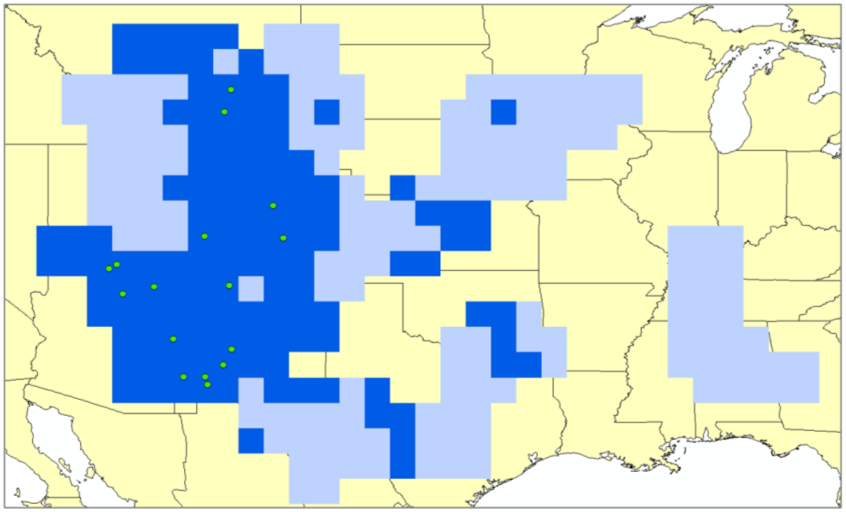


Turonian projection onto Cenomanian environments

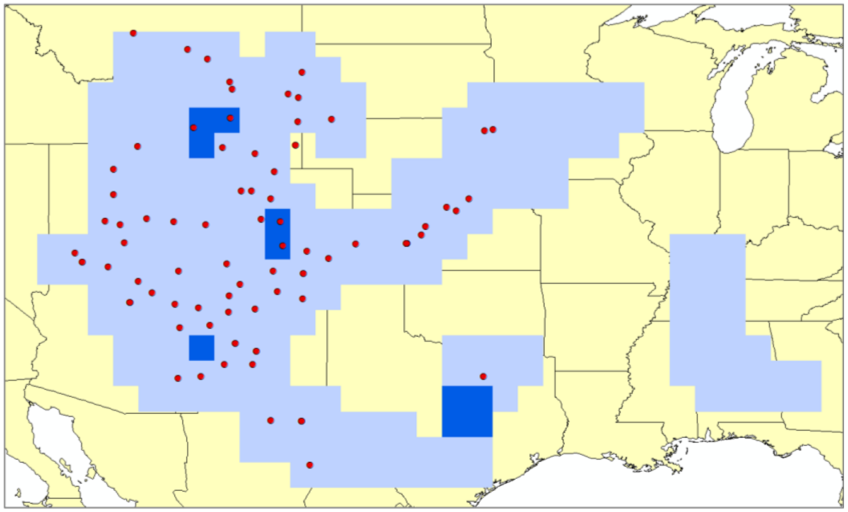


Mytiloides

Cenomanian training region



Cenomanian projection onto Turonian environments



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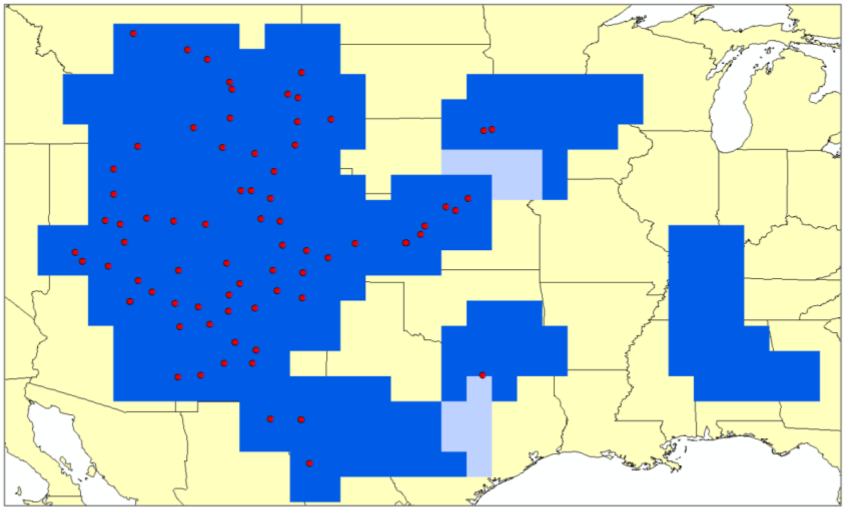
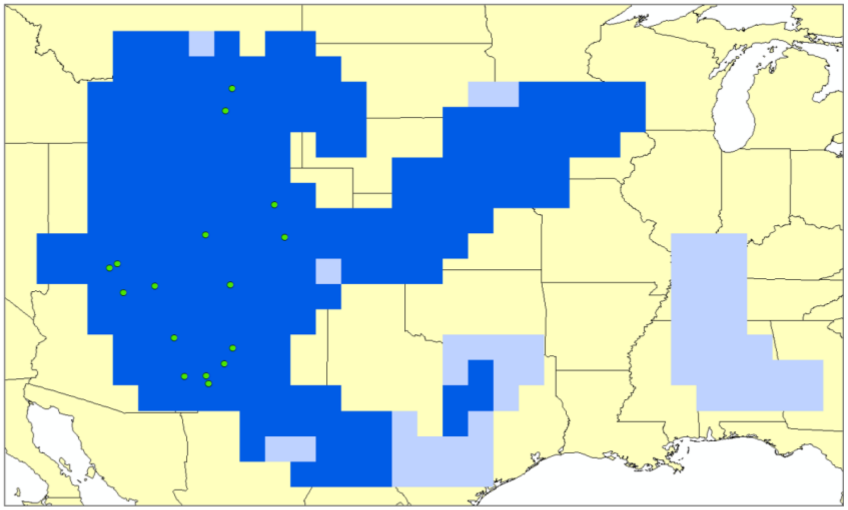
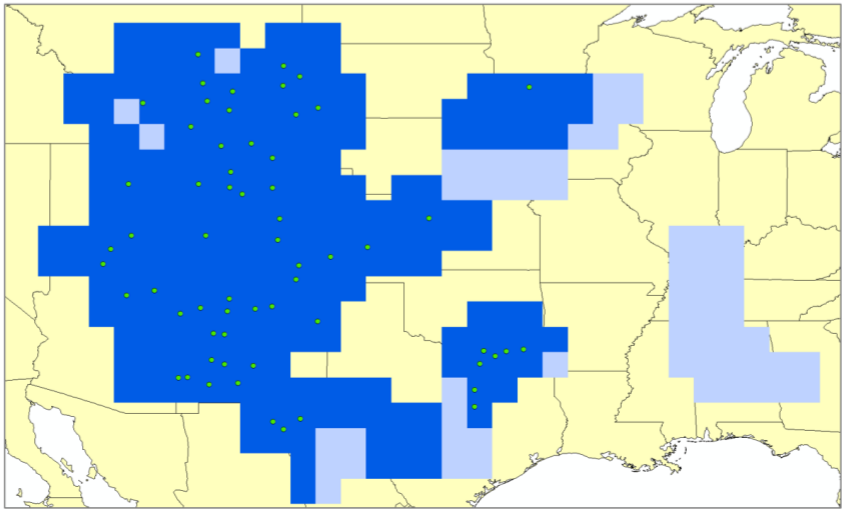


Turonian projection onto Cenomanian environments

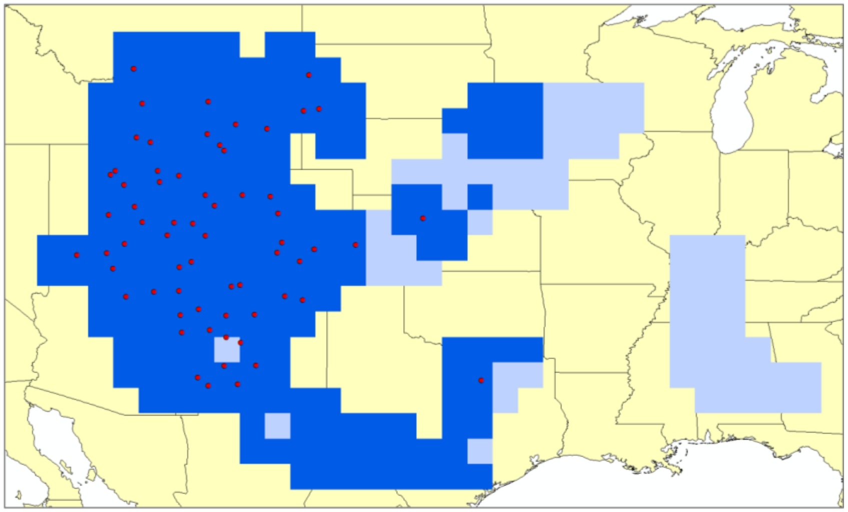


Ostrea

Cenomanian training region



Cenomanian projection onto Turonian environments



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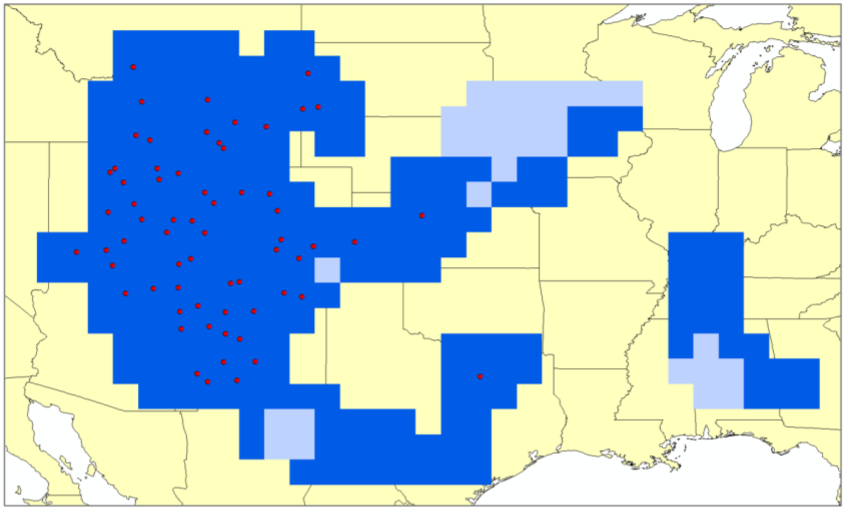

