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Using ecological niche modeling for quantitative biogeographic analysis: a case study of Miocene and Pliocene Equinae in the Great Plains

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Abstract.—The subfamily Equinae in the Great Plains region of North America underwent a dramatic radiation and subsequent decline as climate changed from warm and humid in the middle Miocene to cooler and more arid conditions during the late Miocene. Here we use ecological niche modeling (ENM), specifically the GARP (Genetic Algorithm using Rule-set Prediction) modeling system, to reconstruct the geographic distribution of individual species during two time slices from the middle Miocene through early Pliocene. This method combines known species occurrence points with environmental parameters inferred from sedimentological variables to model each species' fundamental niche. The geographic range of each species is then predicted to occupy the geographic area within the study region wherever the set of environmental parameters that constrain the fundamental niche occurs. We analyze changes in the predicted distributions of individual species between time slices in relation to Miocene/Pliocene climate change. Specifically, we examine and compare distribution patterns for two time slices that span the period from the mid-Miocene (Barstovian) Climatic Optimum into the early Pliocene (Blancan) to determine whether habitat fragmentation led to speciation within the clade and whether species survival was related to geographic range size. Patchy geographic distributions were more common in the middle Miocene when speciation rates were high. During the late Miocene, when speciation rates were lower, continuous geographic ranges were more common. Equid species tracked their preferred habitat within the Great Plains region as well as regionally throughout North America. Species with larger predicted ranges preferentially survived the initial cooling event better than species with small geographic ranges. As climate continued to deteriorate in the late Miocene, however, range size became irrelevant to survival, and extinction rates increased for species of all range sizes. This is the first use of ENM and GARP in the continental fossil record. This powerful quantitative biogeographic method offers great promise for studies of other taxa and geologic intervals.

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Introduction

The subfamily Equinae underwent a major radiation during the Miocene from one species, *Parahippus leonensis*, to 70 species, reaching its highest diversity during the middle Miocene (Clarendonian) with 13 named genera (MacFadden 1992; Hulbert 1993) (Fig. 1). The main interval of equid radiation coincides with the first major cooling event of the Miocene (Zachos et al. 2001), and the equid radiation has been classically attributed to an adaptive response following climate and vegetation change during the Miocene (MacFadden and Hulbert 1988; Hulbert 1993). As the climate became cooler and drier during the Miocene, vegetation shifted from woodland dominated to a mosaic of savanna and riparian forests that supported browsing, grazing, and mixed-feeding horses (Webb 1983). Following the radiation, members of the Equinae exhibit a variety of dental and muzzle morphologies as well as a diverse range of body sizes and limb proportions (MacFadden 1992). It has been previously hypothesized that this morphological diversity arose as equids with overlapping distributions partitioned their niches to exploit different resources as climate changed (MacFadden 1992; Webb et al. 1995). This diversity peak, however, did not last. The equid clade began to decline during the late Miocene, and by the middle of the Pliocene only three genera were extant (Hulbert 1988). Competition with other grazers

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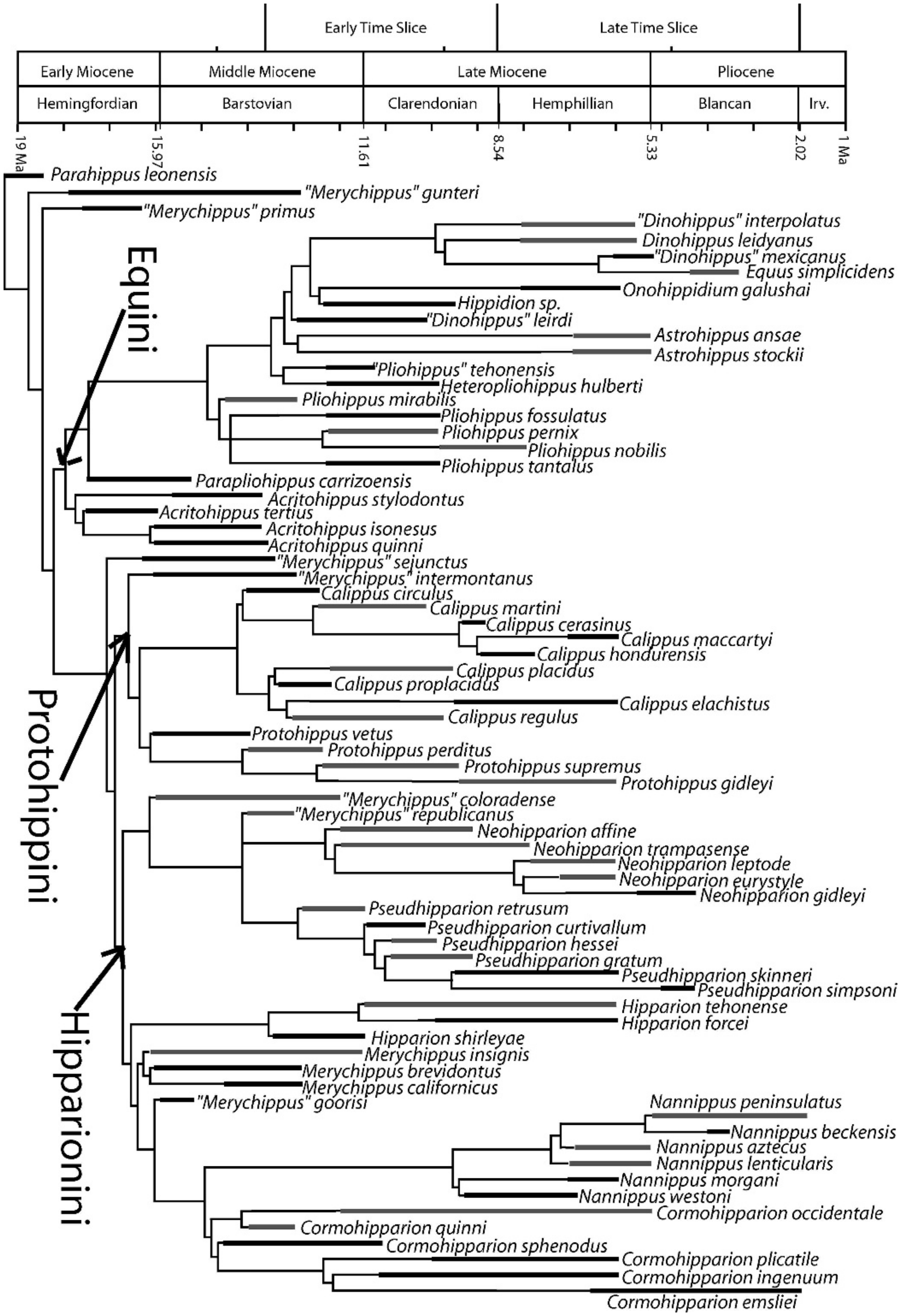

FIGURE 1. Temporally calibrated cladogram of Equinae modified from Maguire and Stigall (2008). Time slice divisions are indicated at the top. Narrow horizontal lines indicate ghost lineages, whereas bold horizontal lines indicate the recorded range. Thick gray lines indicate species whose ranges were modeled in this analysis.

(e.g., artiodactyls, rodents) was previously inferred to have caused the decline of the clade (Simpson 1953; Webb 1969, 1984; Stanley 1974), but it is now attributed to the continuation of cooling temperatures and more arid climatic conditions (MacFadden 1992; Webb et al. 1995).

Most paleobiogeographic studies of equids have focused on large-scale patterns, such as migration patterns from North America to the Old World (e.g., MacFadden 1992). Other paleobiogeographic studies have grouped equids with other Miocene mammalian clades to demonstrate general patterns, such as retreat to the Gulf Coast region as the climate became cooler and more arid in northern areas of North America during the late Miocene (e.g., Webb 1987; Webb et al. 1995). A more focused study examining the distribution of individual equid species can provide a framework in which to analyze habitat fragmentation, niche partitioning, and speciation. Because the radiation is hypothesized to have resulted from climate change, an integrated assessment of the ecology and biogeography is necessary to fully understand evolutionary patterns in the clade. Shotwell (1961) recognized this relationship in his study on the biogeography of horses in the northern Great Basin, in which he observed changes in species composition that coincided with vegetation change. Shotwell concluded that this shift resulted from immigration of equid species adapted to the new vegetative regime from other regions into the Great Basin.

Recent advances in understanding the phylogenetic relationships provide a more robust framework for new analyses. Furthermore, numerous recent studies have investigated the environmental and climatic conditions of the Great Plains during the Miocene. These studies comprise analyses of vegetation type (e.g., Fox and Koch 2003; Strömberg 2004; Thomasson 2005), paleosol composition (e.g., Retallack 1997, 2007), and climate proxies including stable oxygen and carbon isotopes of foraminifera from deep-sea cores (e.g., Woodruff et al. 1981; Zachos et al. 2001) that provide a rich source of environmental information previously unavailable for equid ecological biogeographic analyses.

