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On the role of tectonics in stimulating the Cretaceous diversification of mammals

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A R T I C L E I N F O

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A B S T R A C T

Mammals rose to prominence in terrestrial ecosystems after the Cretaceous–Paleogene mass extinction, but the mammalian lineages characteristic of Paleogene faunas began their evolutionary and ecological diversification in the Late Cretaceous, stimulated by the rise of angiosperms (flowering plants) according to the preeminent hypothesis. The Cretaceous rise of mammals is part of a larger expansion in biodiversity on land that has been termed the Cretaceous (or Angiosperm) Terrestrial Revolution, but the mechanisms underlying its initiation remain opaque. Here, we review data from the fossil and rock records of western North America—due to its relatively continuous fossil record and complete chronology of mountain-building events—to explore the role that tectonism might have played in catalyzing the rise of modern-aspect terrestrial biodiversity, especially that of mammals and angiosperms. We highlight that accelerated increases in mammal and angiosperm species richness in the Late Cretaceous, ca. 100–75 Ma, track the acceleration of tectonic processes that formed the North American Cordillera and occurred during the 'middle-Cretaceous greenhouse' climate. This rapid increase in both mammal and angiosperm diversity also occurred during the zenith of Western Interior Seaway transgression, a period when the availability of lowland habitats was at its minimum, and oscillatory transgression-regression cycles would have frequently forced upland range shifts among lowland populations. These changes to both landscapes and climates have all been linked to an abrupt, global tectonic-plate 'reorganization' that occurred ca. 100 Ma. That mammals and angiosperms both increased in species richness during this interval does not appear to be a taphonomic artifact—some of the largest spikes in diversity occur when the available mammal-bearing fossil localities are sparse. Noting that mountainous regions are engines for generating biodiversity, especially in warm climates, we propose that the Cretaceous/Angiosperm Terrestrial Revolution was ultimately catalyzed by accelerated tectonism and enhanced via cascading changes to landscapes and climate. In the fossil record of individual basins across western North America, we predict that (1) increases in mammalian diversity through the Late Cretaceous should be positively correlated with rates of tectonic uplift, which we infer to be a proxy for topographic relief, and are attended by increased climate heterogeneity, (2) the diversity of mountain-proximal mammalian assemblages should exceed that of coeval mountain-distal assemblages, especially in the latest Cretaceous, and (3) endemism should increase from the latest Cretaceous to early Paleogene as Laramide mountain belts fragmented the Western Interior. Empirical tests of these predictions will require increased fossil collecting in under-sampled regions and time intervals, description and systematic study of existing collections, and basin-scale integration of geological and paleontological data. Testing these predictions will further our understanding of the coevolutionary processes linking tectonics, climate, and life throughout Earth history.

1. Introduction

Terrestrial ecosystems are the most biodiverse habitats on the planet today (e.g., May, 1994; Dawson and Hamner, 2008; Dawson, 2012), and the roots of their modern composition trace to the middle-to-Late Cretaceous when angiosperms (flowering plants), pollinating insects,

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and the major groups of extant terrestrial vertebrates, such as mammals, originated and diversified (e.g., Benton, 2001; Vermeij and Grosberg, 2010). This Cretaceous burst of diversification in the terrestrial realm has been termed the Cretaceous Terrestrial Revolution (Lloyd et al., 2008; Benton, 2010) or, more recently, the Angiosperm Terrestrial Revolution (Benton et al., 2022), and is proposed to span the middle Cretaceous to the early Paleogene (ca. 100–50 million years ago [Ma]). Here, because our focus is the initiation of diversification in the middle–Late Cretaceous, we retain the shorthand of the Cretaceous Terrestrial Revolution (KTR) to broadly refer to this blooming of modern biodiversity. The temporal range proposed for the KTR has shifted from ca. 125–80 Ma (Lloyd et al., 2008; Benton, 2010) to ca. 100–66 Ma (i.e., the Late Cretaceous; Benton et al., 2021), likely to better align with the ecological diversification of angiosperms, which began near the Early–Late Cretaceous boundary, rather than the earliest taxonomic diversification of angiosperms in the Early Cretaceous. We retain this younger temporal range for the KTR here (ca. 100–66 Ma), and we particularly focus on changes in the fossil and rock record that occurred during the onset of the KTR, from the earliest Cenomanian to late Campanian (ca. 100–75 Ma).

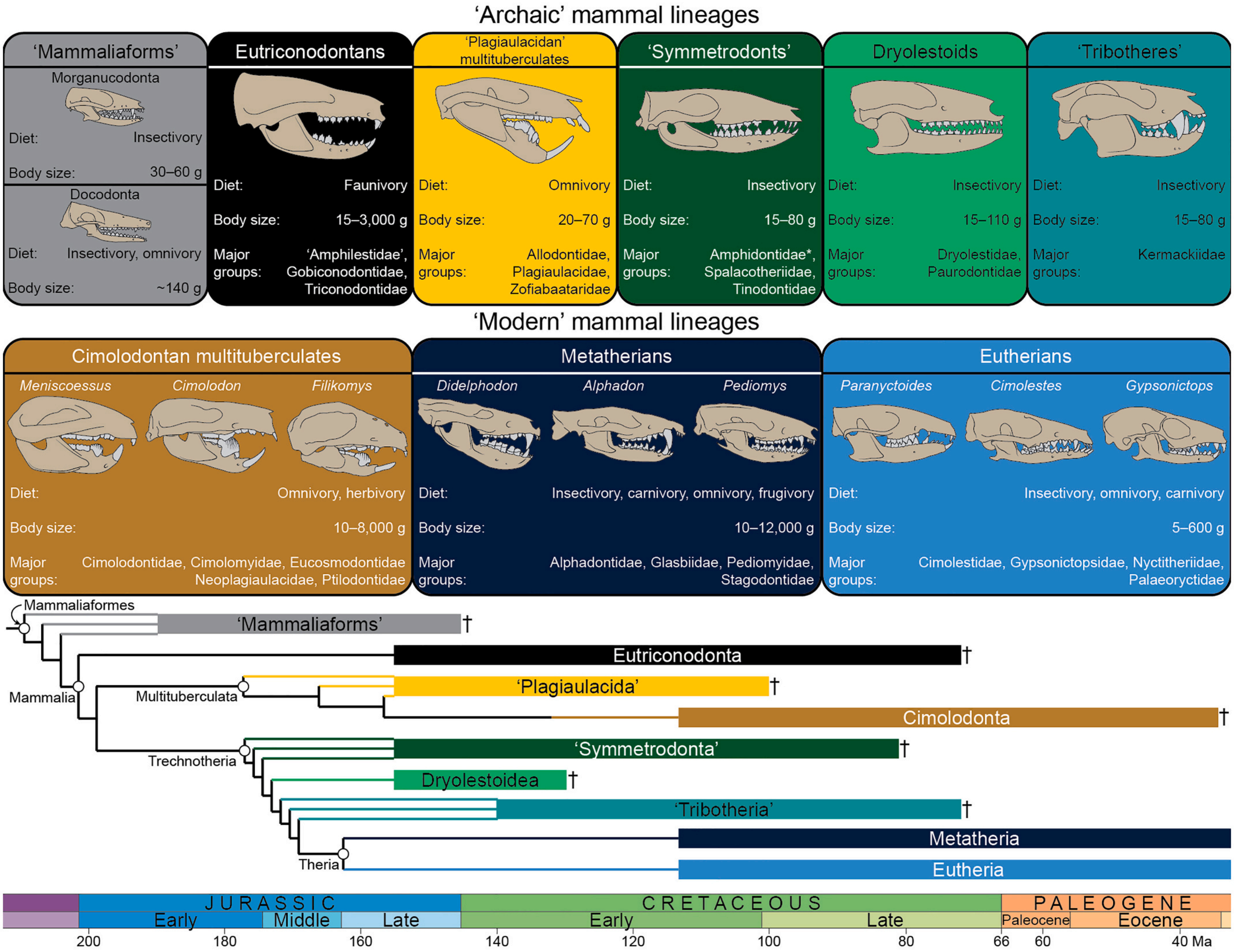

Fig. 1. Major mammalian groups from the Late Jurassic through early Paleogene fossil record of western North America. **Top**, major 'archaic' lineages that mostly went locally extinct in the Early–middle Cretaceous. **Middle**, major 'modern' lineages that characterize mammalian assemblages from the Late Cretaceous and early Paleogene. **Bottom**, generalized cladogram depicting phylogenetic relationships of different mammalian groups and their approximate geologic ranges in western North America (modified from Luo et al., 2002 and Kielan-Jaworowska et al., 2004). Each major mammalian group panel includes estimated dietary preferences, body-size ranges, and major sub-groups (mostly at the family level; for the 'modern' lineages only Late Cretaceous sub-groups are listed). For the 'modern' lineages, three skulls are illustrated to give a sense of the morphological breadth among different Late Cretaceous groups: Cimolodontan multituberculates (left to right)—Cimolomyidae (based on *Meniscoessus robustus*, known from nearly complete skulls [Archibald, 1982]), Cimolodontidae (based on *Cimolodon nitidus*, known only from gnathic fragments [Clemens, 1964]), Neoplagiaulacidae (based on *Filikomys primaevus*, known from nearly complete skulls [Weaver et al., 2021]); Metatherians (left to right)—Stagodontidae (based on *Didelphodon vorax*, known from nearly complete skulls [Wilson et al., 2016]), Alphadontidae (known from partial skulls [Freimuth et al., 2021; Brannick, 2021] but not reconstructed; thus, this illustration is based on *Pucadelphys*), and Pediomyidae (not known from cranial material, illustration based on *Monodelphis*); Eutherians (left to right)—Nyctitheriidae (not known from cranial material, illustration based on *Barunlestes*), Cimolestidae (not known from cranial material, illustration based on *Maelestes*), Gypsonictopidae (not known from cranial material, illustration based on *Ptilocercus*). Diets were informed by Grossnickle and Newham (2016; eutherians), Jäger et al. (2020; eutriconodontans), Kielan-Jaworowska et al. (2004; all groups), Fox (2015; eutherians), Williamson et al. (2014; metatherians), Wilson (2013; eutherians), and Wilson et al. (2012; multituberculates). Body-size ranges were estimated from Clemens (2002; eutherians), Davis et al. (2022; Morganucodonta), Foster (2009; Morganucodonta, eutriconodontans, 'plagiaulacidan' multituberculates, 'symmetrodonts', dryolestoids, and 'tribotheres'), Lyson et al. (2019; metatherians), Smits and Wilson (2011; metatherians), Williamson et al. (2014; metatherians), Wilson (2013; eutherians), and Wilson et al. (2012; multituberculates).

The KTR has been invoked to explain patterns in both the fossil and molecular-genetic records of terrestrial biodiversity. The groups that feature most prominently in discussion of the KTR are angiosperms (e.g., Dilcher, 2000; Willis and McElwain, 2014; Barba-Montoya et al., 2018; Benton et al., 2022), pollinating insects (e.g., Grimaldi, 1999; McKenna et al., 2015), dinosaurs (e.g., Lloyd et al., 2008), and mammals (e.g., Meredith et al., 2011; Wilson et al., 2012; Grossnickle and Polly, 2013; Grossnickle and Newham, 2016; Grossnickle et al., 2019). Although generally characterized as a period of diversification (i.e., speciation in excess of extinction; Lloyd et al., 2008; Benton, 2010), the KTR was also a time of substantial taxonomic turnover, especially near the Early–Late Cretaceous boundary, when numerous incumbent groups (e.g., gymnosperms and ferns, sauropod dinosaurs, and 'archaic' mammals in North America) began to be replaced by newly emerging lineages (e.g., angiosperms, ceratopsian and hadrosaurian dinosaurs, and cimolodontan multituberculates and therians in North America; Lidgard and Crane, 1990; Lupia et al., 1999; Gates et al., 2012; Benson et al., 2013; Grossnickle and Polly, 2013; Nicholson et al., 2015). Here we primarily focus on the patterns among angiosperms and mammals, with the former contextualizing previous explanations of diversification patterns in the latter.

Until now, the diversification of angiosperms has frequently been identified as the ultimate driver of the KTR (e.g., Lloyd et al., 2008; Benton et al., 2022), especially the rise in ecological diversity of angiosperms, which was characterized by their transformation from herbaceous plants to structurally diverse and anatomically complex shrubs and trees in the Late Cretaceous (Wing and Tiffney, 1987; Wing and Sues, 1992; Wing and Boucher, 1998; Eriksson et al., 2000; Philippe et al., 2008). The profound effects of ecological diversification among angiosperms on terrestrial ecosystems are well documented: the rise of angiosperms led to more complex habitats (e.g., Wing and Boucher, 1998; Coiffard et al., 2012), proliferation of new dietary resources in the form of more nutritious leaves, flowers, fruits, and nuts (e.g., Eriksson et al., 2000; Feild et al., 2011), dramatic changes in terrestrial food webs and the coevolution of many groups of fungi and animals (e.g., Wing and Tiffney, 1987; Eriksson, 2016; Benton et al., 2022), and increased plant transpiration affecting the global water cycle (Boyce et al., 2009, 2010).

The middle-to-Late Cretaceous (including the late Early Cretaceous through Late Cretaceous, ca. 110–66 Ma) was also a pivotal period in the evolution of mammals. For much of the Jurassic, mammalian communities comprised a mixture of archaic mammaliaforms, such as morganucodontans and docodontans, eutriconodontans, 'plagiaulacidan' multituberculates, and 'therian-line' lineages (i.e., Trechnotheria) such as spalacotheroids and dryolestoids (e.g., Simpson, 1928, 1929; Lillegraven et al., 1979; Kielan-Jaworowska et al., 2004) (see Fig. 1 for a primer on the major Mesozoic mammal groups discussed here). In the middle Cretaceous (ca. 110–90 Ma), however, the composition of mammalian communities, especially in the northern hemisphere, changed dramatically, with the aforementioned lineages declining or going extinct and the cimolodontan multituberculates, metatherians, and eutherians rising to prominence (e.g., Clemens, 1970; Kielan-Jaworowska et al., 2004; Grossnickle and Polly, 2013; Benson et al., 2013) (Fig. 1). Those latter three groups (though to a lesser degree in eutherians) underwent adaptive radiations that began in the Late Cretaceous (Clauset and Redner, 2009; Wilson et al., 2012; Grossnickle and Newham, 2016; Wu et al., 2017; Cohen et al., 2020), and molecular phylogenies of extant therians continue to find the middle–Late Cretaceous as the time of origin for crown placentals and marsupials (e.g., Hedges et al., 1996; Meredith et al., 2011; dos Reis et al., 2014; Liu et al., 2017; Velazco et al., 2022; Christmas et al., 2023). Note, however, that some researchers contend that the adaptive radiation (and potentially even origin) of crown placental mammals post-dated the Cretaceous–Paleogene (K–Pg) boundary (e.g., Alroy, 1999; Wible et al., 2007; O'Leary et al., 2013; Halliday and Goswami, 2016; Halliday et al., 2019). In either case, mammals are one of the hallmarks of the KTR, and their adaptive radiations prior to the K–Pg mass extinction have been attributed to the ecological expansion of angiosperms (Wilson et al., 2012; Grossnickle and Polly, 2013; Grossnickle and Newham, 2016).

There is little doubt that the rise of angiosperms had a profound effect on the structure of terrestrial ecosystems, yet there is a substantial temporal lag between when angiosperms originated and when they diversified ecologically, raising the question: Why did the burst of terrestrial biodiversity that characterizes the KTR start in the middle Cretaceous? The earliest undisputed angiosperm fossils appear in the earliest Cretaceous (e.g., Friis et al., 2010), but, increasingly, putative angiosperms are being reported from the Jurassic (e.g., Sun et al., 1998; Gang et al., 2016; Cui et al., 2022), and molecular evidence also supports a pre-Cretaceous origin of angiosperms (Barba-Montoya et al., 2018; Coiro et al., 2019; Magallón et al., 2019; Sauquet et al., 2022). Thus, even if we conservatively place the origin of angiosperms at the beginning of the Cretaceous, there is at least a ca. 45-Myr lag between their origin and the onset of their ecological ascendency. A few hypotheses have been proposed to explain this 'ecological lag' in the evolutionary history of angiosperms, most of which invoke a sort of evolutionary or ecological inertia, whereby angiosperms were eventually able to overtake the floral ecomorphospaces gradually vacated (either by extinction or local extirpation) by ferns and gymnosperms due to their more rapid life-history strategies (allowing them to rapidly colonize disturbed habitats) and 'advanced' suite of physiological and ecological adaptations (e.g., insect pollination, flexible seed production and dispersal) (e.g., Wing and Boucher, 1998; Bouchenak-Khelladi et al., 2015; Onstein, 2020; Benton et al., 2022; Carvalho et al., 2021). Whole-genome duplication has also been implicated in the rapid diversification of many angiosperm lineages (e.g., Tank et al., 2015; Landis et al., 2018). That abiotic factors outside of the K–Pg mass extinction (e.g., climate change) were potential drivers has been largely discounted, other than by some researchers who have invoked changing fire regimes in the Cretaceous as a catalyst for the rise of angiosperms (Bond and Scott, 2010).

Whereas paleontologists and evolutionary biologists have focused on angiosperms as the cause of the KTR, geologists in the realms of tectonics and paleoclimate have also identified the middle–Late Cretaceous as a pivotal interval in Earth history. For example, sea-floor-spreading rates increased dramatically and the directions of plate motion changed in response to a global 'plate reorganization' around 100 Ma (e.g., Matthews et al., 2012). This change in global plate motion is manifest in many aspects of the geological record, such as a pulse in ophiolite generation (fragments of oceanic lithosphere that become stranded on continents; e.g., Dilek, 2003), an increase in the exhumation and preservation of blueschists (subduction-specific metamorphic rocks; e.g., Tsujimori and Ernst, 2014), inferred 'flare-ups' in many magmatic arcs (e.g., Nelson and Cottle, 2018; Balgord et al., 2021; Pastor-Galán et al., 2021; Ma et al., 2022), and changes in the structural development of orogenic belts (details for North America to be discussed more below). Along with—and perhaps driven by (e.g., Poulsen et al., 2003; Lee et al., 2013)—this tectonic upheaval, global mean temperature reached an estimated acme of >30 °C during the Cretaceous Thermal Maximum ca. 95 Ma, a temperature never since documented (e.g., Huber et al., 2018; Jones et al., 2022). The role that these landscape and climatic processes might have played in the KTR, however, has been only cursorily noted and often discounted in favor of biotic drivers (i.e., angiosperms; e.g., Benton et al., 2022). Nonetheless, the interplay between tectonics and climate has played a profound role in shaping patterns of biodiversity in terrestrial ecosystems today and in the geologic past. For example, mountainous regions are biodiversity hotspots for both extant plants and mammals (along with other tetrapods, such as birds; e.g., Badgley and Fox, 2000; Badgley, 2010; Hoorn et al., 2010; Mulch, 2016; Hoorn et al., 2018; Quintero and Jetz, 2018; Rahbek et al., 2019), and tectonic activity has been correlated with increases in species richness and cladogenesis in the latter part of the Cenozoic on different continents (e.g., Finarelli and Badgley, 2010; Hoorn et al., 2010).

