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# ASSEMBLAGE-LEVEL STRUCTURE IN MORRISON FORMATION DINOSAURS, WESTERN INTERIOR, USA

**John A. Whitlock, Kelli C. Trujillo, and Gina M. Hanik**

Theme Issue
An Ecosystem We Thought We Knew—
The Emerging Complexities of the Morrison Formation
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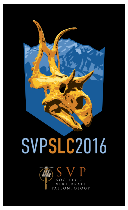

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## Assemblage-level Structure in Morrison Formation Dinosaurs, Western Interior, USA

**John A. Whitlock[1], Kelli C. Trujillo[2], and Gina M. Hanik[1]**
*[1]Department of Science and Mathematics, Mount Aloysius College, Cresson, PA 16630; jwhitlock@mtaloy.edu; gmhst4@student.mtaloy.edu*
*[2]Haub School of Environmental and Natural Resources, The University of Wyoming, Laramie, WY 82071; kellitrujillo@icloud.com*

## ABSTRACT

The Upper Jurassic Morrison Formation is both geographically extensive and well-sampled, making it an ideal candidate for biogeographic analysis at both coarse and finer scales. Historically, however, this has not translated into a consensus on patterns of ecological structure and connectivity, particularly with regard to the characteristic dinosaur faunas. Here, we use both traditional (genus richness, alpha and beta diversity) and bipartite network-based (biogeographic connectivity, local endemism, and average occurrence) measures to examine patterns of structure on a per-locality basis. Given the broad geographic range of the formation, we subdivide the Morrison Formation into four discrete regions based roughly on latitude and lithology—north (Montana, South Dakota, and northern Wyoming), west (Utah and western Colorado), east (central and eastern Colorado and southern Wyoming), and south (Arizona, New Mexico and Oklahoma). Further investigation revealed many coeval sites (ca. 152 Ma) in the east and west regions. Presence-absence data were also compared using network analysis to determine the presence and content of discrete subassemblages within the larger region-level assemblages. Based on our results, we favor reconstructions of the Morrison Formation as a 'mosaic' type environment over most of its depositional history, with patches of open environments interspersed with more closed, forested regions. This is suggested by relatively low rates of local endemism (patches are consistent in plant and animal structure) and connectivity across the majority of the formation, as well as the recovery of three non-overlapping assemblages dominated by different guilds of herbivorous dinosaurs.

## INTRODUCTION

The Late Jurassic Morrison Formation (~157-149 Ma) of North America represents one of the most extensive Mesozoic terrestrial depositional basins yet discovered, covering approximately 1.5 million square miles of territory, although much of the formation remains unexposed (Foster, 2003). As a result, the Morrison Formation has proven to be one of the most productive sources for dinosaur material, with dozens of named taxa inclusive of a wide range of bauplans, body sizes, and ecological habits. Despite the paleontological riches, however, little agreement on the basic ecosystem has been reached, with authors variously claiming a dominant conifer forest habitat, xeric plains-type habitats, or a "Jurassic savanna" habitat dominated by lush, low-growing vegetation and at least seasonally wet climates, or a mosaic of at least two distinct habitat types.

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Here, we show contrasting patterns in distribution between the largest bodied herbivores and all other dinosaurian taxa, and interpret the low degrees of endemism and connectivity as evidence for a 'mosaic' type landscape throughout most of the depositional basin represented by the Morrison Formation.

Prior studies of broad-scale ecological reconstruction in the Morrison Formation have primarily been focused on the abundant macro- and microfossil paleobotanical evidence. Plant fossils representing a diverse flora of cheirolepidiaceans, conifers, ferns, ginkophytes, horsetails, and podocarpaceans are known throughout the formation (Tidwell, 1990; Ash and Tidwell, 1998; Parrish and others, 2004). Between the abundance of drought intolerant plants (e.g., ferns, horsetails) and the known abundance of large herbivores (with their attendant forage requirements), some of the original interpretations of the Morrison Formation paleoenvironment focused on it as a lush, wet floodplain (Tidwell, 1990; Ash and Tidwell, 1998). Additionally, the apparent absence of arrested growth structures in woody remains and the presence of wood-rotting fungi have also been cited as evidence for a generally humid, mesic environment (Tidwell and others, 1998). More recently, however, two separate interpretations have taken root. One camp suggests that the paleoenvironment recorded by the Morrison Formation was xeric or only seasonally wet, with a flora comprised primarily of herbaceous and low- to mid-height woody podocarpaceaean shrubs; taller woody plants would have been restricted to riparian environments (Engelmann and others, 2004; Parrish and others, 2004; Rees and others, 2004). This view interprets the paleoenvironment as roughly equivalent to a modern tropical savanna grassland, with ferns and bryophytes occupying the ground-level browse layer currently dominated by grasses. More recently, some authors have presented evidence for the paleoenvironment of the Morrison Formation as a 'mosaic,' either with a matrix of conifer forest dominating interspersed open habitats (Gee, 2010; Hotton and Baghai-Riding, 2010), or as a primarily open environment with interspersed woodland environments (Whitlock, 2011). In all cases, it seems unlikely that dry-adapted plants such as cheirolepidiaceans would be restricted to riparian lands with wet soils, and indeed the opposite interpretation is now typically accepted (Hotton and Baghai-Riding, 2010).

There has been some attempt to segregate the Morrison Formation into ecological regions, such that the northern exposures of the Morrison (particularly in Montana and South Dakota) represent a substantially wetter paleoenvironment than the exposures to the south (Parrish and others, 2004; Noto and Grossman, 2010). Montana, in particular, houses some localities reconstructed as a unique depositional environment, dominated by mires, coal swamps, and peat bogs (Parrish and others, 2004). Palynological evidence also indicates the presence of a more humid environment in the northern extremes with a potentially higher water table as well (Hotton and Baghai-Riding, 2010). This is corroborated by the more frequent occurrence of semi-aquatic reptiles (e.g., crocodilians, turtles; Foster and McMullen, 2017) in the Morrison Formation of Montana, South Dakota, Wyoming, and eastern Colorado. Furthermore, there has been a suggestion of a longitudinal gradient of drainage and precipitation as well (Demko and others, 2004; Turner and Peterson, 2004), with drier margins and a 'center' with the majority of standing water in the forms of lakes and wetlands.

From the earliest stages of ecological assessment in the Morrison Formation, a 'core' fauna of large diplodocids, *Stegosaurus*, and *Allosaurus* has been recognized, with other taxa appearing with less regularity (Dodson and others, 1980a, 1980b), although there has been little consensus on how those faunas have been constructed. More recently, Noto and Grossman (2010) analyzed the paleoecology of dinosaurs in the Morrison Formation (and other formations), dividing the localities into six "assemblages" based on geographic proximity and using Ecological Structure Analysis (ESA) to identify any potential relationships between the behavior or ecology of the dinosaurs (e.g., body size, locomotor habit) and the regional environment. Although they did not make explicit statements about generic constituencies of any inferred communities, they did identify what they termed a "semi-arid" set of assemblages from the latitudinal center of the formation, bounded by a more arid set of assemblages from the northern and southern extremes. This distinction was largely recognized in the faunas as a function of body size (smaller overall body size in the semi-arid environments) and locomotor habit (semi-arid environments were more dominated by bipedal organisms; Noto and Grossman, 2010).

Here, we attempt to build on this prior work by examining the Morrison Formation on a quarry level to try and pull out any signal that might indicate the presence of distinct communities at the generic level. Using classical ecological inferences (alpha and beta diversity and shared taxonomic scope) in concert with newer bipartite statistical methods (following Sidor and others, 2013), we characterize the dinosaur assemblages at both regional and individual locality scales, and interpret the results in the context of describing the overarching ecological conditions present at the time of Morrison Formation deposition.