Although the diversification of the Equinae is hypothesized to have resulted from climate change and ecological specialization, the interaction between individual species and environmental conditions has not previously been quantitatively analyzed. Here we reconstruct the geographic ranges for individual species of Miocene to early Pliocene horses in concert with environmental conditions to assess how changing climate and shifting habitats affected evolutionary patterns in the Equinae. In order to study the distribution of horses relative to ecological changes, we use ecological niche modeling (ENM). A species' ecological, or fundamental, niche is defined as the set of environmental tolerances and limits in multidimensional space that defines where a species is potentially able to maintain populations (Grinnell 1917; Hutchinson 1957). Determining the ecological niche of a taxon is essential in determining its potential distribution (Peterson 2001) as well as taxon/environment interactions. A species may potentially occupy the entire geographic region in which its ecological niche occurs; although biotic interactions, including competition and predation may limit a species range to a smaller ''realized niche'' (Lomolino et al. 2006). Because determination of these biotic interactions from the fossil record is rarely possible, we turn here instead to modeling species' ecological niches.

Ecological niche modeling is a GIS-based method in which species' environmental tolerances are modeled on the basis of a set of environmental conditions at locations where the species is known to occur. The species range is then predicted to occupy areas where the same set of environmental conditions occurs in the study region. Fundamentally, this approach directly utilizes sedimentary data to determine the likely distribution of taxa, thus providing a framework to examine interactions between abiotic and biotic factors that control species distribution and how these shift through time. ENM-based range prediction provides a framework to test hypotheses about similarities/differences in evolutionary and/or biogeographic patterns exhibited as climate and environments shifts through time (Stigall and Lieberman 2006; Stigall 2008). ENM methods were originally developed for modern taxa, and high levels of predictive accuracy have been documented (Peterson and Cohoon 1999; Peterson 2001; Stockwell and Peterson 2002). In particular, analyzing niche conservatism versus niche shifts in ecological time (e.g., Peterson et al. 2001, 2002; Nunes et al. 2007) and predicting the extent of species occurrences for conservation purposes (e.g., Peterson et al. 1999; Raxworthy et al. 2003) have been highly productive. The only prior use of ENM methods for the fossil record examined the geographic ranges of Late Devonian brachiopods in the north Appalachian Basin across the Frasnian/Famennian (Late Devonian) boundary (Stigall Rode and Lieberman 2005). Results of that study indicated that the computer-learning-based algorithms used in ENM have excellent potential to predict fossil species ranges from sedimentary parameters. This study uses the GARP (Genetic Algorithm using Rule-set Prediction) modeling system, a computer-learning-based analytical ENM package (Stockwell and Peters 1999). GARP has been successfully used with numerous modern mammalian studies investigating ecological and environmental questions (e.g., Lim et al. 2002; Illoldi-Rangel and Sánchez-Cordero 2004) and in studies of marine invertebrates in the fossil record (Stigall Rode and Lieberman 2005). This study represents the first application of ENM and GARP to fossil vertebrates. The fossil record of equids is densely sampled and abundant locality information provides a robust record of where each species lived in North America (MacFadden 1992). This clade, therefore, is an excellent candidate for ENM analysis. Direct mapping of species ranges from known occurrence points may underestimate a species' actual geographic range because of the inherent biases of the paleontological record (Kidwell and Flessa 1996; Stigall Rode 2005). More accurate ranges can be constructed by using ENM to model species ranges on the basis of known occurrence points and environmental parameters estimated from the sedimentary record (Maguire 2008).

In this study, the distribution patterns of individual species are examined to better constrain the rise and fall of the Equinae in relation to environmental and climatic change. We model ecological niches and predict geographic ranges in order to study how species' distributions shifted through time as a result of climatic and vegetative changes. Specifically, we test hypotheses that habitat fragmentation led to the diversification of the clade and that distributional patterns and range size affected the survivorship of individual species are tested.

Methods

Geographic and Stratigraphic Intervals

Geographic Extent.—The geographic distributions of equid species were reconstructed for each of two successive time slices during the middle Miocene through early Pliocene in the Great Plains region of North America (Table 1). The study area incorporated regions of the High Plains, as defined by Trimble (1980), which comprises northern Texas, western Oklahoma, western Kansas, Nebraska, eastern Colorado, southeastern Wyoming, and southern South Dakota (Fig. 2). Although equid species also inhabited regions of North America outside the study area, we focus our analysis on the Great Plains region because there is abundant published data on both the distribution of equid fossil material and the environmental setting of the region during the Miocene and Pliocene. To facilitate analysis of environmental data, we divided the study region into grid boxes of 1° longitude by 1° latitude (Fig. 2). Subdivision of geographic regions at this scale is standard procedure for ENM analyses of modern organisms (e.g., Stockwell and Peterson 2002; Wiley et al. 2003; Illoldi-Rangel and Sánchez-Cordero 2004), and modern environmental data are typically presented in this format. Environmental parameter data were collected for as many 1° grid boxes as possible from literature sources (Tables 2, 3, 4).

Climatic, Temporal, and Stratigraphic Framework.—Data were collected for two time slices (Barstovian–Clarendonian and Hemphillian–Blancan) in order to analyze the distribution of species through the climatic changes of the Miocene and Pliocene. Boundaries for each

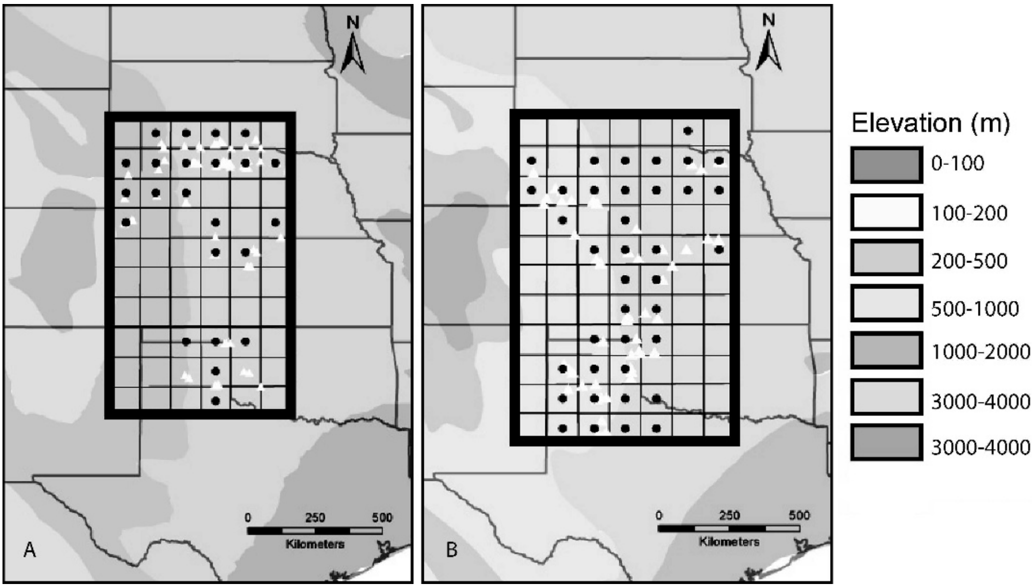

FIGURE 2. Study area overlain with 1° × 1° grid boxes illustrating the distribution of environmental data (black circles) and species occurrence data (white triangles) for the Barstovian–Clarendonian (A) and Hemphillian–Blancan (B) time slices. Base map indicates paleoelevation in meters, modified from Markwick (2007).

time slice (Table 1, Fig. 1) were based on changes in slope or directional reversals of temperature trends in the Cenozoic climate curve of Zachos et al. (2001). This climate curve is a compilation of global deep-sea oxygen and carbon isotope records of benthic foraminifera from over 40 Deep Sea Drilling Project and Ocean Drilling Program sites culled from the literature (Zachos et al. 2001) and is the Cenozoic climate curve most widely used in the literature (e.g., Barnosky and Kraatz 2007; Berger 2007; Costeur and Legendre 2008; Gamble et al. 2008; Williams et al. 2008).

The first interval examined in this analysis spans a 5.5 Ma interval from the middle Barstovian North American Land Mammal Age (NALMA), as temperatures began to drop dramatically following the Mid-Miocene Climatic Optimum (ca. 11.5 Ma), through the

TABLE 1. Species included in niche modeling analysis by time slice. Number in parentheses indicates number of spatially distinct species occurrences included in modeling analysis.

Barstovian–Clarendonian	Hemphillian–Blancan
Calippus martini (25)	*Astrohippus ansae* (9)
Calippus placidus (24)	*Astrohippus stockii* (7)
Calippus regulus (17)	*Cormohipparion occidentale* (8)
Cormohipparion occidentale (44)	*Dinohippus interpolatus* (12)
Cormohipparion quinni (12)	*Dinohippus leidyanus* (8)
Hipparion tehonense (11)	*Equus simplicidens* (19)
Merychippus coloradensis (12)	*Nannippus aztecus* (8)
Merychippus insignis (15)	*Nannippus lenticularis* (18)
Merychippus republicanus (18)	*Nannippus peninsulatus* (8)
Neohipparion affine (30)	*Neohipparion eurystyle* (27)
Neohipparion trampasense (5)	*Neohipparion leptode* (10)
Pliohippus mirabilis (11)	*Pliohippus nobilis* (9)
Pliohippus pernix (28)	*Protohippus gidleyi* (5)
Protohippus perditus (18)	
Protohippus supremus (26)	
Pseudhipparion gratum (37)	
Pseudhipparion hessei (10)	
Pseudhipparion retrusum (24)	

TABLE 2. Environmental variables studied and primary references.