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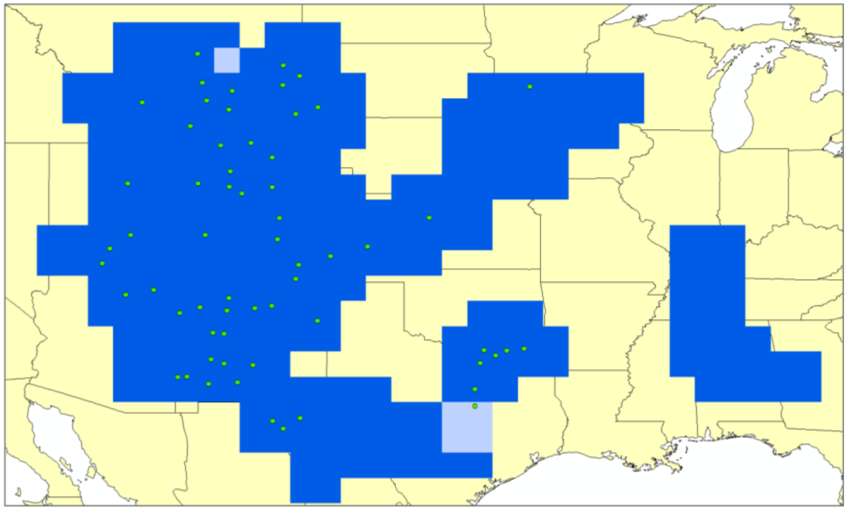
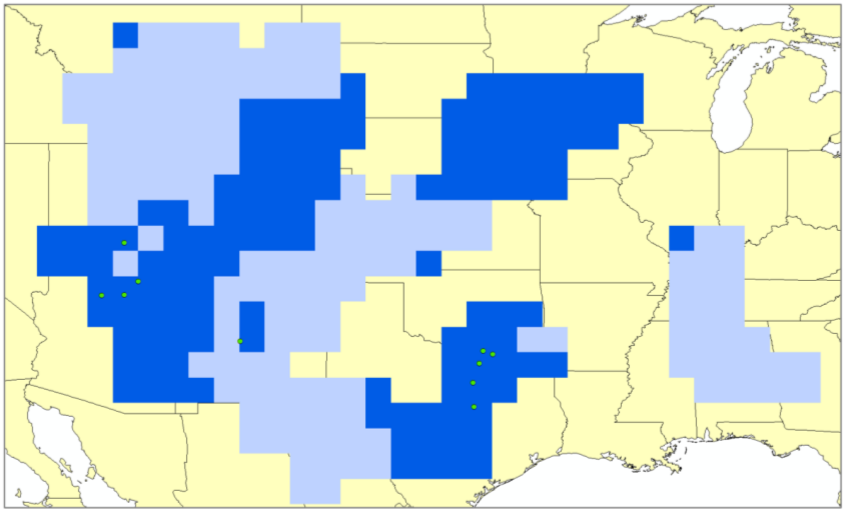


Ostrea soleniscus

Cenomanian training region



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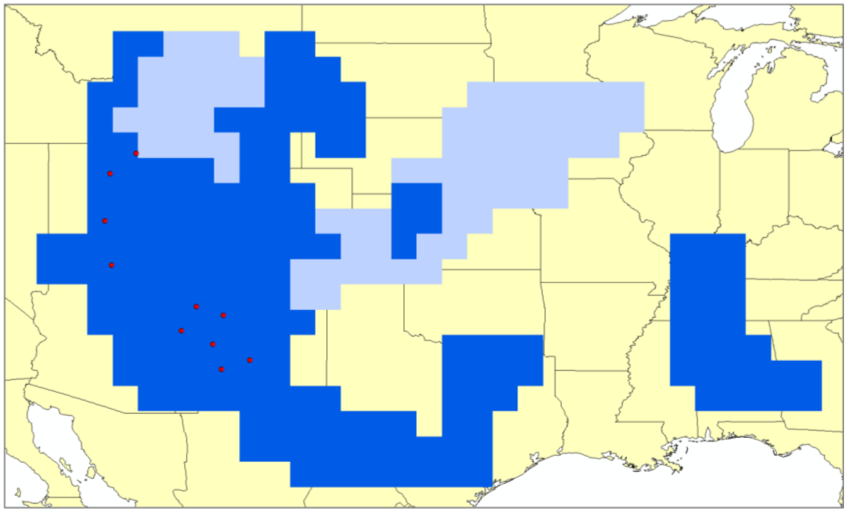

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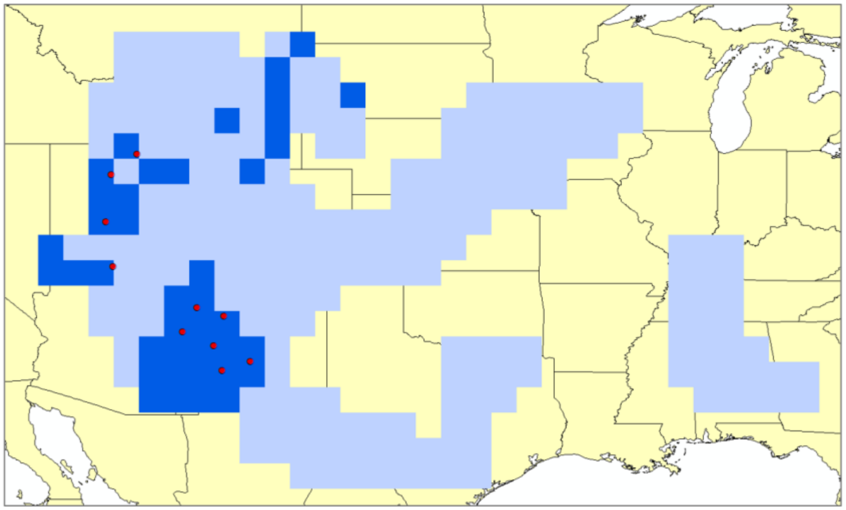
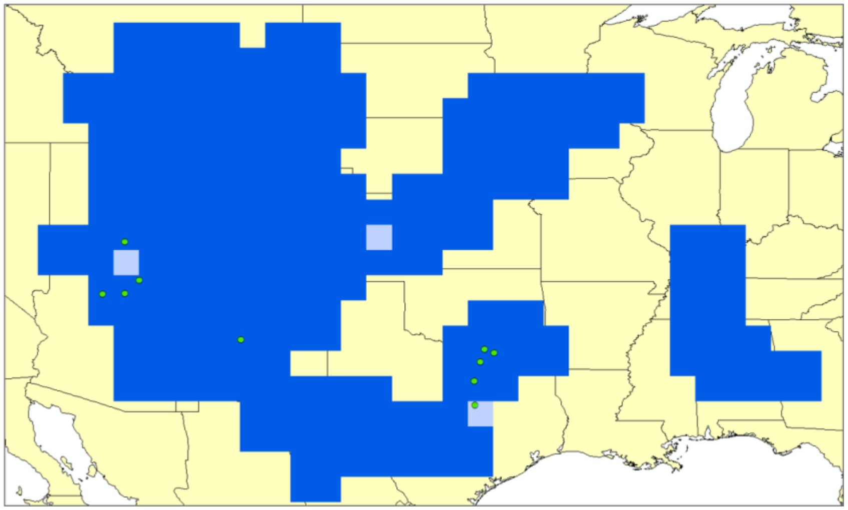
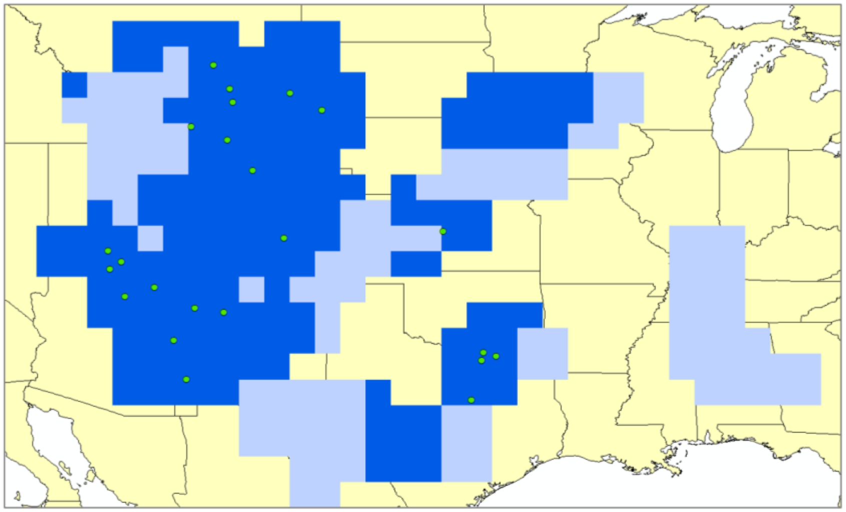
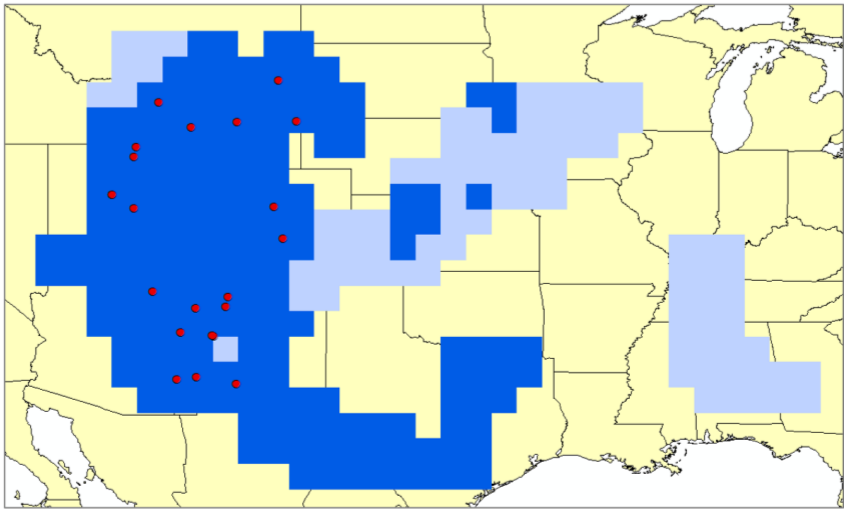