## METHODS

Because the Morrison Formation incorporates both a large geographic and temporal range, the 291 localities sampled were divided into four regions: north (65 localities), inclusive of localities in Montana, South Dakota, and northern Wyoming (above 43°N); west (72 localities), inclusive of localities in Utah and Colorado just east of the city of Gunnison, Colorado (Cabin Creek [see Turner and Petersen, 1999] and westward); east (128 localities), inclusive of Colorado east of Cabin Creek and Wyoming below 43°N and the lithologically similar Snowmass locality (Foster and Wedel, 2014); and south (26 localities), inclusive of localities in Arizona, New Mexico and Oklahoma (figure 1). Differences in recognized members across the formation as well as limitations on the quality of intraformational correlations hamper further subdivision into more definitive age units at this time (Trujillo, 2006). New $^{40}Ar/^{39}Ar$ and U-Pb isotope ages, however, identify 28 localities across the east and west regions that are roughly coeval (ca. 152 Ma; Trujillo and others, 2014, 2015; Trujillo and Kowallis, 2015). These localities are examined independent of the rest of the data set to provide further insight into potential regional differences independent of time dilation effects. Because we are predominantly interested in examining regional patterns of taxonomic structure, we refrain from attempts to group localities into bins of equal number or attempts to filter localities by alpha diversity and other indicators.

Taxonomic data was pooled from the Paleobiology Database (http://fossilworks.org; see supplemental information) and supplemented with additional information from Foster (2003). One caveat with using data of this sort is that we are, at best, two steps removed from the original material (collector->compiler->present authors), each step having the potential to introduce errors ranging from incorrect taxonomic assignment to typographic issues. As it is reasonable to assume the general care of our colleagues with regard to data collation, the biggest concern is misidentification of the fossils themselves. Dinosaur workers in general and those familiar with the Morrison Formation specifically will no doubt already be aware of the difficulty in correctly assigning many fossil specimens, as well as the potential for "hidden" taxonomic diversity (e.g., *Galeamopus*, *"Elaphrosaurus;"* Chure, 2001; Carrano and Sampson, 2008; Tschopp and others, 2015; Tschopp and Mateus, 2017). While recognizing the potential confounding effects of these issues, there is fundamentally little that can be done to resolve them at this level, and thus we note their existence here and calibrate our interpretations accordingly. Similarly, we note the potential for taphonomic bias towards larger bodied taxa, which we attempt to mitigate again by limiting our scope to presence-absence rather than abundance.

Taxonomically unresolved taxa—e.g., "*Elaphrosaurus*"—or records without identification to the genus level were omitted. The recently proposed generic separation between *Apatosaurus* and *Brontosaurus* (Tschopp and others, 2015) is not incorporated into this analysis for reasons of practicality; the records in question predate this proposal, and in lieu of attempting to examine all specimens of *Apatosaurus* in question (some 75 total records composed of untold numbers of individual specimens), we elect to simply continue use of the genus *Apatosaurus.* To examine large-scale trends in connectivity and diversity, alpha diversity (using genus richness), beta diversity (as measured by Sørenson's Index, or SI), and shared taxonomic scope were calculated using the pooled assemblage data from each major region. Sørenson's Index was chosen as a measure of beta diversity vis-à-vis continuity (sensu Koleff and others, 2003). Importantly, SI satisfies the requirement of be-

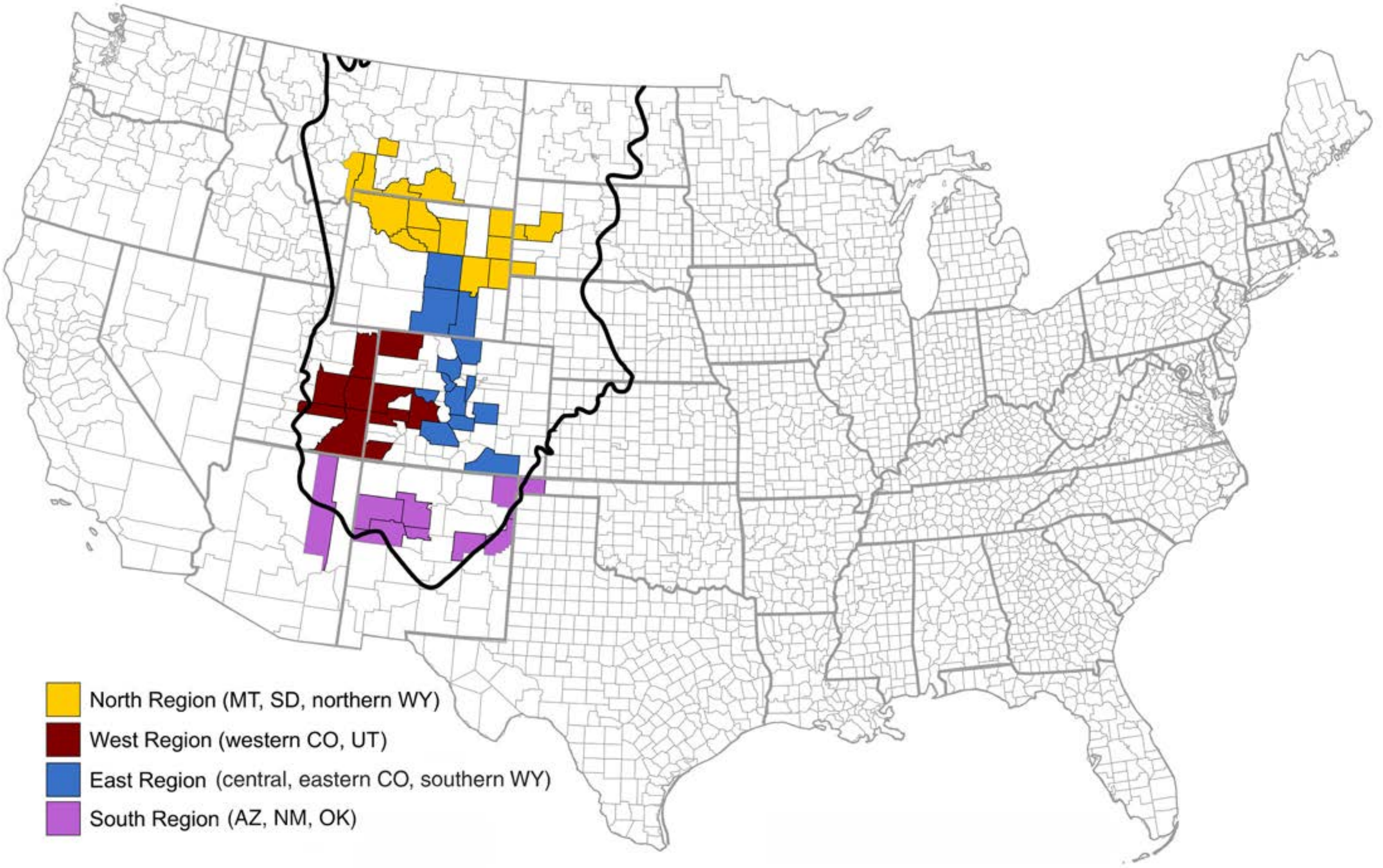


Figure 1. Map of localities by county, color coded by region. Heavy black line indicates approximate geographic extent of the Morrison Formation (modified from Turner and Peterson, 2004). See supplemental information for full details.

ing sensitive only to proportions of species, not to total number (Janson and Vegelius, 1981), the latter being a potential issue given the unequal areas and taxonomic compositions of the regions under consideration. To characterize locality-level connectivity, bipartite resampling methods (following Sidor and others, 2013) were used to calculate three measures: average occurrences per taxon (interpreted as range size, following Sidor and others, 2013), average endemic taxa per locality, and biogeographic connectivity (the number of taxon linkages as a proportion of the maximum possible). Each analysis presents a distribution of scores obtained via 1000 bootstrap replicates (see supplemental information for discussion of replicate choice). A Welch two-sample unequal variances t-test was used to determine statistical significance. To look for potentially distinct assemblages within the taxonomic samples, co-occurrence and edge matrices were computed in R using the cooccur package (Griffith and others, 2016); resultant networks were analyzed for patterns of generic clustering using Gephi (Bastian and others, 2009). For the temporal groupings in the east and west regions, localities with good stratigraphic data were correlated with the nearest precise radiometric age by K.C. Trujillo.