1. Percent C_4 vegetation (stable isotope data based on tooth enamel* or paleosols†)
    - Fox and Fisher 2004*
    - Fox and Koch 2003†
    - Passey et al. 2002*
    - Wang et al. 1994*
    - Clouthier 1994*
2. Mean annual precipitation (MAP)
    - Damuth et al. 2002
    - Retallack 2007
    - Retallack unpublished data
3. Mollic epipedon
    - Retallack 1997
    - Retallack unpublished data
4. Ecotope
    - Axelrod 1985
    - Gabel et al. 1998
    - MacGinitie 1962
    - Strömberg 2004
    - Thomasson 1980, 1983, 1990, 1991, 2005
    - Wheeler and Mayden 1977
5. Crocodilian distribution
    - Markwick 2007

end of the Clarendonian NALMA. Stable oxygen isotope data from benthic foraminifera indicate falling temperatures during this time that fluctuated with an overall drop from 13°C to about 7.5–9.5°C (Cooke et al. 2008). This interval of global cooling was mediated by the formation of permanent ice sheets on Antarctica (Woodruff et al. 1981; Zachos et al. 2001; Rocchi et al. 2006; Lewis et al. 2007). Uplift of the Cordilleran region during the Miocene resulted in development of a rain-shadow effect, which in concert with the cooling temperatures, resulted in increased aridity in the Great Plains during the middle Miocene (Zubakov and Borzenkova 1990; Ward and Carter 1999). Mean annual precipitation fluctuated between 1000 mm and 500 mm during this period, with an overall trend of decreasing precipitation (Retallack 2007). Streams flowing eastward from the Cordillera deposited sediment on the Great Plains forming the Ogallala Group, an east-

TABLE 3. Environmental data for each grid box in the Barstovian–Clarendonian. MAP = mean annual precipitation. Values in parentheses indicate number of data points within the grid box. Coding for environmental variables as follows: Mollic epipedon: 1 = mollic, 2 = near-mollic, 3 = non-mollic. Ecotope: 1 = woodland, 2 = savanna with surrounding woodland, 3 = savanna, 4 = grassland/steppe. Crocodiles: 0 = absence, 1 = presence. Decimal values represent averaged values where multiple data points occur in a single grid box.

Long.	Lat.	% C_4	MAP (mm)	Mollic epipedon	Ecotope	Crocodilian presence
−102.5	43.5	-	-	-	3 (1)	-
−101.5	43.5	-	266.17 (1)	3 (1)	3 (11)	-
−100.5	43.5	-	-	-	-	0 (1)
−99.5	43.5	-	356.31 (17)	2.9 (17)	3 (9)	0 (1)
−97.5	42.5	13 (1)	-	-	-	1 (2)
−98.5	42.5	16 (3)	1590.65 (1)	-	2.5 (2)	1 (1)
−99.5	42.5	18.4 (6)	819.07 (4)	2 (3)	3 (7)	0 (3)
−100.5	42.5	10.6 (5)	519.57 (15)	2.1 (13)	3 (12)	1 (1)
−101.5	42.5	15 (1)	825 (1)	-	2.8 (4)	-
−102.5	42.5	16 (1)	-	-	-	0 (1)
−103.5	42.5	13.5 (3)	410.34 (9)	1 (8)	-	1 (2)
−104.5	41.5	-	325.86 (1)	-	-	0 (1)
−103.5	41.5	18.5 (2)	-	-	-	0 (1)
−102.5	41.5	28 (1)	479.59 (3)	2 (2)	2 (1)	-
−101.5	41.5	16 (1)	-	-	-	-
−98.5	40.5	0 (1)	1888.09 (1)	-	-	0 (1)
−100.5	40.5	23 (1)	-	-	-	-
−103.5	40.5	-	1143.92 (1)	-	1 (1)	-
−104.5	40.5	-	633.87 (1)	-	-	-
−100.5	39.5	21 (1)	402.61 (2)	2.5 (2)	2 (1)	-
−99.5	39.5	-	266.53 (1)	-	-	0 (1)
−99.5	37.5	-	-	-	-	-
−99.5	36.5	17.3 (3)	-	-	-	-
−100.5	36.5	18 (1)	825 (1)	-	-	1 (1)
−101.5	36.5	12 (1)	-	-	-	1 (1)
−100.5	35.5	5 (1)	-	-	-	1 (2)
−100.5	34.5	1 (1)	760 (1)	-	3 (1)	0 (1)
−101.5	33.5	29 (2)	-	-	-	-

TABLE 4. Environmental data for each grid box in the Hemphillian–Blancan time slice. Refer to Table 3 for explanation.

Long.	Lat.	% C_4	MAP (mm)	Mollic epipedon	Ecotope	Crocodilian presence
−98.5	43.5	59 (1)	323.53 (1)	-	-	-
−97.5	42.5	55 (1)	661.38 (2)	-	-	0 (1)
−98.5	42.5	15 (1)	486.91 (2)	-	-	-
−99.5	42.5	37 (3)	379.16 (5)	1.8 (5)	-	0 (1)
−100.5	42.5	0 (1)	393.11 (1)	2 (1)	-	-
−101.5	42.5	58 (1)	-	-	-	-
−103.5	42.5	12 (3)	533.87 (1)	-	-	-
−103.5	41.5	26 (2)	335.94 (6)	2.2 (6)	-	-
−102.5	41.5	27 (5)	349.42 (23)	2.5 (22)	2.7 (3)	-
−101.5	41.5	19 (2)	339.2 (5)	2.3 (4)	2 (1)	-
−100.5	41.5	-	275.54 (1)	-	-	-
−99.5	41.5	15 (1)	-	-	-	-
−98.5	41.5	21 (1)	-	-	-	-
−97.5	41.5	69 (2)	-	-	-	-
−100.5	40.5	12 (1)	820.2 (1)	-	-	-
−102.5	40.5	-	520.47 (1)	-	-	-
−101.5	39.5	-	646.52 (1)	-	4 (1)	-
−100.5	39.5	-	429.28 (17)	1.6 (16)	-	-
−99.5	39.5	-	365.76 (27)	2.3 (27)	2 (2)	-
−97.5	39.5	-	181.26 (1)	-	-	-
−99.5	38.5	-	252.52 (2)	3 (2)	-	-
−100.5	38.5	-	356.51 (27)	2.9 (27)	2 (1)	-
−100.5	37.5	38 (2)	503.01 (42)	2.5 (41)	-	0 (5)
−99.5	37.5	8 (1)	148.43 (1)	-	-	-
−99.5	36.5	4 (1)	-	-	-	0 (2)
−100.5	36.5	9.5 (2)	-	-	3 (1)	0 (3)
−101.5	36.5	-	-	-	-	1 (1)
−102.5	35.5	-	-	-	-	0 (1)
−101.5	35.5	37 (2)	-	-	-	0 (3)
−100.5	35.5	21 (1)	-	-	-	0 (1)
−99.5	34.5	-	-	-	-	0 (1)
−100.5	34.5	0 (1)	-	-	-	-
−101.5	34.5	43 (3)	-	-	-	0 (2)
−102.5	34.5	20 (1)	-	-	-	0 (1)
−102.5	33.5	11 (1)	-	-	-	-
−101.5	33.5	21.5 (2)	-	-	-	1 (3)
−100.5	33.5	-	-	-	-	0 (1)
−99.5	33.5	-	-	-	-	1 (1)

ward sloping wedge of coarse fluvial sediments that eroded from the Laramie and Front Ranges (Condon 2005). The Ogallala Group sediments include braided stream, alluvial fan, low-relief alluvial plain, and lacustrine deposits (Goodwin and Diffendal 1987; Scott 1982; Swinehart and Diffendal 1989; Flanagan and Montagne 1993).

The second time slice comprises 6.5 million years and includes the Hemphillian through the Blancan North American Land Mammal Ages and spans the Miocene-Pliocene boundary. Climate fluctuated during this interval, but an overall cooling trend continued. During the early Hemphillian, temperatures stabilized at approximately 8°C but then continued to decline, reaching a minimum of 4.5°C before rising back to 8°C by the end of the Miocene (Zachos et al. 2001; Cooke et al. 2008). This cooling was associated with increased aridity during the Miocene as mean annual precipitation dropped to 250 mm (Retallack 2007). During the early Pliocene, however, mean annual precipitation increased to approximately 1050 mm although temperatures continued to cool reaching modern temperatures (Chapin and Kelley 1997; Elias and Mathews 2002). Around 4 Ma, temperatures rose by 10°C, leading to the mid-Pliocene thermal optimum (Elias and Mathews 2002). Deposition of the Ogallala Group continued during the first half (late Miocene portion) of this time slice. Erosion of the western mountain ranges slowed during the Pliocene, and as deposition slowed, an unconformity formed above the Ogallala

Group (Condon 2005). Furthermore, the Great Plains region began to slowly uplift (Morrison 1987). As the region rose, sediments in the western Great Plains were eroded and either redeposited on top of the Ogallala Group or removed completely; however, sediments accumulated in Nebraska during the Pliocene due to its northeastward slope at the time (Steven et al. 1997).