Here, we propose that the acceleration of tectonic activity in the middle-to-Late Cretaceous was the ultimate driver of the KTR. To explore this hypothesis, we review and summarize data from the primary literature on the mammalian and angiosperm fossil, tectonic, paleolandscape, and paleoclimate records of western North America. We focus on western North America because it has the most temporally continuous and well-studied fossil and rock records, but we suggest that the patterns observed therein were likely global. We focus on mammals as a test case because (1) they have the most well-sampled, well-studied, and relatively continuous fossil record through the interval of interest relative to other animal groups implicated in the KTR, (2) there is a tight link between the ecomorphological diversity of mammalian communities and environmental conditions (e.g., Polly et al., 2011; Chen et al., 2019; Laméris et al., 2020), and the ways in which mammals respond behaviorally and morphologically to changing environments have been well studied (e.g., Hayward and Phillipson, 1979; Blois and Hadly, 2009), and (3) the concentration of small-bodied mammalian diversity (e.g., among rodents, which are similar in size to most Mesozoic mammals) has been shown to be strongly influenced by tectonic processes and topographic heterogeneity (e.g., Badgley and Fox, 2000; Finarelli and Badgley, 2010). Below, we first summarize the landscape, climate, and vegetation histories of western North America through time in the context of the mammalian fossil record. We then elaborate upon our hypothesis and offer predictions that can be tested empirically at the level of individual basins.

2. Evolution of terrestrial ecosystems in western North America

From the onset of compressional tectonics that ushered in the Sevier Orogeny in the Late Jurassic to the beginning of orogenic collapse that signaled the nearing end of the Laramide Orogeny in the early Eocene, the composition of mammalian communities and indeed the entirety of mammalian evolution were wholly reorganized, shifting from (1) the ‘archaic’ mammalian lineages of the Jurassic and earliest Cretaceous, to (2) the rise of the major ‘modern’ groups in the middle–Late Cretaceous, to (3) the proliferation of extant orders in the early Paleogene. The landscapes in which these evolutionary transformations took place changed dramatically, sculpted by the rising North American Cordillera and the rise and fall of the Western Interior Seaway, as did the climatic regimes, which, although much warmer than most of the Cenozoic, fluctuated substantially over that 100 Myr window. These abiotic changes likely had a significant influence on mammalian evolution, and below we summarize some of the key transformations in early mammalian evolution and their abiotic and vegetational settings. We begin with the Late Jurassic and proceed to the early Eocene, but our focus is on the Late Cretaceous to explore the potential abiotic stimulants of the KTR from the perspective of mammals.

2.1. Late Jurassic

All Late Jurassic mammals from North America come from the Morrison Formation of Wyoming, Colorado, and Utah (Fig. 2) (Kielan-Jaworowska et al., 2004). The Morrison Formation accounts for nearly all continental Late Jurassic deposits in the American west (DeCelles and Burden, 1992; Maidment and Muxworthy, 2019). Fossil assemblages from the Morrison Formation are among the richest and most historically important in the Mesozoic mammal fossil record (e.g., Marsh, 1880, 1887; Simpson, 1929). They comprise primarily ‘archaic’ lineages characteristic of the Middle–Late Jurassic in the northern hemisphere: non-mammalian mammaliaforms (morganucodontans and docodonts), eutriconodonts, ‘plagiaulacidan’ multituberculates, ‘symmetrodonts’ (e.g., spalacotheroids), and dryolestoids (Fig. 1 and Fig. 2) (Kielan-Jaworowska et al., 2004; Davis et al., 2018, 2022). Ecologically, most species were very small (<< 1 kg), and all but the ‘plagiaulacidan’ multituberculates are inferred to have been primarily insectivorous or faunivorous (e.g., Simpson, 1926, 1929; Jäger et al., 2020) (Fig. 1). Most were likely fairly generalized in locomotor habits (e.g., Jenkins Jr and Parrington, 1976), with one notable exception (the mole-like *Fruitafossor*, a specialized burrower; Luo and Wible, 2005).

The lithology and inferred depositional environments of the Morrison Formation vary considerably geographically; for example, the southern facies include a preponderance of coarse-grained, braided-river deposits, whereas more northerly deposits are finer-grained floodplain or lacustrine deposits (Maidment and Muxworthy, 2019). As such, the composition and structure of the Morrison flora were spatially heterogeneous (Hotton and Baghai-Riding, 2010). Broadly speaking, however, landscapes in the latest Jurassic of North America were dominated by conifers (Hotton and Baghai-Riding, 2010) and herbaceous vegetation, forming relatively open, savannah-like habitats in a strongly seasonal and semiarid climate (e.g., Demko et al., 2004; Engelmann et al., 2004; Parrish et al., 2004). Evidence for seasonal and semi-arid climates includes the presence of evaporites, calcareous paleosols, alkaline lakes, and eolian sandstones (e.g., Demko and Parrish, 1998). Diagenesis may prevent quantitative, carbonate-based reconstructions of precipitation seasonality and/or paleotemperatures (Parrish et al., 2019). Topographic heterogeneity was low in the Late Jurassic, with the most prominent tectonic feature on the landscape being the Mogollon Highlands in the southwest (DeCelles, 2004; Yonkee and Weil, 2015). Early initiation of westward movement by the North American plate resulted in only moderate shortening and uplift proceeding from the Pacific margin (Yonkee and Weil, 2015).

2.2. Early Cretaceous

In much of western North America there is a substantial unconformity between Late Jurassic strata (e.g., Morrison Formation) and late Early Cretaceous strata (e.g., Cloverly Formation) representing a period of regional erosion that was caused by either (1) a cessation of subsidence associated with the subduction of oceanic slabs during westward drift of the North American plate (Yonkee and Weil, 2015) or (2) eastward migration of the forebulge after Morrison deposition (DeCelles and Currie, 1996). Regardless of the mechanisms underlying this stratigraphic gap, the result is that our understanding of terrestrial ecosystem evolution in the earliest Cretaceous is sparse, with most preserved continental deposition consisting of coarse conglomerates from proximal alluvial fans that have yet to yield productive vertebrate fossil assemblages (e.g., Gannett Group of Utah, Wyoming, and Idaho). Nonetheless, the Lakota Formation of South Dakota, which is estimated to roughly span the Valanginian through Hauterivian (ca. 140–130 Ma), has produced a modest mammalian assemblage (Cifelli et al., 2014). The taxonomic makeup of the Lakota mammals closely resembles that of the Morrison Formation but appears to be in a state of transition to more ‘typical’ Cretaceous faunas in its absence of non-mammalian mammaliaforms (e.g., docodonts), the decline of dryolestoids, and the appearance of early tribosphenic taxa (Cifelli et al., 2014).

The only mammalian assemblages known from the late Early Cretaceous (i.e., Aptian–Albian) come from the Cloverly Formation of Montana and Wyoming and the Trinity Group of Texas and Oklahoma (Fig. 3) (Kielan-Jaworowska et al., 2004). Lower portions of the Cedar Mountain Formation in Utah span a similar chronostratigraphic interval but, to date, only a single mammalian (or putatively non-mammalian mammaliaform) specimen is known from Early Cretaceous portions of that formation (Huttenlocker et al., 2018). Cloverly mammals have been described in patchwork fashion (e.g., Jenkins Jr and Schaff, 1988; Cifelli et al., 1998; Cifelli and Davis, 2015); many specimens and assemblages have yet to be fully described. Nonetheless, from what has been published, Cloverly mammalian communities apparently constitute a mixture of more ‘archaic’ lineages (eutriconodonts, ‘plagiaulacidan’ multituberculates) and the appearance and early diversification of groups that come to dominate later in the Cretaceous, namely cimolodontan multituberculates (e.g., Oreska et al., 2013). The Trinity mammals are among the most famous Mesozoic mammalian assemblages because they once represented the oldest-known therian fossils (this is

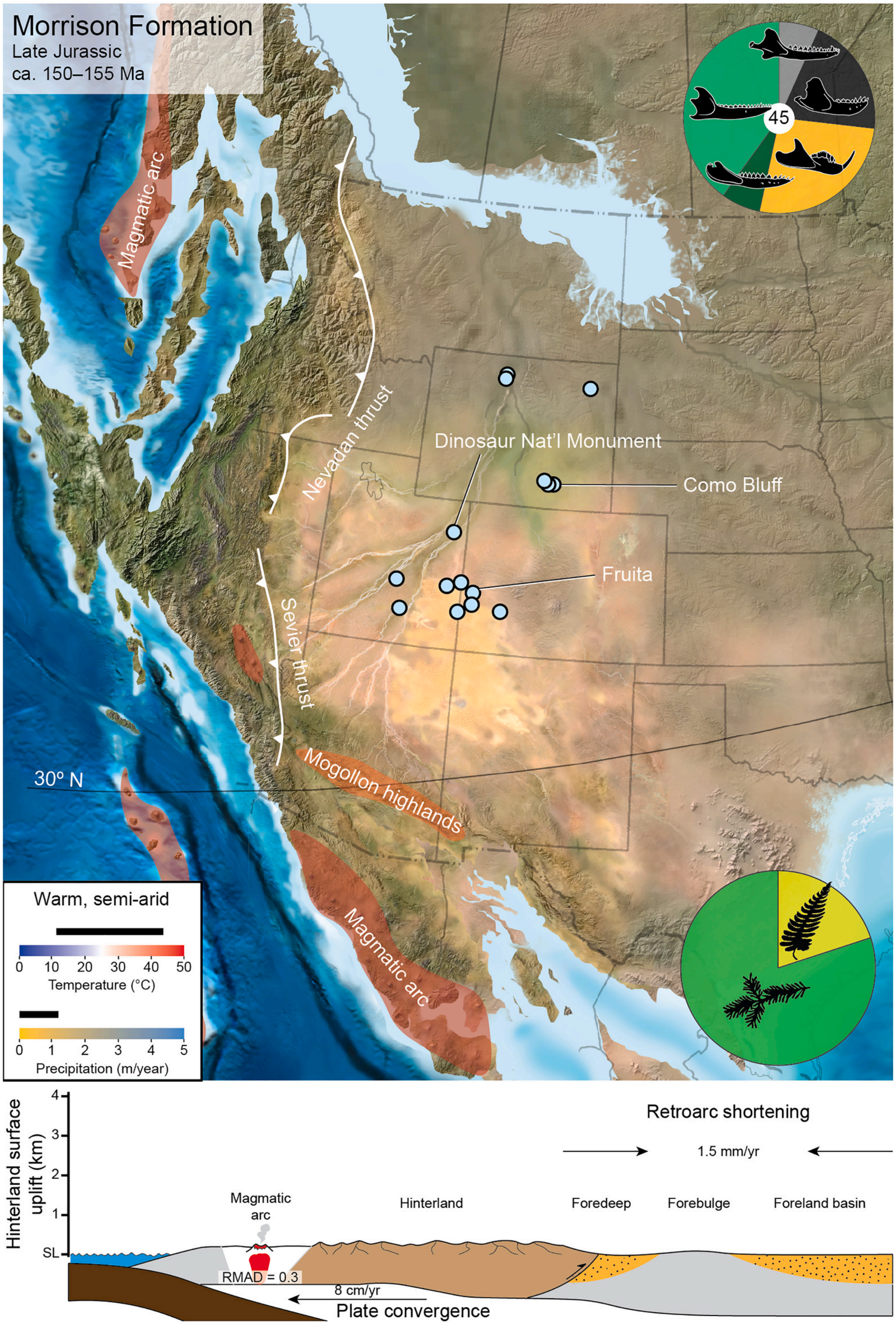

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Fig. 2. Map of mammal-bearing fossil localities (blue circles) of the Morrison Formation (Late Jurassic, ca. 150–155 Ma) in relation to their paleoenvironmental and tectonic setting (Morrison Formation paleoenvironmental reconstruction map from Ron Blakey [Deep Time Maps]; Geographic location of mammal localities derived from the Paleobiology Database; Tectonic annotations derived from DeCelles, 2004, Yonkee and Weil, 2015, Balgord et al., 2021, and Weil and Yonkee, 2023). Leader lines highlight important mammal-bearing areas. Note that these maps are meant to describe broad regional patterns and therefore may not perfectly reflect local paleogeography. **Top right**, relative species richness of major mammalian groups, with approximate total species richness in the center: Gray = non-mammalian Mammaliaformes; Black = Eutriconodonta; Yellow = 'Plagiaulacida', Multituberculata; Dark Green = 'Symmetrodonta'; Light Green = Dryolestoidea. Species richness was approximated from Kielan-Jaworowska et al. (2004) and Davis et al. (2022). **Lower right**, approximate relative abundance of ferns (yellow-green) and conifers (light green) (from Hotton and Baghai-Riding, 2010), **Lower left**, temperature (top) and precipitation (bottom) estimates for this time period, with the black bars representing reported ranges of temperatures or precipitation. Broad temperature categories (hot, warm, cooler) follow Huber et al. (2018), and broad precipitation categories (arid, humid) based on Benton et al. (2021). Temperature ranges come from the western North American portion of the general circulation models of Valdes (1993) and Sellwood and Valdes (2006) and are consistent with those climate estimates by Parrish et al. (2004) generated from Morrison Formation plant, taphonomy, and sedimentology data. Precipitation ranges were similarly drawn from the western North American portion of the general circulation models of Sellwood and Valdes (2006), but also from Myers et al. (2014), who used the chemical index of alteration minus potassium (CIA – K) and the calcium and magnesium weathering index (CALMAG) from Morrison Formation paleosols to estimate paleorainfall. **Bottom panel**, schematic of tectonic setting, including rate of North America-Farallon plate convergence, rate of retroarc shortening, elevation of the hinterland, and relative magmatic addition rate (RMAD; relative to the peak observed magmatic addition rates in the Jurassic and Cretaceous). This schematic is not based on any specific transect; it a generalized west–east cross section of western North America. Tectonic data are derived from DeCelles (2004), Chapman et al. (2015), Yonkee and Weil (2015), Balgord et al. (2021), and Weil and Yonkee (2023).

no longer the case; e.g., Luo et al., 2011), and they were some of the first fossils used to document the early evolution of the tribosphenic molar and therian masticatory apparatus (Patterson, 1956; Davis and Cifelli, 2011). Nonetheless, the most abundant mammalian constituents of Trinity mammalian assemblages, the multituberculates, remain largely undescribed (but see Cifelli, 1997). Despite these conspicuous gaps in our understanding, the late Early Cretaceous is notable in marking the onset of 'typical' Late-Cretaceous-aspect mammalian faunas, characterized by the first appearances of cimolodontan multituberculates and therians (e.g., Cifelli, 1999; Cifelli and Davis, 2015). And although these earliest cimolodontans and therians did not likely differ substantially ecologically from their more archaic precursors—both groups were small in body size, early therians were likely strict insectivores, and early cimolodontans are interpreted as animal-dominated omnivores (e.g., Kielan-Jaworowska et al., 2004; Wilson et al., 2012; Grossnickle and Newham, 2016)—their dental bauplans set the stage for their ecological proliferation in the Late Cretaceous and early Paleogene (e.g., Grossnickle et al., 2019).

In general, the Cloverly Formation and Trinity Group are interpreted as primarily fluvial coastal lowland deposits indicative of a warm and humid (tropical–subtropical) climate, consistent with climatic proxies and models of the Cretaceous 'greenhouse' (e.g., Huber et al., 2002; Poulsen et al., 2003; Huber et al., 2018), with some seasonal drying indicated by the prevalence of red-bed paleosols (e.g., Kvale, 1986; Andrzejewski and Tabor, 2020). Although these Aptian-Albian landscapes were still dominated by ferns and conifers, they document the early diversification of angiosperms, which were mostly herbaceous in form (e.g., Wing and Boucher, 1998; Friis et al., 2010). The middle Aptian also marked the onset of a tectonic flare-up that would continue well into the Late Cretaceous, characterized by pronounced volcanism and the first substantial uplift of the Sevier hinterland (Yonkee and Weil, 2015; Balgord et al., 2021). Nonetheless, topographic gradients from the Cloverly, and especially Trinity, depocenters to the emerging Sevier Thrust Belt were likely shallow, since even approaching the Early–Late Cretaceous boundary there were apparently small elevation differences (< 1 km) between the hinterland and the foreland in western North America (Fetrow, 2022; Fetrow et al., 2022).

2.3. Late Cretaceous

2.3.1. Cenomanian and the '100 Ma event'

Near the Early–Late Cretaceous boundary (early Cenomanian; ca. 100 Ma) (Fig. 4), mammalian assemblages are primarily known from the Mussentuchit Member of the Cedar Mountain Formation in Utah (e.g., Cifelli et al., 1999; Cifelli and Madsen, 1999; Eaton and Cifelli, 2001; Cifelli, 2004; Cifelli et al., 2016), but a mammalian local fauna from the Wayan Formation of Idaho is beginning to expand that perspective (Weaver et al., 2019). Mammals are also known from the Naturita Formation (formerly Dakota Formation) of Utah, which is apparently late Cenomanian in age (e.g., Eaton, 1993, 2009). These Cenomanian assemblages are dominated by cimolodontan multituberculates (including the first appearance of more deeply nested groups, such as the Cimolodontidae; Weaver et al., 2019), a more diverse array of metatherians, eutriconodontans, and a handful of lingering 'plagiaulacidan' multituberculates; the higher relative abundance and species richness of cimolodontan multituberculates, followed by metatherians, relative to all other coeval groups are characteristic of mammalian local faunas for the entirety of the Late Cretaceous in western North America.