## RESULTS

Alpha diversity is consistently high in the north, west, and east regions (21-22 genera) and substantially lower in the south region (10 genera; table 1). Sauropod alpha diversity appears to decrease with decreasing latitude, but this trend is not seen in either theropods or ornithischians. In theropods, there appears to be a 'bulge' in diversity in a central region (west and east regions combined). Beta diversity is highest between the north and east regions (SI = 83% similarity; table 2), but is also notable between the west and east regions (71%). Similarity is lower between the north and west regions (65%), and is lowest between the south region and all others (56-58%), with the north and south being most different. This trend is generally conserved when the samples are restricted by taxonomic group, with the exception of sauropods, where similarity is highest between the south region and the west and east regions (83%), although again the north and south are least similar (63%).

Shared taxonomic scope is reasonably high in the Morrison Formation (figure 2). This is exemplified by the large-bodied sauropods, where 5 of 12 taxa occur in all four regions and 8 of 12 occur in at least two. The regionally endemic taxa, *Dyslocosaurus*, *Dystrophaeus*, *Kaatedocus,* and *Suuwassea*, are also known from only a single locality each, which suggests that their rarity is either a function of their rarity in the fauna as a whole or the rate at which they are misidentified by collectors, or both. Theropod shared taxonomic scope is less robust, with only two of the largest bodied taxa (*Allosaurus* and *Ceratosaurus*) occurring in all four regions, and two others (the very large *Torvosaurus* and the small *Coelurus*) occurring in three. Nearly half (4/10) of theropod taxa are known from a single region only, and there is the possibility of a great many more singleton taxa that would increase this total (e.g., any potential taxa subdivided from the catch-all genus "*Elaphrosaurus,*" *Koparion*). These regionally endemic theropods are invariably small-bodied. Ornithischian-shared taxonomic scope is somewhat intermediate between sauropods and theropods, in that regional endemism is high (4/10 taxa), as in theropods, but as many taxa occur in at least three regions (4/10), a distribution somewhat similar to that seen in sauropods. Two taxa (*Camptosaurus* and *Stegosaurus*) are known from all four regions. For the 152 Ma time bin, absolute taxonomic diversity is highest in the east region (18 taxa vs. 12 taxa in the west). Beta diversity is generally high (0.66), but this is largely driven by the sauropods (1.0). Theropod (0.5) and ornithischian (0.5) assemblages are both relatively less similar. The difference in taxonomic scope is largely due to the absence of many relatively small bodied taxa, particularly theropods (e.g., *Coelurus*) in the west.

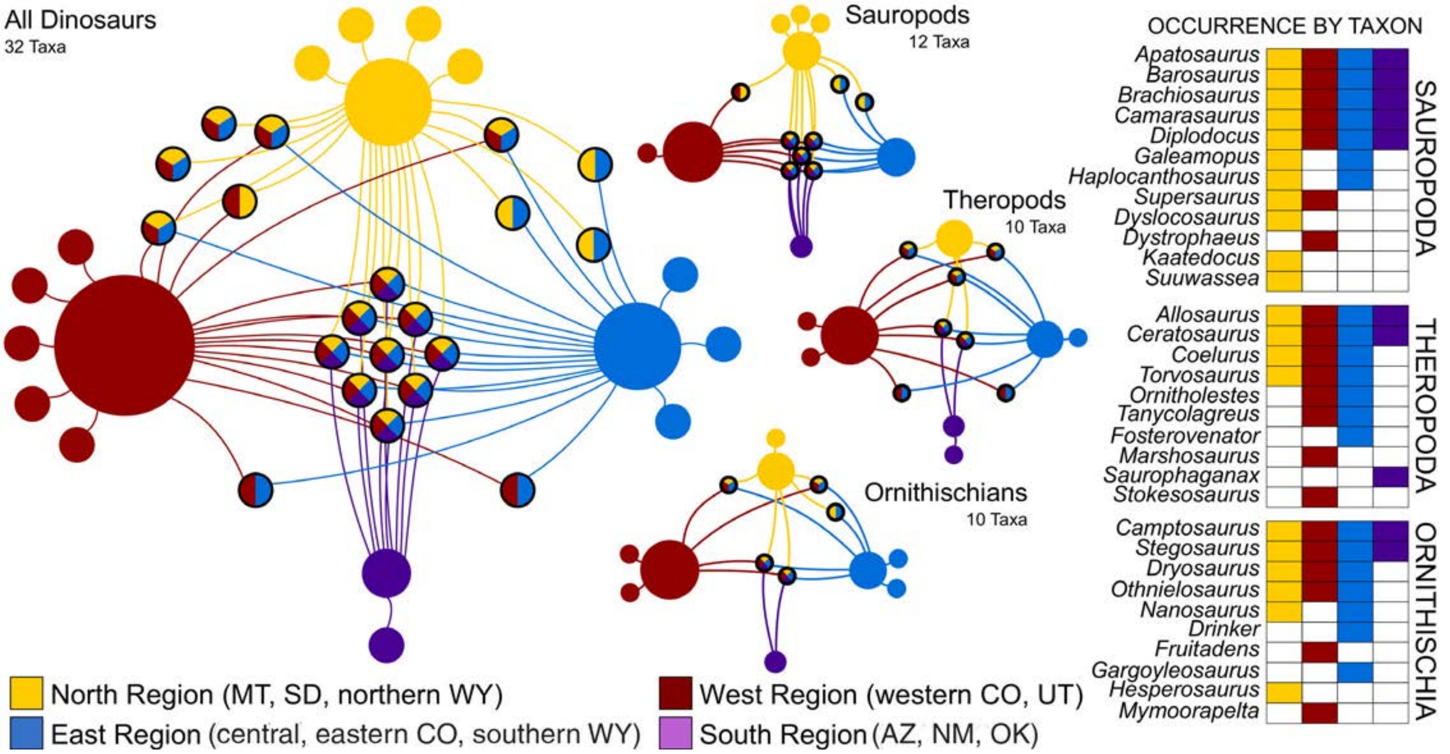
Table 1. Alpha diversity (generic richness) for each of the four study regions.

| | Total Generic Diversity | Sauropods only | Theropods only | Ornithischians only |
|---|---|---|---|---|
| North | 22 | 11 | 4 | 7 |
| West | 21 | 7 | 9 | 5 |
| East | 21 | 7 | 7 | 7 |
| South | 10 | 5 | 3 | 2 |
| 152Ma East | 18 | 6 | 5 | 7 |
| 152Ma West | 12 | 5 | 3 | 4 |

Table 2. Beta diversity (Sørenson's Index) for each of the four study regions.

| | North | West | East | South | |
|---|---|---|---|---|---|
| North | | | | | ALL TAXA |
| West | 65% | | | | |
| East | 83% | 71% | | | |
| South | 56% | 58% | 58% | | |
| | **North** | **West** | **East** | **South** | |
| North | | | | | SAUROPODS |
| West | 67% | | | | |
| East | 78% | 71% | | | |
| South | 63% | 83% | 83% | | |
| | **North** | **West** | **East** | **South** | |
| North | | | | | THEROPODS |
| West | 67% | | | | |
| East | 73% | 80% | | | |
| South | 57% | 36% | 40% | | |
| | **North** | **West** | **East** | **South** | |
| North | | | | | ORNITHISCHIANS |
| West | 62% | | | | |
| East | 86% | 62% | | | |
| South | 44% | 50% | 44% | | |

