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Estimating ancient biogeographic patterns with statistical model discrimination

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Abstract

The geographic ranges in which species live is a function of many factors underlying ecological and evolutionary contingencies. Observing the geographic range of an individual species provides valuable information about these historical contingencies for a lineage, determining the distribution of many distantly related species in tandem provides information about large-scale constraints on evolutionary and ecological processes generally. We present a linear regression method that allows for the discrimination of various hypothetical biogeographical models for determining which landscape distributional pattern best matches data from the fossil record. The linear regression models used in the discrimination rely on geodesic distances between sampling sites (typically geologic formations) as the independent variable and three possible dependent variables: Dice/Sorensen similarity; Euclidean distance; and phylogenetic community dissimilarity. Both the similarity and distance measures are useful for full-community analyses without evolutionary information, whereas the phylogenetic community dissimilarity requires phylogenetic data. Importantly, the discrimination method uses linear regression residual error to provide relative measures of support for each biogeographical model tested, not absolute answers or *p*-values. When applied to a recently published dataset of Campanian pollen, we find evidence that supports two plant communities separated by a transitional zone of unknown size. A similar case study of ceratopsid dinosaurs using phylogenetic community dissimilarity provided no evidence of a biogeographical pattern, but this case study suffers from a lack of data to accurately discriminate and/or too much temporal mixing. Future research aiming to reconstruct the distribution of organisms across a landscape has a statistical-based method for determining what biogeographic distributional model best matches the available data.

KEYWORDS

biogeography, dinosaur, ecology, linear regression, phylogenetics

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1 | INTRODUCTION

Quantifying biodiversity across time and reconstructing the phylogenetic relationships of that biodiversity are the two legs supporting the majority of macroevolution research. Peter Dodson's career has been devoted to bolstering these two pillars, especially in the Cretaceous of North America and Asia. Early in his career, Dodson (1975) used allometry to greatly reduce the assumed biodiversity of hadrosaurids in the, then, Oldman Formation (now the Dinosaur Park Formation) by demonstrating the numerous species of *Prochenosaurus* were juveniles of the genera *Lambeosaurus* and *Corythosaurus*. Since that landmark paper, he set his sights on quantifying the total number of dinosaurs that existed during the Mesozoic, which resulted in a preliminary count of 336 discovered genera (Holmes & Dodson, 1997), with subsequent revised estimates of approximately 1,850 genera (Wang & Dodson, 2006) and 1,936 species (Starrfelt & Liow, 2016) using more complex statistical methods.

Additionally, Peter Dodson considered the role of biodiversity in paleoecology by studying dinosaurs (Dodson, Behrensmeyer, Bakker, & McIntosh, 1980) and the small vertebrates that lived alongside them (Dodson, Currie, & Koster, 1987). Some of his most influential works in paleoecology stem from studies of taphonomy (Dodson, 1971; Dodson et al., 1980), which he used to identify biases in the fossil record that could, once identified, be accommodated in paleoecological interpretations. The contribution presented here follows in the same vein of understanding aspects of ancient ecosystems and biogeography by incorporating known biodiversity data and accommodating preservation biases.

Modeling biotic geographic range distributions across a landscape can inform us about the underlying ecological parameters that shape range boundaries (Brown, Stevens, & Kaufman, 1996). Individual species geographic ranges are expected to vary in shape and size due to the sum of interactions between an organism's phenotype and extrinsic factors such as the abiotic environment or density-dependent biotic influences like competition, predation, and disease (Brown et al., 1996; Gaston, 2003; Lomolino, Riddle, & Brown, 2005). Indeed, biogeography and biodiversity theory rely heavily on observations of geographic range size and shape. For instance, Rapoport's rule states that the latitudinal range size of organisms living at the poles is larger than those living toward the equator (Rapoport, 1982). Researchers have also documented that, within a given latitude, there is greater species diversity in topographically complex regions, compared to flatter regions (Badgley et al., 2017; Finarelli & Badgley, 2010). Each of these generalizations requires species-specific geographic range data, yet the

combination of these data results in emergent properties at larger scales that are often the focus of study and simultaneously complex to model and describe.

Overlaying the geographic ranges of every species within an ecosystem presents in a mosaic of varying range shapes and sizes that morph across a landscape. As a result, geographic localities will differ in the number of species that overlap their range, ultimately producing variability in species composition across a gradient. Likely the most conspicuous of these biodiversity turn-overs is the modern-day latitudinal diversity gradient, which describes the phenomenon of greater species diversity near the equator than observed at the poles (Hillebrand, 2004; Pontarp et al., 2019). Despite being a canonical phenomenon of extant ecology, it remains unclear why the latitudinal biodiversity gradient forms. Records of ancient life have the potential to provide valuable information about ecosystem and geographic range shifts over long time intervals, something unattainable using only extant biotic records and some authors have therefore suggested that paleontological records hold the key to deciphering this pattern (Fraser, 2017; Jablonski & Hunt, 2006; Mittelbach et al., 2007).

As we observe with modern species, a terrestrial ancient species would have occupied a two-dimensional geographic range that covered a region of earth's surface. However, nonrandom and discontinuous preservation of these past ecosystems within sedimentary basins (i.e., in geologic formations) biases this record. In essence, this nonrandom preservation turns near-continuous biotic geographic range distributions into a series of discrete point distributions, each marked by occurrences in fossil localities (Figure 1). Geographic ranges of extant species are interpolated based on many point occurrences, yet the taphonomic filters that bias the fossil record provide many fewer point occurrences (sometimes only a single occurrence) to interpolate for extinct organisms. Nonetheless, paleontologists can utilize the phenomenon of varying species compositions at fossil sites distributed across a landscape to determine generalized range distributions of ancient species. For instance, Jablonski and Hunt (2006) reconstructed the geographic range of extinct mollusks and gastropods, ultimately finding that differences in range distributions played a role in their extinction and speciation rates. Pimiento et al. (2016) approximated the geographic range of the shark *Otodus megalodon* as global, based on the occurrences of fossil teeth from this taxon around the world. Utilizing data from phylogenetics, ecological function, fossil spatial occurrences, and paleoenvironment, García-Girón et al. (2021) predicted the geographic ranges of dinosaur species during the latest Cretaceous of North America was segregated based on ecological gradients and physiology.

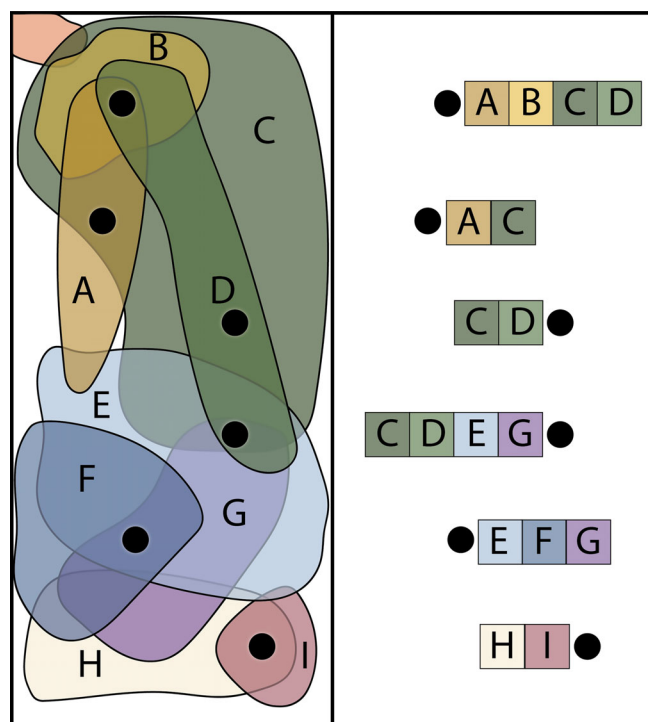


FIGURE 1 Conceptual diagram of overlapping species geographic ranges. (a) Colored shapes represent the geographic ranges of species (letters). Black circles represent the geographic location of sample sites. (b) Species that are present in each locality due to overlapping geographic ranges

Early in the 21st century, Ree and Smith (2008) introduced the Dispersal, Extinction, and Cladogenesis (DEC) model of biogeography that allowed for estimation of biogeographic area evolution across a clade while taking into account the probabilities of various connections between geographic regions at different geologic times (Matzke, 2013). A windfall of subsequent methods followed over the next 15 years that expanded on the basic premise of the DEC model by allowing more complex ecological information to be added to the analysis (e.g., Clarke, Thomas, & Freckleton, 2017; Nuismer & Harmon, 2015), and in some cases, even these supplemental data are utilized in algorithms that estimate biogeographic area shifts through jointly considering phylogenetic and ecological data (Landis, Eaton, et al., 2021; Landis, Edwards, & Donoghue, 2021; Quintero & Landis, 2020). Each of these methods provides critical information about the diversification process of a single clade, even when investigating the role of biome shifts in speciation and dispersal.