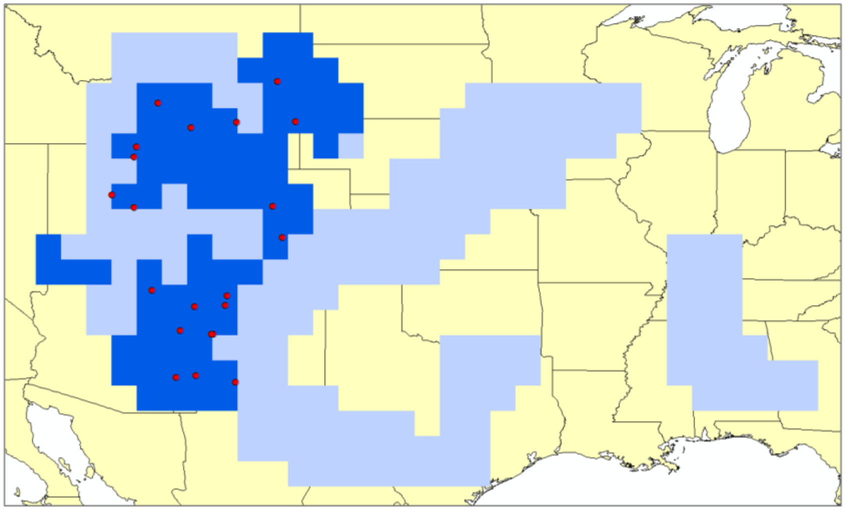
Turonian projection onto Cenomanian environments