Bipartite analyses result in significantly different ($p < 0.0001$; $t$ and df reported in supplemental information) distributions of all three characteristics (average occurrence, average endemics, biogeographic connectivity) for all regions, excluding only biogeographic connectivity between north, east, and west regions ($1 \leq p \leq 0.9994$). Despite this statistical significance, certain characteristics of certain regions appear more similar to each other than others. As noted, biogeographic connectivity is statistically identical in the north, east, and west regions (figure 3), and is significantly lower



| | | | | | |
|---|---|---|---|---|---|
| SAUROPODA | Apatosaurus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Barosaurus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Brachiosaurus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Camarasaurus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Diplodocus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Galeamopus | 🟨 | | 🟦 | |
| | Haplocanthosaurus | 🟨 | | 🟦 | |
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| | Dystrophaeus | | 🟥 | | |
| | Kaatedocus | 🟨 | | | |
| | Suuwassea | 🟨 | | | |
| THEROPODA | Allosaurus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Ceratosaurus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Coelurus | 🟨 | 🟥 | 🟦 | |
| | Torvosaurus | 🟨 | 🟥 | 🟦 | |
| | Ornitholestes | | 🟥 | 🟦 | |
| | Tanycolagreus | | 🟥 | 🟦 | |
| | Fosterovenator | | | 🟦 | |
| | Marshosaurus | | 🟥 | | |
| | Saurophaganax | | | | 🟪 |
| | Stokesosaurus | | 🟥 | | |
| ORNITHISCHIA | Camptosaurus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Stegosaurus | 🟨 | 🟥 | 🟦 | 🟪 |
| | Dryosaurus | 🟨 | 🟥 | 🟦 | |
| | Othnielosaurus | 🟨 | 🟥 | 🟦 | |
| | Nanosaurus | 🟨 | | 🟦 | |
| | Drinker | | | 🟦 | |
| | Fruitadens | | 🟥 | | |
| | Gargoyleosaurus | | | 🟦 | |
| | Hesperosaurus | 🟨 | | | |
| | Mymoorapelta | | 🟥 | | |

Figure 2. Shared taxonomic scope between the four regions of interest with distribution broken down by individual genera.

than in the south region, where connectivity is highest. Despite the lower connectivity scores, locality-level endemism is essentially zero in the central and north regions, with an order of magnitude higher rates recorded in the south region. Average occurrence (AO) scores do increase as the number of localities sampled increases, but none are directly limited by the number of localities (i.e., all AO scores are less than 1/4 of the number of sampled localities). Time-restricted samples show the same general pattern as the broader samples, with the exception of an unusually high connectivity in the east 152 Ma time bin (figure 3).

Assemblage-level structure in the Morrison Formation is generally built around a consistent "core" of taxa (*Allosaurus*, *Apatosaurus*, *Camarasaurus*, *Diplodocus*, and *Stegosaurus*) that are highly connected with the majority of other taxa, and might be considered the 'typical' Morrison fauna (Dodson and others, 1980a, 1980b). *Camptosaurus* and *Ceratosaurus* are also commonly found co-occurring with most other taxa. Larger herbivores (i.e., sauropods, *Camptosaurus*) and some large predators (i.e., *Allosaurus*, *Ceratosaurus*) display little preference with regard to co-occurring taxa, although smaller carnivores (*Coelurus*, *Tanycolagreus*) and many other large predators (*Fosterovenator, Stokesosaurus, Torvosaurus*) do appear to show some segregation. These patterns are most distinct in the central region (figure 4). The most locality level segregation is found among the medium- to small-sized ornithischians in the central region, which appear to sort themselves into three general groups based upon non-overlapping exemplar taxa: (1) a '*Mymoorapelta*' group, which co-occurs with no other smaller herbivores, only large sauropods; (2) an *'Othnielosaurus'* group, which co-occurs with *Camarasaurus*, *Camptosaurus, Drinker*, *Nanosaurus,* and *Stegosaurus*; and (3) a '*Dryosaurus*' group, consisting of *Apatosaurus*, *Camarasaurus, Camptosaurus, Diplodocus, Gargoyleosaurus,* and *Stegosaurus*. In the north region, where connectivity is relatively high, *Dryosaurus* and *Othnielosaurus* do co-occur in a single locality (Howe-Stevens, see supplemental information); the remaining combined 10 occurrences (as measured

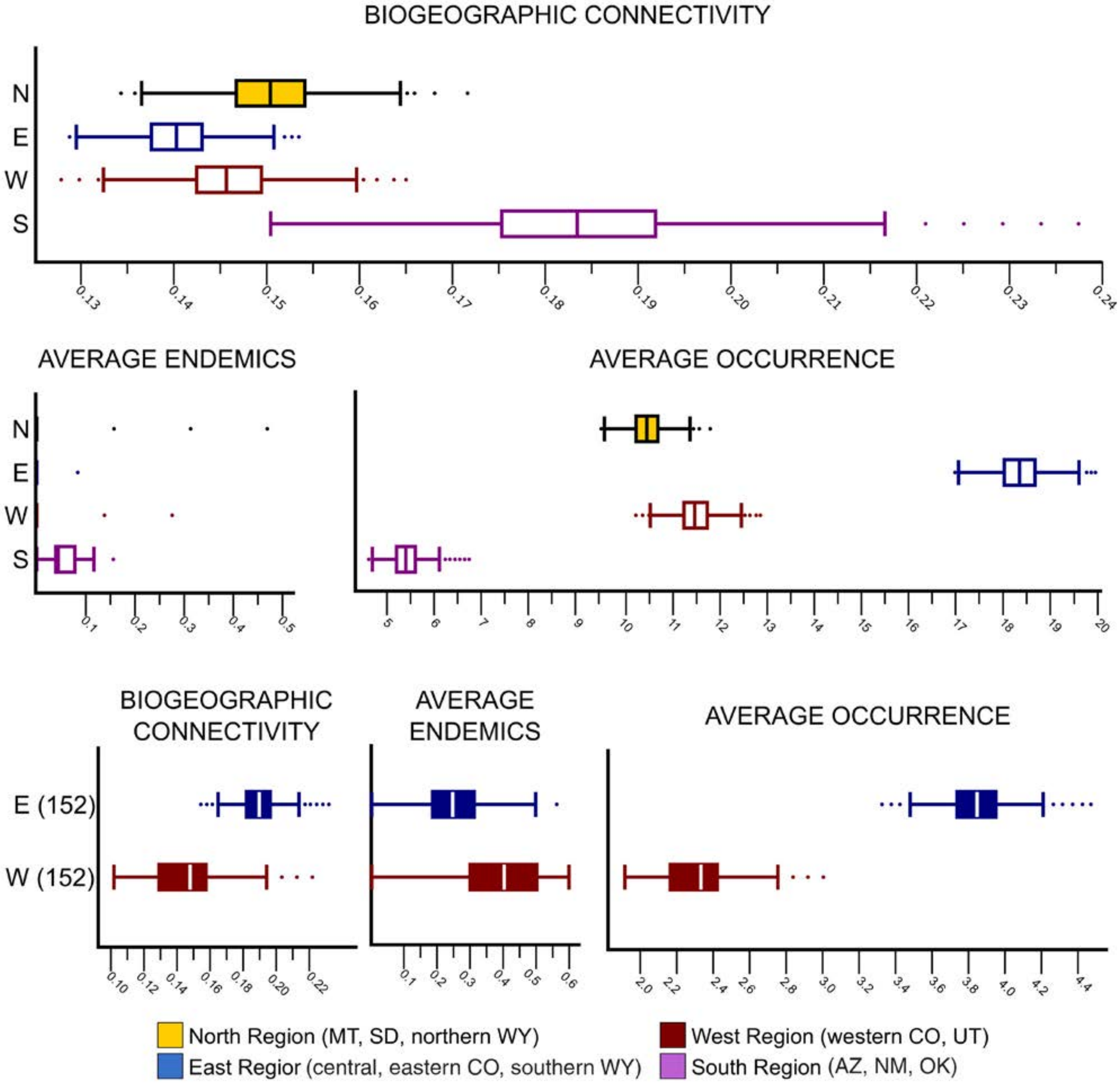

Figure 3. Box and whisker plots representing the results of the bipartite statistical analyses for each sampled region as well as the 152 Ma sample of east and west. Average occurrence represents the average number of localities a randomly selected species would occur in. Average endemics reports the average number of per-locality endemic taxa recovered. Biogeographic connectivity measures the proportion of recovered connections (shared taxa) as a function of the total potential connections. Numbers reported represent distributions over 1000 replicates.