Around 100 Ma, a geologically abrupt global change in subduction-zone dynamics, mid-ocean-ridge spreading rates, and directions of plate movement occurred (for review see Matthews et al., 2012). This global 'plate reorganization', often termed the '100 Ma event', manifested in North America as a rapid acceleration of North American-Farallon plate convergence, growth of the fore-arc accretionary prism, hinterland surface uplift, foreland-basin subsidence, magmatic-arc flare-up, and the eastern progression of the Sevier Thrust Belt (DeCelles, 2004; Yonkee and Weil, 2015; Centeno-García, 2017; Balgord et al., 2021). The resultant construction of a high-elevation orographic barrier led to a complete transformation of terrestrial landscapes in western North America. Foreland subsidence associated with the '100 Ma event' drove flooding of the continental interior by a shallow epeiric sea, the Western Interior Seaway (Fig. 4), the transgression and regression of which would remain tightly linked to plate-boundary dynamics and corresponding subsidence for most of the Late Cretaceous (e.g., Catuneanu et al., 1997; Catuneanu, 2004; Chang and Liu, 2021). In addition to marking the proliferation of marine sedimentation in the Western Interior for most of the Late Cretaceous, the continental inundation by the Western Interior Seaway coupled with rising Sevier-highland sediment sources resulted in marked facies shifts in non-marine deposits west of the paleoshoreline; namely, the preponderance of saturated and hydromorphic paleosols; thinly laminated, often carbonaceous mudstones; and mostly single-storied, trough-crossbedded sandstones, collectively indicative of coastal lowland floodplains, mires and ponds, and low-sinuosity channels (e.g., Wing and Sues, 1992; Fastovsky and McSweeney, 1987; DeCelles and Currie, 1996; Rogers, 1998; Tucker et al., 2022). The acceleration of seafloor spreading and continental reconfiguration associated with the '100 Ma event' (Matthews et al., 2012) has also been implicated as a driver of the early–middle Turonian 'Cretaceous Thermal Maximum' (Poulsen et al., 2003; Lee et al., 2013), the zenith of mean global temperature (> 30 °C) for the past 100 Myr or more (e.g., Huber et al., 2018). The concurrence of a high-elevation orographic barrier to the west, a warm shallow epeiric sea to the east, a hot global climate, and the opening of the Atlantic gateway to invigorate oceanic circulation between more southerly and northerly oceans,

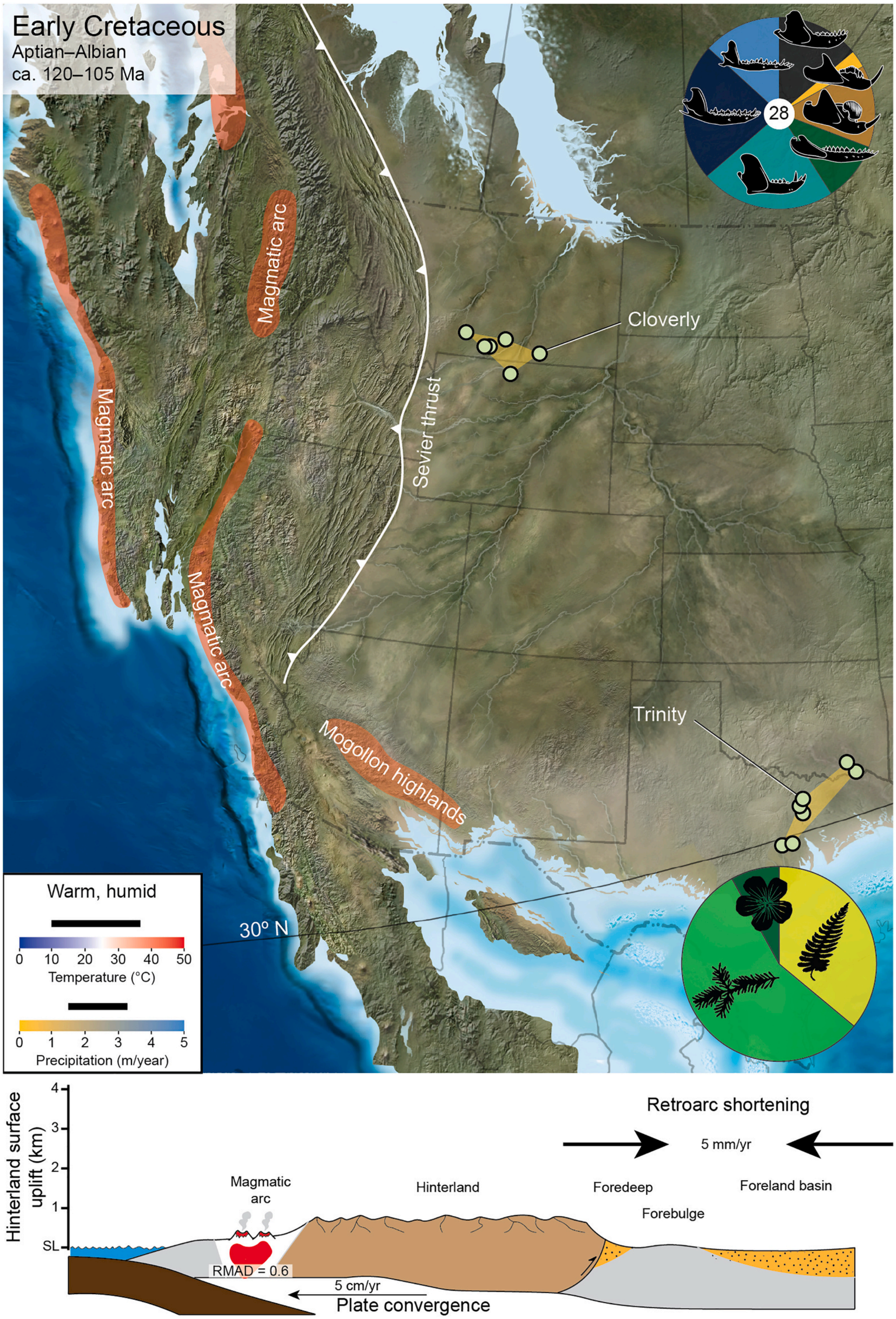

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Fig. 3. Map of mammal-bearing fossil localities (green circles) from the late Early Cretaceous (Aptian–Albian, ca. 120–105 Ma) in relation to their paleoenvironmental and tectonic setting (Aptian–Albian paleoenvironmental reconstruction map from Ron Blakey [Deep Time Maps]; Geographic location of mammal localities derived from the Paleobiology Database; Tectonic annotations derived from DeCelles, 2004, Yonkee and Weil, 2015, Balgord et al., 2021, and Weil and Yonkee, 2023). Leader lines and yellow polygons highlight mammal-bearing units (Cloverly Formation, Trinity Group). **Top right**, relative species richness of major mammalian groups, with approximate total species richness in the center: Black = Eutriconodonta; Yellow = 'Plagiaulacida', Multituberculata; Dark Green = 'Symmetrodonta'; Gold = Cimolodonta, Multituberculata; Teal = Stem Theria ('Tribotheres'); Dark Blue = Metatheria; Light Blue = Eutheria (from Kielan-Jaworowska et al., 2004, Oreska et al., 2013, and Cifelli and Davis, 2015). **Lower right**, approximate relative abundance of ferns (yellow-green), conifers (light green), and angiosperms (dark green) (from Lupia et al., 1999). **Lower left**, temperature (top) and precipitation (bottom) estimates for this time period, with the black bars representing reported ranges of temperatures or precipitation. Broad temperature categories (hot, warm, cooler) follow Huber et al. (2018), and broad precipitation categories (arid, humid) based on Benton et al. (2021). Temperature range comes from $\delta^{18}O_{VPDB}$ values of benthic and planktonic foraminifera in the southern hemisphere (Huber et al., 2018). Precipitation estimates were generated via $\delta^{18}O$ values from sphaerosiderites from the Aptian–Albian and general circulation models (Suarez et al., 2011). **Bottom panel**, schematic of tectonic setting, including rate of North America-Farallon plate convergence, rate of retroarc shortening, elevation of the hinterland, and relative magmatic addition rate (RMAD; relative to the peak observed magmatic addition rates in the Jurassic and Cretaceous). This schematic is not based on any specific transect; it a generalized west–east cross section of western North America. Tectonic data are derived from DeCelles (2004), Chapman et al. (2015), Yonkee and Weil (2015), Balgord et al. (2021), and Weil and Yonkee (2023).

likely initiated a western North American summer monsoon, analogous to the Himalayan-influenced South-Asian monsoon present today (Tardif et al., 2023), that would continue into the Paleocene (e.g., Poulsen et al., 2007; Fricke et al., 2010; Sewall and Fricke, 2013; but the exact timing of the onset of the North American summer monsoon is not addressed in these references except to note that it is linked to high topography, which was likely established in the Cenomanian [Suarez et al., 2014]). In sum, the ca. 100 Ma global tectonic-plate reorganization led to dramatic shifts in topography, geography, climate, and weather patterns, and these changes are clearly documented in the rock record of western North America.

As with the earliest Late Cretaceous mammalian faunas, which are the first to show the ascendency of cimolodontans and metatherians relative to contemporaneous taxa, the suite of landscape and climate transformations that occurred at the dawn of the Late Cretaceous occurred rapidly and then characterized most of the remaining ca. 34 Myr in western North America (i.e., the remainder of the Late Cretaceous). Vegetational structure, in contrast, remained similar to that of late Early Cretaceous, with angiosperms still representing relatively modest components of the flora in terms of ecological dominance (though they continued to increase in taxonomic diversity) (Lidgard and Crane, 1990; Wing and Boucher, 1998; Friis et al., 2010). Thus, the onset of the Late Cretaceous in western North America was apparently discrete and relatively rapid in terms of mammalian faunal composition and the regional landscape and climate, but not in its floral constituency, which did not change markedly until later in the epoch.

2.3.2. Turonian–middle Santonian

The Turonian through middle Santonian represents the most poorly sampled interval in terms of Late Cretaceous mammalian fossil assemblages; to date, our only window into this interval comes from the Straight Cliffs Formation of southwestern Utah (Fig. 5) (e.g., Eaton, 1995, 1999, 2006; Cohen, 2018; Cohen et al., 2020). The Straight Cliffs Formation, however, is lithologically heterogeneous, reflecting a mix of marine and continental deposition that varies laterally and complicates its chronostratigraphy. Straight Cliffs mammalian assemblages are broadly similar to those from later in the Late Cretaceous (i.e., the Aquilan North American Land-Mammal 'age' [NALMA]): they are dominated by the cimolodontid and cimolomyid multituberculates and 'alphadontid' (as well as early stagodontids and pediomyids) metatherians, with a handful of lingering 'archaic' lineages, such as triconodontid eutriconodonts (e.g., Eaton and Cifelli, 1988; Cifelli, 1990a; Eaton, 1995; Cohen et al., 2020). Despite the Straight Cliffs mammalian assemblages being rare and numerically depauperate relative to others from the Late Cretaceous, they are more varied in dental form (e.g., Grossnickle and Newham, 2016; Cohen et al., 2020) than better sampled localities from the early Cenomanian (i.e., Mussentuchit local fauna), and there is likely a cryptic diversity (both taxonomic and ecological) masked by the fragmentary nature of the record. Improved sampling from these Straight Cliffs localities is expected to yield a mammalian fauna that is approaching the species richness of the Aquilan NALMA.

The paucity of mammalian specimens from the Turonian–middle Santonian is mainly due to the paucity of non-marine deposition (and limited sampling in preserved non-marine deposits) across the Western Interior during that time interval, which reflects the maximum transgression of the Western Interior Seaway (Kauffman and Caldwell, 1993). Our understanding of terrestrial ecosystem and landscape structure during the middle Late Cretaceous is therefore limited. Nonetheless, as mentioned above, the Cretaceous Thermal Maximum occurred in the early–middle Turonian, and landscape transformation associated with the Sevier Orogeny occurred relatively rapidly until at least the middle Campanian (e.g., DeCelles, 2004; Yonkee and Weil, 2015). Angiosperm taxonomic diversity continued to increase throughout the Turonian–middle Santonian, as evident primarily through palynological data (e.g., Lupia et al., 1999), but the ecological diversification of angiosperms is typically thought to have occurred in the latter parts of the Late Cretaceous (e.g., Wing and Tiffney, 1987; Wing and Boucher, 1998). Nonetheless, the discovery of a reasonably large (~ 2-m diameter) fossil angiosperm log from the Turonian suggests that, as with mammals, there may have been cryptic ecological diversity among angiosperms by the early–middle Late Cretaceous (Jud et al., 2018).

2.3.3. Late Santonian–Maastrichtian (Aquilan–Lancian NALMAs)

Late Santonian through late Maastrichtian mammalian fossil assemblages are among the best-studied and well-sampled Mesozoic mammal localities in the world (e.g., Kielan-Jaworowska et al., 2004); as such, it is in this latest Cretaceous interval that we have the definition of the only pre-Cenozoic NALMAs (Lillegraven and McKenna, 1986; Cifelli et al., 2004). The Aquilan is the oldest of the NALMAs and is based on assemblages from the Milk River Formation of Verdigris Coulee in southern Alberta (Fox, 1970, 1971, 1976), but Aquilan faunas are also known from the Eagle Formation of northwestern Montana (Davis et al., 2016), the Wahweap Formation of southern Utah (e.g., Cifelli, 1990b, 1990c; Eaton, 2002), and (provisionally) the John Henry Member of the Straight Cliffs Formation in southern Utah (Davis et al., 2016) (Fig. 6). Considered to span roughly the late Santonian through early–middle Campanian (ca. 85–80 Ma), the Aquilan is notable in marking the last occurrences of most 'archaic' mammalian lineages, such as the triconodontid eutriconodonts and spalacotheriid 'symmetrodonts' and the early diversification of mammalian groups that come to dominate later Cretaceous local faunas in terms of relative abundance, such as neoplagiaulacid multituberculates (Cifelli et al., 2004; Davis et al., 2016). The Aquilan has also been interpreted as marking the initiation of adaptive radiations among multituberculates (Wilson et al., 2012) and therians (Grossnickle and Newham, 2016), inferred via pronounced increases in mammalian species richness as well as dietary and body-size disparity (but see Cohen, 2018 and Cohen et al., 2020 who argue that these adaptive radiations may have begun earlier than the late Santonian).

The Judithian NALMA (middle–late Campanian; ca. 80–72 Ma)

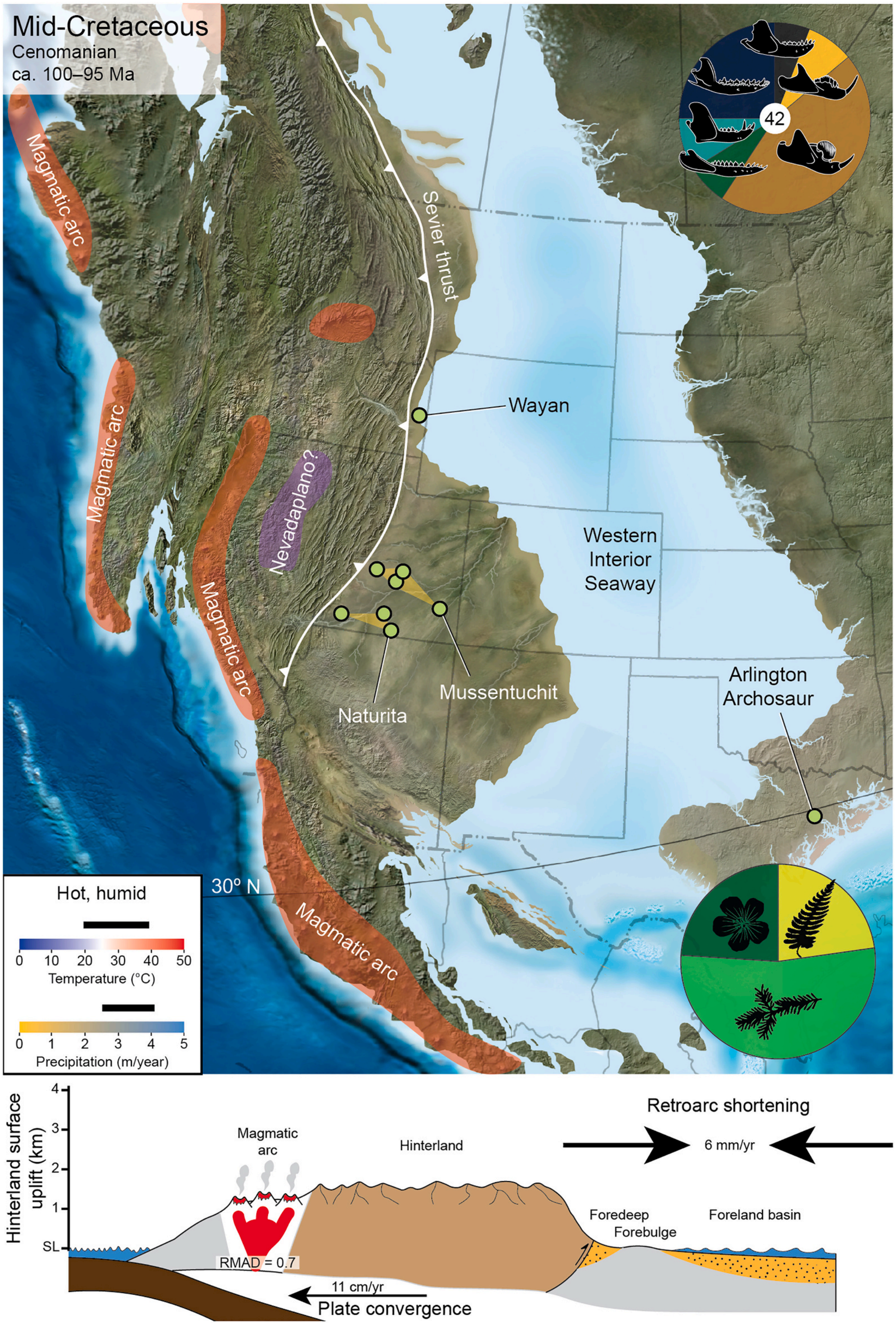

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Fig. 4. Map of mammal-bearing fossil localities (green circles) from near the Early–Late Cretaceous boundary (Cenomanian, ca. 100–95 Ma) in relation to their paleoenvironmental and tectonic setting (Cenomanian paleoenvironmental reconstruction map from Ron Blakey [Deep Time Maps]; Geographic location of mammal localities derived from the Paleobiology Database; Tectonic annotations derived from DeCelles, 2004, Yonkee and Weil, 2015, Balgord et al., 2021, and Weil and Yonkee, 2023). Leader lines and yellow polygons highlight mammal-bearing units (Mussentuchit, Wayan, Naturita) or localities (Arlington Archosaur). **Top right**, relative species richness of major mammalian groups, with approximate total species richness in the center: Black = Eutriconodonta; Yellow = 'Plagiaulacida', Multituberculata; Dark Green = 'Symmetrodonta'; Gold = Cimolodonta, Multituberculata; Teal = Stem Theria ('Tribotheres'); Dark Blue = Metatheria (from Eaton and Cifelli, 2001, Kielan-Jaworowska et al., 2004, Eaton, 2009, Cifelli et al., 2016, Carneiro, 2018, and Weaver et al., 2019). **Lower right**, approximate relative abundance of ferns (yellow-green), conifers (light green), and angiosperms (dark green) (from Lupia et al., 1999). **Lower left**, temperature (top) and precipitation (bottom) estimates for this time period, with the black bars representing reported ranges of temperatures or precipitation. Broad temperature categories (hot, warm, cooler) follow Huber et al. (2018), and broad precipitation categories (arid, humid) based on Benton et al. (2021). Temperature range comes from $\delta^{18}O$ values of benthic and planktonic foraminifera in the southern hemisphere (Huber et al., 2018) and clumped isotope paleotemperatures from North America (Jones et al., 2022). Precipitation estimates were generated via $\delta^{18}O$ values of sphaerosiderites from the eastern margin of the Western Interior Seaway (White et al., 2001). **Bottom panel**, schematic of tectonic setting, including rate of North America-Farallon plate convergence, rate of retroarc shortening, elevation of the hinterland, and relative magmatic addition rate (RMAD; relative to the peak observed magmatic addition rates in the Jurassic and Cretaceous). This schematic is not based on any specific transect; it a generalized west–east cross section of western North America. Tectonic data are derived from DeCelles (2004), Chapman et al. (2015), Yonkee and Weil (2015), Balgord et al. (2021), and Weil and Yonkee (2023).

follows the Aquilan and represents the first time in which mammalian assemblages are known from throughout the Western Interior (Lillegraven and McKenna, 1986; Cifelli et al., 2004) (Fig. 7), although the NALMA was erected on the basis of the Clam Bank Hollow local fauna in northcentral Montana (Sahni, 1972). In terms of faunal composition, the Judithian is remarkable in marking the regional extinction of all 'archaic' lineages (save for a putative 'plagiaulacidan' multituberculate from New Mexico; Flynn, 1986) and the first mammalian communities consisting almost entirely of cimolodontan multituberculates, metatherians, and eutherians (although there are a few lingering 'tribotheres'). As such, the succeeding NALMAs are henceforth mostly differentiated by the appearance/disappearance of subgroups nested within these larger lineages, rather than wholesale appearance/disappearance of major groups or branches.