Species Occurrence Data

Species occurrence data were collected from the primary literature as well as online databases (Miocene Mammal Mapping Project [MIOMAP]; Carrasco et al. 2005) and the Paleobiology Database [PBDB]). Species name, geographic occurrence (latitude and longitude), and stratigraphic position were recorded for each species assigned to the subfamily Equinae (see Supplementary Material online at http://dx.doi.org/10.1666/08048.s1:). Alroy's (2002, 2007) reidentifications of several specimens in the PBDB record were honored. The occurrence data were split into the two times slices described above. Although species occurrence data were collected for all species considered valid in recent phylogenetic hypotheses (e.g., Hulbert 1993; Kelly 1995, 1998; Prado and Alberdi 1996; Woodburne 1996) (Fig. 1), species with fewer than five spatially distinct occurrences in the study region per time slice were excluded from the analysis. This cutoff number has been determined from modeling experiments to be the minimum data required to produce robust ecological niche models using the GARP modeling system (Peterson and Cohoon 1999; Stockwell and Peterson 2002). A recent revision of *Cormohipparion* by Woodburne (2007) was not included in this study because that revision utilized highly typological species concepts that differ from all previous analyses.

Environmental Data

A variety of environmental factors (e.g., temperature, climate, vegetation, resource availability) may determine the ecological niche of a horse species. Although biotic competition may have played a role in further constraining the ranges of certain species, particularly species with sympatric ranges (e.g., *Calippus regulus*, *C. placidus*, and *C. martini*), it is not possible to model these interactions within a paleobiologic framework or with ENM methods. This analysis, therefore, focuses on reconstructing a species' fundamental niche and not its realized niche. To model fundamental niches of extinct species, environmental factors are estimated from sedimentological variables collected from the sedimentary record (Stigall Rode and Lieberman 2005). This study focused on five environmental parameters: percent C_4 vegetation, mean annual precipitation, soil type, ecotope, and crocodilian occurrence (a temperature proxy). Each of these parameters can be determined from the sedimentary record, either through fossils or directly from sedimentary deposits. The combination of these variables produces a robust data set of environmental and climatic factors that can be used to reconstruct the distribution of horse species. The use of five environmental variables is consistent with standard ENM methodology; analyses with the GARP modeling system have been successful with as few as four and as many as 19 environmental factors (e.g., Peterson and Cohoon 1999; Anderson et al. 2002; Feria and Peterson 2002). Although covariation among these environmental variables exists (e.g., ecotope and percent C_4 vegetation), GARP is not sensitive to covariation among environmental variables because it is a Bayesian-based system that produces accurate results for a wide range of domains, such as numerical function optimization, adaptive control system design, and artificial intelligence tasks (Stockwell and Peters 1999). Classical and parametric statistics, on the other hand, are sensitive to covariation within data and, therefore, are not applicable for this study. The five environmental parameters are discussed individually below, and data are presented in Tables 3 and 4.

Stable Carbon Isotopes.—During the Cenozoic, the dominant vegetation type shifted from enclosed forests with leafy shrubs and trees (C_3 plants) to grasslands (C_4 plants). This shift in vegetation created a mosaic of food sources for equid taxa during the Miocene, promoting a diverse range of morphological feeding adaptations in the Equinae clade (MacFadden 1992; Webb et al. 1995). The distribution of a species' food resource is the primary factor determining its ecological niche and geographic range (Fox and Fisher 2004; Lomolino et al. 2006). Carbon isotope composition ($\delta^{13}C$) can be used as a proxy for vegetation type (C_3 or C_4) in the Great Plains. C_3 and C_4 plants use different photosynthetic pathways (Calvin cycle and Hatch-Slack cycle, respectively) for fixing atmospheric CO_2 (Cerling and Quade 1993). Each pathway fractionates carbon isotopes to a different degree, producing nonoverlapping carbon isotope compositions. Modern C_3 plants exhibit a $\delta^{13}C$ range of −22‰ to −35‰ with an average of −27‰ (O'Leary 1988; Tieszen and Boutton 1989), whereas modern C_4 plants exhibit a range of −10‰ to −14‰ with an average of −13‰ (O'Leary 1988; Tieszen and Boutton 1989). A third pathway, crassulacean acid metabolism (CAM), results in carbon isotope compositions intermediate to the other two pathways, but it is primarily utilized by succulent plants in arid conditions (Cerling and Quade 1993) and uncommon in the study area.

Stable carbon isotope data included in this study were assembled from published literature sources that analyzed $\delta^{13}C$ primarily from paleosols (Table 2). Stable carbon isotope data from tooth enamel of equids and proboscideans were also used to supplement the larger paleosol data set (Table 2). The use of stable carbon isotope values from tooth enamel has been used as a vegetation proxy in previous analyses (e.g., Wang et al. 1994; Cerling et al. 1997; Passey et al. 2002). While we recognize that values from tooth enamel may be more indicative of diet type than of overall environment in certain taxa, we have combined stable carbon isotope data from multiple taxa in order to prevent bias in the data set. Studies of carbon isotopes in paleosols applied an enrichment value of +14–17‰ to all values according to Cerling et al. (1989, 1991). Enamel studies applied an enrichment factor of +14‰ to all values according to Cerling and Harris (1999). Published $\delta^{13}C$ values also control for the 1.5‰ decrease in the atmospheric composition of CO_2 that has occurred since the onset of human fossil fuel burning (Friedli et al. 1986). We used the results of Fox and Koch (2003) and Passey et al. (2002) to convert raw stable carbon isotope data into percent C_4 vegetation. Percent C_4 vegetation was used as an index of the vegetative composition. Low C_4 percentages are interpreted as predominantly leafy vegetation preferred by browsers, high percentages are interpreted as predominantly grassy vegetation preferred by grazers, and intermediate percentages represent vegetation preferred by mixed feeders.

Mean Annual Precipitation.—Rainfall would have directly influenced the vegetation and water resources available to equid species and thus represents a fundamental parameter of a species' ecological niche (e.g., Anderson et al. 2002; Illoldi-Rangel and Sánchez-Cordero 2004). Mean annual precipitation (MAP) values determined from paleosols, ungulate tooth size, and vegetation were compiled for analysis (Table 2). The depth of the Bk horizon in paleosols can be utilized to estimate MAP with the equation: $p = 137.24 + 6.45D - 0.013D^2$, where D is depth in cm (Jenny 1941; Retallack 1994, 2005). A second measure of MAP, which uses ungulate tooth size within a community, is "per-species mean hypsodonty" (PMH). Developed by Damuth et al. (2002), PMH is the average hypsodonty of the ungulate fauna divided by the number of all mammalian species present in a community (Janis et al. 2004). Lastly, we used MAP ranges interpreted from plant assemblages (Axelrod 1985; Thomasson 1980).

Mollic Horizon.—Soil horizons can provide information about precipitation, climate, and vegetation cover. As discussed above, these factors influence the distribution of species. Modern soils supporting grassy vegetation have a mollic epipedon, a surface layer consisting of dark organic clayey soil about 2–5 mm thick (Retallack 1997). In paleosols, mollic epipedons are recognized by common dark, thin, clayey rinds to abundant small rounded soil peds and by abundant fine root traces. In addition, fossilized mollic epipedons are nutrient-rich and often contain carbonate or easily weathered minerals. Retallack (1997, personal communication 2007) divided paleosols containing calcareous nodules from the Great Plains during the Miocene into three categories. The first category, mollic, contained all paleosols that adhered to the above criteria. The second category, near-mollic, was assigned to paleosols that had surface horizons with ''a structure of subangular to rounded peds some 5–10 mm in size, along with abundant fine root traces and darker color than associated horizons'' (Retallack 1997). Near-mollic epipedons are found under bunch grasslands of woodlands or under desert grasslands (Retallack 1997). The third category, non-mollic, was assigned to all other paleosols included in the study. This third group consisted primarily of paleosols similar to soils of deserts and woodlands (Retallack 1997). We coded the vegetation cover interpreted from the three categories of mollic epipedons as 1, 2, and 3, respectively.