by presence/absence) in the north region and all 15 occurrences in the central region are mutually exclusive. *Othnielosaurus* is a relatively rare taxon, but it is substantially more common in the northern Morrison (five localities vs. two each in the west and east). *Coelurus* is found exclusively with the *Othnielosaurus* assemblage, and *Tanycolagreus* is found exclusively with the *Dryosaurus* assemblage, although the two taxa do co-occur (in the absence of both *Dryosaurus* and *Othnielosaurus*) in the west region.

Within the 152 Ma time bin, we observe this segregation in the east (figures 4E and 4F), but not in the west

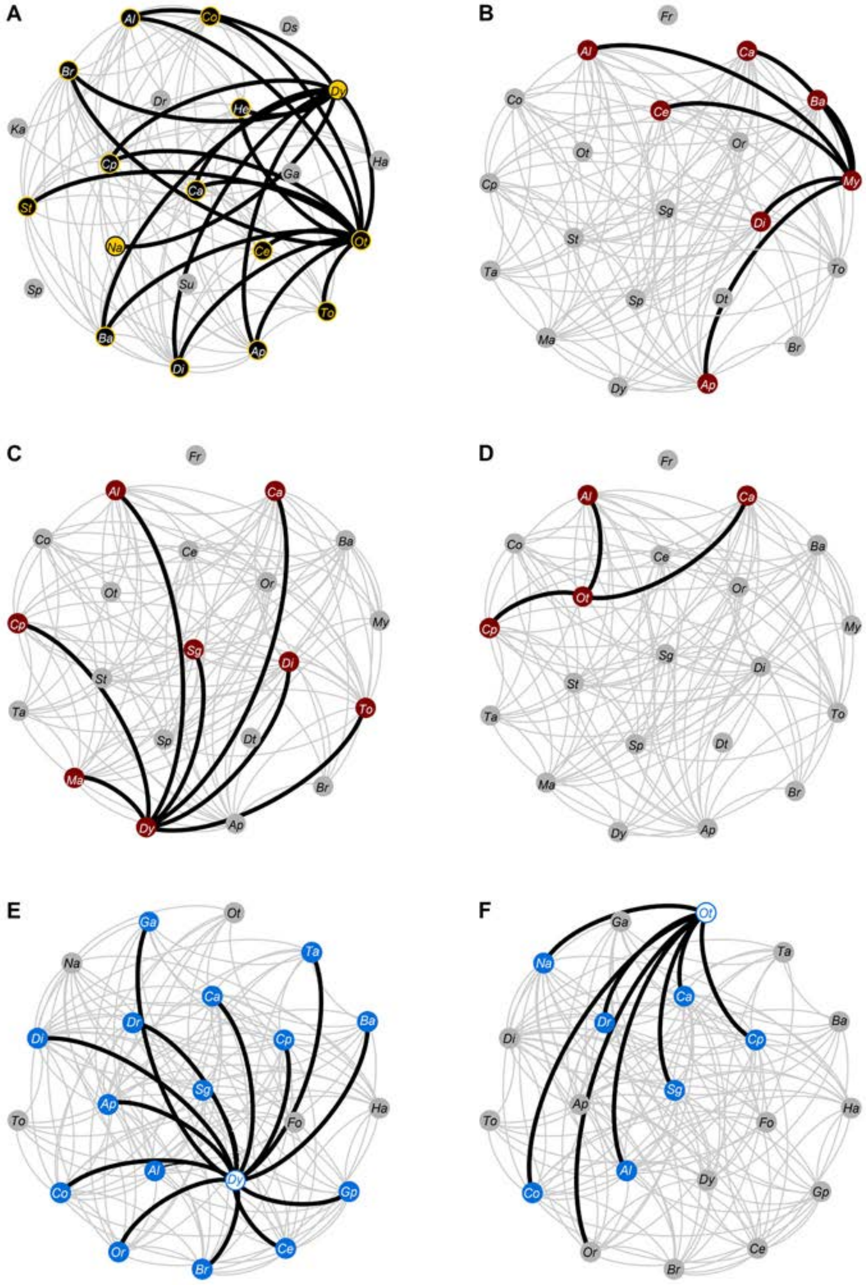

Figure 4. Network diagrams illustrating co-occurrence between genera in the central Morrison Formation. (A) Network diagram of the north region, with conjoined *Dryosaurus* and *Othneilosaurus* network highlighted. (B) Network diagram of the west region, with *Mymoorapelta* assemblage highlighted. (C) Network diagram of the west region, with *Dryosaurus* assemblage highlighted. (D) Network diagram of the west region, with *Othnielosaurus* assemblage highlighted. (E) Network diagram of the east region, with *Dryosaurus* assemblage highlighted. (F) Network diagram of the east region, with *Othnielosaurus* assemblage highlighted. Abbreviations: Al = *Allosaurus*; Ap = *Apatosaurus*; Ba = *Barosaurus*; Br = *Brachiosaurus*; Ca = *Camarsaurus*; Ce = *Ceratosaurus*; Co = *Coelurus*; Cp = *Camptosaurus*; Di = *Diplodocus*; Dr = *Drinker*; Ds = *Dyslocosaurus*; Dt = *Dystrophaeus*; Dy = *Dryosaurus*; Fo = *Fosterovenator*; Fr = *Fruitadens*; Ga = *Gargoyleosaurus*; Gp = *Galeamopus*; Ha = *Haplocanthosaurus*; He = *Hesperosaurus*; Ka = *Kaatedocus*; Ma = *Marshosaurus*; My = *Mymoorapelta*; Na = *Nanosaurus*; Or = *Ornitholestes*; Ot = *Othneilosaurus*; Sg = *Stegosaurus*; St = *Stokesosaurus*; Su = *Suuwassea*; Ta = *Tanycolagreus*; To = *Torvosaurus*.

(figure 4D). Furthermore, *Dryosaurus* does not co-occur with any other taxa in this sample and so provides no information relevant to its participation in discrete assemblages. Aside from a slightly lower taxonomic diversity, the 152 Ma time bin is representative of the regions as a whole with regard to taxonomic assemblages.

## DISCUSSION

Diversity metrics (genus richness, SI) generally suggest similar diversity levels in localities in the northern and central parts of the Morrison Formation, with the greatest diversity occurring in the central region. Regional interconnectivity appears to be tied to some combination of body size and ecological habit. Large-bodied herbivores (such as sauropods, and certain ornithiscians like *Camptosaurus*) tend to occur in more regions overall (lower rates of endemism), and have a wider individual distribution (weighted towards occurrence in four regions over occurrence in two). *Camptosaurus* is itself potentially cosmopolitan not simply within the Morrison Formation, but also may appear in coeval basins in Europe as well (Foster, 2013). This would be a substantial geographic range for a single taxon, although representatives of other Morrison Formation genera such as *Allosaurus*, *Ceratosaurus, Stegosaurus,* and *Torvosaurus* have been reported from Iberia (Mateus, 2006; Mateus and others, 2006; Escaso and others, 2007; Hendrickx and Mateus, 2014). Whether this is a true distribution or simply a matter of taxonomic 'lumping' (e.g., '*Elaphrosaurus;*' Carrano and Sampson 2008) is unclear, however.