The middle–late Campanian is geologically one of the best-studied intervals in the Late Cretaceous (e.g., Catuneanu et al., 1997; Rogers, 1998; Dettman and Lohmann, 2000; Fricke et al., 2010; Burgener et al., 2019). It is in this interval that we see the final expression of many of the tectonic trends and landscape features that characterized the preceding portions of the Late Cretaceous—the Sevier hinterland reaches its acme, retroarc shortening rates are near their pre-Cenozoic peak, and the transgression of the Bearpaw Sea marks the last major transgression of the Western Interior Seaway (e.g., Kauffman and Caldwell, 1993; DeCelles, 2004; Yonkee and Weil, 2015). Climatically, it is from the middle–late Campanian that we have the best evidence for the Western Interior Monsoon (discussed in section '2.3.1 Cenomanian and the 100 Ma event' above) and this interval also records the last very high paleotemperatures that characterized most of the middle–Late Cretaceous (e.g., Huber et al., 2018; Jones et al., 2022).

The 'Edmontonian' NALMA is poorly characterized (hence the scare quotes) but was originally argued (Lillegraven and McKenna, 1986) to capture assemblages that were compositionally intermediate between those of the Judithian and the Lancian. Spanning the early Maastrichtian, it is currently thought that these local faunas are more similar to the older Judithian local faunas than to those of the Lancian (Hunter et al., 2010), but the interval remains poorly sampled (Cifelli et al., 2004).

The Lancian NALMA (ca. 68–66 Ma) documents mammalian communities and evolution immediately preceding the K–Pg mass extinction, composed entirely of cimolodontan multituberculates, metatherians, and eutherians (e.g., Clemens, 1964, 1966, 1973; Archibald, 1982; Wilson et al., 2010; Wilson, 2013, 2014). Like the Judithian, Lancian mammalian assemblages are known from throughout the Western Interior Basin (Fig. 8). In general, Lancian mammals continue the trend of increasing ecological diversity that began at least in the Aquilan, but they are notable in including some of the largest known Mesozoic mammals, such as the badger-like metatherian *Didelphodon vorax* and the marmot-like multituberculate *Meniscoessus robustus* (Fig. 1). In the Hell Creek Formation of eastern Montana, mammalian evenness (i.e., the balance in relative-abundance structure among different mammalian taxa) declines in the lead-up to the K–Pg boundary, signaling a decline in ecosystem stability that may have made ecosystems especially vulnerable to the Chicxulub bolide impact that ultimately ushered in the K–Pg mass extinction (Wilson, 2014).

Numerous changes to landscapes and climates occurred in the last ca. 2 Myr of the Cretaceous; indeed, these changes were often invoked to explain the K–Pg mass extinction and corresponding changes in the makeup of terrestrial ecosystems (e.g., Jepsen, 1963; Bakker, 1977; Archibald, 2012). Most salient in the sedimentary rock record is the final regression of the Western Interior Seaway, which although persisting as the Cannonball Sea in the Dakotas well into the Paleocene (e.g., Brown and Lemke, 1948; Peppe et al., 2009), never again bisected North America nor transgressed far westward. This final regression is intimately linked with the southwest to northeast path of the Laramide Orogeny (e.g., Copeland et al., 2017) which, although beginning ca. 80 Ma in the southern Colorado Plateau (e.g., Weil and Yonkee, 2023), did not substantially modify the landscapes coeval with mammalian fossil assemblages until near the end of the Cretaceous (e.g., Heller et al., 2013; Weil and Yonkee, 2023). Climatically, the late Maastrichtian experienced a continued cooling trend leading to the K–Pg boundary (e.g., Tobin et al., 2014; Tabor et al., 2016; Jones et al., 2022). The biotic consequences of these myriad environmental changes in the latest Cretaceous have been explored in detail, especially in the past few years, via the application of ecological-niche and trophic-network modelling (e.g., Chiarenza et al., 2019; García-Girón et al., 2022). It is in this dynamic context that angiosperms exhibit their greatest taxonomic and ecological diversity of the Cretaceous, finally exceeding ferns and gymnosperms in terms of species richness and ecological disparity, exhibiting a broad and abundant array of arborescent forms (e.g., Wing and Sues, 1992; Wing and Boucher, 1998; Eriksson et al., 2000; Philippe et al., 2008).

2.4. Early Paleogene

The K–Pg mass extinction dramatically transformed terrestrial ecosystems, most famously by marking the demise of non-avian dinosaurs and the ascendancy of mammals (Archibald, 1982; Clemens, 2002; Schulte et al., 2010; Wilson, 2014). At the dawn of the Puercan NALMA (Fig. 9), which roughly spans the first 1 Myr of the Paleocene and is known from mammalian assemblages across the Western Interior (Lofgren et al., 2004; Sprain et al., 2015, 2018), the taxonomic makeup of mammalian communities was, as in the Late Cretaceous, dominated by cimolodontan multituberculates (e.g., Smith et al., 2018; Claytor et al., 2023). However, nearly all North American metatherians went extinct at the K–Pg boundary (e.g., Lillegraven, 1969), whereas eutherians diversified rapidly and rivaled multituberculates in terms of both species richness and relative abundance (e.g., Simpson, 1937; Van Valen, 1978; Archibald, 1982; Clemens, 2002; Wilson, 2013, 2014). In

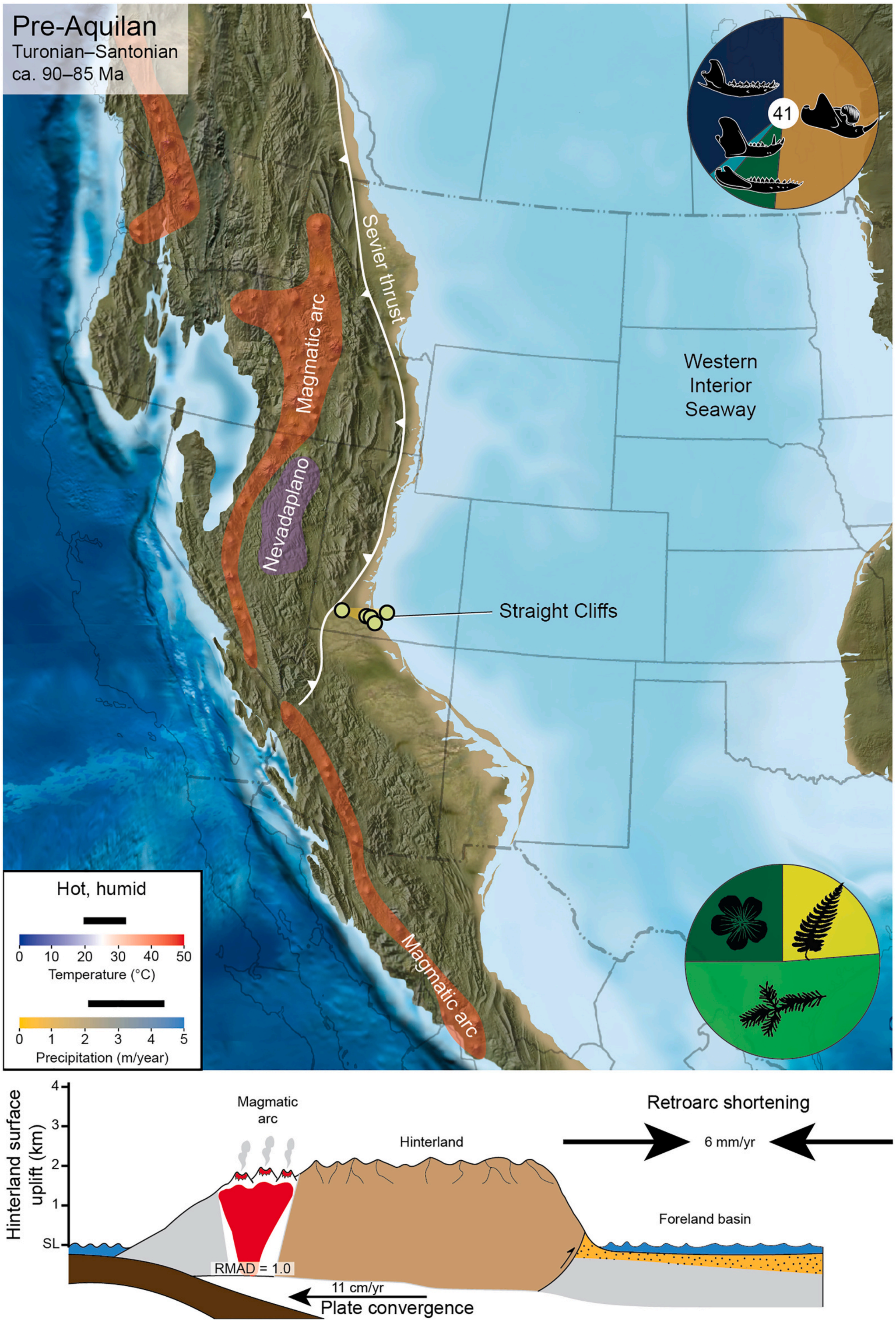

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Fig. 5. Map of mammal-bearing fossil localities (green circles) from the Turonian–middle Santonian (ca. 90–85 Ma) in relation to their paleoenvironmental and tectonic setting (early Santonian paleoenvironmental reconstruction map from Ron Blakey [Deep Time Maps]; Geographic location of mammal localities derived from the Paleobiology Database; Tectonic annotations derived from DeCelles, 2004, Yonkee and Weil, 2015, Balgord et al., 2021, and Weil and Yonkee, 2023). Leader line and yellow polygon highlight the mammal-bearing Straight Cliffs Formation. **Top right**, relative species richness of major mammalian groups, with approximate total species richness in the center: Dark Green = 'Symmetrodonta'; Gold = Cimolodonta, Multituberculata; Teal = Stem Theria ('Tribotheres'); Dark Blue = Metatheria (from Kielan-Jaworowska et al., 2004, Eaton, 2006, Cohen, 2018, and Cohen et al., 2020). **Lower right**, approximate relative abundance of ferns (yellow-green), conifers (light green), and angiosperms (dark green) (Lupia et al., 1999). **Lower left**, temperature (top) and precipitation (bottom) estimates for this time period, with the black bars representing reported ranges of temperatures or precipitation. Broad temperature categories (hot, warm, cooler) follow Huber et al. (2018), and broad precipitation categories (arid, humid) based on Benton et al. (2021). Temperature range comes from $\delta^{18}O$ values of benthic and planktonic foraminifera in the southern hemisphere (Huber et al., 2018) and clumped isotope paleotemperatures from North America (Jones et al., 2022). Precipitation estimates were generated via $\delta^{18}O$ values of sphaerosiderites from the eastern margin of the Western Interior Seaway (White et al., 2001) and the general circulation model of Sewall and Fricke (2013); Fig. 3) for western North America in the Campanian. **Bottom panel**, schematic of tectonic setting, including rate of North America-Farallon plate convergence, rate of retroarc shortening, elevation of the hinterland, and relative magmatic addition rate (RMAD; relative to the peak observed magmatic addition rates in the Jurassic and Cretaceous). This schematic is not based on any specific transect; it a generalized west–east cross section of western North America. Tectonic data are derived from DeCelles (2004), Chapman et al. (2015), Yonkee and Weil (2015), Balgord et al. (2021), and Weil and Yonkee (2023).

particular, archaic ungulates (i.e., 'condylarths') diversified rapidly and within ca. 300 kyr of the K–Pg boundary exceeded the body sizes of the largest Mesozoic mammals (e.g., Lyson et al., 2019). From the Puercan through the Wasatchian, eutherians continued to diversify both taxonomically and ecologically, culminating in the appearance of lineages from most modern orders near the Paleocene-Eocene boundary (e.g., Rodentia, Primates, Perissodactyla, Artiodactyla) (Rose, 1981; Gingerich, 2006). Metatherians persisted through this early Paleogene interval but only in very low species richness and relative abundance (e.g., Lofgren et al., 2004; Rose, 2006). Multituberculates continued to diversify through the Tiffanian NALMA (middle–late Paleocene), but their diversity plummeted in the Clarkforkian NALMA, roughly 1 Myr prior to the Eocene (Krause, 1986; Wilson et al., 2012; Weaver and Wilson, 2021). Thus, from the early Eocene onwards, eutherian mammals alone dominated mammalian faunas in western North America.

Following a moderate decline in taxonomic richness and ecological diversity among floral communities in the early aftermath of the K–Pg mass extinction (Johnson, 2002; Nichols and Johnson, 2008; Wilson Deibel, 2022), the floras of the early Paleogene document the continued ecological proliferation of angiosperms, and by the early Eocene there were as disparate forms as exist in modern tropical ecosystems today (e.g., Benton et al., 2022; Carvalho et al., 2021). Global temperatures from the K–Pg boundary to the early Eocene were generally much cooler than the Late Cretaceous (e.g., Westerhold et al., 2020), with the most substantial climatic perturbation being the abrupt global warming event at the Paleocene-Eocene boundary, the Paleocene-Eocene Thermal Maximum (Kennett and Stott, 1991; McInerney and Wing, 2011). The Laramide and Sevier orogenies continued to deform the continental interior well into the early Eocene (e.g., Solum and van der Pluijm, 2007). What was once a north–south corridor of coastal plains along the foreland of the Sevier Thrust Belt gave way to a patchwork of intermontane basins bordered by an anastomosing network of basement-cored mountain ranges across the Western Interior (e.g., Dickinson et al., 1988; Weil and Yonkee, 2023). What role these dramatic landscape changes played in stimulating the rise of mammals in the Cenozoic remains to be explored, but disentangling landscape-driven from post-K–Pg-extinction-driven changes to mammalian diversity in the early Paleogene is challenging.

3. Tectonics as a catalyst of the Cretaceous Terrestrial Revolution

3.1. *Increases in Mammalian Diversity Track Tectonic Processes in the Late Cretaceous*

3.1.1. *Mammalian and angiosperm diversity accelerated between 100 and 75 Ma*

Following the appearance of the major 'modern' mammalian groups (cimolodontan multituberculates and therians) in the late Early Cretaceous, raw mammalian species richness increased dramatically from near the Early–Late Cretaceous boundary to the middle Campanian in western North America, with the estimated species richness of the Aquilan more than double that of the early Cenomanian, and that of the Judithian nearly double that of the Aquilan (Fig. 10; Supplementary Material). Species richness then declined slightly from the Judithian to the K–Pg boundary. Thus, there was an over threefold increase in mammalian taxonomic diversity from ca. 100 to 75 Ma (Supplementary Material). Whether mammalian ecological diversity tracked taxonomic diversity during this interval, however, is unclear. Previous studies have proposed that mammals did not diversify appreciably ecologically (i.e., in terms of dietary or body-size diversity) until ca. 85–80 Ma (in the Aquilan) (Wilson et al., 2012; Grossnickle and Newham, 2016); taxonomic diversification thus preceded ecological diversification in that scenario. The decoupling of taxonomic and ecological diversification in Cretaceous mammals, however, may in part reflect differences in the intensity of sampling or study of Turonian–Santonian versus Campanian–Maastrichtian mammalian fossil assemblages. For example, metatherian assemblages from the Smoky Hollow Member of the Straight Cliffs Formation (middle Turonian) of Utah have been interpreted to be nearly as ecologically rich as those from the Lancian (late Maastrichtian) (Cohen et al., 2020), and the morphological disparity (i.e., range of different shapes) of cimolodontan multituberculate dentitions from the Turonian–Santonian is on par with those from the Judithian and Lancian (Eaton, 1995; Weaver and Wilson, 2021). Thus, raw mammalian species richness increased dramatically from 100 to 75 Ma (Fig. 10), and mammalian ecological richness either followed or occurred in tandem with this burst in taxonomic diversification. Future work sampling and describing Turonian–Santonian mammalian assemblages and quantifying their ecological diversity should illuminate which of these scenarios is most likely.

Angiosperm within-flora diversity (both species richness and relative abundance) closely resembles the trend in raw mammalian species richness over that same interval in western North America (Fig. 10): angiosperm within-flora richness and abundance increased substantially from <20% of floral composition in the early Cenomanian to nearly 50% of floral composition by the middle Campanian, when richness then levelled off leading up to the K–Pg boundary (but note that these data are derived from pollen assemblages [Lupia et al., 1999]. In some macrofloral fossil assemblages angiosperms make up >75% of plant morphotypes in the latest Cretaceous [e.g., Lidgard and Crane, 1990; Nichols and Johnson, 2008]). The ecological diversification of angiosperms, however, continued through the end of the Cretaceous and into the early Paleogene (Wing and Boucher, 1998; Benton et al., 2022).