Another interesting approach presented by Meseguer, Lobo, Ree, Beerling, and Sanmartín (2015) uses ecological niche modeling in combination with phylogenetic information to determine biogeographical history based on the estimation of appropriate ecological parameters for the species under study. Ecological niche modeling has gained further traction in paleontological studies to

predict the extent of environmental conditions that were favorable to a species, all in an effort to estimate how large geographic ranges could be for ancient taxa (Chiarenza et al., 2019; Saupe et al., 2019; Dudgeon, Landry, Callahan, Mehling, & Ballwanz, 2021; García-Girón et al., 2021).

In some cases, environmental predictions from ecological niche models or observing the spread of fossil occurrences across a study area might suggest large-scale eco-evolutionary drivers that could affect diversification rates. Describing the pattern of taxonomic turnover between biomes or across a landscape is prevalent in paleontology. Perhaps the most studied biogeographic pattern is the provinciality of various biotas throughout geologic time, especially in relation to phylogenetic configurations (e.g., Boucot, 1975; Ezcurra, 2010; Hallam, 1974; Systra & Jensen, 2006; Varela, Tambusso, Patiño, Di Giacomo, & Fariña, 2018). Hypotheses of provinciality within the Late Cretaceous (Campanian) Western Interior Basin of North America have a particularly contentious history. Russell (1967) initially proposed that the continent was divided into northern and southern regions composed of different dinosaur species. Subsequent studies concurred with these findings (Lehman, 1987, 1997; Sloan, 1969, 1976), and some suggested that the biogeographic distribution of multiple vertebrate species (Gates et al., 2010) and plant groups (Burgener et al., 2021) was more complicated than a simple north-south division. Opposition to the provinciality hypothesis centered on the lack of spatiotemporally contiguous faunal and temporal data (Chiarenza et al., 2019; Dean, Chiarenza, & Maidment, 2020; Lucas, Sullivan, Lichtig, Dalman, & Jasinski, 2016; Maidment, Dean, Mansergh, & Butler, 2021; Sullivan & Lucas, 2006), or on phylogenetic trees of dinosaur clades defying expectations of a simple two-zone distribution system (Berry, 2018; Longrich, 2014). Other studies (Fowler & Fowler, 2020; Gates, Jinnah, Levitt, & Getty, 2014; McDonald, Wolfe, Fowler, & Gates, 2021) present results that support the hypothesis of separate biotas in the Western Interior Basin based on clade-specific phylogenetic trees.

We present here a new approach in which the ecological community makeup is used as primary data to reconstruct the pattern of species turnover across an ancient landscape within a model-discrimination framework. Our proposed methodology provides an evidence-based approach, akin to the philosophy of Bayesian biogeographic methods (Matzke, 2013), in order to assess the possibility of one geographic range model versus other candidate models. Importantly, the data analytic philosophy utilized here does not prescribe to a single answer but provides concordance error of actual fossil occurrence data compared to idealized species distribution models.

We demonstrate the proof of concept for this method from simulation studies that validate the procedure, discuss its use in time-series analyses, and analyze a dataset of pollen and dinosaurs from the Late Cretaceous Western Interior Basin of North America.

2 | MATERIALS AND METHODS

2.1 | Presence-absence matrices

Binary presence-absence (PA) matrices form the backbone of the analytical methods. A single binary matrix of fossil occurrence data is compared to at least two simulated matrices of known occurrence, in order to determine which of two simulated matrices most closely matches the fossil data. In the analyses for this study, we focused on PA matrices that represent idealized versions of biogeographic distribution patterns discussed in the paleontological literature, including: Random; Cosmopolitan; Gradational change; Two isolated biotic zones (Bizonal); and three variations of the Bizonal model in which a transition zone exists between the main biotic regions (see below for a description of each model). The R code, available in the Supplementary Material, allows complete customization of the PA matrix to fit any hypothetical biogeographic distribution.

Computation of the idealized PA matrices begins with an assumption that each locality is placed in rows that correspond to their placement along a linear transect (i.e., the locality at the top of the idealized matrix is the greatest geographic distance from the locality at the bottom of the matrix). Next, a series of 1's is placed in each row so that there are no species shared with another locality (equal to the total number of species within the entire matrix divided by the number of localities). Amount of species overlap is determined by two values, *prelap* and *postlap*, which represent the number of species shared between a focal locality and the site above it in the matrix (*prelap*) or below it in the matrix (*postlap*). All positive values of *prelap* and *postlap* will increase the number of species shared with the respective adjacent localities, whereas negative values will decrease the shared species. Any hypothetical distribution matrix can be created by modifying these two parameters.

This study focuses on discriminating more “classic” biogeographic distribution models. Figure 2 provides a visual representation of the PA matrix for each of the distribution models. We focus on these particular distributions because they are ones cited in prior paleobiogeographic studies. The three transitional models were deemed necessary distributions to test in our model discrimination framework because they are subtle alterations of a single theme and

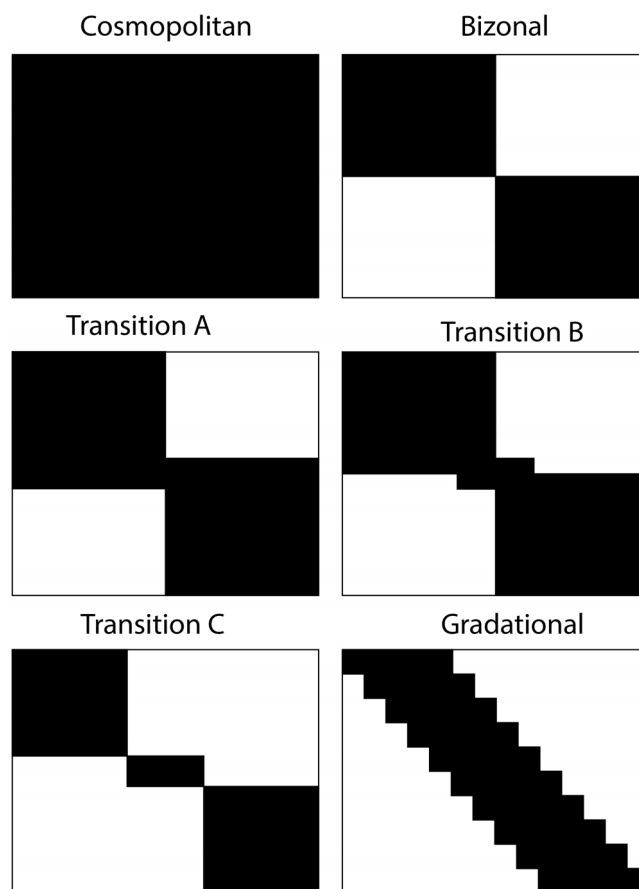


FIGURE 2 Biogeographic distribution models visualized as presence-absence matrices. Black regions represent presences (1's) in the matrix, whereas white regions are absences (0's)

allowed us to investigate the power of these methods to differentiate biogeographic nuance.

In an effort to more accurately reflect the fossil record, binary matrices can be produced to replicate the non-discovery of a taxon at a particular site by randomly adding 0's to the simulated matrix. We refer to this modification as Noise.

2.2 | Community biogeography models

We tested six species distributional models in this study (Figure 2). As an initial distributional model we included a Random model that stochastically assigns species to sites. In addition to providing a convenient null model for biotic distribution, the Random model could be an indication of temporal mixing in which different times are being sampled in different parts of the ecological gradient. A Cosmopolitan model posited that every organism in our hypothetical study area occurs in every sampling site, which would mean that the environment was suitable for all species identified. The Gradational model

assumes that the biotic community that occurs at one end of our hypothetical ecological gradient is different from the community at the opposite end of the gradient, and that the change between the two end-members changes gradually and continuously. Continuous change in the abiotic environment across the ecological gradient could be a reason that would explain this distributional pattern. The Bizonal model is one where the ecological gradient is divided into two equal pieces in which each has a unique fauna/flora that do not have any similarity with each other. This dichotomous distribution could occur if an abiotic boundary prevented interaction between two communities. Three variations of transitional zones provide subtle differences that highlight ecologically important distinctions between species. Transitional A has all the taxa present in the study occur in a few sites at the center of the ecological gradient, whereas the other sampling sites on either side of the transition zone have otherwise distinct biotic communities. Transitional B greatly reduces the number of species that mix between the dichotomous communities. Transitional C takes the differentiation even further by having three distinct biotic communities, but the central community is much smaller than either sandwiching community. These transitional zones could occur if, respectively, the environment in the central portion of the gradient was ideal for all taxa, or a few species in the two major communities had slightly greater eurytopic environmental tolerances that allowed them to occupy greater geographic ranges than other species in their community, or as in the last case, if the central portion of the ecological gradient contained such unique environmental conditions that only a uniquely adapted suite of species could live there.