Ecotope.—The fourth environmental variable included in this analysis is ecosystem type as determined from paleobotanical studies (Table 2). Although an extensive collection of paleobotanical occurrences and taxonomic descriptions exists in the literature, only studies that included a paleoenvironmental description were included in the data set for this analysis. These environmental descriptions were coded and divided into four categories:

1. Woodland (e.g., ''deciduous valley and riparian forests with scattered grasslands'' [Axelrod 1985])
2. Savanna or subtropical grassland with surrounding wooded areas (e.g., ''subtropical grassland with associated mesic and woody components'' [Thomasson 2005])
3. Savanna or subtropical grassland (e.g., ''grassland savanna'' [Gabel et al. 1998])
4. Dominantly grassland/Steppe (e.g., ''grassland, shrubs, with limited trees'' [Thomasson 1990])

Crocodilian Distribution.—In the fossil record, crocodilian occurrence has traditionally been used as a paleotemperature proxy (Lyell 1830; Owen 1850). Ecological analysis of modern crocodilians indicates that temperature is the most influential factor determining their distribution (Woodburne 1959; Martin 1984; Markwick 1996). The data set used in this analysis is derived from the comprehensive work of Markwick (1996, 2007). Markwick (1996) compiled a global database of vertebrate assemblages and used the distribution of crocodilians as a paleotemperature proxy from the Cretaceous through the Neogene. Markwick (1996) includes crocodilians that belong to the ''crown group'' (Alligatoridae, Crocodylidae, and Gavialidae families). The climatic tolerance of the modern American alligator, *Alligator mississippiensis*, was used as the minimum temperature tolerance of extinct crocodilians. *Alligator mississippiensis* can tolerate a mean temperature range of 25–35°C. Because crocodilians are well documented in the fossil record and Markwick (1996, 2007) includes vertebrate sites lacking crocodilians as a control group, crocodilian absences in his database are considered true absences. This study includes 95 assemblages from Markwick (2007) that fall within the study area. For this study, crocodilian presence and absences were coded 1 and 0, respectively.

Creation of Environmental Layers

For analysis of environmental data, the study region was divided into 1° grid boxes using latitude and longitude coordinates, as discussed above, and environmental parameters derived from the literature were assigned to the appropriate grid box. When multiple data points occurred in one grid box, the values were averaged to account for environmental variability. This method of intermediate coding has been successful with ENM analysis and is an effective method of representing environmental variability (Stigall Rode and Lieberman 2005). Raw data are included in the supplementary material.

Environmental data points for both time slices were imported into ArcGIS 9.2 (ESRI Inc. 2006). For each environmental variable we used four data points to create an interpolated surface using inverse distance weighting, a method that allows us to use a set of scattered points to assign values to unknown points. Each interpolated surface had a power of 3 (exponent of distance) and

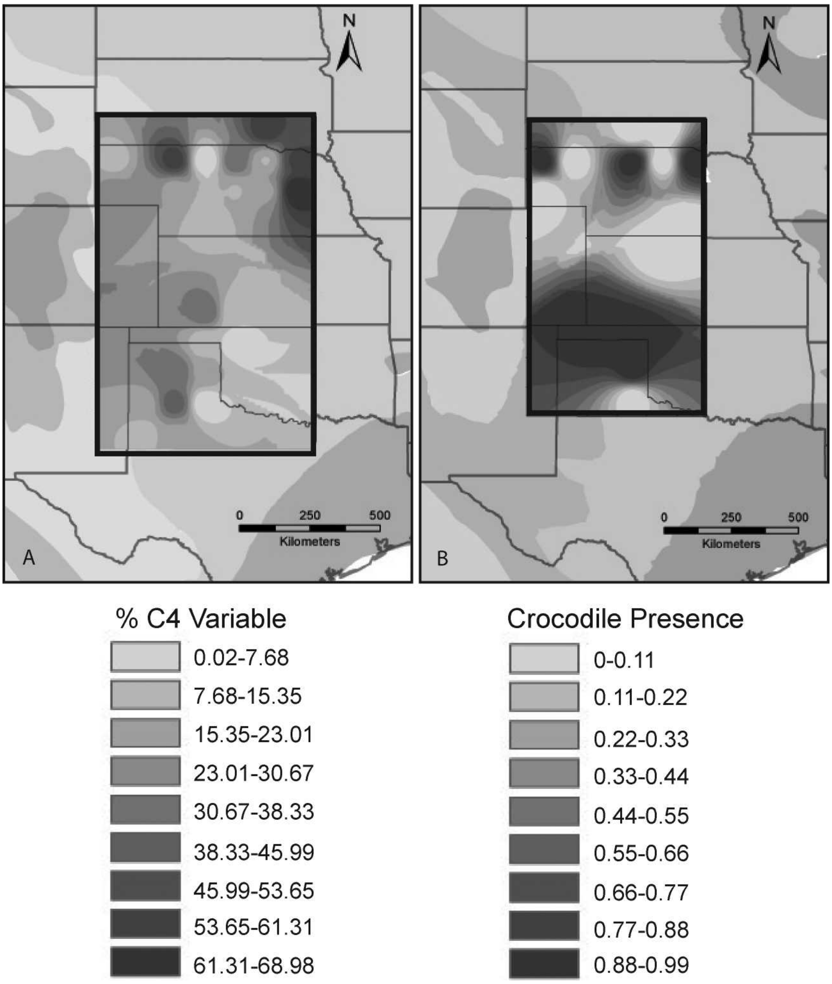

FIGURE 3. Examples of environmental variable interpolations. A, Interpolation of the percentage of C_4 vegetation derived from stable isotope data in the Hemphillian–Blancan time slice. B, Interpolation of crocodilian presence/absence data for Barstovian–Clarendonian; 0 = absence, 1 = presence. See Figure 2 for base map explanation.

an output cell size of 0.1° (8 × 11 km). Interpolation was based on four data points because this was the largest number of data points appropriate for interpolation that were available from all environmental data sets. The interpolated environmental area for the Barstovian–Clarendonian and the Hemphillian–Blancan time slices covered from 104°W,44°N to 98°W,34°N and from 104°W,44°N to 97°W,33°N, respectively. Examples of interpolated environmental coverages are shown in Figure 3.

Distribution Modeling

A genetic algorithm approach was chosen to model the distribution of Equinae species. Genetic algorithms have been successfully used in previous niche modeling analyses of paleontological data (Stigall Rode and Lieberman 2005) because genetic algorithms are effective for data sets with unequal sampling and poorly structured domains (Stockwell and Peterson 2002). Other statistical methods such as multiple regression and logistic regression, assume multivariate normality and true absence data. Because absence in paleontological data does not necessarily represent true absence and multivariate normality is unlikely with paleontological data, these methods are not suitable here. Genetic algorithms apply a series of rules in an iterative, evolving manner to the data set until maximum significance is reached (Stockwell and Peters 1999). GARP was specifically designed to predict a species' range from its fundamental niche as estimated from environmental variables (Peterson and Vieglais 2001). Another advantage of the GARP modeling system is that it was originally designed to accommodate for data from museum collections; in particular, GARP is able to analyze non-uniformly distributed, sparse, or patchy data (Peterson and Cohoon 1999; Stockwell and Peters 1999). Furthermore, covariance between environmental variables does not negatively affect the model's results (Stockwell and Peters 1999).

All species distribution modeling was performed using DesktopGARP 1.1.4 (www.nhm.ku.edu/desktopgarp). GARP is composed of eight programs that include data preparation, model development, model application, and model communication (Stockwell and Peters 1999). The GARP system divides the data in half to create two groups, the test group and the training group. A rule (e.g., logit, envelope) is randomly selected and applied to the training set. The accuracy of the rule is assessed by using 1250 points from the test data set and 1250 points randomly resampled from the area as a whole. The rule is then modified (mutated) and tested again. If accuracy increases, the modified rule is incorporated into the model; if not, it is excluded. GARP creates separate rule sets for each region within the study area, rather than forcing a global rule across the data. The resulting models are more accurate and precise than those using global rule methods (Stockwell and Peters 1999; Stockwell and Peterson 2002). The algorithm continues until further modification of the rules no longer results in improved accuracy or the maximum number of iterations set by the operator is reached (Stockwell and Noble 1992; Stockwell and Peters 1999).

Prior to performing the modeling analysis, the statistical significance of each environmental variable was tested using a jackknifing procedure. This was accomplished by selecting all combinations of rules and selected layers for the GARP analysis following Stigall Rode and Lieberman (2005). The five most abundant species from the Barstovian–Clarendonian time slice (*Cormohipparion occidentale*, *Neohipparion affine*, *Pliohippus pernix*, *Protohippus supremus*, *Pseudhipparion gratum*) were used in the jackknifing procedure. The contribution of each environmental variable to model error, measured by omission and commission, was analyzed using a multiple linear regression analysis in Minitab 14 (Minitab Inc. 2003). An environmental variable was inferred to increase error in the model if it was significantly correlated with either omission or commission. A multiple linear regression analysis was conducted for the five species in the Barstovian–Clarendonian time slice together as well as each individual species in the Barstovian–Clarendonian time slice. Although each environmental variable is significantly correlated with error with at least one species; no environmental variable contributed significant error in all species. All variables were therefore considered valid as environmental predictors and were included in the niche modeling analysis.