The interval of ca. 100 to 75 Ma that shows these pronounced increases in both mammal and angiosperm diversity is henceforth (for the ease of discussion) referred to as the 'onset' of the KTR, which we highlight in yellow on Fig. 10. Note that our data are from western North America, and it is possible that they are not reflective of global

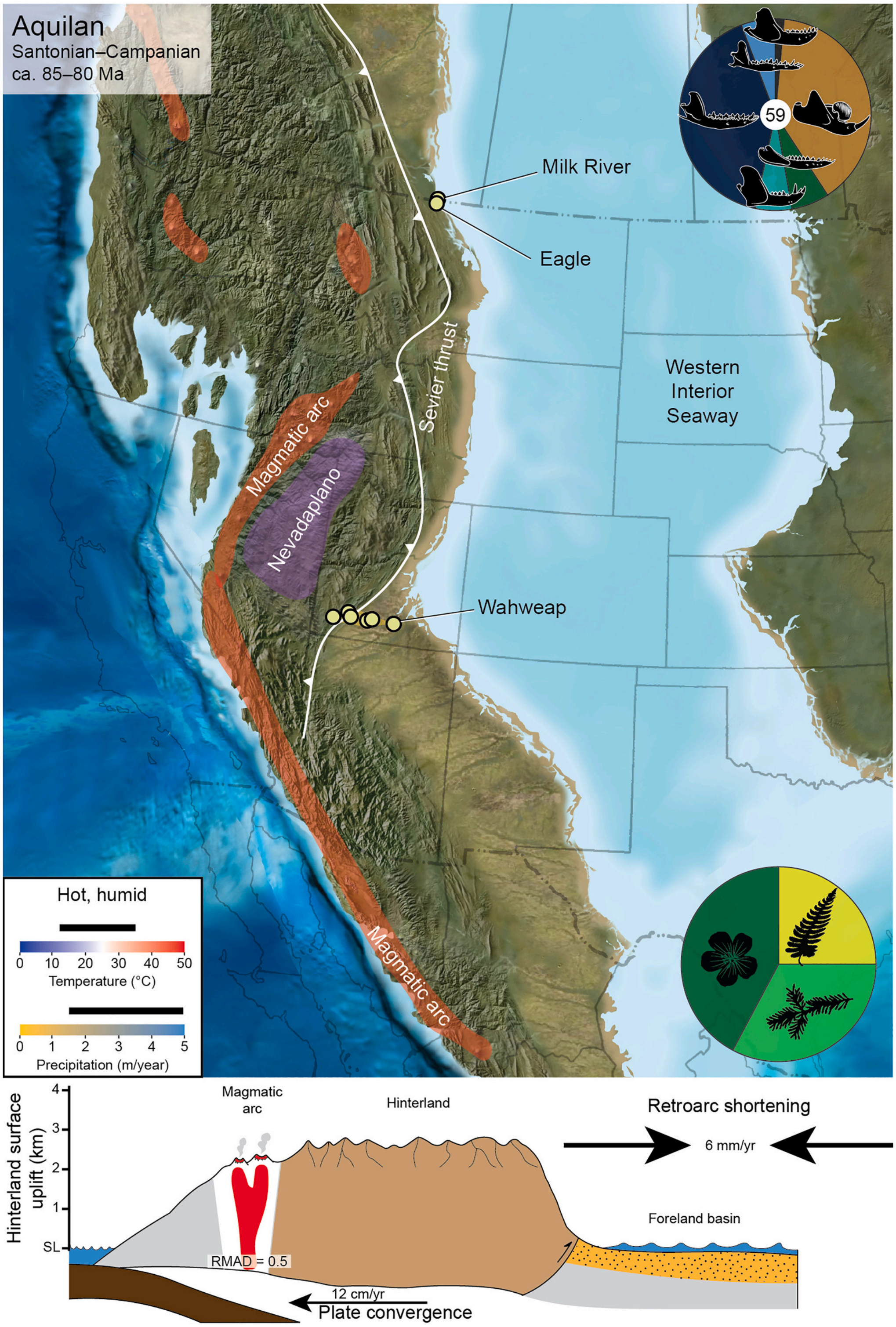

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Fig. 6. Map of mammal-bearing fossil localities (green circles) from the Aquilan NALMA (late Santonian–middle Campanian, ca. 85–80 Ma) in relation to their paleoenvironmental and tectonic setting (early Campanian paleoenvironmental reconstruction map from Ron Blakey [Deep Time Maps]; Geographic location of mammal localities derived from the Paleobiology Database; Tectonic annotations derived from DeCelles, 2004, Yonkee and Weil, 2015, Balgord et al., 2021, and Weil and Yonkee, 2023). Leader lines and yellow polygons highlight mammal-bearing formations. **Top right**, relative species richness of major mammalian groups, with approximate total species richness in the center: Gold = Cimolodonta, Multituberculata; Dark Blue = Metatheria; Light Blue = Eutheria (from Kielan-Jaworowska et al., 2004 and Davis et al., 2016). **Lower right**, approximate relative abundance of ferns (yellow-green), conifers (light green), and angiosperms (dark green) (Lupia et al., 1999). **Lower left**, temperature (top) and precipitation (bottom) estimates for this time period, with the black bars representing reported ranges of temperatures or precipitation. Broad temperature categories (hot, warm, cooler) follow Huber et al. (2018), and broad precipitation categories (arid, humid) based on Benton et al. (2021). As in Figs. 3–5, temperature range is informed by Huber et al. (2018), but here also organic geochemical (TEX_{86}) paleotemperature estimates from Linnert et al. (2014; Mississippi Embayment) and clumped-isotope paleotemperature estimates Petersen et al. (2016; Western Interior Seaway). Precipitation range is based on the general circulation model of Sewall and Fricke (2013); Fig. 3) for western North America in the Campanian. **Bottom panel**, schematic of tectonic setting, including rate of North America-Farallon plate convergence, rate of retroarc shortening, elevation of the hinterland, and relative magmatic addition rate (RMAD; relative to the peak observed magmatic addition rates in the Jurassic and Cretaceous). This schematic is not based on any specific transect; it a generalized west–east cross section of western North America. Tectonic data are derived from DeCelles (2004), Chapman et al. (2015), Yonkee and Weil (2015), Balgord et al. (2021), and Weil and Yonkee (2023).

biodiversity trends (e.g., Flannery-Sutherland et al., 2022). Nonetheless, because the mechanisms we propose as biodiversity simulants in the Late Cretaceous should have global relevance, we suggest that this interval likely captured the onset of the KTR globally. Regardless, the correlation between these mammalian and angiosperm patterns fits the prevalent interpretation that mammalian diversification in the Late Cretaceous was driven by the diversification of angiosperms (e.g., Wilson et al., 2012; Grossnickle and Newham, 2016; Chen et al., 2019; Grossnickle et al., 2019; see also the Supplementary Materials), but that putatively causal relationship requires reevaluation when abiotic factors are also considered.

3.1.2. *The onset of the KTR coincided with the '100 Ma event'*

Increases in mammalian and angiosperm diversity during the onset of the KTR track major changes to terrestrial landscapes and climate, all of which have been linked to the '100 Ma event' (e.g., Poulsen et al., 2003; Matthews et al., 2012; Lee et al., 2013; Balgord et al., 2021; see section '2.3.1 Cenomanian and the 100 Ma event' above for more details). Between 100 and 75 Ma, there were increases in critical tectonic processes (Fig. 10)—plate-convergence rates, relative magmatic addition rates (consistent with a global flare-up in arc magmatism), retroarc shortening rates (a proxy for topographic complexity), crustal thickness (a proxy for topographic relief), and hinterland surface uplift (i.e., overall peak elevation of the Sevier Orogenic Belt)—that occurred during the peak warm period of the Cretaceous, the 'middle-Cretaceous greenhouse' climate, epitomized by the Cretaceous Thermal Maximum. The onset of the KTR also coincided with the maximum transgression of the Western Interior Seaway (Fig. 10), which was caused by both tectonic loading and dynamic topography that increased subsidence of the Western Interior Basin (e.g., Catuneanu et al., 1997; Catuneanu, 2004; Chang and Liu, 2021). Following the onset of the KTR, when both mammalian and angiosperm taxonomic diversity plateaued, arc magmatism began to shut down, retroarc shortening rates decreased, hinterland surface uplift plateaued, global and regional temperatures cooled, and the Western Interior Seaway began its final oscillatory regression (Fig. 10). Thus, the rapid accumulation of both mammalian and angiosperm diversity in the Late Cretaceous of western North America occurred during a period of accelerated building of the North American Cordillera, peak global and regional climatic warmth, and peak transgression of the Western Interior Seaway.

3.1.3. *Taphonomic considerations*

The raw taxonomic richness patterns that we highlight here among mammals and angiosperms are almost certainly influenced by differential (i) preservation, (ii) sampling (temporally and geographically), and (iii) taxonomic emphasis. Subsidence and concomitant sediment-accumulation rates increased substantially in response to the growth of the North American Cordillera in the Late Cretaceous (e.g., Yonkee and Weil, 2015), increasing both the stratigraphic opportunities for fossil preservation and their likelihood of preservation (e.g., Behrensmeyer, 1982; Kidwell, 1986; Badgley et al., 1995; Rogers et al., 2007). Indeed, we see that the number and geographic breadth of mammal-bearing fossil localities increases substantially when comparing, for example, the Cenomanian to the Judithian (Fig. 4 vs. Fig. 7). Nonetheless, it is possible that the increase in mammalian fossil localities and species are driven by a common cause. Increased Sevier uplift and associated increases in total precipitation amounts or monsoonal precipitation patterns drove a major increase in sediment input to the Western Interior Basin (Fricke et al., 2010; Yonkee and Weil, 2015; Chang and Liu, 2021), and that increased sediment load was also nutrient-rich (e.g., Lee et al., 2018) and likely increased the carrying capacity of both plants and animals living on the eastern flanks of the Sevier front (analogous to western Amazonia and the eastern flanks of the northern Andes; Hoorn et al., 2010). Changes to erosion and sedimentation dynamics may have therefore amplified the biological patterns we observe in the fossil record, rather than obscure them (e.g., Peters and Gaines, 2012).

Many studies have addressed the problem of sampling bias in the Cretaceous fossil record (e.g., Butler et al., 2011; Benson et al., 2013; Chiarenza et al., 2019; Maidment et al., 2021) and have made clear that uneven stratigraphic and spatial sampling biases biodiversity patterns. In terms of the mammalian fossil record, the Judithian and Lancian have been sampled much more than any of the preceding Late Cretaceous intervals, as evident by the geographic breadth of mammal-bearing fossil localities from the middle Campanian–late Maastrichtian (e.g., Figs. 7 and 8 vs. Figs. 4–6). Nonetheless, early Cenomanian (mostly from the Mussentuchit Member of the Cedar Mountain Formation) and Aquilan (mostly from the Milk River Formation) mammalian fossil assemblages have been sampled to a similar, moderate degree (e.g., Eaton and Cifelli, 2001; Davis et al., 2016), yet mammalian species richness in the Aquilan is more than double that in the early Cenomanian (59 species vs. 28 species, respectively; Supplementary Material). Morphological disparity in therian molars (a measure of ecological disparity given the close relationship between tooth shape and diet), which is less biased by sampling than raw richness, also shows a marked increase in the Aquilan relative to the earlier Late Cretaceous (Grossnickle and Newham, 2016). Further, despite Lancian fossil assemblages being much better sampled than those in the Judithian (e.g., Kielan-Jaworowska et al., 2004; Wilson et al., 2010), raw species richness is lower in the Lancian than in the Judithian (Fig. 7 vs. Fig. 8; Supplementary Material). Although sampling bias in both the mammalian and angiosperm fossil record certainly deserves further scrutiny, our qualitative comparisons suggest that these patterns, approximate though they may be, represent actual changes in mammalian diversity.

Taxonomic emphasis also likely plays a major role in biasing the diversity patterns presented here (e.g., Nanglu and Cullen, 2023). Therians and other tribosphenic or 'therian-line' (i.e., trechnotherian) mammals have received more systematic and descriptive study than have non-therian groups. For example, the tribosphenic mammals ('tribotheres' and therians) from the Early Cretaceous Trinity Group of

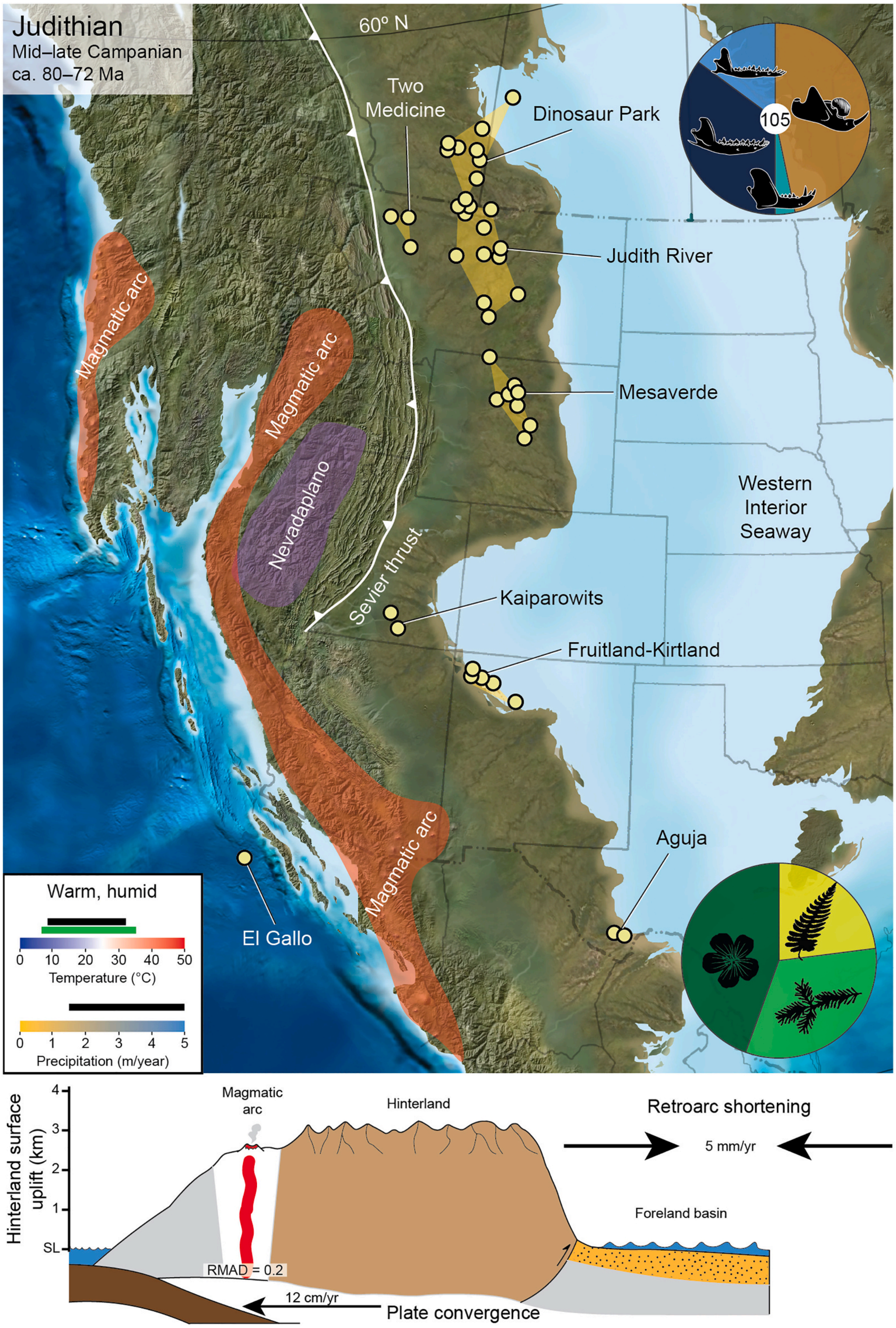

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Fig. 7. Map of mammal-bearing fossil localities (green circles) from the Judithian NALMA (mid–late Campanian, ca. 80–72 Ma) in relation to their paleoenvironmental and tectonic setting (late Campanian paleoenvironmental reconstruction map from Ron Blakey [Deep Time Maps]; Geographic location of mammal localities derived from the Paleobiology Database; Tectonic annotations derived from DeCelles, 2004, Yonkee and Weil, 2015, Balgord et al., 2021, and Weil and Yonkee, 2023). Leader lines and yellow polygons highlight mammal-bearing formations. **Top right**, relative species richness of major mammalian groups, with approximate total species richness in the center: Gold = Cimolodonta, Multituberculata; Dark Blue = Metatheria; Light Blue = Eutheria (from Kielan-Jaworowska et al., 2004 and Weaver et al., 2021). **Lower right**, approximate relative abundance of ferns (yellow-green), conifers (light green), and angiosperms (dark green) (Lupia et al., 1999). **Lower left**, temperature (top) and precipitation (bottom) estimates for this time period, with the bars representing reported ranges of temperatures or precipitation. Broad temperature categories (hot, warm, cooler) follow Huber et al. (2018), and broad precipitation categories (arid, humid) based on Benton et al. (2021). Temperature range in black is drawn from the same sources as Fig. 6, plus clumped isotope paleotemperature estimates from Meyer et al. (2018; Mississippi Embayment) and Gao et al. (2021; Western Interior Seaway); temperature range in green is the non-marine paleotemperature estimate from clumped isotope analysis of paleosol carbonates in the Kaiparowits and Two Medicine formations (Burgener et al., 2019). Precipitation range is the same as Fig. 6. **Bottom panel**, schematic of tectonic setting, including rate of North America-Farallon plate convergence, rate of retroarc shortening, elevation of the hinterland, and relative magmatic addition rate (RMAD; relative to the peak observed magmatic addition rates in the Jurassic and Cretaceous). This schematic is not based on any specific transect; it a generalized west–east cross section of western North America. Tectonic data are derived from DeCelles (2004), Chapman et al. (2015), Yonkee and Weil (2015), Balgord et al. (2021), and Weil and Yonkee (2023).

Texas have a long and influential history of research (e.g., Patterson, 1956; Davis and Cifelli, 2011), yet multituberculates are the most abundant taxa represented in the Trinity assemblages (Patterson, 1956) but have never been described. That taxonomic preference can bias biodiversity patterns has been well-documented (Raup, 1979; Adrain and Westrop, 2000; Alroy, 2010; Nanglu and Cullen, 2023), and it has almost certainly dampened our tally of raw species richness.

Directionality, however, is an important consideration for these potential sources of bias in the taxonomic record of mammals (and angiosperms)—if these preservation, sampling, and taxonomic-emphasis biases did not exist, would that reinforce or refute the hypothesis presented here? We argue that these various biases actually dampen our expected biodiversity patterns rather than inflate them. For example, tectonic activity began accelerating around 100 Ma, but the taxonomic diversity of mammals does not exceed that of pre-Late Cretaceous intervals until the Aquilan (approximately 15 Ma later; Fig. 10; Supplementary Material). This lag in taxonomic diversification (and potentially also ecological diversification, see section '3.1.1 Mammalian and angiosperm diversity accelerated between 100 and 75 Ma') is likely due, at least in part, to the relatively meager fossil record from the Turonian–middle Santonian (e.g., Fig. 5). Indeed, as the Turonian–middle Santonian interval has received greater attention in recent years (in terms of both fossil collecting and study), it increasingly appears that the major leaps in both mammalian and angiosperm diversity began much closer to the Early-Late Cretaceous boundary (e.g., Cohen, 2018; Jud et al., 2018; Cohen et al., 2020), reinforcing our conclusions. Finally, we emphasize that smaller scale case studies at the level of individual basins, where it is easier to contend with those biases, hold the greatest promise for illuminating macroevolutionary trends in the future (e.g., Maidment et al., 2021; see section '4.1 The Way Forward').

3.2. *The Tectonic Catalyst Hypothesis*

3.2.1. *A 'perfect storm' for diversification*

We propose that the acceleration of tectonic activity in the middle–Late Cretaceous (initiated by the '100 Ma event'; Matthews et al., 2012) was the ultimate catalyst of the KTR. The idea that tectonic processes in the Cretaceous stimulated the evolution of terrestrial ecosystems has been proposed in the past (e.g., Bakker, 1977) but, at the global scale, typically in the context of continental breakup (e.g., Hedges et al., 1996; Christmas et al., 2023). In western North America, many researchers have investigated north-south provincialism among Late Cretaceous terrestrial faunas (particularly non-avian dinosaurs; e.g., Sloan, 1969; Lehman et al., 1997, Lehman, 2001; Gates et al., 2010) and have attributed patterns of endemism and diversification to Laramide mountain-building (Gates et al., 2012), transgression-regression cycles of the Western Interior Seaway (e.g., Horner et al., 1992; Loewen et al., 2013), or climatic zonation (e.g., Burgener et al., 2021). Here we propose a different mechanism: tectonism triggered increases in topographic complexity (e.g., the rising North American Cordillera), fluctuations in sea level (e.g., the waxing and waning of the Western Interior Seaway), and changes in climate (e.g., Cretaceous Thermal Maximum, Western-Interior Monsoon) that would have collectively created a 'perfect storm' for diversification (sensu Jablonski et al., 2017; Jablonski and Edie, 2023; Fig. 11). In other words, we contend that changes to Late Cretaceous landscapes and climate are all related and were ultimately triggered by accelerated tectonism beginning ca. 100 Ma, setting in motion a positive feedback that can explain patterns of diversification at both the regional (i.e., western North America) and global scale (Fig. 11). Below we elaborate on various aspects of this hypothesis, including the specific roles that mountains, sea-level change, tropical climates, and vegetation likely played in stimulating the diversification of mammals and terrestrial biota more broadly in the Late Cretaceous.