2.3 | Biogeographic model distribution

Model discrimination between the fossil distribution data and the hypothesized distribution models is implemented through linear regression with a choice of three dependent variables. At least two hypothetical biogeographic models must be tested in the model discrimination process (although users can input as many hypothetical models as desired). For model testing purposes, we recommend that the number of localities chosen in the hypothetical distributions equal the number of actual sites in the fossil dataset.

Dependent variables within the linear regressions are produced by calculating a pairwise similarity between localities. The first linear regression method utilizes PA biodiversity similarity measures to produce pairwise values between each formation in the PA matrix. Our

preference is the Dice/Jaccard index because of its relative reliability in providing accurate similarity values between localities despite missing data or rare taxa (Archer & Maples, 1987; Hurbalek, 1982; Maples & Archer, 1988; Shi, 1993), although any similarity measure can be used.

The second linear regression method obtains the dependent variable by calculating the pairwise Euclidean distance between each site, which is calculated from the eigenvectors derived from a detrended correspondence analysis on each PA matrix being tested.

Our final method for obtaining dependent variables is by utilizing phylogenetic community dissimilarity (PCD; Ives & Helmus, 2010). In this method, PCD is derived via the product of the similarity of the community of shared taxa between pairwise sites and the phylogenetic similarity of the taxa not shared between pairwise sites. In addition to a PA matrix, calculation of this value also requires a time-scaled phylogenetic tree of all taxa present in the PA matrix. PCD is calculated here in the R package *caper* v. 1.0.1.

Independent variables are the geodesic distance between localities calculated in the R package *fossil* v. 0.4.0. Although fossil localities are not distributed equally in space, we assume that the distribution of organisms across our hypothetical model space is continuous, meaning that distance between sites will provide the distribution pattern of an ideal situation.

Model discrimination within the linear regression framework is accomplished by use of either mean absolute error (MAE) or root mean square error (RMSE). The latter has the property of penalizing residuals with exponential error corresponding to the distance they occur from the regression line. MAE, on the other hand, treats residuals linearly.

2.4 | Simulation tests

Analysis of covariance was performed using R (R Core Team, 2021) via RStudio version 1.4.1717 on all hypothetical models listed above to test which of the geographic distributions could be differentiated reliably via the linear regression methods (i.e., which of the slopes and intercepts for each geographic distribution were statistically distinct).

To ground-truth these methods, we tested each geographic distribution with a copy of the Bizonal distribution model. In addition to running tests of the data without modification, we also modified the geographic positions of the localities as well as increased the noise in the data. Site locations were first run as evenly distributed across the study region, then randomized with retaining the locality order, run with the locations of

fossil sites in pollen data published in Burgener et al. (2021; see below), both with and without the East Fork Formation, and finally, all sites and locations across the hypothetical gradient randomized. We tested the impact of noise on the fidelity of model discrimination by randomly increasing the number of 0's and 1's in the Bizonal dataset by 25, 50, and 75%. In each linear regression test, we used the RMSE because it shows the most dramatic differences between models.

Simulation of the PCD required both a PA matrix and a phylogenetic tree. For the former, we used the evenly distributed PA matrix; for the latter, we used the ceratopsid phylogenetic time-averaged tree (see below).

2.5 | Pollen data

As a test of the model-discrimination methods on fossil data, we used the Campanian pollen dataset from Burgener et al. (2021), producing a matrix of 26 localities and 1,312 palynotaxa. Additionally, we followed Burgener et al. (2021) in including both species-level and genus-level occurrences within the data to provide “paraphylogenetic” data. In order to test the sensitivity of our data, we removed a series of localities chosen non-randomly. To test the sensitivity of locality position along the hypothetical ecological gradient, we ran the model discrimination technique after removing the East Fork Formation since this locality is greater than 1,000 km further north than the next nearest locality and its removal would more evenly distribute the fossil sites across the landscape. Finally, we performed tests to see the effect of removing pollen taxa that had minimal overlap with other formations. Columns with only one, two, and three taxa were iteratively removed from the database, repeating the calculations at each iteration.

2.6 | Ceratopsian data

Occurrence data for all Campanian ceratopsid dinosaurs was collected from the literature and a phylogenetic tree grafted using Fowler and Fowler (2020) and Dalman, Lucas, Jasinski, and Longrich (2022). One hundred time-scaled trees were produced using the cal3 method in the R package paleotree v. 3.3.25, which we then averaged all branch lengths to produce a single consensus time-tree (Supplementary Material).

3 | RESULTS

The majority of all geographic distributions can be differentiated from each other using linear regression analysis

(Figure 3; Supplementary Material). Random and Cosmopolitan models both have a slope near zero, so are indistinguishable based on slopes, but their intercepts were drastically different. Most difficult to parse are the models with subtle differences in the transition from one distinct region to another. Using the Similarity measure, the only models that cannot be statistically separated are the Bizonal-Transitional B and the Bizonal-Transitional C. The distance measure has more difficulty parsing the Bizonal and transitional models; no combination of these models can be differentiated with the distance measure. Given the subtle difference in species prelap and postlap in these three models, Figure 3 shows that the difference in slope is similar between Bizonal, Transitional B, and Transitional C.

Increasing noise (either increased absences or randomly allotting 0's or 1's) in PA matrices makes biogeographic distributions trend toward Random (Figure 4). This is not surprising, but reinforces the importance of taxonomy and adequate sampling in studies that rely on biodiversity as data.

3.1 | Simulation tests

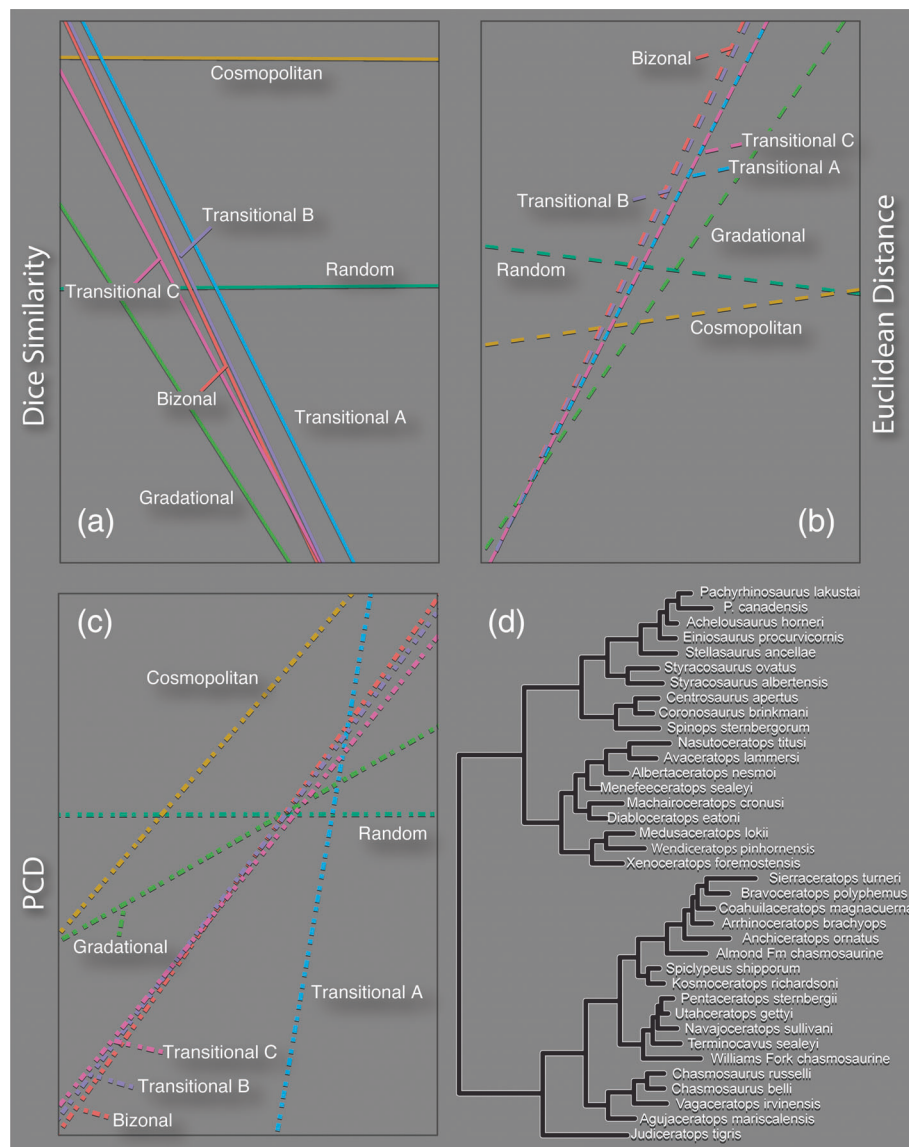
As expected, the linear regression discrimination method performed admirably when testing the pure Bizonal model against all others, with zero error in the similarity metric and 0.05 for the distance metric error (well-below the next closest model). Applying the locality distributions to match the Burgener et al. (2021) localities yielded closer error values for the similarity metric, but a much more distinct preference for the Bizonal model using the distance metric. The Random model was the preferred model under the similarity metric when we randomized the distance and placement of the sites. Interestingly, the distance metric managed to retain the Bizonal signal (Table 1).