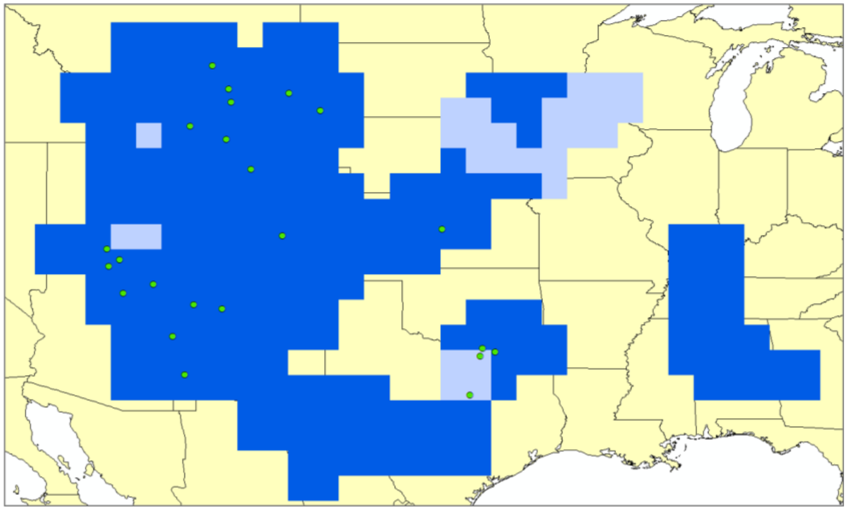


Phelopteria


Cenomanian training region

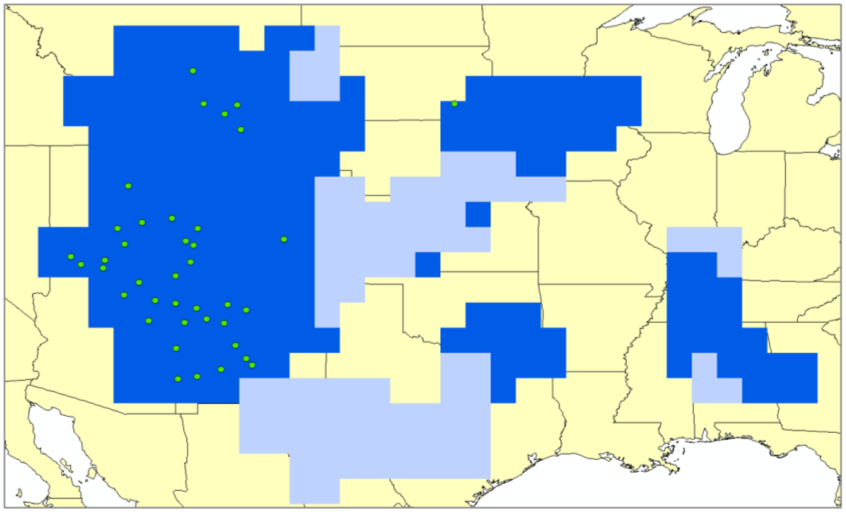

Cenomanian projection onto Turonian environments


Turonian training region

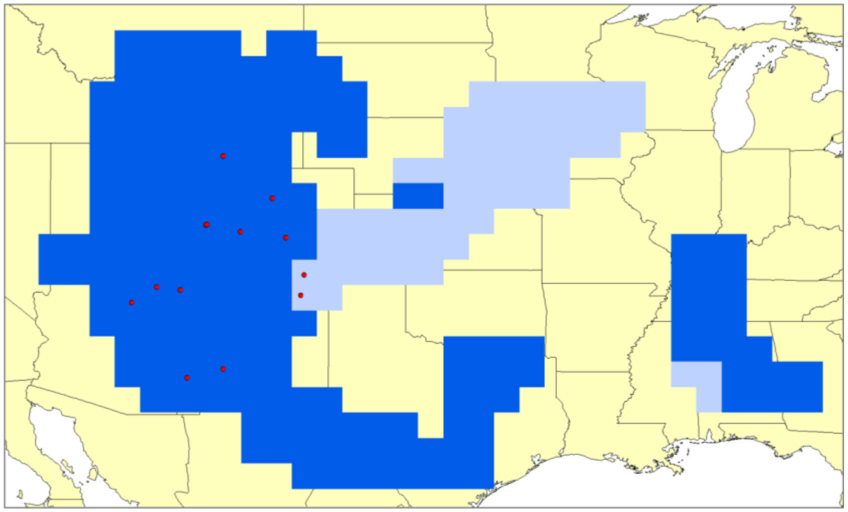

Turonian projection onto Cenomanian environments

Pycnodonte

Cenomanian training region



Cenomanian projection onto Turonian environments



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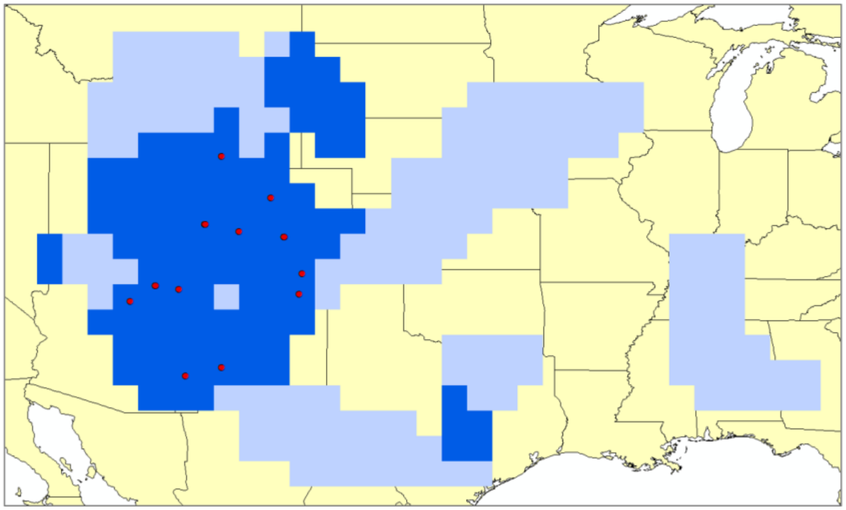
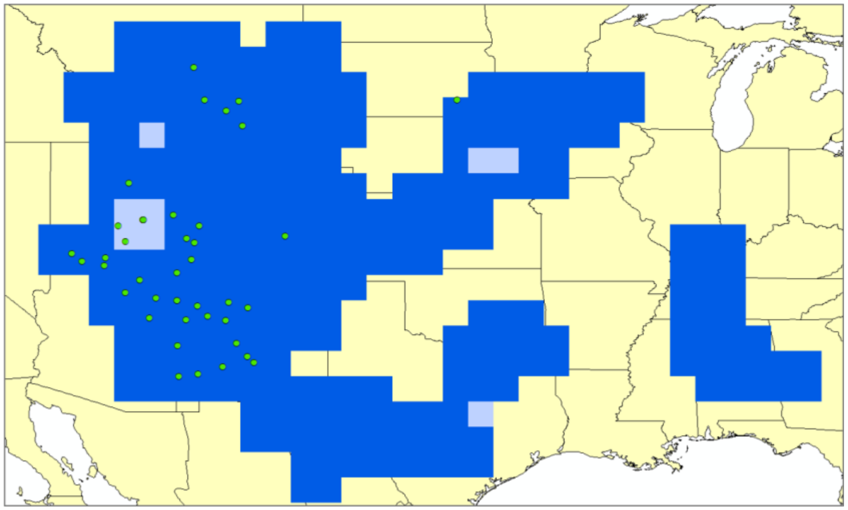
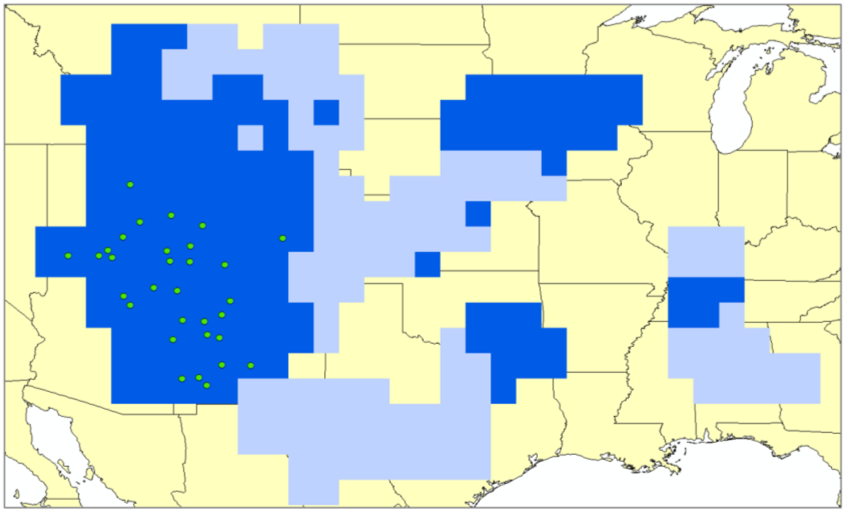
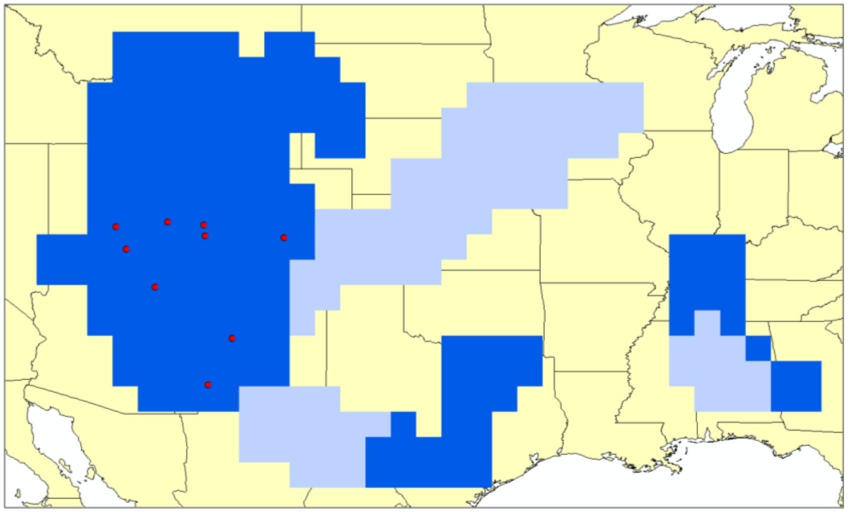


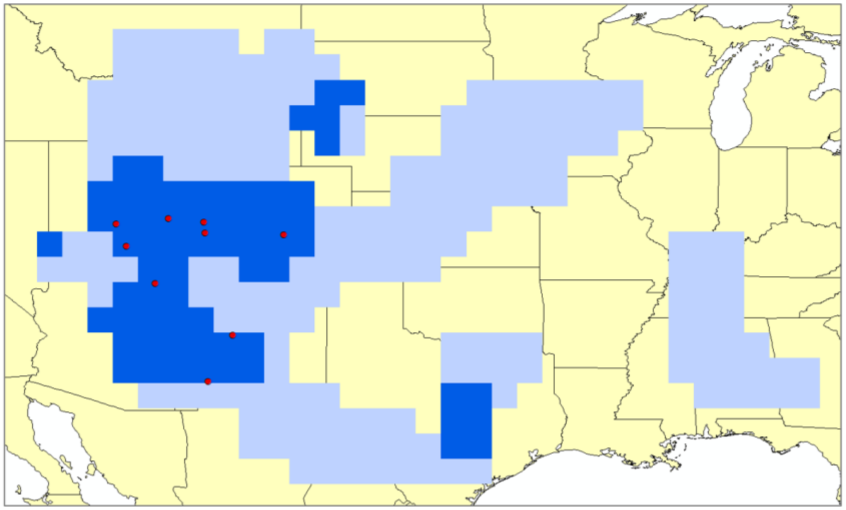
Turonian projection onto Cenomanian environments



Pycnodonte newberryi


Cenomanian training region


Cenomanian projection onto Turonian environments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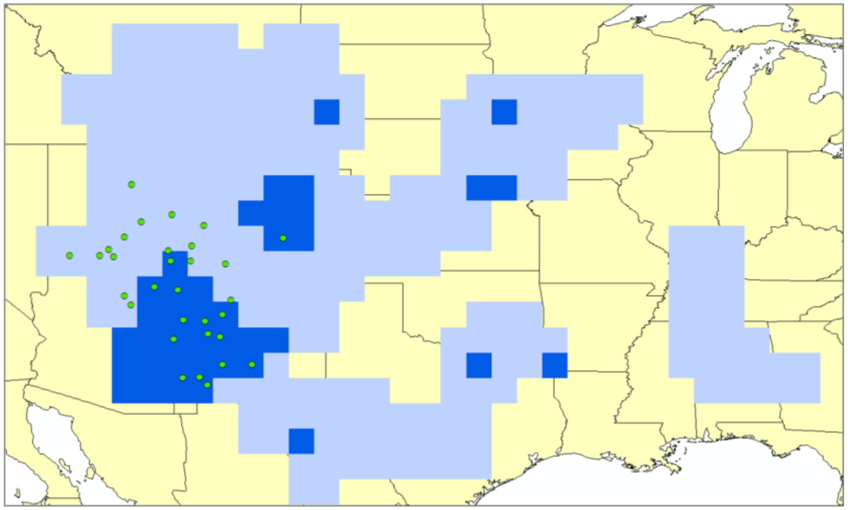
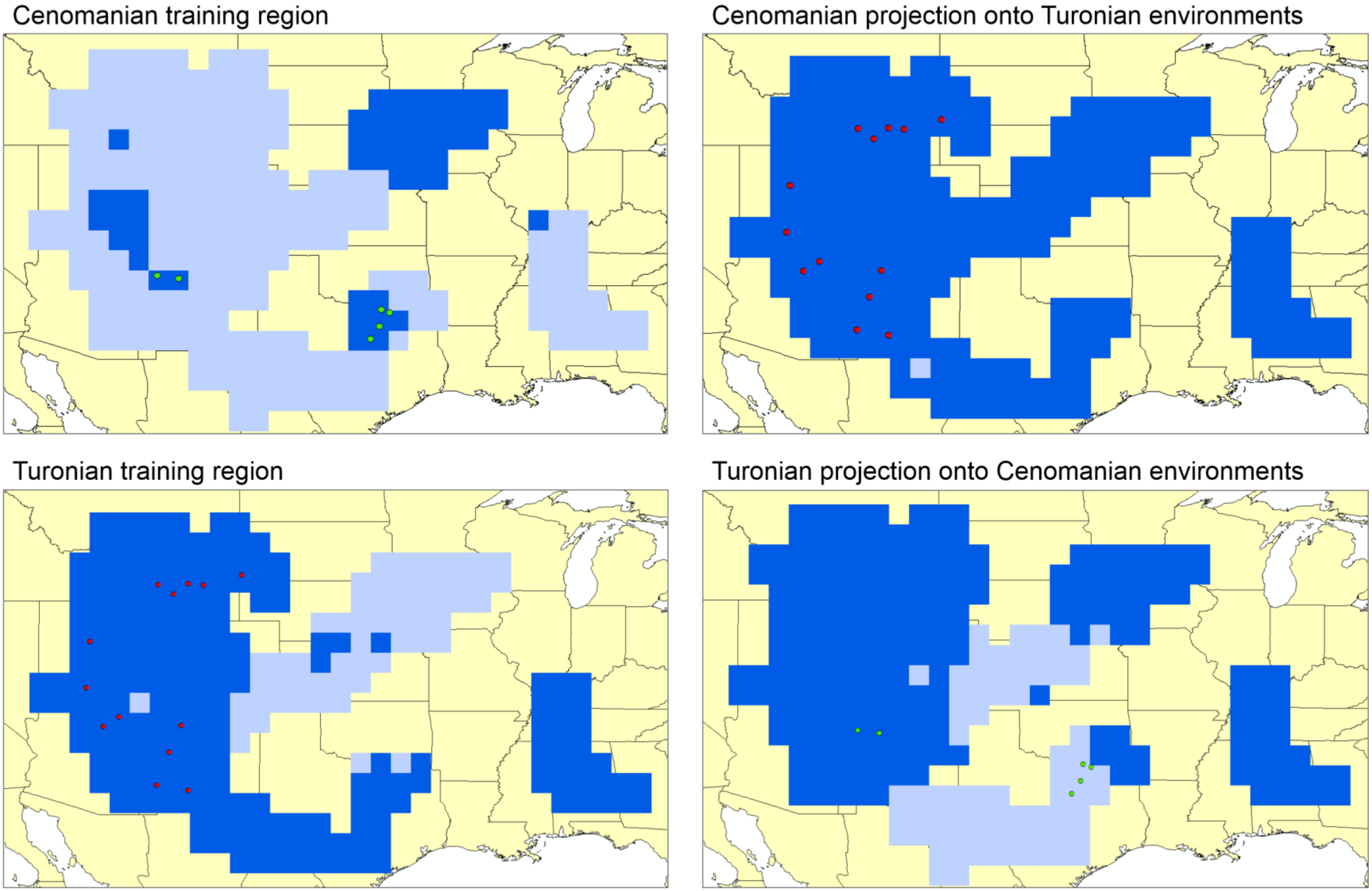