Niche modeling was performed individually for each species in each time slice. All rules and all environmental layers to be used were selected, and 500 replicate models were run for each species with the convergence interval set at 0.01. Training points were set to 50% as discussed above. The best subset selection was utilized so that the ten best models were chosen, with an omission threshold of 10% and a commission threshold of 50%. Range predictions were output as ASCII grids and the ten best models were imported into ArcGIS 9.2. The ASCII grids were converted into raster files and weight-summed to derive the final range prediction maps (Fig. 4). The geographic area occupied by each species was quantified for biogeographic analysis by using the Zonal Geometry Tool in the Spatial Analyst Toolbox of ArcGIS and then converting the number of rasters occupied into percent area occupied in km^2 (Table 5).

Examination of Distributional Patterns and Habitat Tracking

Habitat Fragmentation.—We analyzed the relative prevalence of patchy ranges, ranges

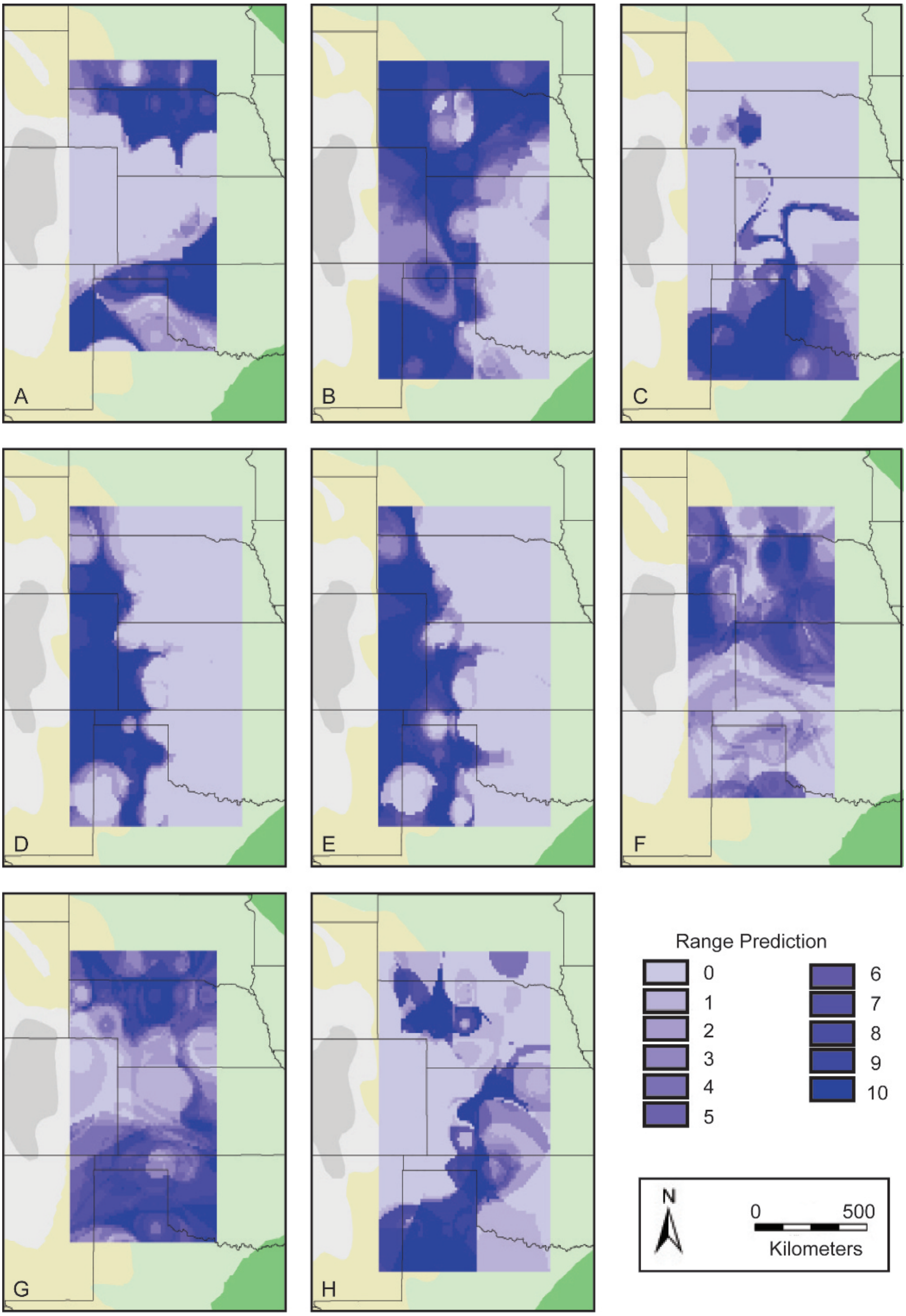

FIGURE 4. GARP predicted species distribution maps for *Pseudhipparion gratum* in the Barstovian–Clarendonian time slice (A), *Nannippus lenticularis* in the Hemphillian–Blancan time slice (B), *N. azetecus* in the Hemphillian–Blancan time slice (C), *Astrohippus ansae* in the Hemphillian–Blancan time slice (D), *Dinohippus interpolatus* in the Hemphillian–Blancan time slice (E), *Pliohippus mirabilis* in the Barstovian–Clarendonian time slice (F), *P. pernix* in the Barstovian–Clarendonian time slice (G), and *P. nobilis* in the Hemphillian–Blancan time slice (H). Color ramp indicates number of the ten best models predicting species occurrence.

TABLE 5. Geographic ranges predicted for species in the Barstovian–Clarendonian and Hemphillian–Blancan time slices from GARP modeling. Explanation of column headings and abbreviations: Area (km^2), total area of predicted species range. Coverage, percentage of the study region that is occupied by the predicted species range. Survivor, species survival. S, species survived the NALMA boundary. E, species went extinct by the NALMA boundary. Southern coverage, percentage of area below 39°N (Hemphillian–Blancan time slice) or 38.5°N (Barstovian–Clarendonian time slice) in the study region that is occupied by the predicted species range. No. of populations, the number of distinct populations within a predicted species range. NALMA boundary abbreviations: Bar, Barstovian; Clar, Clarendonian; Hemph, Hemphillian; Bla, Blancan.

Species	Area (km^2)	Coverage (%)	Survivor Bar/Clar	Survivor Clar/Hemph	Southern coverage (%)	No. of populations	Time slice
Cormohipparion occidentale	2.29×10^5	37.45	S	S	36.97	2	Bar–Clar
Calippus martini	2.32×10^5	37.88	S	E	44.83	2	Bar–Clar
Calippus placidus	2.64×10^5	43.07	S	E	50.07	3	Bar–Clar
Calippus regulus	9.15×10^4	14.93	S	E	7.13	4	Bar–Clar
Cormohipparion quinni	6.45×10^4	10.53	E	-	0.17	2	Bar–Clar
Hipparion tehonense	1.17×10^5	27.93	S	S	36.93	3	Bar–Clar
Merychippus coloradensis	6.76×10^4	11.03	E	-	0.00	3	Bar–Clar
Merychippus insignis	1.10×10^5	17.95	E	-	1.33	3	Bar–Clar
Merychippus republicanus	8.40×10^4	12.70	E	-	0.00	2	Bar–Clar
Neohipparion affine	1.67×10^5	27.25	S	E	12.93	3	Bar–Clar
Neohipparion trampasense	9.34×10^4	15.25	S	S	19.20	2	Bar–Clar
Pliohippus mirabilis	1.49×10^5	24.28	E	-	3.57	2	Bar–Clar
Pliohippus pernix	2.66×10^5	43.35	S	E	54.20	2	Bar–Clar
Protohippus perditus	1.52×10^5	24.76	E	-	6.10	2	Bar–Clar
Protohippus supremus	1.31×10^5	21.30	S	E	14.43	2	Bar–Clar
Pseudhipparion gratum	2.23×10^5	36.42	-	E	37.23	2	Bar–Clar
Pseudhipparion hessei	2.05×10^5	33.40	-	E	49.10	1	Bar–Clar
Pseudhipparion retrusum	6.83×10^4	11.13	E	-	0.00	3	Bar–Clar
Astrohippus ansae	2.35×10^5	29.33	-	S	31.27	1	Hemph–Bla
Astrohippus stockii	2.11×10^5	26.40	-	S	46.83	1	Hemph–Bla
Cormohipparion occidentale	2.58×10^5	32.21	-	S	36.47	1	Hemph–Bla
Dinohippus interpolatus	2.65×10^5	33.13	-	S	33.79	1	Hemph–Bla
Dinohippus leidyanus	3.11×10^5	38.87	-	S	22.52	1	Hemph–Bla
Equus simplicidens	2.82×10^5	35.30	-	-	52.00	3	Hemph–Bla
Nannippus aztecus	1.19×10^5	23.87	-	-	39.25	1	Hemph–Bla
Nannippus lenticularis	4.34×10^5	54.13	-	-	33.04	1	Hemph–Bla
Nannippus peninsulatus	2.00×10^5	24.96	-	-	39.25	1	Hemph–Bla
Neohipparion eurystyle	4.29×10^5	53.53	-	-	30.42	2	Hemph–Bla
Neohipparion leptode	3.67×10^5	45.80	-	-	36.62	2	Hemph–Bla
Pliohippus nobilis	2.24×10^5	28.00	-	S	33.45	1	Hemph–Bla
Protohippus gidleyi	2.64×10^5	32.91	-	S	29.12	1	Hemph–Bla

in which a species' distribution includes multiple discrete areas of occurrence, versus widespread continuous ranges. Habitat fragmentation has been hypothesized to contribute to the radiation of numerous clades (e.g., birds [Mayr 1942]; fishes [Wiley and Mayden 1985]; mammals [Vrba 1992]). If geographic patchiness did promote speciation in equids, species should exhibit a higher frequency of discrete patches in their predicted ranges during the Barstovian–Clarendonian time slice when speciation rates were higher (Hulbert 1993), than species in the Hemphillian–Blancan time slice, when the clade was in decline. For each species in each time slice, we counted the number of discrete populations or patches occupied (Table 5). The extent of a population or patch was defined by a contained area that did not have a geographic connection with a second population. The number of populations per species for each time slice was statistically analyzed using a two-sample *t*-test (Table 6).