There does not appear to be a clear size-distribution relationship for theropods, as in general large- and small-bodied individuals are recovered as both widely distributed (e.g., *Allosaurus*, *Coelurus*) and regionally endemic (e.g., *Saurophaganax*, *Stokesosaurus*). This may be due to increased competitive pressures facing carnivores, access to appropriate prey, and/or reinforcing behaviors such as territorialism. We agree with Foster (2000) in that we find little evidence to suggest drastic differences in environment with latitude, particularly with regard to the northern Morrison Formation as an environmental outlier, as has been previously suggested (Parrish and others, 2004; Hotton and Baghai-Riding, 2010; Whitlock, 2011). Sauropod diversity does decline with declining latitude, but the differences between the north and central regions are not substantial and are primarily driven by the presence of two north region endemics, *Kaatedocus* and *Suuwassea*. These two taxa are both very recently described (Harris and Dodson, 2004; Tschopp and Mateus, 2013) and are represented by a single specimen each; consequently, it is not implausible that additional specimens from other regions are either undiscovered or misidentified in existing collections.

Bipartite statistics predict greater provincialism when biogeographic connectivity and range sizes are small and average endemism is high (Sidor and others, 2013). In the south region, we find agreement between range size and endemism—both of which predict a high degree of provincialism—but disagreement with biogeographic connectivity, which would predict a very cosmopolitan distribution of taxa. Similarly, range sizes and endemism predict a more cosmopolitan distribution in the north, east, and west regions, but the comparatively lower biogeographic connectivity in those regions predicts provincialism. Some of these effects may be attributable to time dilation effects; i.e., substantial turnover in environmental structure may result in these statistics capturing discordant effects due to overlaying different environmental structures on top of each other, both in physical space (as a function of deposition) and in 'statistical space' (as a function of data pooling). However, we postulate that these results may be still interpretable due to a highly fractured environments. Extremely patchy ecosystems would result in smaller ranges and increased regional endemism. If substantial corridors connecting similar patches did not exist (or were outside the depositional area recorded), these patches would be isolated from each other in the fossil record, which is consistent with a low per-locality connectivity measurement, as observed. We do interpret some degree of connectivity, largely driven by the cosmopolitan sauropod fauna, as complete balkanization of depositional environments has been shown to correspond to even lower degrees of connectivity than observed here (Sidor and others, 2013). In the case of the widely distributed taxa (sauropods, large theropods like *Allosaurus*), it seems likely that their large size would have made them largely immune to barriers, inclusive of larger patches of less suitable habitat. In modern ecosystems, large rivers present barriers to dispersal for many organisms, including such varied groups as African Buffalo (Naidoo and others, 2012), elephants (Robertson, 2013), lions and other African carnivores (Cozzi and others, 2013), wolves (Blanco and others, 2005), passerine birds (Ayres and Clutton-Brock, 1992; Hayes and Sewlal, 2004; but see Gascon and others, 2000), and primates (Goodman and Ganzhorn, 2004; Harcourt and Wood, 2012), although there is some evidence that larger bodied taxa are less affected, particularly when the river in question is small or seasonally low (Cozzi and others, 2013; Robertson, 2013). The river itself does not need to be impassable to be a barrier; in many cases the ecosystem on either side of the river is significantly different as to be a barrier unto itself (Oates, 1998; Meijard and Groves, 2006). A more continuous environment would result in a signal with low regional endemism and high connectivity, as there would be no barrier regions where a variety of ecomorphs would be less likely to occur or be preserved.

When restricted to localities deposited at or near 152 Ma, however, our results paint a more consistent picture. The west region scores lower in range size and connectivity and higher in endemism than the east, all of which suggest that the west was more provincial at this time. This fragmentation supports the idea that there was no 'rain shadow' effect caused by coeval and preceding uplift and erosion of rift shoulders associated with a magmatic arc west of the Morrison Formation's depositional area (Turner and Fishman, 1998; Dickinson, 2006). Such uplift could have potentially created a 'rain shadow' on the leeward basin, resulting in an arid region without significant permanent riparian structure. Due to the high rate of sediment deposition attributable to erosion from those highlands (Turner and Fishman, 1998), however, it seems unlikely that there was a significant rain shadow effect on the west region at this time (Turner and Peterson, 2004). In addition, a rain shadow would likely have resulted in a relatively homogenous, 'savanna' type environment without major river systems to serve as dispersal barriers for smaller dinosaurs (Ash and Tidwell, 1998; Parrish and others, 2004). Instead, the apparently robust riparian structure in that region may well have provided significant (if ephemeral on geologic time scales) barriers to dispersal in the form of major river systems and alkaline-saline wetlands (e.g., "Lake" Tooʼdiʼchiʼ in southwest Colorado and southeast Utah; Fishman and others, 1995; Turner and Peterson, 2004), which could potentially have limited the range sizes and regional distribution of smaller dinosaurs (e.g., smaller theropods, ornithischians). The riparian structure would have been less restrictive to the extremely large sauropods and larger theropods like *Allosaurus*, which do indeed have a more cosmopolitan distribution. Range size is also strongly correlated with body size in extant mammals (McNab, 1966; Swihart and others, 1988), largely as a function of energetics, which would further explain the consistently cosmopolitan distribution of these larger organisms.

The larger range sizes and degree of connectivity overall in the east, however, suggest greater environmental homogeneity, consistent with reconstructions of this region dominated by a broad alluvial plain (Turner and Peterson, 2004). Therefore, we favor the nuanced interpretation many modern studies have put forward, such that the geographically large region recorded by the Morrison Formation likely included a diverse array of habitats and habitat structures inclusive of both drier, 'savanna'-type environments and wetter, riparian-dominated environments, consistent with regional tectonic and eustatic changes at the time. However, the patchiness (or 'mosaic' distribution) of these environments as well as the effects of time dilation make direct comparisons to modern ecosystems (e.g., 'savanna') somewhat problematic, particularly as the geographic scale of the study increases.

The interpretation of our bipartite analysis results is consistent with the network analysis which recovered three distinct ornithischian assemblages in the central region—a '*Mymoorapelta*' assemblage, a '*Dryosaurus*' assemblage, and an '*Othnielosaurus*' assemblage—as well as with prior work (Noto and Grossman, 2010). The *Mymoorapelta* group appears to be more 'open' adapted, based upon the feeding preferences of the locally dominant diplodocid sauropods (Stevens and Parrish, 1999; Upchurch and Barrett, 2000; Stevens and Parrish, 2005; Whitlock, 2011), although the *Mymoorapelta* type locality does feature abundant evidence for conifers

(Tidwell and others, 1999; Hotton and Baghai-Riding, 2010). The *Dryosaurus* and *Othnielosaurus* assemblages both contain more closed-adapted genera, including a wide variety of other medium-sized ornithischians, but they differ regarding sauropod content. *Dryosaurus* assemblages include both diplodocids and the mid- to high-browser *Camarasaurus* (Fiorillo, 1998; Upchurch and Barrett, 2000; Whitlock, 2011); *Othnielosaurus* assemblages are strongly associated with *Camarasaurus.* This suggests the preference of *Dryosaurus* for edge environments (where open and closed adapted taxa would be expected to intermingle) and closed environments for *Othnielosaurus*. As *Othnielosaurus* is reconstructed as substantially smaller than *Dryosaurus* (e.g., Farlow and others, 2010), this is a reasonable assumption to make. There is some evidence for habitat preference in theropods as well, with many large-bodied taxa appearing to prefer open environments and medium- to small theropods choosing closed or edge environments. This association is not as strong, however, suggesting that habitat choice is more labile. This is consistent with observations of modern animals, which often display variance in habitat preference largely dependent on nonbiotic environmental factors such as local temperature (May and others, 2010; van Beest and others, 2012).