Turonian projection onto Cenomanian environments

Tellina



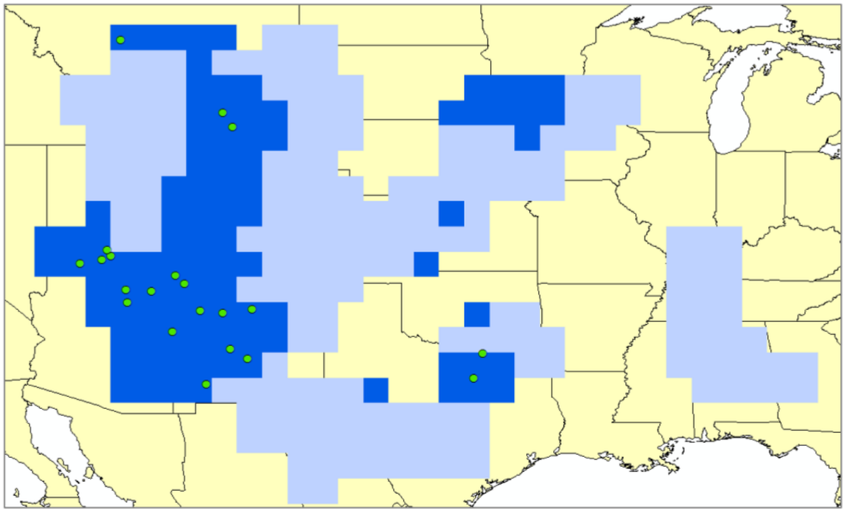
Cenomanian training region

Cenomanian projection onto Turonian environments

Turonian training region

Turonian projection onto Cenomanian environments

Turritella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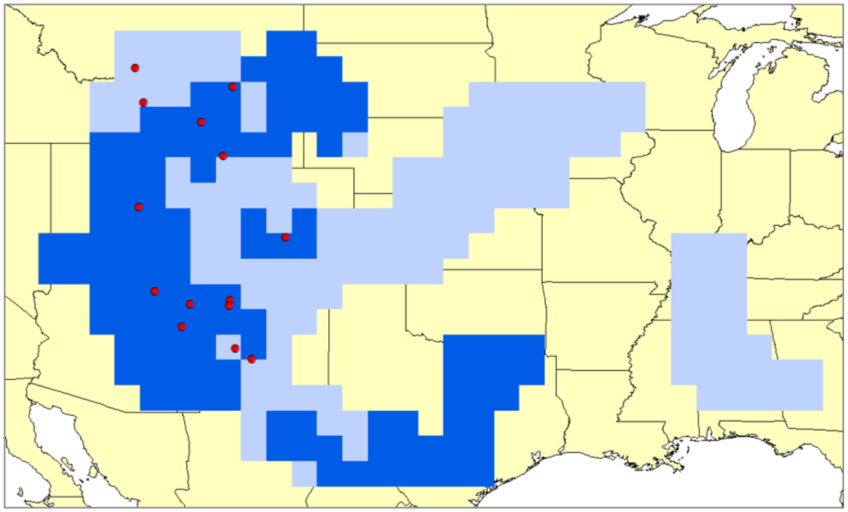
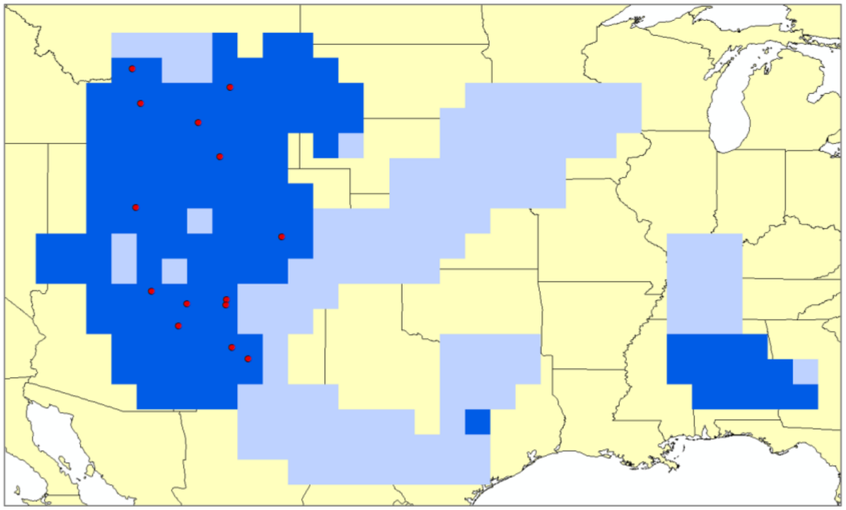

Cenomanian projection onto Turonian environments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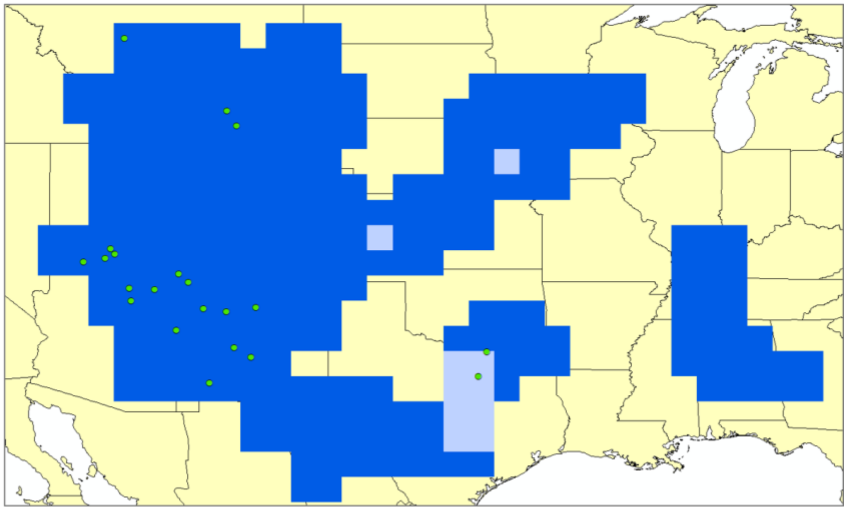
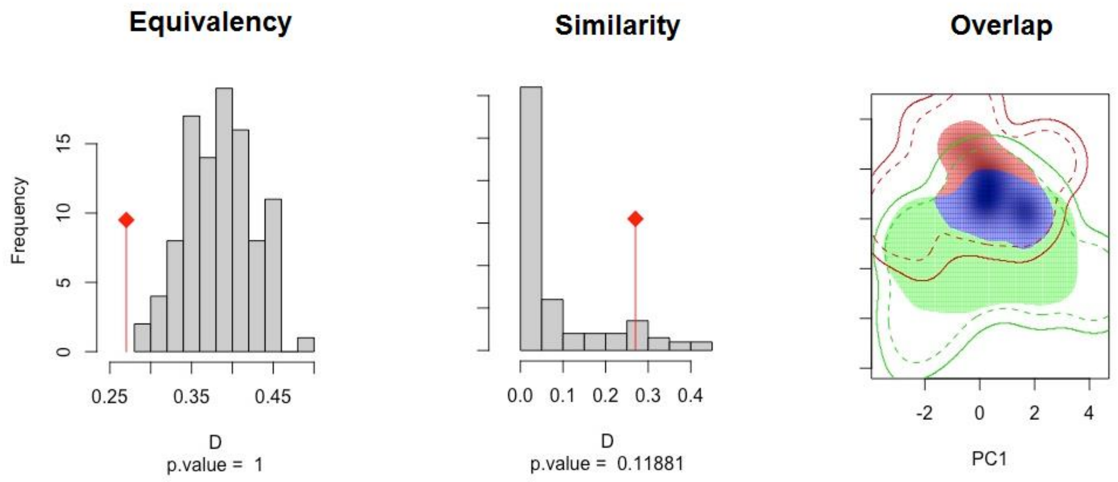

Turonian projection onto Cenomanian environments

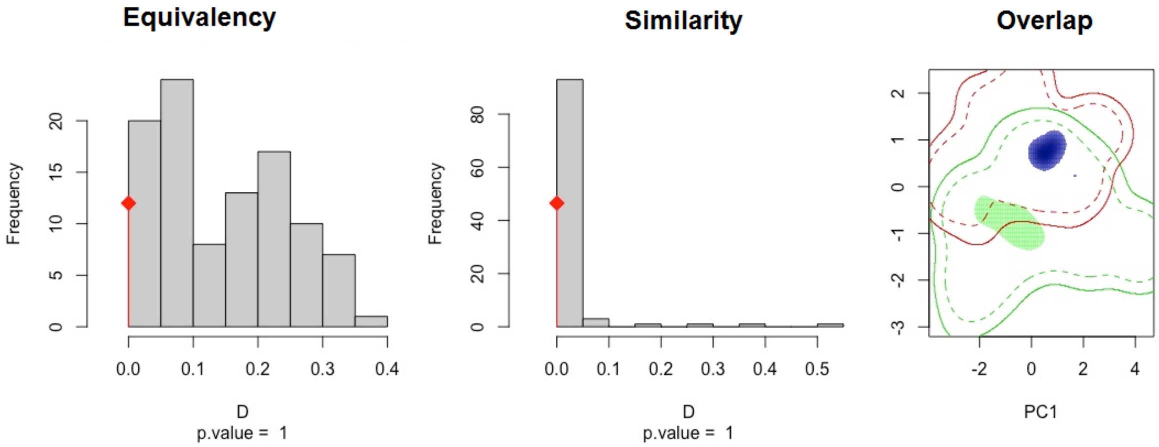
Appendix 5 – Ecospat results

Figures from Ecospat output for each taxon per column. Taxon name is labeled at the top, followed by niche equivalency, similarity, and overlap (with green = Cenomanian, red = Turonian) in descending order.