Applying an increasing number of taxon absences to the Bizonal model indicates that with moderate (~25%) levels of noise both the linear regression similarity and distance metrics preferred the Bizonal model. At 50% and greater, only the distance metric supported the Bizonal model, but this model preference is marginal at high levels of noise.

3.2 | Campanian Western Interior Basin pollen

Linear regression RMSE results differed between the similarity index and distance measure calculations (Table 2). The former measure consistently retrieved the Random model as the most preferred in four out of the five data

FIGURE 3 Linear regression representation of each idealized biotic distributional model. Panel (a) shows the linear regression lines produced from using the Dice/Sorensen similarity index, whereas, Panel (b) shows the linear regression lines obtained from using the same data but analyzing with Euclidean distance. Panel (c) contains the equivalent linear regression lines from the phylogenetic community dissimilarity metric and Panel (d) has the phylogenetic topology of ceratopsid dinosaurs used in the phylogenetic community dissimilarity (PCD)



transformations. A Gradational model was the second most preferred in these same data iterations. When the East Fork Formation was removed from the analysis both the Random and Gradational models were equally likely. MAE results differed from the RMSE in that the Gradational model was preferred in three of the five iterations. The third most likely model was the Transition C model in all instances with the Dice/Sorensen similarity measure.

The Euclidean distance measure provided a different discrimination of the models compared to the Dice/Sorensen measure (Table 2). Interestingly, the Bizonal, Transitional A, and Transitional B models were the top three most preferred with RMSE when we analyzed the original dataset, but these followed behind a Random model when discriminating with MAE. In short, at least one of the Bizonal, Transitional A, or Transitional B

models were always of the most preferred models throughout the data manipulations and discriminating with either RMSE or MAE. In all linear regression analyses, less data equates to a stronger Random model signal.

3.3 | Campanian Western Interior Basin ceratopsid dinosaurs

Incorporating both community dissimilarity and phylogenetic similarity of the ceratopsid dinosaurs inhabiting the Cretaceous Western Interior Basin unambiguously supported a Random model using the RMSE and MAE (Table 3). A gradational model came out as the second-best option, followed by Transitional C with almost twice as much error.

4 | DISCUSSION

Much of the paleobiogeographic discourse in recent years revolves around determining the global immigration and emigration of individual clades using phylogenetic-centered methods (e.g., Matzke, 2013; Lam, Stigall, & Matzke, 2018; Lam, Sheffield, & Matzke, 2021; Gates,

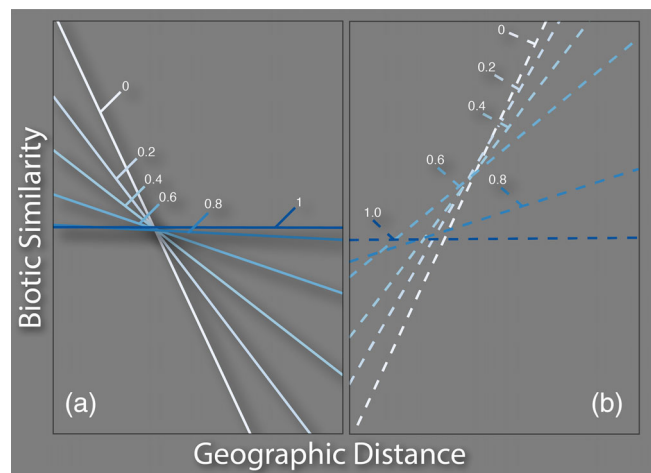


FIGURE 4 Analytical effect of adding random absences to the Bizonal presence-absence matrix. (a) Linear regression Dice-Sorensen similarity method and (b) linear regression Euclidean distance method. In all cases, increasing absences in a presence-absence matrix moves candidate distributional models toward random distribution. Phylogenetic community dissimilarity was not included here because the results are the mirror of the Dice similarity regressions with decreasing similarity between sites as the dissimilarity proceeds to 1, which is exacerbated by the phylogeny obtaining more randomness

Gorscak, & Makovicky, 2019; Ding et al., 2020; Landis, Edwards, & Donoghue, 2021; Landis, Eaton, et al., 2021). Additionally, speciation and extinction rates among clades is an area of biogeographic interest for ecological turnover as well as phylogenetically because the methods mentioned above each require a time-calibrated phylogeny that can be extremely affected by extinction rates (Bapst, 2013; Sanmartín & Meseguer, 2016). In many clades, however, a reliable phylogeny is not available for fossil taxa, so methods utilizing PA ordination, faunal similarity metrics, or simply visual approximations of species biogeography are used to hypothesize the ecosystem-scale interactions within and between formations. The Western Interior Basin of North America is no exception, with most of the biogeographic research being conducted through these methods (e.g., Burgener et al., 2021; Fowler, 2017; Gates et al., 2010; Lehman, 1997; Lucas et al., 2016; Russell, 1967; Sloan, 1969). Other research has centered on the quality of the dataset itself—that is, the adequacy of the fossil record—for determining the biogeographic distribution of organisms, most of which proposes that the record is simply not good enough (Chiarenza et al., 2019; Dean et al., 2020; Maidment et al., 2021).

Arguments purported for abandoning the practice of deciphering the geographic distributional pattern of extinct organisms due to an inadequate fossil record are persuasive in so much as the incomplete ecosystem data, asynchronicity of faunal comparisons, and incorrect taxonomy are limitations to paleontological data that continue to be updated with more research. All prior concerns, indeed, need to be considered carefully before attempting such a focus, still there are critical biogeographic data that can be leveraged. The model-

TABLE 1 RMSE results obtained from running analyses on a Bizonal distribution across a variety of site distances. Equal distribution has equal spacing between locations. Random distribution places each site randomly among the hypothetical gradient. Fossil distribution replicates the site locations from Burgener et al. (2021). Sim and Dist refer to RMSE values using the similarity index or the Euclidean distance measure, respectively. Percentage columns show the error values after adding that number of 0's to the matrix prior to running the linear regression analyses. The preferred model for each iteration is designated by a white box

	Equal distribution		Random distribution		Fossil distribution		25%		50%		75%	
	Sim	Dist	Sim	Dist	Sim	Dist	Sim	Dist	Sim	Dist	Sim	Dist
Random	0.500	0.559	0.503	0.561	0.500	0.536	0.382	0.896	0.289	1.050	0.390	1.655
Cosmo	0.703	0.576	0.709	0.558	0.519	0.541	0.624	0.919	0.741	1.098	0.869	1.733
Grad	0.460	0.435	0.633	0.429	0.387	0.369	0.192	0.884	0.166	1.105	0.189	1.771
Bizonal	0.00	0.053	0.515	0.035	0.238	0.038	0.121	0.713	0.238	0.951	0.366	1.631
Trans A	0.395	0.413	0.588	0.418	0.395	0.290	0.274	0.826	0.350	1.040	0.478	1.694
Trans B	0.264	0.286	0.508	0.120	0.304	0.156	0.143	0.728	0.259	0.965	0.388	1.644
Trans C	0.432	0.447	0.628	0.421	0.405	0.322	0.274	0.824	0.286	1.044	0.326	1.700

Abbreviation: RMSE, root mean square error.