3.2.2. *Mountains and biodiversity*

Mountain building is an engine for generating biodiversity (e.g., Badgley, 2010; Hoorn et al., 2013; Badgley et al., 2017; Hoorn et al., 2018; Perrigo et al., 2020). As mountain belts grow, they create elevational differences in climate and fragment landscapes, which together increase habitat complexity and diversity in montane regions (e.g., Badgley et al., 2017, 2018). Consequently, terrestrial biodiversity is concentrated in topographically complex regions (e.g., Simpson, 1964; Badgley and Fox, 2000; Hoorn et al., 2013; Rahbek et al., 2019) and the formation of mountainous or topographically complex landscapes has been implicated in speciation pulses in the geologic past (e.g., Finarelli and Badgley, 2010; Hoorn et al., 2010; Bedoya et al., 2021). Fossils do not usually preserve or accumulate in montane regions, however, and in the Cretaceous record of the Western Interior Basin of North America most fossil assemblages come from lowland paleoenvironments. Nonetheless, montane species ranges typically extend into adjacent lowlands (e.g., Badgley and Fox, 2000) and mountainous regions are often cradles of diversification from which species later disperse (e.g., Badgley et al., 2017). As such, lowlands adjacent to mountain belts, where fossils do accumulate, frequently capture a significant portion of the diversity stimulated in topographically complex and higher-elevation (but taphonomically inhospitable) regions (e.g., Hoorn et al., 2010).

3.2.3. *The North American Cordillera as an engine for generating Cretaceous biodiversity*

During the onset of the KTR, topographic complexity, relief, and elevation increased dramatically, resulting in the establishment of the North American Cordillera (what is today the Rocky Mountains), which ran roughly north to south through what today is Alberta and British Columbia to Nevada and Utah (Burchfiel and Davis, 1972; DeCelles, 2004; Yonkee and Weil, 2015). The rapid establishment of a montane western North America would have generated an abundance of new habitats along elevational gradients and across the fragmented and heterogeneous landscape. Further, frequent and abundant sediment delivery from the Cordilleran uplands would have promoted the

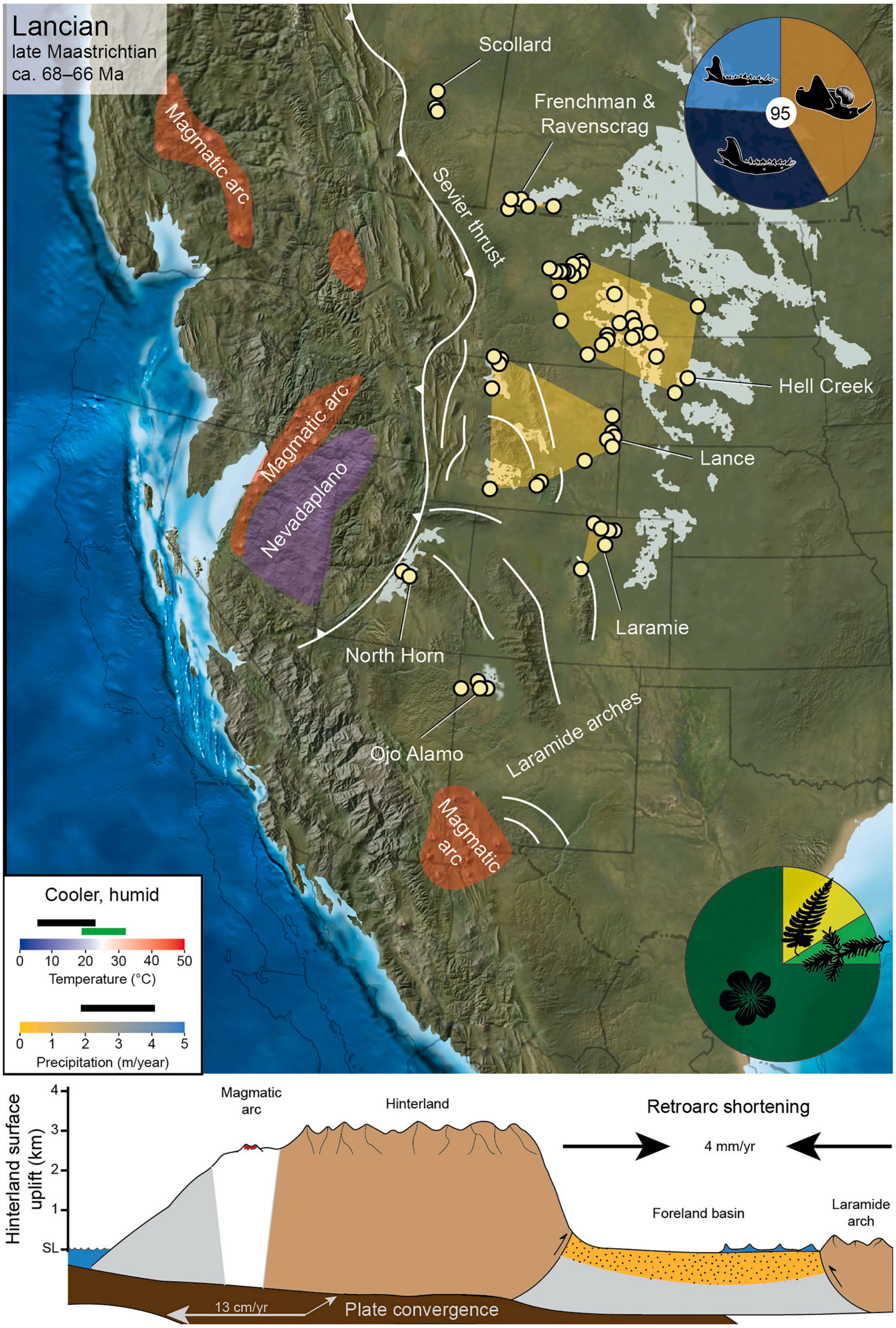

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Fig. 8. Map of mammal-bearing fossil localities (green circles) from the Lancian NALMA (late Maastrichtian, ca. 68–66 Ma) in relation to their paleoenvironmental and tectonic setting (late Maastrichtian paleoenvironmental reconstruction map from Ron Blakey [Deep Time Maps]; Geographic location of mammal localities derived from the Paleobiology Database; Tectonic annotations derived from DeCelles, 2004, Yonkee and Weil, 2015, Balgord et al., 2021, and Weil and Yonkee, 2023). Leader lines and yellow polygons highlight mammal-bearing formations. **Top right**, relative species richness of major mammalian groups, with approximate total species richness in the center: Gold = Cimolodonta, Multituberculata; Dark Blue = Metatheria; Light Blue = Eutheria (from Kielan-Jaworowska et al., 2004 and Wilson et al., 2010). **Lower right**, approximate relative abundance of ferns (yellow-green), conifers (light green), and angiosperms (dark green) (from Johnson, 2002, Nichols, 2002, and Nichols and Johnson, 2008). **Lower left**, temperature (top) and precipitation (bottom) estimates for this time period, with the bars representing reported ranges of temperatures or precipitation. Broad temperature categories (hot, warm, cooler) follow Huber et al. (2018), and broad precipitation categories (arid, humid) based on Benton et al. (2021). Temperature range in black is drawn from the same sources as Fig. 6 (except without data from Gao et al., 2021); temperature range in green shows non-marine paleotemperature estimates from clumped isotope analysis of freshwater molluscs in the Hell Creek Formation (Tobin et al., 2014). Precipitation range is for western North America from the general circulation model of Hunter et al. (2008): Fig. 5). **Bottom panel**, schematic of tectonic setting, including rate of North America-Farallon plate convergence, rate of retroarc shortening, and elevation of the hinterland (arc magmatism ceased with the onset of flat-slab subduction associated with the Laramide Orogeny). This schematic is not based on any specific transect; it a generalized west–east cross section of western North America. Tectonic data are derived from DeCelles (2004), Chapman et al. (2015), Yonkee and Weil (2015), Balgord et al. (2021), and Weil and Yonkee (2023).

development of more nutrient-rich soils in the Western Interior Basin compared to those of the earlier Cretaceous (e.g., Lee et al., 2018), when sediment accumulation rates (and thus the frequency of nutrient delivery to the lowlands) were much lower (e.g., Quesada et al., 2009; Chang and Liu, 2021), thus promoting the establishment of richer floras and faunas (e.g., ter Steege, 2009).

The waxing and waning of the Western Interior Seaway, which were ultimately driven by cycles of orogenic loading and quiescence, respectively, in the Sevier Orogenic Belt (e.g., Catuneanu et al., 1997; Catuneanu, 2004; Chang and Liu, 2021), also likely had a pronounced influence on the evolution of mammals and plants during the onset of the KTR. During lowstands of the Western Interior Seaway, a broad, roughly continuous stretch of coastal plains would have run north to south along the front of the rising Sevier Orogenic Belt. In contrast, during highstands the availability of lowland habitat would have diminished substantially, and the continuity of the coastal plain was likely interrupted by the transgression of shallow seas into the foothills of the North American Cordillera. As such, during Western Interior Seaway lowstands, population connectivity in the Western Interior Basin was likely high since there was abundant lowland habitat that was virtually uninterrupted from present-day Mexico to Canada. During Western Interior Seaway highstands, however, lowland populations would have been forced upland, fragmenting population continuity and likely promoting genetic divergence (e.g., Horner et al., 1992; Loewen et al., 2013). Transgressions and regressions of the Western Interior Seaway were also not always latitudinally uniform, with transgressions sometimes beginning in the south before advancing north (or vice versa) (e.g., Kauffman and Caldwell, 1993), which would have further modulated Late Cretaceous landscapes of western North America. Together, there would have been a cyclical and reinforcing cascade of landscape changes (i.e., the 'Haug Effect'; Johnson, 1971; Bakker, 1977) that could stimulate allopatric speciation, whereby: (i) A pulse of tectonic uplift grows topography to the west, promoting greater biodiversity and (ii) increases crustal loading and retroarc foreland flexure, resulting in greater foreland subsidence. (iii) That greater subsidence in turn drives the transgression of the Western Interior Seaway, flooding coastal lowlands, (iv) fragmenting lowland population continuity and forcing populations upland into the growing foothills and mountains, (v) which ultimately promotes increased rates of allopatric speciation. (vi) As foreland subsidence rebounded and the Western Interior Seaway regressed, populations could once again colonize coastal lowlands, (vii) until another pulse of uplift set the cascade in motion again, with the downstream biotic consequences being now amplified by the ever-growing topography to the west (Fig. 11).

3.2.4. *Climate change and the KTR*

Global climate warmed considerably from the Early to middle Cretaceous (ca. 115–95 Ma), reaching a peak at the Cretaceous Thermal Maximum (ca. 95 Ma) when mean global temperatures exceeded 30 °C (e.g., Huber et al., 2018; Tierney et al., 2020; Jones et al., 2022; Burgener et al., 2023), and some continental temperature estimates for North America exceeded 50 °C (Fetrow, 2022). There were no dramatic swings in paleotemperature for much of the remaining Late Cretaceous (unless they were short in duration and have, to date, been missed by the sampling density of the global benthos; c.f., Cretaceous oceanic anoxic events; e.g., Leckie et al., 2002) until the late Campanian–early Maastrichtian when global temperatures began to cool leading up to the K–Pg boundary (Tobin et al., 2014; Bodin et al., 2015; Jones et al., 2022). Thus, global mean temperature alone cannot account for the observed changes in the fossil records of mammals and angiosperms. The 'middle-Cretaceous greenhouse' itself was likely a consequence of the same tectonic processes implicated here for the acceleration of mammal and plant diversity (i.e., due to changes in ocean-circulation patterns and increased magmatism; Poulsen et al., 2003; Lee et al., 2013). Nonetheless, elevated global temperatures in the middle–Late Cretaceous may have driven northward geographic range shifts among species (e.g., Wing et al., 2005), increasing species richness in mid-to-high latitudes and promoting interspecific interactions (e.g., competition, new trophic links), and perhaps opening high-latitude dispersal corridors (analogous to those in the early Eocene; e.g., Beard, 2002). Indeed, high-latitude land corridors likely existed between North America and Asia in the Early–middle Cretaceous (e.g., Blakey, 2014), which might explain the apparently sudden appearance of cimolodontan multituberculates and therians in the late Early Cretaceous of North America (since both groups have putative ancestors known from older deposits in eastern Asia; Kielan-Jaworska et al., 1987; Luo et al., 2003, 2011; Bi et al., 2018).

Although shifts in global climate alone are unlikely to have triggered the KTR, the interactions among mountains, warm temperatures, and enhanced hydrological cycles do have a substantial influence on patterns of biodiversity (e.g., Perrigo et al., 2020), beyond tropical and topographically complex regions simply being the most biodiverse modern terrestrial ecosystems. The steepest gradients in temperature and precipitation amounts on the surface of the Earth are due to topography (Roe, 2005; Fick and Hijmans, 2017), and as topography grows it can alter local, regional, and global precipitation patterns, including by inducing monsoonal rainfall (e.g., Fricke et al., 2010; Sewall and Fricke, 2013; Tardif et al., 2023). The rise and fall of the Western Interior Seaway (or other shallow epicontinental seas) also likely altered regional precipitation patterns (e.g., Gates et al., 2010; Burgener et al., 2021); for example, monsoonal precipitation amounts were likely higher along the eastern flanks of the Sevier Orogenic Belt during highstands of the Western Interior Seaway than during lowstands. There are thus numerous tectonic-climate feedbacks that likely played a role in structuring patterns of biodiversity in the Late Cretaceous.

Although not the focus of this paper, the latest Cretaceous cooling trend that is observed in the Maastrichtian has been proposed to explain the destabilization of mammalian (and potential other vertebrate) communities leading up the K-Pg boundary (e.g., Tobin et al., 2014; Wilson, 2014; Sprain et al., 2015). Thus, just as we propose that climatic

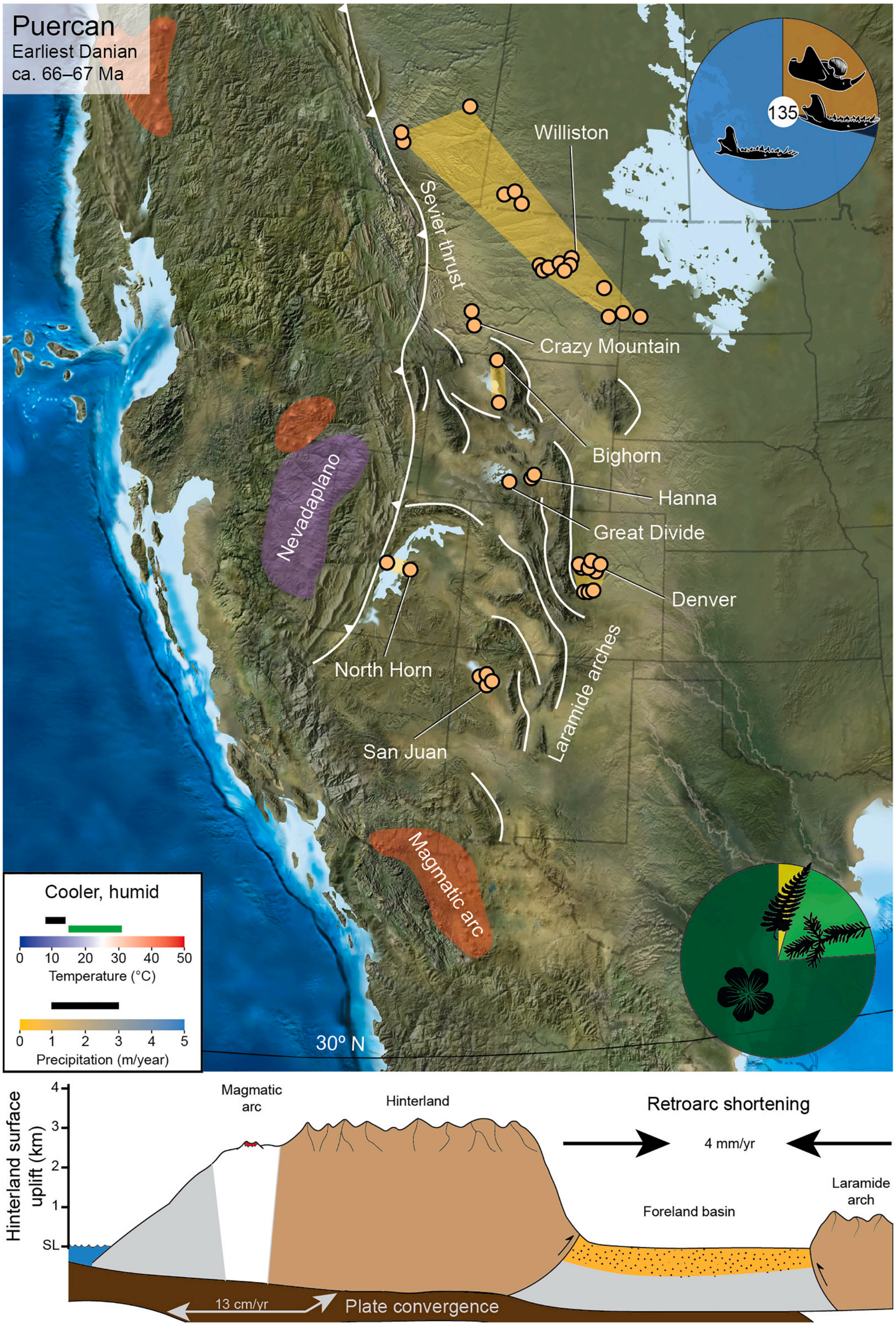

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Fig. 9. Map of mammal-bearing fossil localities (orange circles) from the Puercan NALMA (earliest Danian, ca. 66–65 Ma) in relation to their paleoenvironmental and tectonic setting (early Danian paleoenvironmental reconstruction map from Ron Blakey [Deep Time Maps]; Geographic location of mammal localities derived from the Paleobiology Database; Tectonic annotations derived from DeCelles, 2004, Yonkee and Weil, 2015, Balgord et al., 2021, and Weil and Yonkee, 2023). Leader lines and yellow polygons highlight mammal-bearing basins. **Top right**, relative species richness of major mammalian groups, with approximate total species richness in the center: Gold = Cimolodonta, Multituberculata; Dark Blue = Metatheria; Light Blue = Eutheria (from Lofgren et al., 2004, Silviria, 2019, and Weaver and Wilson, 2021). **Lower right**, approximate relative abundance of ferns (yellow-green), conifers (light green), and angiosperms (dark green) (Johnson, 1992). **Lower left**, temperature (top) and precipitation (bottom) estimates for this time period, with the bars representing reported ranges of temperatures or precipitation. Broad temperature categories (hot, warm, cooler) follow Huber et al. (2018), and broad precipitation categories (arid, humid) based on Benton et al. (2021). Temperature range in black derived from Huber et al. (2018) (same as Figs. 3–6) plus TEX$_{86}$ paleotemperature estimates from Linnert et al. (2014; Mississippi Embayment) and benthic foraminifera stable-isotope paleotemperature estimates from Barnet et al. (2018; South Atlantic); temperature range in green shows non-marine paleotemperature estimates derived from clumped isotope analysis of freshwater molluscs in the Fort Union Formation (Tobin et al., 2014) and the distribution of branched tetraether lipids from fossil peats in southern Saskatchewan (O'Connor et al., 2023). Precipitation range estimated via leaf-fossil traits from Johnson and Ellis (2002) and Flynn and Peppe (2019). **Bottom panel**, schematic of tectonic setting, including rate of North America-Farallon plate convergence, rate of retroarc shortening, and elevation of the hinterland (arc magmatism ceased with the onset of flat-slab subduction associated with the Laramide Orogeny). This schematic is not based on any specific transect; it a generalized west–east cross section of western North America. Tectonic data are derived from DeCelles (2004), Chapman et al. (2015), Yonkee and Weil (2015), Balgord et al. (2021), and Weil and Yonkee (2023).