## CONCLUSIONS

A picture of the Morrison Formation paleoecosystem emerges as a mosaic of diverse communities and environmental structures in a massive, long-lived depositional basin, regionally dominated by distinct populations of relatively small-bodied ornithischian herbivores and theropod carnivores, with widespread and potentially migratory populations of large-bodied sauropods and certain other exemplar taxa such as *Allosaurus* and *Camptosaurus*. Where temporal restriction is possible, distinct regional differences emerge between the western and eastern regions of the basin, consistent with coeval tectonic events, such that uplift and extensive riparian development to the west created greater habitat fractionation and provincialization in dinosaurian assemblages. Direct comparisons to modern ecosystems (e.g., use of analogs such as 'savanna') are likely of limited application, at least at this geographic scale. The apparent patchiness of much of the Morrison basin suggests a 'mosaic' type environment, and as such we must look to different approaches, such as this one, to gain a better understanding of the community-level dynamics in the megafauna.

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## REFERENCES

Ash, S.R., and Tidwell, W.D., 1998, Plant megafossils from the Brushy Basin Member of the Morrison Formation near Montezuma Creek Trading Post, southeastern Utah: Modern Geology, v. 22, p. 321–339.

Ayres, J.M., and Clutton-Brock, T.H., 1992, River boundaries and species range size in Amazonian primates: The American Naturalist, v. 140, p. 531–537.

Bastian, M., Heymann, S., and Jacomy, M., 2009, Gephi—an open source software for exploring and manipulating networks, *in* Proceeding of the third international conference on weblogs and social media (ICWSM): Association for the Advancement of Artificial Intelligence, p. 361–362.

Blanco, J.C., Cortés, Y., and Virgós, E., 2005, Wolf response to two kinds of barriers in an agricultural habitat in Spain: Canadian Journal of Zoology, v. 83, p. 312–323.

Carrano, M.T., and Sampson, S.D., 2008, The phylogeny of Ceratosauria (Dinosauria: Theropoda): Journal of Systematic Palaeontology, v. 6, no. 2, p. 183–236.

Chure, D.J., 2001, The second record of the African theropod *Elaphrosaurus* (Dinosauria, Ceratosauria) from the Western Hemisphere: Neues Jahrbuch für Geologie und Paläontologie, v. 2001, p. 565–576.

Cozzi, G., Broekhuis, F., McNutt, J.W., and Schmid, B., 2013, Comparison of the effects of artificial and natural barriers on large African carnivores—implications for interspecific relationships and connectivity: Journal of Animal Ecology, v. 82, p. 707–715.

Demko, T.M., Currie, B.S., and Nicoll, K.A., 2004, Regional paleoclimatic and stratigraphic implications of paleosols and fluvial/overbank architecture in the Morrison Formation (Upper Jurassic), Western Interior, USA: Sedimentary Geology, v. 167, p. 115–135.

Dickinson, W.R., 2006, Geotectonic evolution of the Great Basin: Geosphere, v. 2, no. 7, p. 353–368.

Dodson, P., Behrensmeyer, A.K., and Bakker, R.T., 1980a, Taphonomy of the Morrison Formation (Kimmeridgian-Portlandian) and Cloverly Formation (Aptian-Albian) of the western United States: Mémoir Societé Géologique de France, v. 139, p. 87–93.

Dodson, P., Behrensmeyer, A.K., Bakker, R.T., and Mcintosh, J.S., 1980b, Taphonomy and paleoecology of the dinosaur beds of the Jurassic Morrison Formation: Paleobiology, v. 6, no. 2, p. 208–232.

Engelmann, G.F., Chure, D.J., and Fiorillo, A.R., 2004, The implications of a dry climate for the paleoecology of the fauna of the Upper Jurassic Morrison Formation: Sedimentary Geology, v. 167, no. 3–4, p. 297–308.

Escaso, F., Ortega, F., Dantas, P., Malafaia, E., Pimentel, N.L., Pereda-Suberbiola, X., Sanz, J.L., Kullberg, J.C., Kullberg, M.C., and Barriga, F., 2007, New evidence of shared dinosaur across Upper Jurassic Proto-North Atlantic—stegosaurus from Portugal.: Die Naturwissenschaften, v. 94, no. 5, p. 367–374.

Farlow, J.O., Coroian, I.D., and Foster, J.R., 2010, Giants on the landscape—modelling the abundance of megaherbivorous dinosaurs of the Morrison Formation (Late Jurassic, western USA): Historical Biology, v. 22, no. 4, p. 403–429.

Fiorillo, A.R., 1998, Dental microwear patterns of the sauropod dinosaurs *Camarasaurus* and *Diplodocus*—evidence for resource partitioning in the Late Jurassic of North America: Historical Biology, v. 13, no. 1, p. 1–16.

Fishman, N.S., Turner, C.E., and Brownfield, I.K., 1995, Authigenic albite in a Jurassic alkaline, saline lake deposit, Colorado Plateau—evidence for early diagenetic origin: U.S. Geological Survey Bulletin 1808, 14 p.

Foster, J.R., 2000, Paleobiogeographic homogeneity of dinosaur faunas during the Late Jurassic in western North America: New Mexico Museum of Natural History and Science Bulletin 17, p. 47–50.

Foster, J.R., 2003, Paleoecological analysis of the vertebrate fauna of the Morrison Formation (Upper Jurassic), Rocky Mountain Region, U.S.A.: New Mexico Museum of Natural History and Science Bulletin 23, p. 1–95.

Foster, J.R., 2013, Ecological segregation of the Late Jurassic stegosaurian and iguanodontian dinosaurs of the Morrison Formation in North America—pronounced or subtle?: PalArch's Journal of Vertebrate Palaeontology, v. 10, p. 1–11.

Foster, J.R., and McMullen, S.K., 2017, Paleobiogeographic distribution of Testudinata and neosuchian Crocodyliformes in the Morrison Formation (Upper Jurassic) of North America—evidence of habitat zonation?: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 468, p. 208–215.

Foster, J.R., and Wedel, M.J., 2014, *Haplocanthosaurus* (Saurischia: Sauropoda) from the lower Morrison Formation (Upper Jurassic) near Snowmass, Colorado: Volumina Jurassica, v. 12, no. 2, p. 197–210.

Gascon, C., Malcolm, J.R., Patton, J.L., da Silva, M.N.F., Bogart, J.P., Lougheed, S.C., Peres, C.A., Neckel, S., and Boag, P.T., 2000, Riverine barriers and the geographic distribution of Amazonian species: Proceedings of the National Academy of Sciences, v. 97, p. 13672–13677.

Gee, C.T., 2010, Dietary options for the sauropod dinosaurs from an integrated botanical and paleobotanical perspective, *in* Gee, C.T., editor, Plants in Mesozoic time: Bloomington, Indiana University Press, p. 34–56.

Goodman, S.M., and Ganzhorn, J.U., 2004, Biogeography of lemurs in the humid forests of Madagascar—the role of elevational distribution and rivers: Journal of Biogeography, v. 31, p. 47–55.

Griffith, D.M., Veech, J.A., and Marsh, C.J., 2016, Cooccur—probabilistic species co-occurrence analysis in R: Journal of Statistical Software, v. 69, no. Code Snippet 2, p. 1–17.

Harcourt, A.H., and Wood, M.A., 2012, Rivers as barriers to primate distributions in Africa: International Journal of Primatology, v. 33, p. 168–183.

Harris, J.D., and Dodson, P., 2004, A new diplodocoid sauropod dinosaur from the Upper Jurassic Morrison Formation of Montana, USA: Acta Palaeontologica Polonica, v. 49, no. 2, p. 197–210.

Hayes, F.E., and Sewlal, J-A.N., 2004, The Amazon River as a dispersal barrier to passerine birds—effects of river width, habitat and taxonomy: Journal of Biogeography, v. 31, p. 1809–1818.