TABLE 2 RMSE results of pollen data from Burgener et al. (2021). Biogeographic models that were tested against the fossil pollen data are listed in rows and the data manipulations are listed in columns. Colors grade from dark to light with the lighter cells showing the most likely biogeographic models of those tested

	Original data		Without East Fork		Without East Fork min overlap of 2		Without East Fork min overlap of 3		Without East Fork min overlap of 4	
	Similarity	Distance	Similarity	Distance	Similarity	Distance	Similarity	Distance	Similarity	Distance
RMSE										
Random	0.369	6.580	0.365	2.867	0.333	2.065	0.290	1.911	0.263	1.114
Cosmopolitan	0.832	6.630	0.832	2.974	0.789	2.194	0.746	2.022	0.703	1.188
Gradational	0.376	6.595	0.364	2.992	0.364	2.206	0.365	2.003	0.373	1.206
Bizonal	0.675	6.548	0.630	2.931	0.610	2.152	0.594	1.963	0.579	1.198
Transitional A	0.686	6.556	0.619	2.942	0.589	2.152	0.564	1.958	0.537	1.176
Transitional B	0.649	6.547	0.578	2.926	0.554	2.140	0.535	1.952	0.516	1.177
Transitional C	0.560	6.560	0.516	2.954	0.496	2.166	0.479	1.971	0.464	1.177
MAE										
Random	0.351	3.736	0.349	2.452	0.309	1.929	0.270	1.535	0.222	0.885
Cosmopolitan	0.825	3.844	0.823	2.567	0.775	1.904	0.733	1.643	0.689	1.076
Gradational	0.297	3.881	0.283	2.619	0.286	1.951	0.292	1.674	0.301	1.022
Bizonal	0.546	3.771	0.503	2.514	0.495	1.858	0.489	1.587	0.484	0.979
Transitional A	0.620	3.803	0.530	2.545	0.504	1.887	0.482	1.613	0.462	0.973
Transitional B	0.552	3.778	0.472	2.520	0.453	1.861	0.437	1.590	0.422	0.965
Transitional C	0.469	3.804	0.394	2.555	0.383	1.894	0.374	1.622	0.367	0.978

Abbreviation: RMSE, root mean square error.

TABLE 3 Residual error of Campanian Western Interior Basin ceratopsid dinosaurs using the phylogenetic community dissimilarity measure

	RMSE	MAE
Random	0.343	0.291
Cosmopolitan	3.268	1.439
Gradational	0.686	0.582
Bizonal	1.754	1.694
Transitional A	3.202	1.808
Transitional B	1.439	1.340
Transitional C	1.299	1.005

Abbreviations: MAE, mean absolute error; RMSE, root mean square error.

discrimination methods described here provide an opportunity to use available data to its utmost potential, while allowing for uncertainty to play a role in choosing which distributional models best fit the available data. Specifically, the MAE and RMSE values provide measures of differentiation between models, a method quite distinct from traditional null-hypothesis, *p*-value-centered statistical treatments. Model discrimination methods do not provide a definitive answer to what the *correct* biogeographic distribution model is, but they provide a measure of the most *likely* model(s) given: (a) the available data; and (b) the array of models tested by the researcher.

Of all the PA distributions tested in this study, only the Bizonal and two transitional models were difficult to distinguish from one another. These results show some limitation to the linear regression method, but other more complex analyses may be brought to bear (see below). Nonetheless, it can be determined if a paleobiota is best described as possessing a transitional zone, with further discussion about the type of transition being supported by small changes derived from these methods.

As with any analysis, the linear regression-based model discrimination methods described here perform better with more data. Nonetheless, the knowledge that randomness in absences leads to greater preference for the Random model in the discrimination process can be utilized when making final assessments of which models best fit the available biogeographic data. Additionally, researchers utilizing these methods should be aware of the hypothesis they are testing, then make test distributional models that correspond. For example, if one suspects that a boundary isolates 75% of the biota in a particular ecological gradient, then the hypothetical distribution models should reflect this (especially those such as the transitional and Bizonal models). Finally, we advise using this method to discriminate, and in some cases eliminate, models of biotic distribution, not use this

as the sole source of information about how organisms were arrayed across a landscape. Resulting statistical errors will only be as good as the data that is input.

4.1 | Late Cretaceous Western Interior Basin

Burgener et al. (2021) presented evidence of a steep climatic shift in the Late Cretaceous Western Interior Basin likely created by the mixing of warm and cool waters in the adjacent Western Interior Seaway. In order to test if the climatic boundary had any effects on biotic distributions the authors used a sliding window approach of calculating the variance of Dice/Sorensen similarity index values to the north, south, and overlapping a series of latitudes. Compiled results suggested that plant species were indeed restricted to northern and southern regions because of the climatic boundary. However, it was unclear if a transitional zone existed between the different regions and how a potential zone may have been distributed geographically.

Here, we reanalyzed the pollen distribution data from Burgener et al. (2021) to determine if: (a) parallel results for a climatic influence on plant distribution would be obtained; and (b) if so, whether the boundary between the northern and southern plant biomes resembled a sharp demarcation or a larger transitional zone. Overall, the available fossil data fit most closely with a Random model of pollen distribution. Certainly, a paucity of fossil pollen data has played some role in the Random model discrimination (as shown above, decreasing the number of fossil occurrences moves a bizonal model toward a random distribution). Another factor that likely contributed to the selection of a random plant distribution model is that a subset of the pollen species are found throughout the Western Interior Basin (Burgener et al., 2021). If there is a sample of data points that occurs throughout a region and another set of data points restricted to either a southern or northern zone, along with non-equal species absences, a random model does indeed make sense.

There are also intriguing clues that a more complex distribution is present, especially from the distance metric. A transitional model is one of the top three contending models in each iteration, and in many cases, the transitional model is either most preferred or second in preference. RMSE using the distance measure has the Bizonal model as the preferred model when using the entire dataset, with two transitional models trailing as the second and third preferred models.

Overall, the results of these analyses support both a random distribution as well as bifid northern and

southern plant biozones. We interpret the opposing results as a consequence of missing data and a mismatch between the data distribution and that of the tested models. For instance, in the initial pollen analysis the more northerly location of the East Fork Formation compared to other localities provided a better distributional match to the Bizonal/Transitional models, whereas when the East Fork Fm. was removed, the same distribution represented in the Bizonal/Transitional models was offset from the distribution of the data with the climatic transition zone occurring more northerly (Burgener et al., 2021). More rigorous testing of this hypothesis would involve creating hypothetical PA matrices with the switch between bioregions matching the fossil distribution more closely.

Data sparsity is one issue in fossil PA matrices that leads to Random models being preferred regardless of the actual biotic distribution. The calculation of the Dice-Sorensen similarity index inherently leads toward a preference of randomness as datasets become more homogeneous, because the numerator in the Dice-Sorensen equation stays relatively constant (or minorly decreasing) with the removal of taxa that occur in only a few formations. Simultaneously, the denominator decreases because absolutely more taxa are removed from the total dataset, making the Dice-Sorensen index approach 1 in all cases, irrespective of geographic distance individual formations lie from one another. This phenomenon explains the decreasing RMSE values in Table 2 as more pollen taxa are removed from the data.

An important lesson in this example is that large sample sizes are better for determining biogeographic patterns, especially incorporating taxa that are found in single formations. Therefore, when RMSE scores from the distance measures and the similarity measures are taken together, our initial results parallel those from Burgener et al. (2021) suggesting that plants from the Campanian of the Western Interior Basin indeed show a distribution with different taxonomic compositions in the north versus the south with a transition zone of unknown width between them.

Ceratopsid dinosaur data are much sparser than pollen data during the Campanian of the Western Interior Basin. Yet, unlike pollen, these dinosaurs have a relatively well-understood phylogeny that contains further information that could be incorporated to unravel their greater biogeographic distribution. We incorporated the evolutionary information with the PCD metric (Ives & Helmus, 2010), finding that a Random model again supported the available data best. In addition to data sparsity being a contributing factor in the resulting model discrimination, the fact that differential fossil preservation causes ceratopsid fossils to be unevenly distributed across the study area and study time means that inherently the

null hypothesis should be a random distribution. Phylogenetic information should be able to fill in some of the holes with more ceratopsid data. Regardless if ceratopsids were randomly distributed in time and space or had distinct geographic ranges bounded by the same climatic boundary as the plant communities, the PCD proposed here is another tool that can aid paleontologists in discriminating biogeographic models.