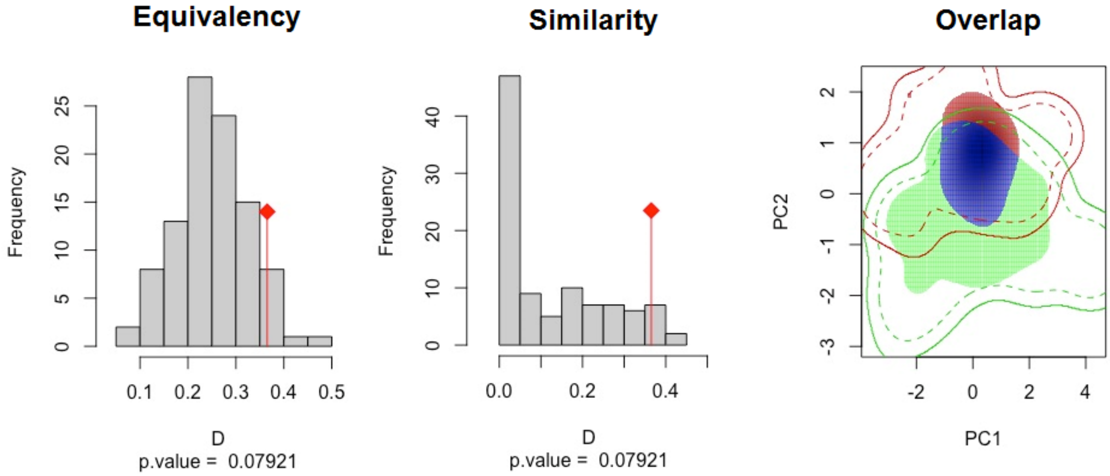
Baculites



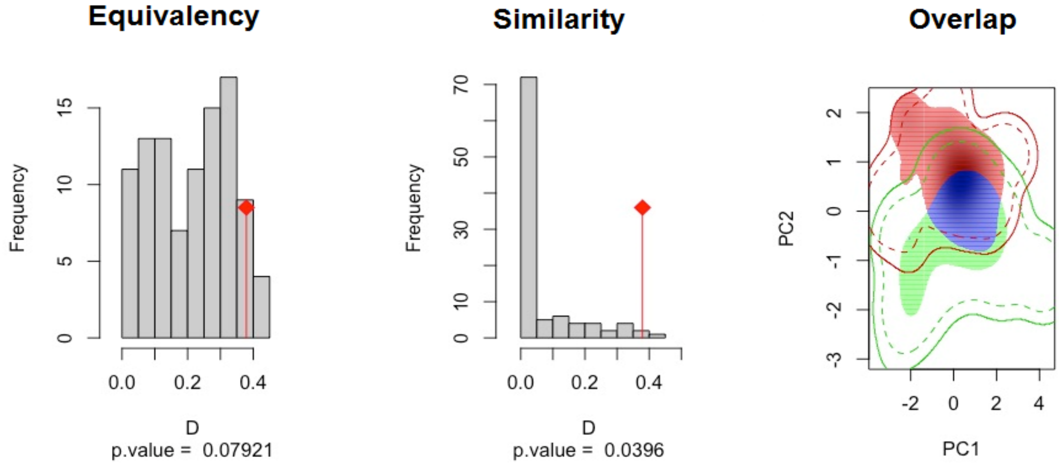
Baculites yokoyamai



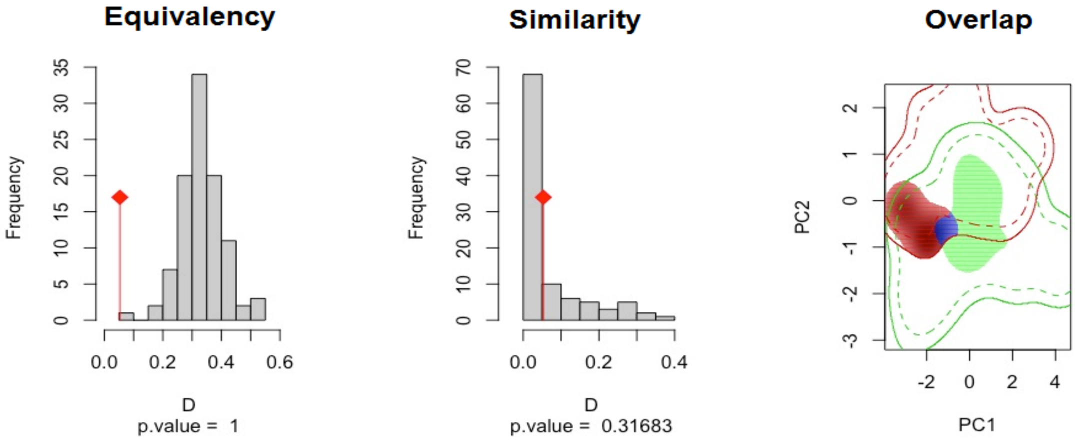
Fagesia



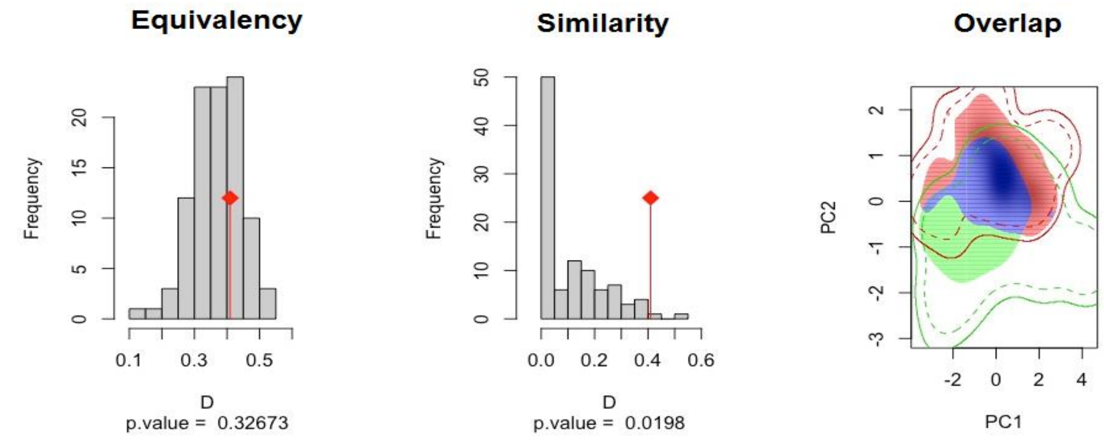
Mammites



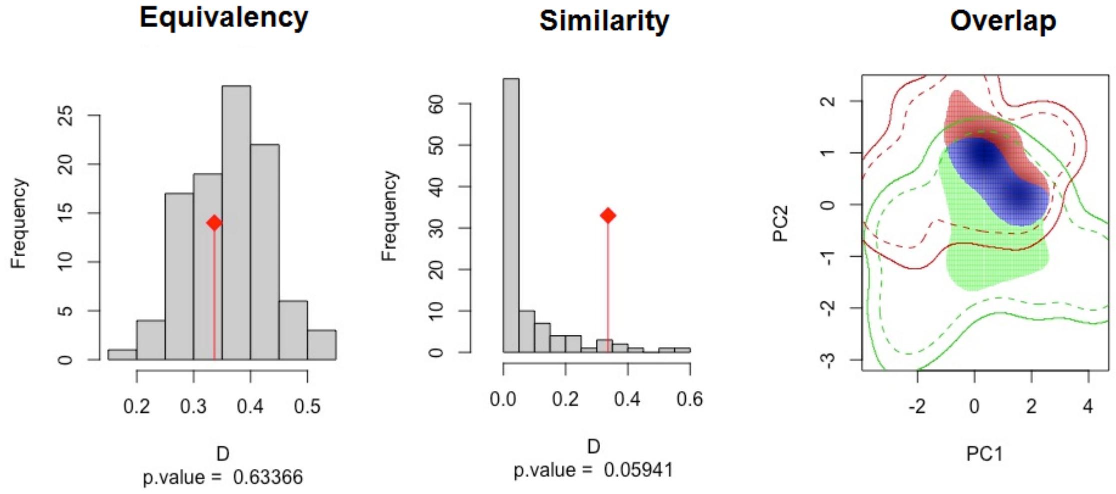
Placenticeras



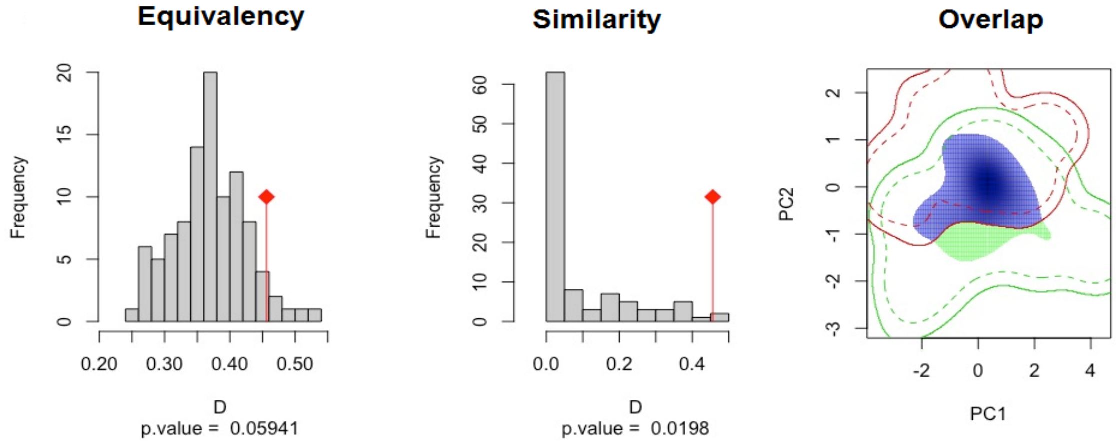
Scaphites



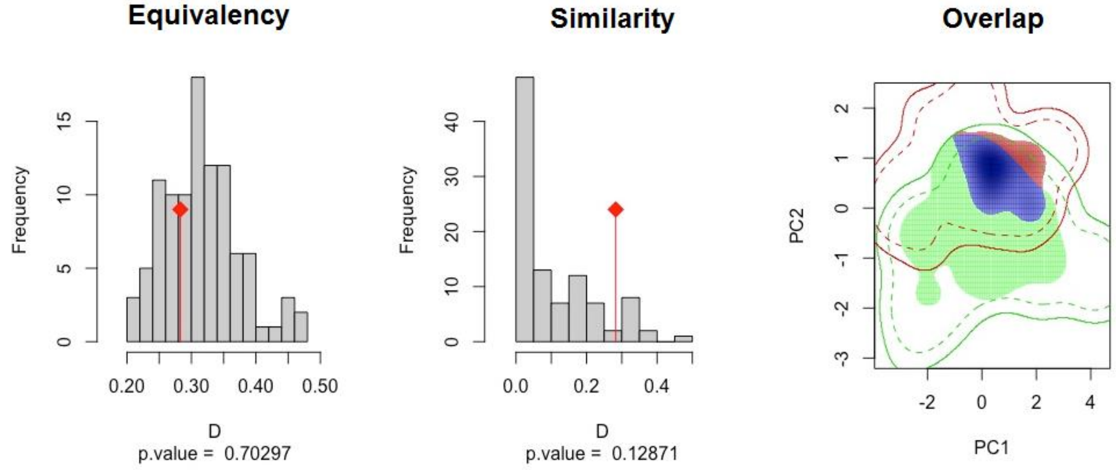
Corbula



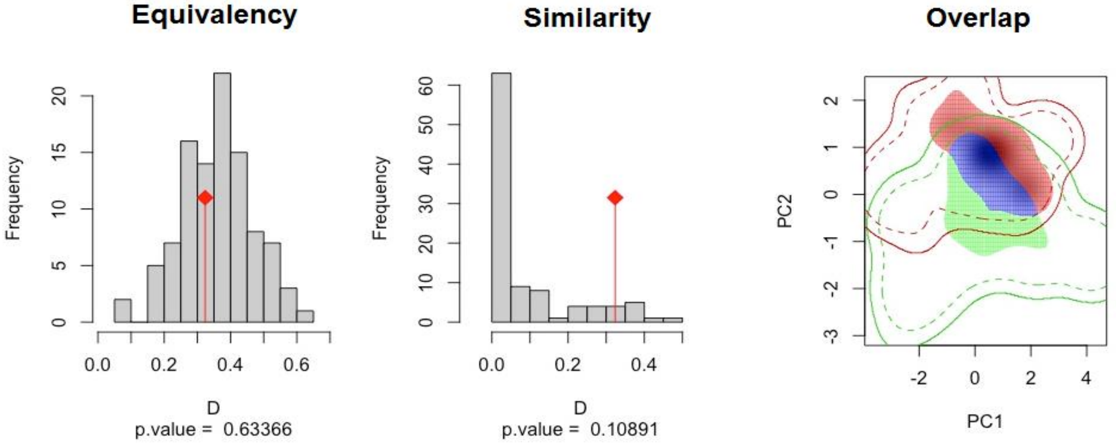