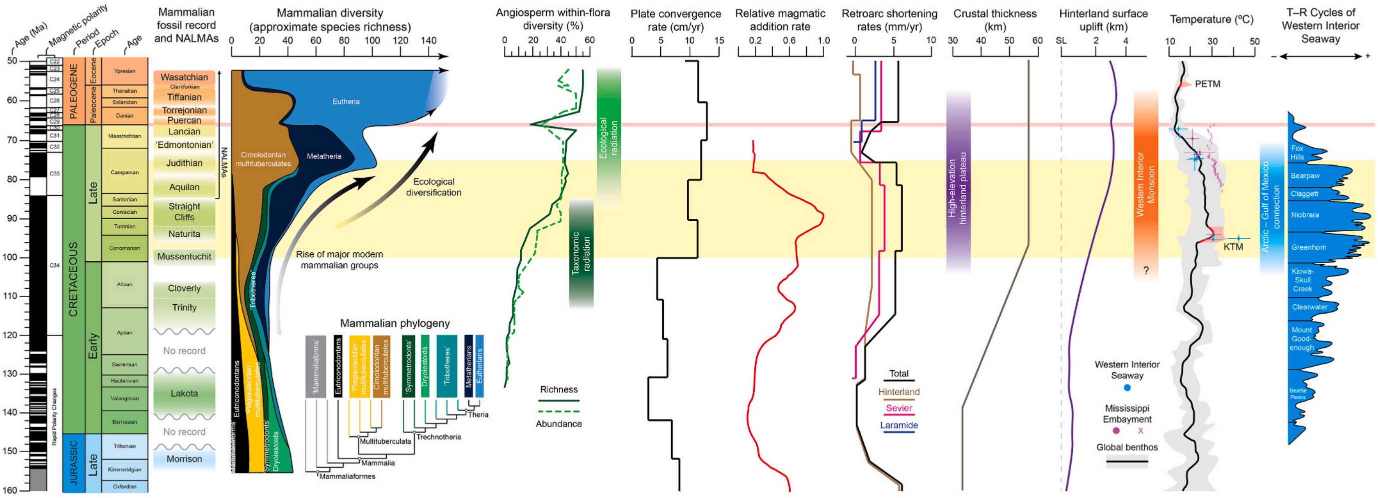

Fig. 10. Mammalian diversity patterns from the latest Jurassic through early Paleogene (ca. 160–50 Ma) of western North America in relation to (from left to right): (1) angiosperm within-flora diversity, (2) major tectonic processes associated with the Sevier and Laramide orogenies including the establishment of high relief between the Cordillera and foreland (approximated via crustal thickness) and formation of a high-elevation hinterland plateau (Nevadaplano), (3) global mean benthic and regional sea-surface temperatures, the establishment of monsoonal precipitation in the Western Interior, and (4) the transgression–regression (T–R) cycles of the Western Interior Seaway including the estimated duration of oceanic connection between the Artic and Gulf of Mexico. The red line indicates the Cretaceous–Paleogene boundary, and the yellow band highlights the temporal coincidence between mammal and angiosperm diversification, a flare-up of tectonic activity, the 'middle-Cretaceous greenhouse', and the high-stand of the Western Interior Seaway. Geologic time scale based on Walker et al. (2018). Major mammal-bearing formations and North American Land-Mammal 'ages' (NALMAs) based on Kielan-Jaworowska et al. (2004), Cifelli et al. (2004), and Lofgren et al. (2004). Mammalian species richness patterns were estimated from Bown et al. (1994; Wasatchian), Eaton and Cifelli (2001; Mussentuchit), Kielan-Jaworowska et al. (2004; Mesozoic), Lofgren et al. (2004; Puercan–Clarkforkian), Eaton (2006; Straight Cliffs), Eaton (2009; Naturita), Wilson et al. (2010; Lancian), Oreska et al. (2013; Cloverly), Cifelli et al. (2014; Lakota), Cifelli and Davis (2015; Cloverly, Trinity), Cifelli et al. (2016; Mussentuchit), Davis et al. (2016; Aquilan), Carneiro (2018; Naturita), Cohen (2018; Straight Cliffs stagodontids), Silviria (2019; Puercan eutherians), Weaver et al. (2019; mid-Cretaceous multituberculates), Cohen et al. (2020; Straight Cliffs metatherians), Weaver and Wilson (2021; Paleogene multituberculates), Weaver et al. (2021; Judithian multituberculates), and Davis et al. (2022; Morrison mammaliaforms)—note that eutherian species richness is much higher in the Wasatchian than is shown (> 400 spp.), indicated by the faded bar. Timing of the Late Cretaceous ecological diversification of mammals estimated from Wilson et al. (2012), Grossnickle and Newham (2016), and Grossnickle et al. (2019), and the mammalian phylogeny follows Luo et al. (2002). Angiosperm within-flora species richness and abundance modified from Lupia et al. (1999) for the Cretaceous and estimated from Wing et al. (1995) and Wing (1998) for the early Paleogene. Global mean temperature curve derived from benthic foraminifera and modified from Veizer et al. (2000), Zachos et al. (2001), Zachos et al. (2008), and Prokoph et al. (2008) (following Kergoat et al., 2014 and Benton et al., 2022), Western Interior Seaway temperatures modified from Petersen et al. (2016), Gao et al. (2021), and Jones et al. (2022), Mississippi Embayment temperatures modified from Meyer et al. (2018; circles) and Linnert et al. (2014; x's, derived from TEX$_{86}$), and the duration of the Cretaceous Thermal Maximum is based on O'Brien et al. (2017). Timing of the Western Interior monsoon based on Poulsen et al. (2007) and Fricke et al. (2010). North American-Farallon-plate convergence rates, retroarc shortening rates, hinterland surface uplift, and establishment of a high-elevation hinterland plateau modified from Yonkee and Weil (2015) and informed by DeCelles (2004), Sewall and Fricke (2013), Chapman et al. (2015), Paterson and Ducea (2015), and Balgord et al. (2021). Relative magmatic addition rate modified from Balgord et al. (2021), and crustal thickness modified from Chapman et al. (2015). Transgression–regression cycles of the Western Interior Seaway modified from Kauffman and Caldwell (1993). Artic-Gulf of Mexico connection informed by Blakey (2014).

warming likely contributed to the KTR, climatic cooling may have been an important contributing factor, along with the global deceleration of tectonism and the retreat of epicontinental seaways, to the purported increasing vulnerability of terrestrial ecosystems to a sudden and dramatic environmental perturbation (i.e., the 'press-pulse' hypothesis; e.g., Arens et al., 2014; Wilson, 2014).

3.2.5. *Were mountain passes 'higher' in the Late Cretaceous?*

One of the most salient hypotheses about the relationship between mountains, climates, and speciation is that mountain passes are 'higher' in the tropics, or simply the 'Janzen Hypothesis' (Janzen, 1967). In tropical climates, which experience a narrow range of diurnal and seasonal temperature variation, the warmer range of annual temperatures

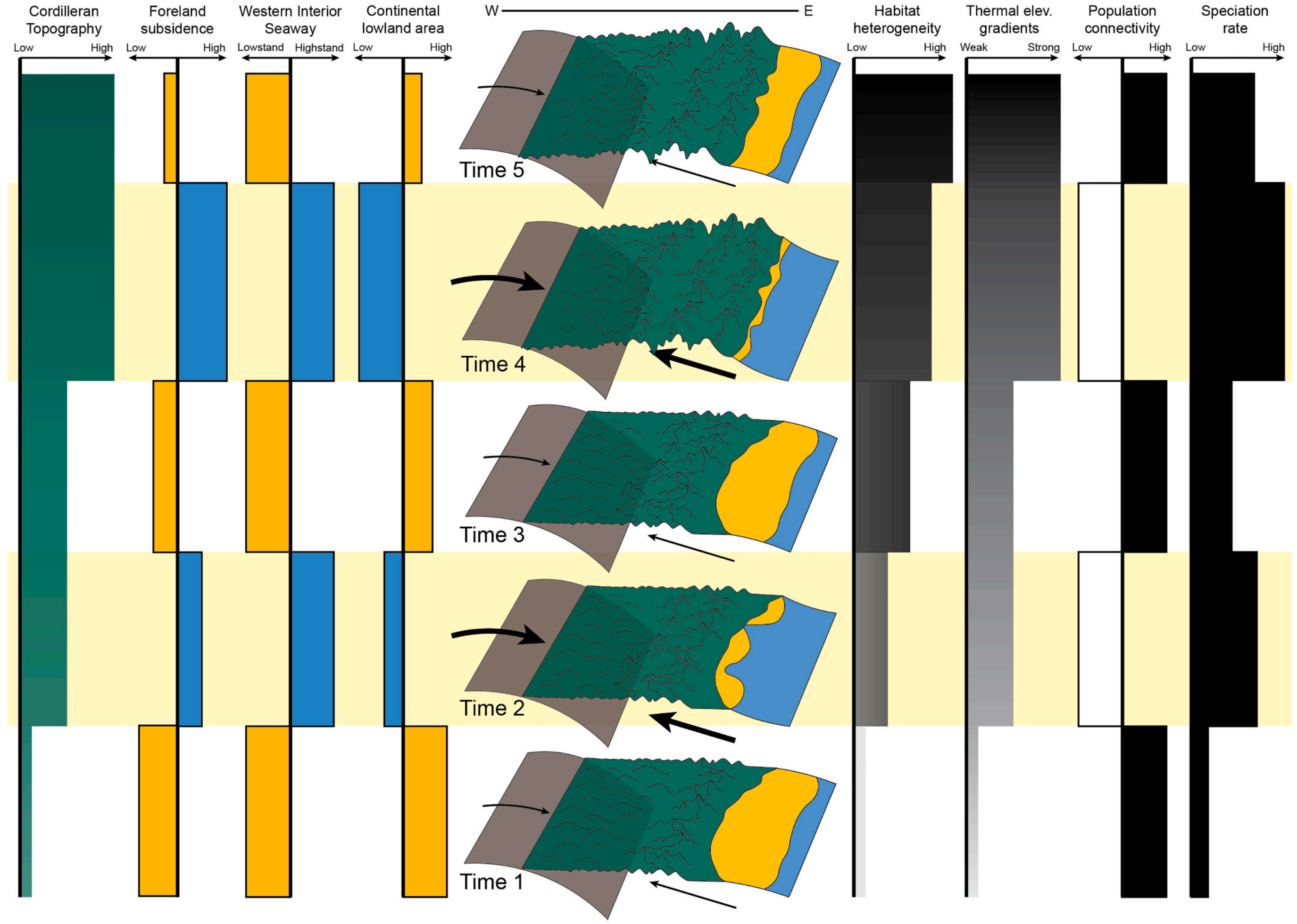

Fig. 11. Illustration of our proposal that mountain building created a 'perfect storm' for increases in biodiversity in the Late Cretaceous (here focusing on North America). With each pulse of Cordilleran topographic build-up to the west, foreland basin subsidence should increase, driving a transgression of the Western Interior Seaway and a decrease the available area of continental lowland habitats. As the foreland basin rebounded, the Western Interior Seaway regressed, and continental lowland area increased. As Cordilleran topography grew to the west, so did habitat heterogeneity and the strength of thermal elevational gradients. When the coastal lowland area was low, so too was population connectivity. Thus, speciation rates are expected to increase from Time 1 to Time 5, and to be highest following pulses of orogenic loading, when population connectivity was at its lowest (Time 2 and Time 4; see section '3.2 The Tectonic Catalyst Hypothesis' for details).

at low elevations never overlaps with the colder range of annual temperatures at high elevations; as such, organisms living in low vs. high elevations have narrower physiological tolerances, increased costs to dispersal along elevational and climatic gradients, lower gene flow among populations, and, as a result, narrower geographic ranges and higher rates of allopatric speciation compared to temperate taxa which, at both low and high elevations, experience substantial diurnal and annual variation in temperature and hence have broader physiological tolerances and dispersal capabilities (Janzen, 1967; Sheldon et al., 2018). Although some have challenged this hypothesis (e.g., Sklenář et al., 2023) or proposed that temperature is not the best mechanism to explain the dichotomy in tropical versus temperate montane diversity (e.g., Freeman et al., 2022 invoke interspecific competition), it has been supported empirically by studies of extant tropical versus temperate taxa in mountainous regions (e.g., Polato et al., 2018), and in the geologic past we see that tectonically active regions promote biodiversity more substantially during warmer intervals (e.g., Finarelli and Badgley, 2010; Smiley et al., 2018).

If mountain passes are indeed 'higher' in the tropics, then the relatively rapid rise of the Sevier Orogenic Belt during a greenhouse climate might have accelerated allopatric speciation in the Late Cretaceous of western North America. Whether global greenhouse climates are in fact more 'equitable' regarding seasonal variations in temperature is incompletely resolved (e.g., Hyland et al., 2018); there is some evidence for seasonal temperature variations in the Campanian on par with those in modern climates and in line with predictions from global climate models on land and in the ocean (e.g., Burgener et al., 2019; De Winter et al., 2021). Nonetheless, relatively high seasonality near the end of the Cretaceous could be a consequence of the late Campanian–Maastrichtian global cooling trend, whereas warmer climates from earlier in the Late Cretaceous apparently experienced much less seasonal temperature variation (Steuber et al., 2005). More Cretaceous continental paleotemperature data, especially from earlier in the Late Cretaceous, are thus needed to further explore whether the 'Janzen Hypothesis' played a role in stimulating speciation during the KTR.

3.2.6. *Recent analogues to the Cretaceous North American Cordillera*

The Andean Orogeny in northern South America is often cited as a recent analogue to the Sevier Orogeny in the North America Cordillera during the Late Jurassic through Late Cretaceous (e.g., DeCelles, 2004; DeCelles et al., 2009), and the role that Andean uplift played in stimulating biotic diversification in Amazonia is well documented (e.g., Hughes and Eastwood, 2006; Antonelli et al., 2009; Hoorn et al., 2010; Lagomarsino et al., 2016; Quintero and Jetz, 2018; Bedoya et al., 2021; Vallejos-Garrido et al., 2023). Andean uplift occurred over tens of millions of years, yet pronounced topographic growth accelerated near the end of the middle Miocene and proceeded rapidly through the remainder of the Cenozoic (e.g., Mora et al., 2010; Garzione et al., 2017), resembling in western North America the protracted growth of the North American Cordillera in the Late Jurassic through Early Cretaceous and its rapid uplift in the Late Cretaceous (e.g., DeCelles, 2004; Snell et al., 2014; Chapman et al., 2015; Yonkee and Weil, 2015). Andean uplift in the Miocene transformed northern South American landscapes from largely paludal to fluvial waterways, with Andean rivers delivering nutrient-rich sediments that later became fertile soils in the adjacent lowlands of western Amazonia (e.g., Quesada et al., 2009). It stands to reason that the rise of the North American Cordillera had a similar effect on western North American ecosystems in the Late Cretaceous. Increases in crustal thickening and concomitant surface uplift similarly transformed the continental landscape, spurring the inundation of the Western Interior Seaway into the continent and establishing a network of west-to-east-trending river systems that formed a latitudinally extensive coastal plain (e.g., Lawton, 1986; DeCelles, 2004; Rogers, 1998; Jinnah and Roberts, 2011; Hartman et al., 2014; Yonkee and Weil, 2015; Blakey and Ranney, 2017; Beveridge et al., 2020; Enriquez St. Pierre and Johnson, 2022; Rogers et al., 2023).

Changes to available continental lowland versus upland habitats in western North America during the Western Interior Seaway transgression-regression cycles of the Late Cretaceous resemble those in Sundaland (southeast Asia) during the glacial-interglacial cycles of the Pleistocene. The Indonesian Orogeny in Sundaland is another recent analogue to the Sevier Orogeny in western North America (e.g., DeCelles, 2004), and Sundaland is also one of the most diverse terrestrial regions on Earth today (e.g., Verma et al., 2020). Sundaland was a contiguous subaerial landmass during glacial maximums, but during interglacial periods, such as today, continental lowlands were flooded by shallow seas and mountainous regions were isolated as island archipelagos (e.g., Hanebuth et al., 2000; Voris, 2000). This expansion, contraction, and isolation of subaerial habitats has had a profound effect on terrestrial ecosystem structure and biodiversity in southeast Asia. For example, rainforests that were contiguous over much of Sundaland during glacial maximums became fragmented and isolated on island archipelagos during glacial minimums (e.g., Cannon et al., 2009), and the repeated expansion-contraction of lowland habitats during glacial-interglacial cycles apparently drove speciation and genetic divergence among many populations of small- to medium-bodied mammals (e.g., Campbell et al., 2004; Gorog et al., 2004; Campbell et al., 2006; Lucchini et al., 2005).

An inverted pattern to that observed in the Pleistocene rise and fall of sea level on Sundaland is that observed in the retreat and advance of glaciers in northern latitudes: continental lowland population continuity was highest during periods of glacial retreat and lowest during periods of glacial advance, which forced many populations into small refugia (but note that this pattern was reversed for montane species, which had higher population connectivity during glacial advance; e.g., Flantua and Hooghiemstra, 2018). These cyclical patterns in habitat connectivity had similarly pronounced effects on population connectivity and stimulated allopatric speciation or population divergence among terrestrial species (e.g., Hewitt, 1996; Flantua and Hooghiemstra, 2018; Morales-Barbero et al., 2018). In sum, frequent cyclical expansions and contractions of continental habitat promote speciation, and the tectonically induced oscillations of the Western Interior Seaway likely accelerated increases in biodiversity in the Late Cretaceous of western North America (Fig. 11) (see also Horner et al., 1992; Loewen et al., 2013).