4.2 | Influence of narrow geographic ranges

The geographic range size of a taxon is dependent on attributes of the local to regional environment and the tolerances of individuals of that taxon to the environment (Brown et al., 1996; Gaston, 2003; Lomolino et al., 2005). Low tolerance for environmental variations results in species or populations that have small geographic ranges compared to other taxa that proliferate in a variety of environmental conditions. Prior work on fossil assemblages (Badgley et al., 2017; Burgener et al., 2021; Darroch & Saupe, 2018; Finarelli & Badgley, 2010; Gates et al., 2010; Gates, Prieto-Márquez, & Zanno, 2012; Jablonski & Hunt, 2006), provided data that suggest that some species occur over a large geographic area whereas others are much more restricted.

Within the context of the methodology described here, taxa restricted to a single geologic formation are essential to be included in order to understand the best representation of community distribution. In the most extreme example, a complete cosmopolitan distribution is represented by every taxon occurring everywhere, whereas at the opposite extreme the complete isolation pattern is where each taxon occurs in only a single formation. Both of these extremes will produce a zero slope on the similarity linear regressions (with the former providing a consistent y-intercept of 1 and the latter intercepting at 0; note that both of these cases cannot be calculated in the detrended correspondence analysis).

The cautionary point of including taxa with narrow geographic ranges (e.g., those that only occur in a single geologic unit) is that the RMSE values will often suggest a Random model as a highly rated model, but examination of the intercepts within the linear regression models can help discern a true Random model (y-intercept $\gg 0.5$) from the Cosmopolitan and nonoverlapping geographic distribution.

Finally, taxonomy plays a crucial role in the acquisition of preferred biotic distribution models. For instance, upon studying a specimen from a particular site, a researcher will decide that the evidence either most supports the inclusion of that specimen in the hypodigm of a

currently existing taxon or create a new species (e.g., Gates & Sampson, 2007; Gates & Scheetz, 2015; Prieto-Márquez, 2014; Zanno, Varricchio, O'Connor, Titus, & Knell, 2011). These decisions can result in either increased similarity between sites that house specimens of the taxon or decreased similarity between sites because a new taxon is included the species data. Additionally, the decision of a researcher to include (as we have done) the generic taxonomic level in the biodiversity data will increase the similarity of geologic units that contain species of the genus, even if each of those sites contain different species.

The use of a phylogenetic tree in the PCD offers a different mathematical approach to the taxonomy considerations above. The community dissimilarity portion of the PCD metric compares taxa that are same between communities and the phylogenetic component incorporates the amount of shared ancestry of taxa that are not equivalent between communities. This means that using genera and species separately in the community PA matrix is not possible, as well as the fact that by making the decision to subsume a specimen from a new sampling site into a current species hypodigm will cause that specimen to not be utilized in the phylogenetic component of the PCD calculation. Inversely, making it a new taxon will mean that it will not be part of the shared taxa in the community dissimilarity calculation. In short, taxonomic decisions of researchers have real ramifications for quantitative paleoecology that impacts calculations involving biodiversity, standard models of phylogenetic relationships, and geographic ranges; all of which feedback to support hypotheses about evolutionary mechanisms.

4.3 | Use in time series

Another use of the model discrimination method described here is to detect the number and types of changes to ecosystems within a single geographic location through time by employing data from individual layers through a stratigraphic section. This can be done by creating biotic PA matrices for as many stratigraphic levels as possible, and then performing the model-discrimination analysis as above using the mean age (or height above the lowest sample) for each layer for which data are being included. Results suggesting a Random distribution could be evidence for rapid, frequent faunal turnover through time (or sparse data), a Bizonal model could suggest a single rapid replacement event, whereas Transitional models and the Gradational model would signal for a much slower transition from one paleocommunity to another. These model-discrimination results could then support inferences about abiotic (e.g., emplacement/removal of physical (e.g., geodispersal; Lieberman & Eldredge, 1996)

or climatic [e.g., Burgener et al., 2021] barriers), biotic (e.g., invasive species [Holland & Patzkowsky, 2007; Patzkowsky & Holland, 2007], or habitat tracking [Brett, Hendy, Bartholomew, Bonelli Jr, & McLaughlin, 2007; Raia, Passaro, Fulgione, & Carotenuto, 2012]) controls on community evolution.

5 | CONCLUSIONS

Biogeographic distributions of organisms hold vital clues about the structuring of ancient ecosystems. To date, there has been limited ability to test different hypotheses of faunal distributions in fossil assemblages, with the most analytically rigorous being those incorporating Bayesian inference with phylogenetic trees. The biggest limitation to these methods is that they are focused largely on single clades, not entire communities. We present here model discrimination methods that allow for differentiation of various geographic distributional hypotheses using information about entire communities.

Simulation tests of the method show that model discrimination is accurate with complete datasets, but has sensitivity to missing data, making randomness more preferred. Notwithstanding the latter observation, it seems that the Euclidean distance metric method may preserve more of the geographic distribution signal than using a similarity measure (such as the Dice/Sorensen used in this study) when missing data pervade.

A recent study (Burgener et al., 2021) suggested that the North American Cretaceous Western Interior Basin had two climatic regimes, a warmer southern and a cooler northern regime, divided from each other by a sharp temperature gradient. Model discrimination analysis of Campanian pollen from this region provided compelling evidence that indeed plants had distinct biotic distributions related to the climatic regimes. As with most paleontological data, missing data are prevalent, yet the Euclidean distance metric consistently showed a divided model as one of the most likely. Ceratopsid dinosaur distribution data over the same time period is likely too sparse to provide accurate model discrimination; nonetheless, linear regression that incorporates PCD suggested that Random biotic distribution was the most preferred followed by gradational latitudinal change.

A potential analytical extension of this linear regression method is to incorporate the epsilon matrix in generalized least squares regression to provide a priori association or dissociation between fossil sites, irrespective of the similarity provided by the raw data. In some cases, this might be similar to the probability matrices used in the DEC biogeographic analysis (Ree & Smith, 2008). New computational power has also allowed

the implementation of machine learning algorithms for ecological datasets. These computational tools may be ideal for the types of questions and data offered in this study (e.g., Olden, Lawler, & Poff, 2008; Thessen, 2016; Viana, Keil, & Jeliaskov, 2022). With additional fossils, environmental data, and refinement of computational techniques we can advance our understanding of ancient biome constraints and their downstream evolutionary ramifications.

Incomplete preservation of biotic data is a perennial problem for paleontological analyses that has led previous studies (e.g., Dean et al., 2020; Lucas et al., 2016; Maidment et al., 2021) to question the very practice of attempting to decipher paleobiogeographic patterns. The model discrimination method presented here accepts the fundamental issues presented in previous studies and provides a means to use the data at hand in order to find out which geographic distribution hypotheses are more likely than others without abandoning the practice all together. Phylogeneticists have utilized this methodological philosophy for decades, continuing to refine analyses with more data and taxa. Biogeographers similarly can continue to expand datasets, refine biogeographic distribution models, and increase the resolution of our paleoecological picture.

AUTHOR CONTRIBUTIONS

Terry Allen Gates: Conceptualization (lead); data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); resources (lead); software (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Hengrui Cai:** Formal analysis (supporting); methodology (equal); software (supporting); writing – original draft (supporting). **Yifei Hu:** Formal analysis (supporting); methodology (supporting); software (supporting); writing – original draft (supporting). **Xu Han:** Formal analysis (supporting); methodology (supporting); software (supporting); writing – original draft (supporting). **Emily Griffith:** Methodology (supporting); writing – review and editing (supporting). **Landon Burgener:** Conceptualization (supporting); resources (supporting); writing – review and editing (supporting). **Ethan Hyland:** Writing – original draft (supporting); writing – review and editing (supporting). **Linday E. Zanno:** Methodology (supporting); writing – review and editing (supporting).