Range Shift and Habitat Tracking.—Initial examination of range models indicated an apparent southward shift of species between the time slices, which we analyzed statistically. The study area for each species was divided in half along the 39°N latitudinal in the Barstovian–Clarendonian time slice time slice and the 38.5°N latitudinal in the Hemphillian–Blancan time slice. For both time slices, the percent area occupied by each species was calculated using ArcGIS (Ta-

TABLE 6. Two-sample t-test comparing number of discrete populations per time slice.

Source	Sample size (n)	Mean	Standard deviation	SE mean
Barstovian–Clarendonian	18	2.389	0.698	0.16
Hemphillian–Blancan	13	1.308	0.630	0.17

t statistic = −4.50.
$p = 1.154 \times 10^{-4}$.
d.f. = 24.

ble 5). A two-sample t-test was applied to determine whether species in the Hemphillian–Blancan time slice occupied a statistically larger portion of the southern region of the Great Plains than species of the Barstovian–Clarendonian time slice, indicating a range shift to the south (Table 7).

Only one species, *Cormohipparion occidentale*, was extant in both time slices. To determine whether the shifting distribution of *C. occidentale* from one time slice to another was a function of habitat tracking, the niche model for the Barstovian–Clarendonian time slice was projected onto the Hemphillian–Blancan time slice environmental layers (Peterson et al. 2001) (Fig. 5). If the resulting distributional pattern matches the original predicted distribution of *C. occidentale* for the Hemphillian–Blancan time slice, then *C. occidentale* tracked its preferred habitat from the Barstovian–Clarendonian time slice to the Hemphillian–Blancan time slice (i.e., niche conservatism). If the distributional patterns do not have a high degree of overlap, *C. occidentale* did not occupy the same niche in both time slices, and the species would be interpreted to have altered its fundamental niche through time (i.e., niche evolution). To determine whether the distributions were equivalent, the area of overlap and areal extent not shared were measured in ArcGIS and compared as a percentage of the total study area.

Examination of Species Survival versus Range Size.—Whether a general relationship between species longevity and predicted distribution area occurs was also assessed through regression analysis (Table 8). Specifically, we tested the hypothesis that species with larger range sizes live longer. The longevity of each species was determined from the literature as illustrated in the stratocladogram in Figure 1. We also examined the relationship between species survival across NALMA divisions and the geographic extent of a species' distributional range. Statistical analyses were performed for each Land Mammal Age division within the temporal extent of this study (Barstovian/Clarendonian, Clarendonian/Hemphillian, and Hemphillian/Blancan boundaries). Survival across the boundary was compared with the size of the species' predicted range. The area of each species range was determined within ArcGIS by calculating the sum of the areas in which seven or more of the ten best models predict occurrence (Table 5). Previous methods have summed three of the five best (Lim et al. 2002), six of the ten best (e.g., Stigall Rode and Lieberman 2005), or all of the ten best (Peterson et al. 2002; Nunes et al. 2007), so our approach is more conservative. Raw area counts were converted into percentage of total model areas for the time slice because the extent of the niche modeling area differs slightly between time slices (Table 5). A nonparametric statistical method, Kruskal-Wallis, was used to analyze the relationship between survival and area because the data

TABLE 7. Two-sample t-test comparing the area of a species' geographic range in the Southern Great Plains per time slice.

Source	Sample size (n)	Mean	Standard deviation	SE mean
Barstovian–Clarendonian	18	20.80	20.40	4.8
Hemphillian–Blancan	13	35.69	7.62	2.1

t statistic = −2.84.
$p = 0.009$.
d.f. = 23.

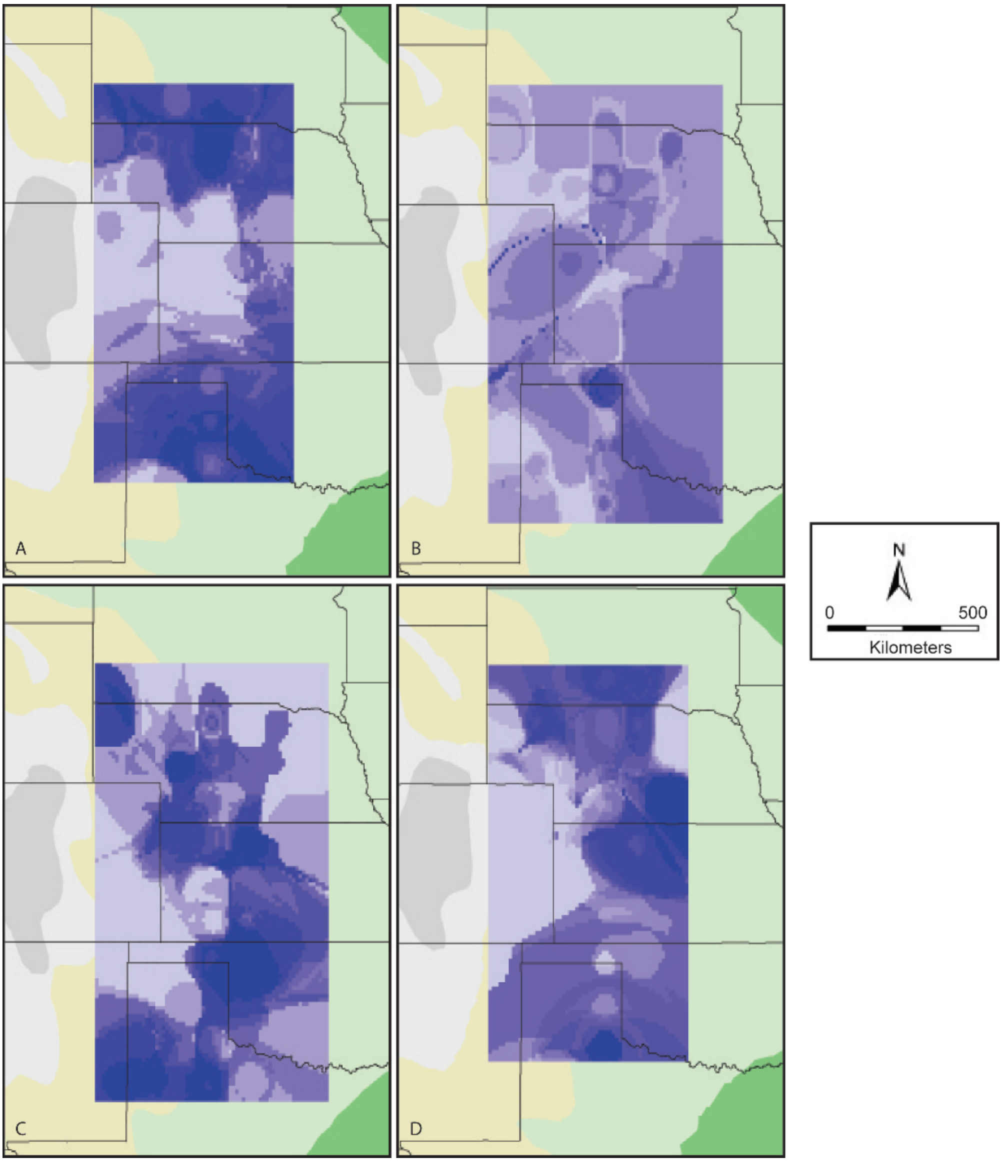

FIGURE 5. GARP predicted distribution maps. A, *Cormohipparion occidentale* Barstovian–Clarendonian model projected onto the Barstovian–Clarendonian environmental layers. B, *C. occidentale* range when the Barstovian–Clarendonian model is projected onto the Hemphillian–Blancan environmental layers. C, *C. occidentale* Hemphillian–Blancan model projected onto the Hemphillian–Blancan environmental layers. D, *C. occidentale* range when the Hemphillian–Blancan model is projected onto the Barstovian–Clarendonian environment.

are not normally distributed even after log, square root, and arcsine transformations were applied (Tables 9, 10).