3.2.7. *The role of angiosperms*

Whether the Late Cretaceous diversification of mammals (and terrestrial animals more broadly) was driven directly by changes to landscapes and climate or indirectly by tracking vegetational responses to those abiotic changes is difficult to disentangle. Most likely, both abiotic and biotic scenarios played a role in stimulating mammalian diversity, since modern small-bodied-mammal diversity patterns are strongly influenced by both topographic heterogeneity (e.g., Simpson, 1964; Badgley and Fox, 2000; Badgley, 2010; Badgley et al., 2018; Smiley et al., 2020) and vegetational structure (e.g., Stoddart, 2012; Chen et al., 2019). It is notable, however, that although mammalian ecological disparity increased substantially near the end of the Cretaceous, the most common and species-rich groups in western North America (e.g., neoplagiaulacid multituberculates, alphadontid metatherians) were small-bodied omnivores or insectivores (e.g., Wilson et al., 2012; Brannick et al., 2023). Only a handful of Late Cretaceous lineages expanded into larger body sizes and herbivorous dietary guilds (e.g., Wilson et al., 2012; Grossnickle and Polly, 2013; Grossnickle and Newham, 2016; Grossnickle et al., 2019; Cohen et al., 2020), and many taxa exhibited a trend towards greater carnivory rather than herbivory (e.g., Fox and Naylor, 2003; Wilson, 2013; Grossnickle and Newham, 2016; Wilson et al., 2016; Brannick and Wilson, 2020; Cohen et al., 2020; Brannick et al., 2023). Increasing topographic complexity (and its associated abiotic consequences) can therefore account for aspects of the Late Cretaceous mammalian radiation that newly emerging plant-based dietary resources alone cannot; namely, by increasing habitat and substrate heterogeneity, thus promoting locomotor and/or dietary niche partitioning over relatively small geographic areas (e.g., Badgley and Fox, 2000; Badgley et al., 2018). Nonetheless, the co-diversification of pollinating insects and increases in habitat complexity that attended the rise of angiosperms likely still provide, in part, a causal link between the ecological ascendency of angiosperms and increases in non-herbivorous ecological disparity among Cretaceous mammals (e.g., Wilson et al., 2012; Grossnickle and Newham, 2016). In sum, tectonism set diversification in motion, and cascading effects to landscapes, climate, and vegetation all likely coalesced to stimulate the rise of mammals in the Late Cretaceous.

3.2.8. *Preliminary quantitative tests of the Tectonic Catalyst Hypothesis*

That increases in both mammalian and angiosperm species richness during the Late Cretaceous were driven by increases in tectonic activity is supported by preliminary linear regression analyses (Supplementary Material). We find that mammalian species richness is significantly correlated with both relative magmatic addition rate and hinterland surface uplift (Supplementary Material), and angiosperm species richness is significantly correlated with hinterland surface uplift, plate-convergence rate, and crustal thickness (Supplementary Material). In contrast, global mean-annual temperature is a significant predictor of neither mammalian nor angiosperm species richness (Supplementary Material). These preliminary results reinforce the hypothesis that mammals and angiosperms were both responding to dynamic landscape changes in the Late Cretaceous and that climate change alone cannot explain changes in Cretaceous mammalian diversity.

4. Towards empirical tests of the tectonic catalyst hypothesis

We offer a series of predictions for the mammalian fossil record that follow from the hypothesis that accelerated tectonism catalyzed the Cretaceous Terrestrial Revolution (Fig. 12):

(1) Taxonomic and ecological richness should increase from the Early Cretaceous to the K–Pg boundary at a rate that is positively correlated with the rate of tectonic uplift.
(2) Mountain-proximal assemblages should have higher taxonomic and ecological richness compared to mountain-distal assemblages for any given time-slice from the Late Cretaceous onwards.
(3) Endemism should increase from the middle Late Cretaceous to the Paleocene as Laramide uplift formed montane barriers to dispersal in the Western Interior.

Implicit in testing these predictions is the assumption that fossil assemblages preserved in Cretaceous depositional environments can capture or reflect biodiversity generated in mountainous regions. High

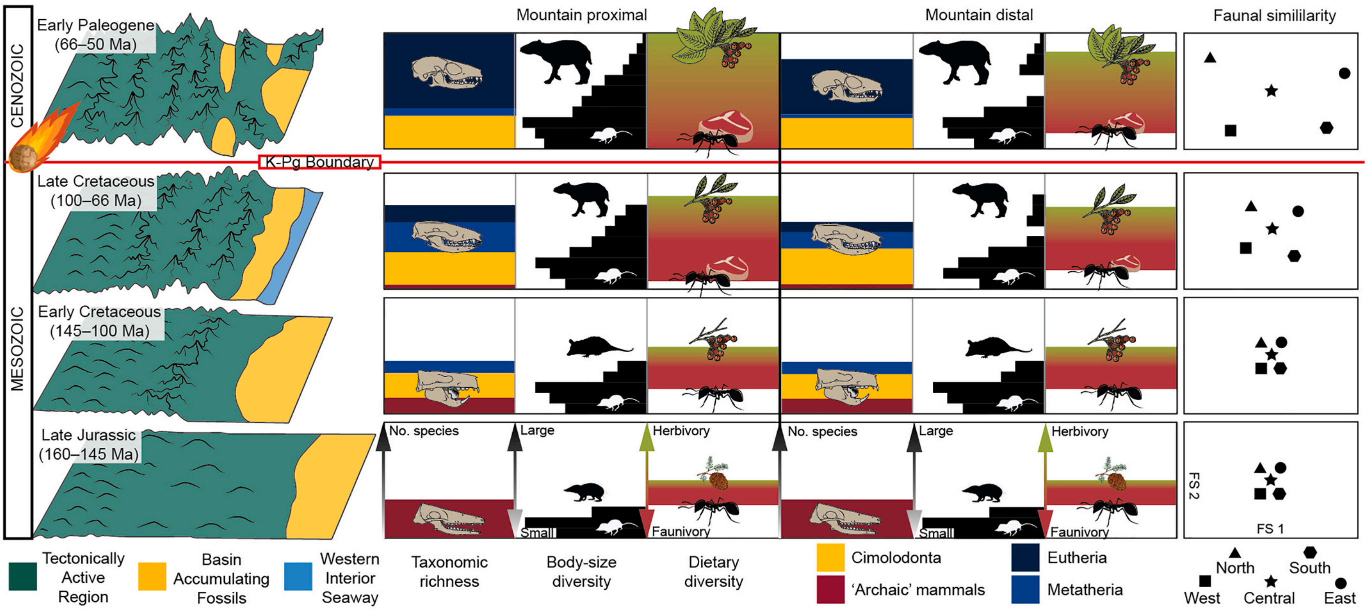

Fig. 12. Illustration of our predictions that follow from the Tectonic Catalyst Hypothesis, which can be tested at the level of individual basins. (1) Taxonomic and ecological richness should increase from the Early Cretaceous to the K–Pg boundary at a rate that is positively correlated with the rate of tectonic uplift, (2) Mountain-proximal assemblages should have higher taxonomic and ecological richness compared to mountain-distal assemblages for any given time-slice from the Late Cretaceous onwards, (3) Endemism should increase from the middle Late Cretaceous to the Paleocene as Laramide uplift formed montane barriers to dispersal in the Western Interior. Taxonomic richness corresponds to the height of the colored bars (which correspond to different mammalian groups). Body-size diversity is illustrated by histograms, with smaller taxa at the bottom and larger taxa at the top, and the left-hand width of the bar representing frequency of individuals (in an assemblage or local fauna) in a given (hypothetical) size bin. Dietary diversity is represented by a widening bar that represents an increasing range of diets on the faunivory–herbivory spectrum. The faunal similarity illustration is modeled after correspondence analysis plots, wherein different localities or regions plot in ordination space based on the faunal constituents (e.g., species) they share in common. In this illustration, FS 1 and FS 2 represent arbitrary faunal similarity axes, and the greater distance between points represents greater faunal dissimilarity.

elevation or montane paleoenvironments do not persist into the deep-time fossil record (e.g., Peters, 2006), but the biodiversity of lowland habitats, which can be detected in the fossil record, is still influenced by nearby mountains. For example, high-elevation mammals often have species ranges that extend into the adjacent lowlands (e.g., Badgley and Fox, 2000; Rahbek et al., 2019), and sediments shed from montane highlands promote a rich lowland biodiversity proximal to mountain ranges (e.g., Hoorn et al., 2010). Thus, a topographic diversity gradient among mammalian fossil assemblages should be detectable, with standing diversity increasing as a function of mountain uplift and mountain-proximal assemblages being more diverse than mountain-distal assemblages. Indeed, in the Paleocene paleobotanical record of the Denver Basin, floras close to the Rocky Mountain front range are much richer than those farther out on the Great Plains (Johnson et al., 2003). Although we predict that the topographic diversity gradient should be detectable among mammalian assemblages from the Late Cretaceous to early Paleogene, we expect that the strength of that gradient—meaning the relative difference between the taxonomic and ecological richness of mountain-proximal vs. mountain-distal mammalian assemblages—would change over time. Specifically, the strength of the topographic diversity gradient should (i) increase from the early Cenomanian to the middle Campanian as the Sevier hinterland reached its maximum elevation, (ii) level off from the middle Campanian to K–Pg boundary, and (iii) decrease in the early Paleogene as Laramide arches grew and created topographic relief in places that were previously coastal lowlands (i.e., the 'background' [or regional] diversity of mammals would increase in response to more broadly dispersed topographic complexity).

4.1. *The Way Forward*

Rigorous, empirical tests of these predictions will require (1) increased fossil-collecting efforts, especially in under-sampled regions and time intervals, (2) description and systematic study of existing collections, and (3) basin-scale integration of paleontological data with reliable records of topographic relief and attendant variation in temperature, precipitation, and alluvial sedimentation. The Cretaceous mammalian fossil record from western North America has greater temporal continuity and abundance of specimens than anywhere else in the world (e.g., Kielan-Jaworowska et al., 2004), yet addressing macroevolutionary questions like those posed here requires greater sampling, both stratigraphically and geographically. Stratigraphically, the Aptian-Albian through lower Campanian intervals are woefully under-sampled despite there being extensive outcrops of mammal-bearing formations throughout the Western Interior. For example, the Straight Cliffs Formation of Utah is essentially our only window into post-Cenomanian but pre-Aquilan mammalian faunas (e.g., Eaton and Cifelli, 1988; Cifelli, 1990a; Eaton, 1995; Cohen et al., 2020), yet other formations that are entirely or partly continental, such as the Frontier Formation of Montana and Wyoming, have been only cursorily explored. Geographically, the vast majority of Cretaceous (especially Late Cretaceous) mammal fossils come from localities from coastal lowland depositional environments (e.g., Clemens, 1964; Rogers et al., 2017), with mammals from more mountain-proximal, inland or upland paleoenvironments being known only from a handful of localities (e.g., Egg Mountain, Two Medicine Formation [Montellano, 1988; Montellano et al., 2000; Freimuth et al., 2021; Weaver et al., 2021]; Black Butte Station, Lance Formation [Donohue et al., 2013]). These stratigraphic and geographic gaps in our record of Cretaceous mammals are in part likely due to sparseness or low productivity of fossil localities from the middle Cretaceous and mountain-proximal regions. Indeed, those two gaps may be related since more upland, mountain-proximal environments are typically higher-energy depositional settings, which may preclude the dense accumulation of vertebrate fossils (e.g., Downey et al., 2021), and the availability of coastal lowland depositional environments was limited in the middle Cretaceous due to the highstand of the Western Interior Seaway. But although building substantial samples of mammalian fossils from these sparser stratigraphic intervals and geographic settings may be more laborious, the effort will inevitably yield new and exciting specimens and taxa and will enable us to investigate these earth-life processes in rigorous ways much deeper in the geologic past than ever before.

Detailed descriptions and alpha taxonomic studies of fossil collections have waned in recent years as computational advances have enabled more sophisticated analyses of data from the published literature and online databases (e.g., Nanglu and Cullen, 2023). Nonetheless, museum drawers are packed with unpublished specimens and, in some cases, entire collections from key stratigraphic or geographic windows, such as those described above (see section ‘2. Evolution of Terrestrial Ecosystems in Western North America’). Ultimately, testing of biogeographic and macroevolutionary questions requires solid primary data, and those primary data are the fossils themselves. The need for more descriptive, systematic, and phylogenetic studies in paleontology is not specific to Cretaceous mammals, but it is especially daunting in this context because, unlike mammalian assemblages from later in the Cenozoic, Cretaceous mammals are largely represented by isolated teeth and do not often have good modern analogues, so teasing apart generic, let alone specific, distinctions among a handful of tiny isolated teeth is challenging. To build a strong foundation upon which we can deploy computational analyses and hypothesis-testing, we must nevertheless prioritize systematic paleontology and bring to light the data already hiding in museum cabinets.

Deliberate and a priori integration of paleontological and geological data at the basin scale is the final necessary piece to explore how landscape and climate change influence macroevolutionary patterns in the fossil record (see also Maidment et al., 2021), and more broadly to illuminate the interplay between tectonic, climatic, and biological processes (e.g., Davies and Gibling, 2010; National Academies of Sciences, Engineering, and Medicine, 2020). Paleontologists, geologists, and evolutionary biologists have all emphasized in recent years the need for stronger integration between the earth and life sciences (e.g., Badgley, 2010; Hoorn et al., 2010, 2013; Mulch, 2016; Dolby et al., 2022). In the case of the hypothesis proposed here, it is necessary to integrate fossil data with (1) sedimentological and stratigraphic data to interpret depositional environments and terrestrial landscape heterogeneity, (2) geochemical data to infer paleoclimatic variables like mean and seasonal temperature and precipitation, as well as paleoelevation, (3) tectonic-proxy data to link changes in distal sedimentary basins to proximal mountain belts, and (4) geochronological data to correlate among these different datasets through time and space. Even among paleontologists, there needs to be a more integrated approach to uniting, for example, the vertebrate paleontological with the paleobotanical records. Interdisciplinary fieldwork efforts are an ideal way to achieve this sort of data integration, because experts in their respective fields can interact in real time on the outcrop and devise ways to merge what can otherwise be divergent approaches or objectives.

5. Conclusion

The Cretaceous Terrestrial Revolution marked the dawn of modern terrestrial ecosystems, with flowering plants, therian mammals, pollinating insects, and a host of other organisms diversifying rapidly in the lead-up to the K–Pg mass extinction. This flourishing of life near the end of the Cretaceous coincided with a tectonic revolution (e.g., Matthews et al., 2012; Balgord et al., 2021) that changed subduction-zone dynamics, accelerated plate motions, formed new mountain ranges, flooded continental interiors with shallow seas, and perhaps even induced climatic warming. That these two revolutions—one biotic, one abiotic—were linked should be expected. Continental drift can separate populations and promote continental endemism. Rising mountains increase habitat heterogeneity, steepen environmental gradients, and create barriers to dispersal. Waxing and waning epeiric seas modulate species distributions and drive populations into upland refugia, and warm climates promote high-latitude dispersal and speciation along elevational gradients. We contend that mountainous areas specifically were likely centers of biotic innovation in the Late Cretaceous, setting the stage for the ascendancy of modern terrestrial ecosystems in the Cenozoic, and the fossil records that accumulated at the feet of those mountains can provide glimpses into those cradles of biodiversity.

Here we have focused primarily on the mammalian fossil record of western North America, but the mechanisms that we pose as drivers of their Late Cretaceous diversification were likely at play for most terrestrial taxa around the world. The middle-to-Late Cretaceous (ca. 110–66 Ma) was a time of orogenesis globally (e.g., South America—Gianni et al., 2018, Horton, 2018; Europe—Zanchetta et al., 2012; Asia—Yin and Harrison, 2000; Africa—Andreoli et al., 2009, Gaina et al., 2013), likely related (at least in part) to the ‘100 Ma event’ (Matthews et al., 2012; Nelson and Cottle, 2018; Balgord et al., 2021; Pastor-Galán et al., 2021; Ma et al., 2022), and nearly every major continental landmass was flooded by waxing and waning epeiric seas (Cooper, 1977; Haq et al., 1987). The ‘middle-Cretaceous greenhouse’ climate and the Cretaceous Thermal Maximum were also global events (e.g., Poulsen et al., 2003; Huber et al., 2018). Thus, we expect that the Tectonic Catalyst Hypothesis proposed here can explain the onset of the Cretaceous Terrestrial Revolution in continental regions around the world. Further, although the focus here was on the mammalian and (to a lesser degree) angiosperm fossil records, the influence of mountain building on terrestrial biodiversity is a broader phenomenon (e.g., Hoorn et al., 2018; Rahbek et al., 2019); as such, we expect that the acceleration of tectonic activity in the middle–Late Cretaceous promoted diversification among most (if not all) terrestrial lineages, and the predictions outlined above for the fossil record of mammals could easily apply to, for example, the fossil records of plants, squamates, amphibians, dinosaurs, insects, and other groups. Nonetheless, we emphasize that empirically testing the Tectonic Catalyst Hypothesis will require invigorated efforts in fossil collection and study and concerted integration between paleontological and geological datasets.

Topographically complex and geologically active landscapes sustain the highest biodiversity on Earth, and the mechanisms that drive their generation and maintenance of species richness are not exclusive to the present or recent geologic past; instead, they have been at play for hundreds of millions of years, and have likely always been a major driver in shaping the distribution and diversity of life. Looking even further back in time, the diversification of early eukaryotes in the Paleoproterozoic Era (e.g., Porter, 2004; Javaux and Lepot, 2018), as well as the emergence of animals in the Neoproterozoic Era (e.g., Erwin et al., 2011), correlate with shifts in the types and diversity of igneous and metamorphic rocks (proxies for large-scale tectonic processes; e.g., Stern, 2018; Holder and Viete, 2023), increases in atmospheric oxygen (e.g., Kump, 2008; Lyons et al., 2014), and global glaciation (‘Snowball Earth’ events: e.g., Hoffman, 2013; Hoffman et al., 2017). These correlations support the provocative hypothesis that tectonic, climatic, and biological evolution are strongly tied across a range of temporal and geographic scales. Identifying and testing the role of mountain building in driving diversification events, however, becomes more difficult as we delve into the deep geologic past. Whereas landscapes formed in the last ca. 20 million years have rich fossil records and the availability of genetic data from extant lineages that allow us to more clearly test the relationship between geologic and biologic processes, the quality and abundance of both datasets decline the further back we go in geologic time as older continental deposits erode and diminish. Nonetheless, the mechanisms ascribed to tectonically mediated diversification have predictable corollaries that can be documented and tested even in spottier paleontological or geological records. By finding creative ways to examine the relationships between mountain-building and biodiversity in the geologic past we can more clearly illuminate the macroevolutionary processes that gave rise to the terrestrial ecosystems we see today.

Author contributions

LNW and CB conceived of the project, JRK provided expertise on paleoclimate, RMH and NAN provided expertise on tectonics, CB provided expertise on mountains and biodiversity, LNW provided expertise on the early mammal fossil record, and LNW wrote the manuscript and created the figures with substantial input from all coauthors.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data used here are drawn from the primary literature and are cited appropriately in the text. See 'Appendix A. Supplementary data' for more details.

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Appendix A. Supplementary data

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