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REFERENCES

- Archer, A. W., & Maples, C. G. (1987). Monte Carlo simulation of selected binomial similarity coefficients (I): Effect of number of variables. *PALAIOS*, 2, 609–617.
- Badgley, C., Smiley, T. M., Terry, R., Davis, E. B., DeSantis, L. R., Fox, D. L., Hopkins, S. S., Jezkova, T., Matocq, M. D., & Matzke, N. (2017). Biodiversity and topographic complexity: Modern and geohistorical perspectives. *Trends in Ecology & Evolution*, 32, 211–226.
- Bapst, D. W. (2013). A stochastic rate-calibrated method for time-scaling phylogenies of fossil taxa. *Methods in Ecology and Evolution*, 4(8), 724–733.
- Berry, K. (2018). Paleontological evidence against a major geographic barrier at about the paleolatitude of Colorado, USA, during the Late Campanian (Late Cretaceous): The conspicuous absence of endemic subclades of chasmosaurine ceratopsid (horned) dinosaurs and its significance. *The Mountain Geologist*, 55, 5–18.
- Boucot, A. J. (1975). Standing diversity of fossil groups in successive intervals of geologic time viewed in the light of changing levels of provincialism. *Journal of Paleontology*, 49, 1105–1111.
- Brett, C. E., Hendy, A. J., Bartholomew, A. J., Bonelli, J. R., Jr., & McLaughlin, P. I. (2007). Response of shallow marine biotas to sea-level fluctuations: A review of faunal replacement and the process of habitat tracking. *PALAIOS*, 22, 228–244.
- Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: Size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, 27, 597–623.
- Burgener, L., Hyland, E., Griffith, E., Mitášová, H., Zanno, L. E., & Gates, T. A. (2021). An extreme climate gradient-induced ecological regionalization in the Upper Cretaceous Western Interior Basin of North America. *GSA Bulletin*, 133, 2125–2136.
- Chiarenza, A. A., Mannion, P. D., Lunt, D. J., Farnsworth, A., Jones, L. A., Kelland, S.-J., & Allison, P. A. (2019). Ecological niche modeling does not support climatically-driven dinosaur diversity decline before the Cretaceous/Paleogene mass extinction. *Nature Communications*, 10, 1–14.
- Clarke, M., Thomas, G. H., & Freckleton, R. P. (2017). Trait evolution in adaptive radiations: Modeling and measuring interspecific competition on phylogenies. *The American Naturalist*, 189, 121–137.
- Dalman, S. G., Lucas, S. G., Jasinski, S. E., & Longrich, N. R. (2022). *Sierraceratops turneri*, a new chasmosaurine ceratopsid from the Hall Lake Formation (Upper Cretaceous) of south-central New Mexico. *Cretaceous Research*, 130, 105034.
- Darroch, S. A., & Saupe, E. E. (2018). Reconstructing geographic range-size dynamics from fossil data. *Paleobiology*, 44, 25–39.

- Dean, C. D., Chiarenza, A. A., & Maidment, S. C. (2020). Formation binning: A new method for increased temporal resolution in regional studies, applied to the Late Cretaceous dinosaur fossil record of North America. *Palaeontology*, 63, 881–901.
- Ding, A., Pittman, M., Upchurch, P., O'Connor, J., Field, D. J., & Xu, X. (2020). The biogeography of coelurosaurian theropods and its impact on their evolutionary history. *Bulletin of the American Museum of Natural History*, 440, 117–157.
- Dodson, P. (1971). Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada). *Palaeogeography Palaeoclimatology Palaeoecology*, 10, 21–74.
- Dodson, P. (1975). Taxonomic implications of relative growth in lambeosaurine hadrosaurs. *Systematic Biology*, 24, 37–54.
- Dodson, P., Behrensmeyer, A. K., Bakker, R. T., & McIntosh, J. S. (1980). Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation. *Paleobiology*, 6, 208–232.
- Dodson, P., Currie, P. J., & Koster, E. (1987). Microfaunal studies of dinosaur paleoecology, Judith River Formation of southern Alberta. Fourth Symposium on Mesozoic Terrestrial Ecosystems, Short Papers. Occasional Papers of the Tyrrell Museum of Palaeontology. pp. 71–75.
- Dudgeon, T. W., Landry, Z., Callahan, W. R., Mehling, C. M., & Ballwanz, S. (2021). An Appalachian population of neochoristoderes (Diapsida, Choristodera) elucidated using fossil evidence and ecological niche modelling. *Palaeontology*, 64, 629–643.
- Ezcurra, M. D. (2010). Biogeography of Triassic tetrapods: Evidence for provincialism and driven sympatric cladogenesis in the early evolution of modern tetrapod lineages. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2547–2552.
- Finarelli, J. A., & Badgley, C. (2010). Diversity dynamics of Miocene mammals in relation to the history of tectonism and climate. *Proceedings of the Royal Society B*, 277, 2721–2726.
- Fowler, D. W. (2017). Revised geochronology, correlation, and dinosaur stratigraphic ranges of the Santonian-Maastrichtian (Late Cretaceous) formations of the Western Interior of North America. *PLoS One*, 12, e0188426.
- Fowler, D. W., & Fowler, E. A. F. (2020). Transitional evolutionary forms in chasmosaurine ceratopsid dinosaurs: Evidence from the Campanian of New Mexico. *PeerJ*, 8, e9251.
- Fraser, D. (2017). Can latitudinal richness gradients be measured in the terrestrial fossil record? *Paleobiology*, 43, 479–494.
- Gaston, K. J. (2003). *The structure and dynamics of geographic ranges* (p. 266). Oxford University Press.
- García-Girón, J., Heino, J., Alahuhta, J., Chiarenza, A. A., & Brusatte, S. L. (2021). Palaeontology meets metacommunity ecology: the Maastrichtian dinosaur fossil record of North America as a case study. *Palaeontology*, 64(3), 335–357.
- Gates, T. A., Gorscak, E., & Makovicky, P. J. (2019). New sharks and other chondrichthyans from the latest Maastrichtian (Late Cretaceous) of North America. *Journal of Paleontology*, 93, 512–530.
- Gates, T. A., Jinnah, Z., Levitt, C., & Getty, M. A. (2014). New hadrosaurid specimens from the lower-middle Campanian Wahweap Formation of Utah. In D. C. Evans & D. A. Eberth (Eds.), *Hadrosaurs* (pp. 156–173). Indiana University Press.
- Gates, T. A., Prieto-Márquez, A., & Zanno, L. E. (2012). Mountain building triggered Late Cretaceous North American megaherbivore dinosaur radiation. *PLoS One*, 7, e42135.
- Gates, T. A., & Sampson, S. D. (2007). A new species of *Gryposaurus* (Dinosauria: Hadrosauridae) from the Late Campanian Kaiparowits Formation. *Zoological Journal of the Linnean Society*, 151, 351–376.
- Gates, T. A., Sampson, S. D., Zanno, L. E., Roberts, E. M., Eaton, J. G., Nydam, R. L., Hutchison, J. H., Smith, J. A., Loewen, M. A., & Getty, M. A. (2010). Biogeography of terrestrial and freshwater vertebrates from the Late Cretaceous (Campanian) Western Interior of North America. *Palaeogeography Palaeoclimatology Palaeoecology*, 291, 371–387.
- Gates, T. A., & Scheetz, R. (2015). A new saurolophine hadrosaurid (Dinosauria: Ornithomimidae) from the Campanian of Utah, North America. *Journal of Systematic Palaeontology*, 13, 711–725.
- Hallam, A. (1974). Changing patterns of provinciality and diversity of fossil animals in relation to plate tectonics. *Journal of Biogeography*, 1, 213–225.
- Hillebrand, H. (2004). On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163, 192–211.
- Holland, S. M., & Patzkowsky, M. E. (2007). Gradient ecology of a biotic invasion: Biofacies of the type Cincinnati Series (Upper Ordovician), Cincinnati, Ohio region, USA. *PALAIOS*, 22, 392–407.
- Holmes, T., & Dodson, P. (1997). Counting dinosaurs—How many kinds are there (1996)? In D. L. Wolberg, E. Stump, & G. D. Rosenberg (Eds.), *Dinofest international* (pp. 125–128). Academy of Natural Sciences.
- Hurbalek, Z. (1982). Coefficients of association and similarity based on binary (presence-absence) data: An evaluation. *Biological Reviews*, 57, 669–689.
- Ives, A. R., & Helmus, M. R. (2010). Phylogenetic metrics of community similarity. *The American Naturalist*, 176, E128–E142.
- Jablonski, D., & Hunt, G. (2006). Larval ecology, geographic range, and species survivorship in Cretaceous mollusks: Organismic versus species-level explanations. *The American Naturalist*, 168, 556–564.
- Lam, A. R., Sheffield, S. L., & Matzke, N. J. (2021). Estimating dispersal and evolutionary dynamics in diploporan blastozoans (Echinodermata) across the great Ordovician biodiversification event. *Paleobiology*, 47, 198–220.
- Lam, A. R., Stigall, A. L., & Matzke, N. J. (2018). Dispersal in the Ordovician: Speciation patterns and paleobiogeographic analyses of brachiopods and trilobites. *Palaeogeography Palaeoclimatology Palaeoecology*, 489, 147–165.
- Landis, M., Edwards, E. J., & Donoghue, M. J. (2021). Modeling phylogenetic biome shifts on a planet with a past. *Systematic Biology*, 70, 86–107.
- Landis, M. J., Eaton, D. A., Clement, W. L., Park, B., Spriggs, E. L., Sweeney, P. W., Edwards, E. J., & Donoghue, M. J. (2021). Joint phylogenetic estimation of geographic movements and biome shifts during the global diversification of Viburnum. *Systematic Biology*, 70, 67–85.
- Lehman, T. M. (1987). Late Maastrichtian paleoenvironments and dinosaur biogeography in the Western Interior of North America. *Palaeogeography Palaeoclimatology Palaeoecology*, 60, 189–217.
- Lehman, T. M. (1997). Late Campanian dinosaur biogeography in the western interior of North America. In D. L. Wolberg, E. Stump, & G. D. Rosenberg (Eds.), *Dinofest international* (pp. 223–240). Academy of Natural Sciences.