Cymbophora



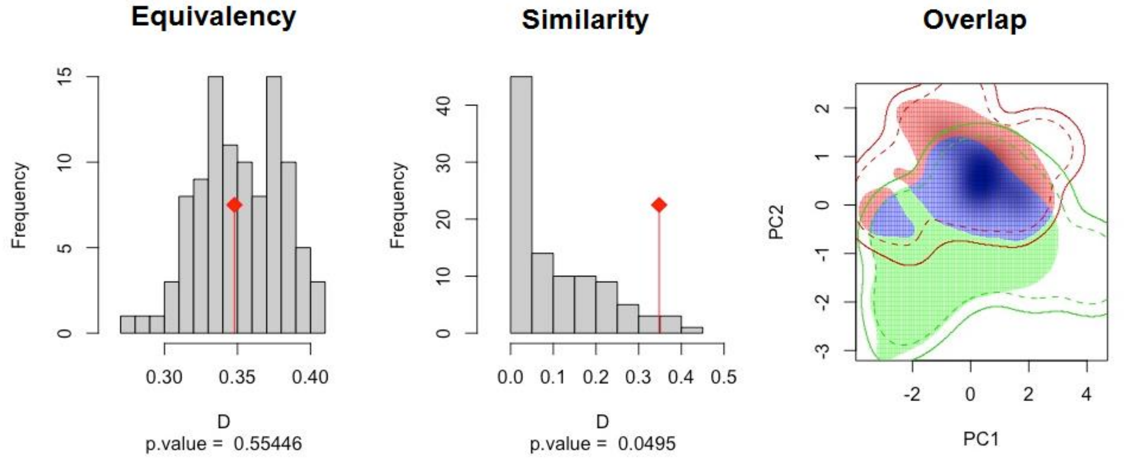
Exogyra



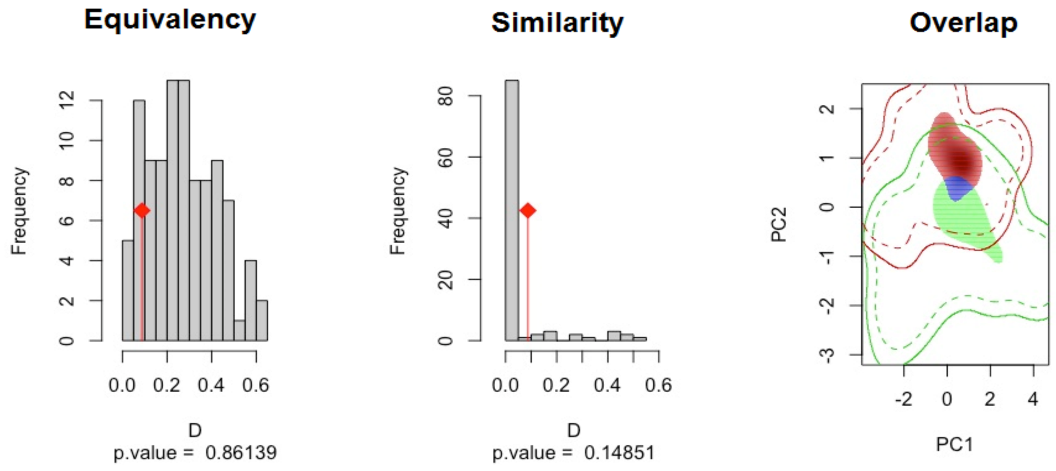
Gyrodes



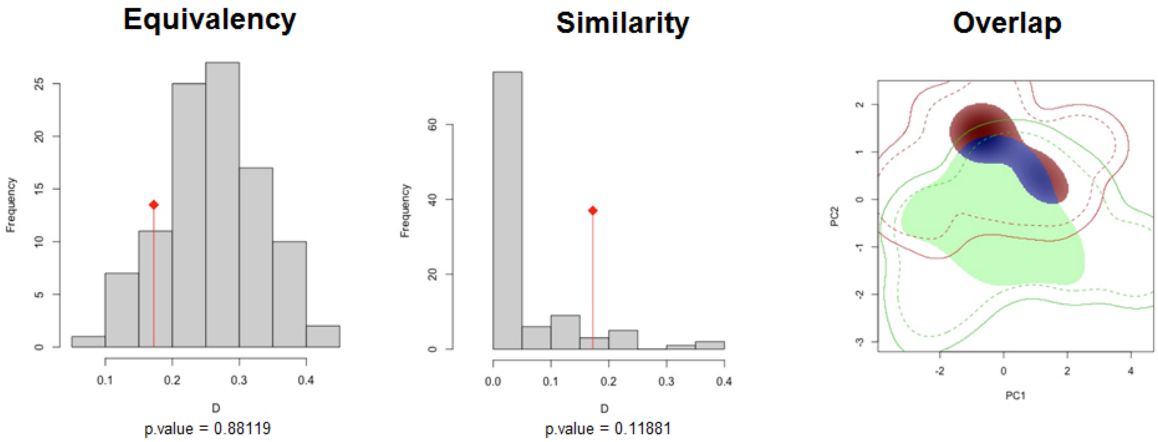
Inoceramus



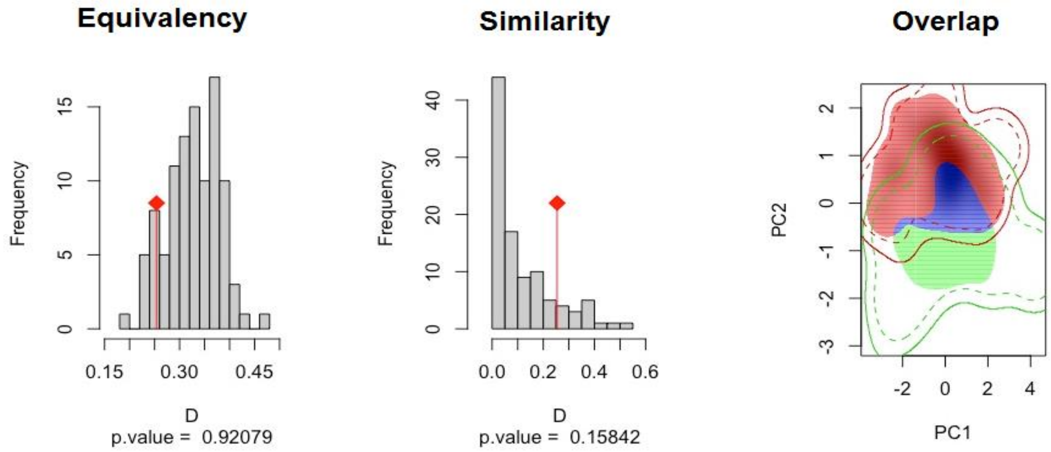
Legumen



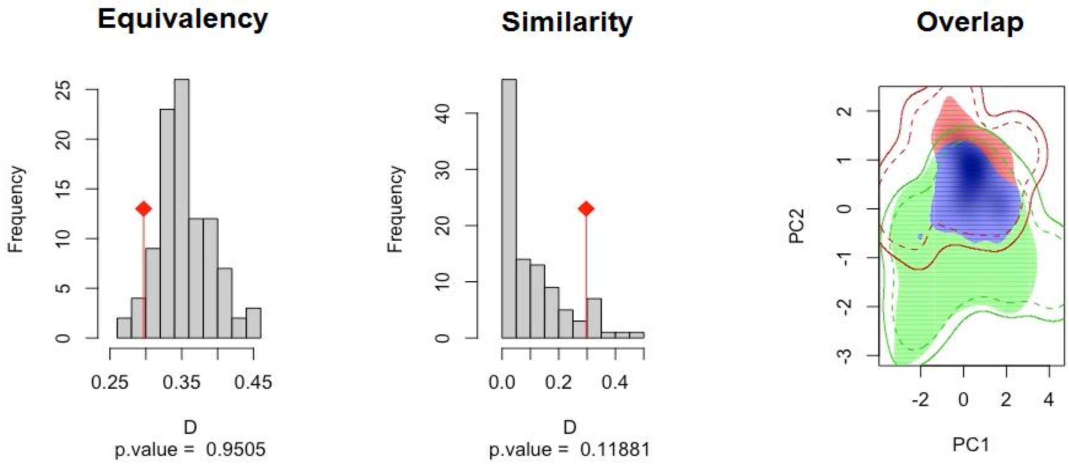
Lucina



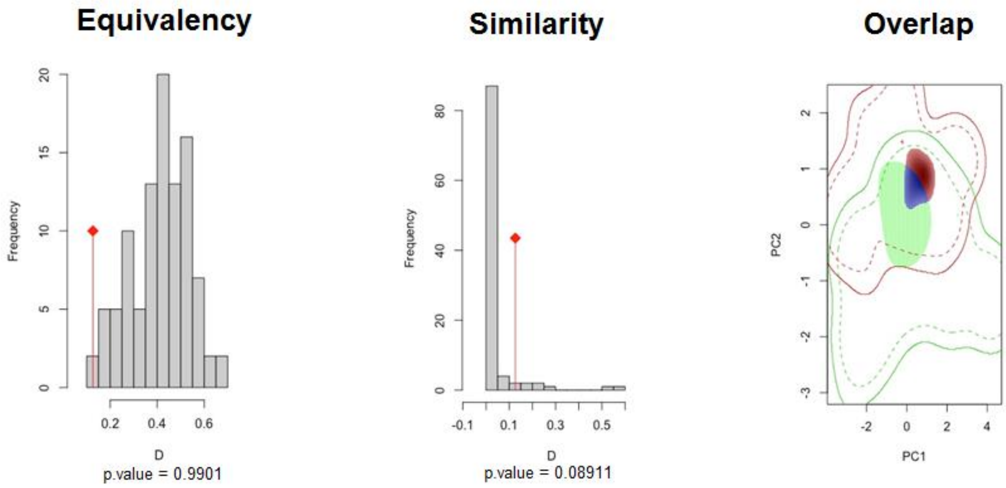
Mytiloides



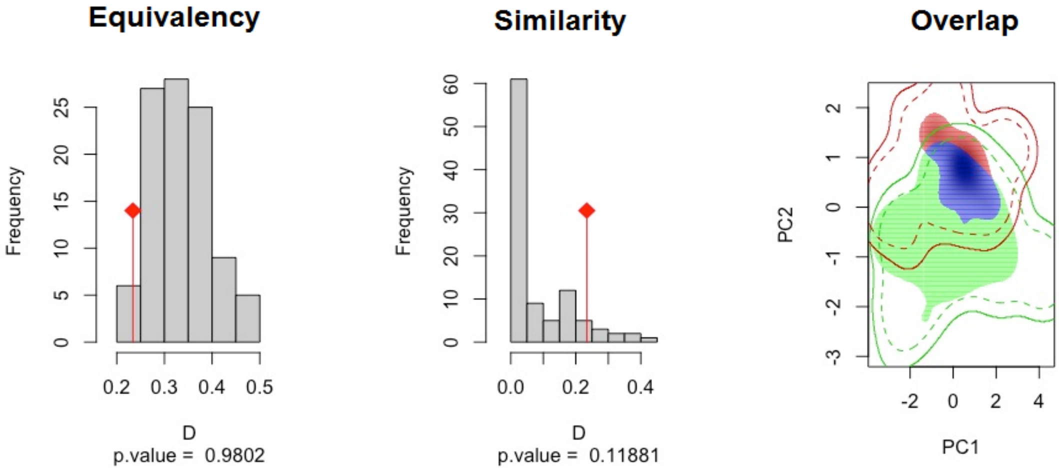
Ostrea



Ostrea soleniscus



Phelopteria