Hendrickx, C., and Mateus, O., 2014, *Torvosaurus gurneyi* n. sp., the largest terrestrial predator from Europe, and a proposed terminology of the maxilla anatomy in nonavian theropods: PLoS One, v. 9, no. 3, p. e88905.

Hotton, C.L., and Baghai-Riding, N.L., 2010, Palynological evidence for conifer dominance within a heterogenous landscape in the Late Jurassic Morrison Formation, U.S.A., *in* Gee, C.T., editor, Plants in Mesozoic time: Bloomington, Indiana University Press, p. 295–328.

Janson, S., and Vegelius, J., 1981, Measures of ecological association: Oecologia, v. 49, p. 371–376.

Koleff, P., Gaston, K.J., and Lennon J.J., 2003, Measuring beta diversity for presence-absence data: Journal of Animal Ecology, v. 72, p. 367–382.

Mateus, O., 2006, Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinhã and Alcobaça Formations (Portugal), and the Tendaguru Beds (Tanzania)—a comparison: New Mexico Museum of Natural History and Science Bulletin 36, p. 223–231.

Mateus, O., Walen, A., and Antunes, M.T., 2006, The large theropod fauna of the Lourinhã Formation (Portugal) and its similarity to the Morrison Formation, with a description of a new species of *Allosaurus*: New Mexico Museum of Natural History and Science Bulletin 36, p. 123–130.

May, R., van Dijk, J., Landa, A., and Andersen, R., 2010, Spatio-temporal ranging behaviour and its relevance to foraging strategies in wide-ranging wolverines: Ecological Modeling, v. 221, p. 936–943.

McNab, B.K., Bioenergetics and the determination of home range size: The American Naturalist, v. 97, p. 133–140.

Meijard, E., and Groves, C.P., 2006, The geography of mammals and rivers in mainland southeast Asia, *in* Lehman, S.M., and Fleagle, J.G., editors, Primate biogeography: New York, Springer, p. 725–732.

Naidoo, R., Du Preez, P., Stuart-Hill, G., Jago, M., and Wegmann, M., 2012, Home on the range—factors explaining partial migration of African Buffalo in a tropical environment: PLoS ONE, v. 7, e36527.

Noto, C.R., and Grossman, A., 2010, Broad-scale patterns of Late Jurassic dinosaur paleoecology.: PLoS One, v. 5, no. 9, p. e12553.

Oates, J.F., 1988, The distribution of *Cercopithecus* monkeys in West African forests, *in* Gautier-Hion, A., Bourlière, and Gautier, J.P., editors, A primate radiation—evolutionary biology of the African guenons: Cambridge, Cambridge University Press, p. 79–103.

Parrish, J.T., Peterson, F., and Turner, C.E., 2004, Jurassic "savannah"—plant taphonomy and climate of the Morrison Formation (Upper Jurassic, western USA): Sedimentary Geology, v. 167, no. 3–4, p. 137–162.

Rees, P.M., Noto, C.R., Parrish, J.M., and Parrish, J.T., 2004, Late Jurassic climates, vegetation, and dinosaur distributions: The Journal of Geology, v. 112, no. 6, p. 643–653.

Robertson, K., 2013, Do anthropogenic and natural features act as barriers to African elephant (*Loxodonta africana*) space use?: Johannesberg, South Africa, University of the Witwatersrand, M.S. thesis, 77 p.

Sidor, C.A., Vilhena, D.A., Angielczyk, K.D., Huttenlocker, A.K., Nesbitt, S.J., Peecook, B.R., Steyer, J.S., Smith, R.M.H., and Tsuji, L.A., 2013, Provincialization of terrestrial faunas following the end-Permian mass extinction: Proceedings of the National Academy of Sciences, v. 110, no. 20, p. 8129–8133.

Swihart, R.K., Slade, N.A., and Bergstrom, B.J., 1988, Relating body size to the rate of home range use in mammals: Ecology, v. 69, p. 393–399.

Stevens, K.A., and Parrish, J.M., 1999, Neck posture and feeding habits of two Jurassic sauropod dinosaurs: Science, v. 284, no. 5415, p. 798–800.

Stevens, K.A., and Parrish, J.M., 2005, Neck posture, dentition, and feeding strategies in Jurassic sauropod dinosaurs, *in* Tidwell, V., and Carpenter, K.E., editors, Thunder lizards—the sauropodomorph dinosaurs: Bloomington, Indiana University Press, p. 212–232.

Tidwell, W.D., 1990, Preliminary report on the megafossil flora of the Upper Jurassic Morrison Formation: Hunteria, v. 2, p. 1–12.

Tidwell, W.D., Britt, B.B., and Ash, S.R., 1998, Preliminary floral analysis of the Mygatt-Moore Quarry, in the Upper Jurassic Morrison Formation, west-central Colorado: Modern Geology, v. 22, p. 341-378.

Trujillo, K.C., 2006, Clay mineralogy of the Morrison Formation (Upper Jurassic-?Lower Cretaceous), and its use in long distance correlation and paleoenvironmental analyses: New Mexico Museum of Natural History and Science Bulletin 36, p. 17–24.

Trujillo, K.C., Carrano, M.T., and Chamberlain, K.R., 2015, A U-Pb zircon age for Reed's Quarry 9, Upper Jurassic Morrison Formation, Albany County, WY [abs.]: Journal of Vertebrate Paleontology, Program and Abstracts, p. 226.

Trujillo, K.C., Foster, J.R., Hunt-Foster, R.K., and Chamberlain, K.R., 2014, A U/Pb age for the Mygatt-Moore Quarry, Upper Jurassic Morrison Formation, Mesa County, Colorado: Volumina Jurassica, v. 12, p. 107–114.

Trujillo, K.C., and Kowallis, B.J., 2015, Recalibrated legacy $^{40}$Ar/$^{39}$Ar ages for the Upper Jurassic Morrison Formation, Western Interior, U.S.A.: Geology of the Intermountain West, v. 2, p. 1–8.

Tschopp, E., and Mateus, O., 2013, The skull and neck of a new flagellicaudatan sauropod from the Morrison Formation and its implication for the evolution and ontogeny of diplodocid dinosaurs: Journal of Systematic Palaeontology, v. 11, no. 7, p. 853–888.

Tschopp, E., Mateus, O., and Benson, R.B.J., 2015, A specimen-level phylogenetic analysis and taxonomic revision of Diplodocidae (Dinosauria, Sauropoda): PeerJ, v. 3, p. e857.

Turner, C.E., and Fishman, N.S., 1998, Late Jurassic lacustrine deposits and implications for paleohydrology—deposition to early compaction, *in* Pitman, J.K., and Carroll, A.R., editors, Modern and ancient lake systems: Utah Geological Association Publication 26, p. 31–49.

Turner, C.E., and Peterson, F., 1999, Biostratigraphy of dinosaurs in the Upper Jurassic Morrison Formation of the Western Interior, U.S.A., *in* Gillette, D.D., editor, Vertebrate paleontology in Utah: Utah Geological Survey Miscellaneous Publication 99-1, p. 77–114.

Turner, C.E., and Peterson, F., 2004a, Reconstruction of the Upper Jurassic Morrison Formation extinct ecosystem—a synthesis: Sedimentary Geology, v. 167, no. 3–4, p. 309–355.

Upchurch, P., and Barrett, P.M., 2000, The evolution of sauropod feeding mechanisms, *in* Sues, H-D., editor, Evolution of herbivory in terrestrial vertebrates—perspectives from the fossil record: Cambridge, Cambridge University Press, p. 79–122.

van Beest, F.M., van Moorter, B., and Milner, J.M., 2012, Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate: Animal Behavior, v. 84, p. 723–735.

Whitlock, J.A., 2011, Inferences of diplodocoid (Sauropoda: Dinosauria) feeding behavior from snout shape and microwear analyses: PLoS ONE, v. 6, no. 4, p. e18304.