- Lieberman, B. S., & Eldredge, N. (1996). Trilobite biogeography in the middle Devonian; geological processes and analytical methods. *Paleobiology*, 22, 66–79.
- Lomolino, M. V., Riddle, B. R., & Brown, J. H. (2005). *Biogeography* (3rd ed., p. 845). Sinauer Publishers.
- Longrich, N. R. (2014). The horned dinosaurs Pentaceratops and Kosmoceratops from the upper Campanian of Alberta and implications for dinosaur biogeography. *Cretaceous Research*, 51, 292–308.
- Lucas, S. G., Sullivan, R. M., Lichtig, A. J., Dalman, S. G., & Jasinski, S. E. (2016). Late Cretaceous dinosaur biogeography and endemism in the Western Interior Basin, North America: A critical re-evaluation. *New Mexico Museum of Natural History & Science Bulletin*, 71, 195–213.
- Maidment, S. C., Dean, C. D., Mansergh, R. I., & Butler, R. J. (2021). Deep-time biodiversity patterns and the dinosaurian fossil record of the Late Cretaceous Western Interior, North America. *Proceedings of the Royal Society B*, 288, 20210692.
- Maples, C. G., & Archer, A. W. (1988). Monte Carlo simulation of selected binomial similarity coefficients (II): Effect of sparse data. *PALAIOS*, 3, 95–103.
- Matzke, N. J. (2013). Probabilistic historical biogeography: New models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography*, 5, 242–248.
- McDonald, A. T., Wolfe, D. G., Fowler, E. A. F., & Gates, T. A. (2021). A new brachylophosaurin (Dinosauria: Hadrosauridae) from the Upper Cretaceous Menefee Formation of New Mexico. *PeerJ*, 9, e11084.
- Meseguer, A. S., Lobo, J. M., Ree, R., Beerling, D. J., & Sanmartin, I. (2015). Integrating fossils, phylogenies, and niche models into biogeography to reveal ancient evolutionary history: The case of Hypericum (Hypericaceae). *Systematic Biology*, 64, 215–232.
- Mittelbach, G. G., Schemske, D. W., Cornell, H. V., Allen, A. P., Brown, J. M., Bush, M. B., Harrison, S. P., Hurlbert, A. H., Knowlton, N., & Lessios, H. A. (2007). Evolution and the latitudinal diversity gradient: Speciation, extinction and biogeography. *Ecology Letters*, 10, 315–331.
- Nuismer, S. L., & Harmon, L. J. (2015). Predicting rates of inter-specific interaction from phylogenetic trees. *Ecology Letters*, 18, 17–27.
- Olden, J. D., Lawler, J. J., & Poff, N. L. (2008). Machine learning methods without tears: A primer for ecologists. *The Quarterly Review of Biology*, 83, 171–193.
- Patzkowsky, M. E., & Holland, S. M. (2007). Diversity partitioning of a late Ordovician marine biotic invasion: Controls on diversity in regional ecosystems. *Paleobiology*, 33, 295–309.
- Pimiento, C., MacFadden, B. J., Clements, C. F., Varela, S., Jaramillo, C., Velez-Juarbe, J., & Silliman, B. R. (2016). Geographical distribution patterns of *Carcharocles megalodon* over time reveal clues about extinction mechanisms. *Journal of Biogeography*, 43, 1645–1655.
- Pontarp, M., Bunnefeld, L., Cabral, J. S., Etienne, R. S., Fritz, S. A., Gillespie, R., Graham, C. H., Hagen, O., Hartig, F., & Huang, S. (2019). The latitudinal diversity gradient: Novel understanding through mechanistic eco-evolutionary models. *Trends in Ecology & Evolution*, 34, 211–223.
- Prieto-Márquez, A. (2014). Skeletal morphology of *Kritosaurus navajovius* (Dinosauria: Hadrosauridae) from the Late Cretaceous of the North American south-west, with an evaluation of the phylogenetic systematics and biogeography of Kritosaurini. *Journal of Systematic Palaeontology*, 12, 133–175.
- Quintero, I., & Landis, M. J. (2020). Interdependent phenotypic and biogeographic evolution driven by biotic interactions. *Systematic Biology*, 69, 739–755.
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing Retrieved from <https://www.R-project.org/>
- Raia, P., Passaro, F., Fulgione, D., & Carotenuto, F. (2012). Habitat tracking, stasis and survival in Neogene large mammals. *Biology Letters*, 8, 64–66.
- Rapoport, E. H. (1982). *Areography: Geographical strategies of species* (p. 269). Pergamon Press.
- Ree, R. H., & Smith, S. A. (2008). Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology*, 57, 4–14.
- Russell, D. A. (1967). *A census of dinosaur specimens collected in western Canada* (Vol. 36, pp. 1–13). National Museum of Canada.
- Sanmartin, I., & Meseguer, A. S. (2016). Extinction in phylogenetics and biogeography: from timetrees to patterns of biotic assemblage. *Frontiers in genetics*, 7, 35.
- Saupe, E. E., Farnsworth, A., Lunt, D. J., Sahoo, N., Pham, K. V., & Field, D. J. (2019). Climatic shifts drove major contractions in avian latitudinal distributions throughout the Cenozoic. *Proceedings of the National Academy of Sciences of the United States of America*, 116, 12895–12900.
- Shi, G. (1993). A comparative study of 39 binary similarity coefficients. *Memoir - Association of Australasian Paleontologists*, 15, 329–341.
- Sloan, R. E. (1969). Cretaceous and Paleocene terrestrial communities of western North America. *Proceedings of the North American Paleontological Convention*, 427–453.
- Sloan, R. E. (1976). The ecology of dinosaur extinction. In C. S. Churcher (Ed.), *Athlon: Essays on Palaeontology in Honour of Loris Shano Russell* (pp. 134–154). Ontario.
- Starrfelt, J., & Liow, L. H. (2016). How many dinosaur species were there? Fossil bias and true richness estimated using a Poisson sampling model. *Philosophical Transactions of the Royal Society B*, 371, 20150219.
- Sullivan, R. M., & Lucas, S. G. (2006). The Kirtlandian land-vertebrate ‘age’-faunal composition, temporal position and biostratigraphic correlation in the nonmarine Upper Cretaceous of western North America. In S. G. Lucas & R. M. Sullivan (Eds.), *Late Cretaceous Vertebrates from the Western Interior* (Vol. 35, pp. 7–30). New Mexico Museum of Natural History and Science Bulletin.
- Systra, Y. J., & Jensen, S. (2006). Trace fossils from the Dividalen group of northern Finland with remarks on early Cambrian trace fossil provincialism. *GFF*, 128, 321–325.
- Thessen, A. (2016). Adoption of machine learning techniques in ecology and earth science. *One Ecosystem*, 1, e8621.
- Varela, L., Tambusso, P. S., Patiño, S. J., Di Giacomo, M., & Fariña, R. A. (2018). Potential distribution of fossil xenarthrans

in South America during the late Pleistocene: Co-occurrence and provincialism. *Journal of Mammalian Evolution*, 25, 539–550.

Viana, D. S., Keil, P., & Jeliaskov, A. (2022). Disentangling spatial and environmental effects: Flexible methods for community ecology and macroecology. *Ecosphere*, 13, e4028.

Wang, S. C., & Dodson, P. (2006). Estimating the diversity of dinosaurs. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 13601–13605.

Zanno, L. E., Varricchio, D. J., O'Connor, P. M., Titus, A. L., & Kneel, M. J. (2011). A new troodontid theropod, *Talos sampsoni* gen. et sp. nov., from the Upper Cretaceous Western Interior Basin of North America. *PLoS One*, 6, e24487.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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