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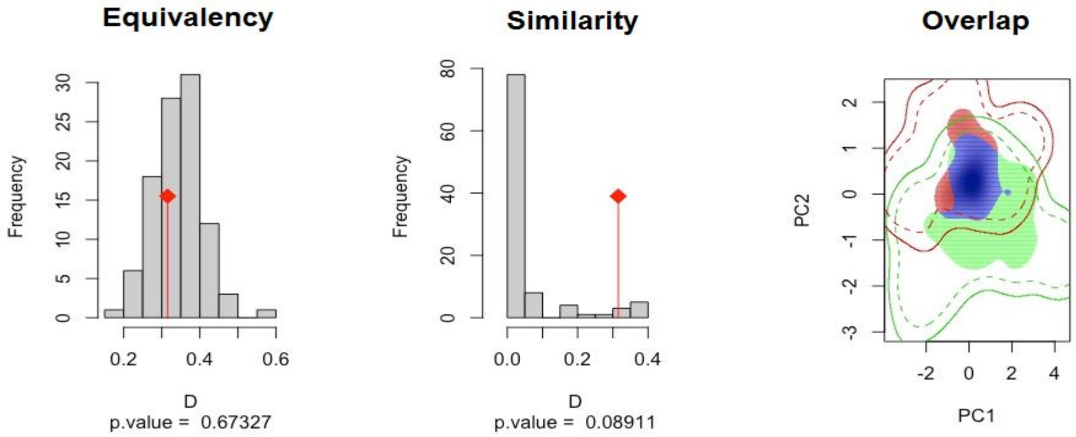
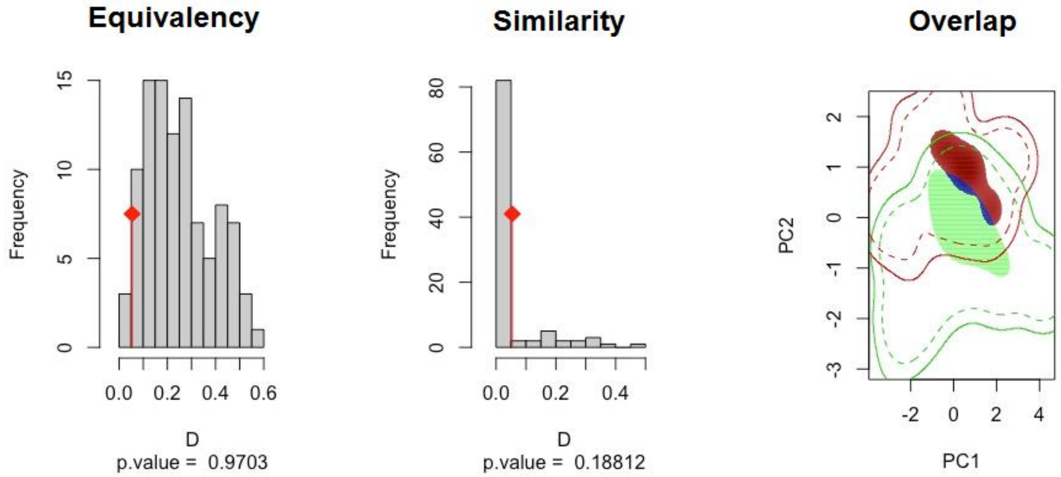
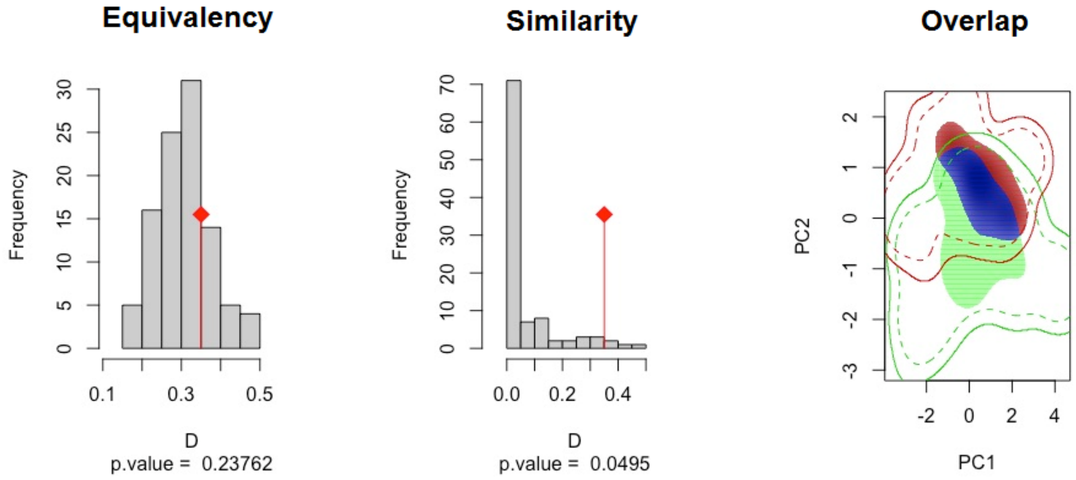


Tellina



Turritella



Appendix 6 – Environmental layer references

Full references for Cenomanian and Turonian environmental layers (see Appendices 1 and 3 for state information).

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