Results and Discussion

Geographic ranges were modeled for 18 equid species from the Barstovian–Clarendonian time slice and 13 species from the Hemphillian–Blancan time slice (Table 1, Fig. 4). All modeled ranges are included in the online Supplementary Material.

Habitat Fragmentation

During the Barstovian–Clarendonian time slice, species ranges were divided into more discrete populations or patches than during the Hemphillian–Blancan time slice (two-sample *t*-test, $p = 1.15 \times 10^{-4}$) (Table 6, cf.

TABLE 8. Linear regression analysis of species longevity versus the area of a species' geographic range.

Predictor	Coefficient	SE coefficient	t	p
Constant	2.84	0.81	3.51	0.001
Area	0.01	0.03	0.43	0.670

Longevity = 2.84 + 0.01(Area).
SD = 1.66.
$R^2 = 0.6$.

Fig. 4A,F vs. 4B,E). The relative abundance of patchy habitats in the Barstovian–Clarendonian time slice correlates with the mid-Miocene interval of rapid cooling. Rapid cooling has been shown to promote local response of the plant communities resulting in fragmentation of the previously widespread woodlands into isolated patches (Vrba 1992). Speciation was high during the Barstovian–Clarendonian time slice and the Equinae reached its highest diversity at this time (MacFadden 1992; Hulbert 1993). Fragmentation of habitats would necessarily have resulted in patchy species distributions. This in turn would have promoted niche partitioning and speciation via vicariance, giving rise to the diverse group of mixed feeders, browsers, and grazers that inhabited the mosaic of vegetation in the Great Plains (Webb et al. 1995).

Environmental coverages of the Barstovian–Clarendonian time slice indicate an area of low precipitation, high percentage of C_4 plants, and an absence of crocodilians that spans the central part of the Great Plains (Fig. 3B). In several predicted ranges for the Barstovian–Clarendonian time slice, this area is unoccupied (e.g., Fig. 4A). The environmental coverages for the Hemphillian–Blancan time slice indicate a return to wetter conditions in this area and a more uniform environmental distribution throughout the study area. Chapin and Kelley (1997) reported increased precipitation in the Pliocene based on the establishment of drainage systems, the erosion of Mesozoic and Cenozoic sediments, the opening of previously closed basins, and stable isotope compositions of paleosol carbonates in arid lands. Modeled species ranges for the Hemphillian–Blancan time slice predict species occurrence in the central area resulting in more continuous ranges from the northern to southern part of the study area (Fig. 4B).

TABLE 9. Kruskal-Wallis test comparing the area of species' geographic range versus species survival across the Barstovian/Clarendonian boundary.

Source	Sample size (n)	Median	Average rank	Z value
Survive	9	27.93	11.1	2.49
Extinct	7	13.70	5.1	−2.49

$H = 6.19$.
$p = 0.013$.
d.f. = 1.

TABLE 10. Kruskal-Wallis test comparing the area of species' geographic range versus species survival across the Clarendonian/Hemphillian boundary.

Source	Sample size (n)	Median	Average rank	Z Value
Survive	9	33.40	10.0	0.40
Extinct	9	32.21	9.0	−0.40

$H = 0.16$.
$p = 0.691$.
d.f. = 1.

Increased continuity of species ranges of the Hemphillian–Blancan time slice may result partly from the spreading of grasslands ca. 6–7 Ma into wetter climatic regions (Retallack 1997). As grasslands spread throughout the Great Plains in the late Miocene and Pliocene, habitats became more homogeneous (Axelrod 1985; Webb et al. 1995). The available range for species adapted to open grassland and steppe habitats increased, promoting large continuous geographic distributions. Continuous ranges resulting from lack of geographic barriers between populations may have contributed to the reduced speciation rates observed within the clade (Hulbert 1993) by eliminating opportunities for geographic isolation by vicariance, a pattern previously observed in Late Devonian marine taxa (Stigall 2009).

Whereas the diversification of the Equinae has been attributed to habitat fragmentation and niche partitioning (MacFadden 1992), its decline has been attributed to the inability of species to adapt to climatic deteriorations during the late Miocene and Pliocene (Webb 1983; MacFadden 1992). In Hulbert's (1993) analysis of biodiversity overturn in Miocene to Pliocene Equinae, the observed high extinction rates in the late Miocene were coupled with low speciation rates that eventually decline to zero. Although climatic deterioration, as hypothesized by MacFadden (1992), may explain the increased rate of extinction, the increase in continuous habitat following the spread of grasslands, and the concomitant reduction in opportunities for speciation, likely contributed significantly to the observed reduction in speciation. Maguire and Stigall (2008) previously noted that speciation by vicariance occurred much less frequently in equids than in modern continental taxa (e.g., Wiley and Mayden 1985). Consequently, this additional reduction in the amount of vicariant speciation in the Equinae due to geographic continuity during the late Miocene and early Pliocene may have been influential in the decline of the clade.

Habitat Tracking

As temperatures decreased during the Miocene and the climate became more arid, several species adapted to woodlands and savannas rather than open grasslands retreated to warmer and wetter regions of North America, specifically the southern Great Plains and Gulf Coast regions (e.g., *Nannippus aztecus*, Fig. 4C) (Webb et al. 1995). Using data from carbonate nodules, Retallack (2007) identified a climatic gradient from warm and humid in the coastal regions to cool and arid in the northern Great Plains region. Species of Equinae in the Hemphillian–Blancan time slice of this study occupied larger ranges south of 38.5°N, than species of the Barstovian–Clarendonian time slice below 39°N (two-sample *t*-test, $p = 0.009$) (Table 7). This southward biogeographic shift indicates that species tracked their preferred habitat toward the south as climate changed more drastically in the northern regions of North America. This demonstrates the potential use of ENM and the fossil record as tools to track patterns of climate change and biogeographical responses. Further examination of morphological differences and dietary adaptations between species that migrated south and those that retained a northern range would further test this hypothesis. The southward range shift may partially result from the distribution of species occurrence points (Fig. 2). The early time slice has a higher concentration of species occurrence points in the northern part of the Great Plains, whereas the late time slice has a more even distribution of points across the Great Plains. Because the GARP algorithm is designed to analyze data from poorly structured domains including unevenly distributed species occurrence data (Stockwell and Peterson 2002), the uneven data distribution is unlikely to skew the resulting range predictions significantly. Furthermore, the distribution of occurrence points in the early time slice may in fact be an accurate representation of the distribution of Equinae species, and thus the more northern range of equids relative to the late time slice.

By the Hemphillian, the southwestern region of North America was semiarid and dominated by shrubland vegetation (Axelrod 1985). Many ungulates retreated from this region into the Great Plains (Webb et al. 1995). This included five species that were modeled in the Hemphillian–Blancan time slice: *Dinohippus leidyanus*, *Dinohippus interpolatus*, *Equus simplicidens*, *Astrohippus ansae*, and *Astrohippus stockii* (Maguire and Stigall 2008). Maguire and Stigall (2008) determined that speciation of these five taxa was a result of geodispersal across the Rocky Mountains from the Southwest to the Great Plains. Predicted geographic distributions of these five species are similar and occur predominantly on the western edge of the Great Plains region (Fig. 4D,E). During the Neogene, the uplift of the Rocky Mountains was interrupted by intervals of tectonic quiescence (Condon 2005). Consequently, during these intervals of quiescence and erosion, equid species could migrate across the Cordilleran region, whereas orogenic pulses resulted in barriers to species movement. The distribution patterns predicted from niche modeling supports the conclusion of Maguire and Stigall (2008) that speciation of these five species was a result of a cyclical geodispersal process as habitat tracking occurred across the Rocky Mountains during these tectonic cycles.

As mentioned previously, one species, *Cormohipparion occidentale*, was extant during both time slices. The species' predicted distributions for the Barstovian–Clarendonian and Hemphillian–Blancan time slices are illustrated in Figure 5A and 5C, respectively. Any ecological niche model, for example the Barstovian–Clarendonian time slice model, is based on the relationship between a species and its inferred habitat. Once the ecological niche of a species is quantified through GARP, it is possible to project the model of species occurrence onto either the set of environmental variables for the same time slice (which was conducted for all taxa in the data set) or a different time slice. To test for patterns of habitat tracking, the ecological niche model of *C. occidentale* developed from the Barstovian–Clarendonian time slice was projected onto the environmental layers of both the Barstovian–Clarendonian and Hemphillian–Blancan time slices, as illustrated in Figure 5A and 5B, respectively. Similarly, the ecological niche model developed from the Hemphillian–Blancan time slice environmental data for *C. occidentale* was projected onto both the Barstovian–Clarendonian and Hemphillian–Blancan time slices, as illustrated in Figure 5C and 5D, respectively. The percentage of overlap of the original projection and the new prediction in the second time slice indicates the extent to which the relationship between the species and its preferred habitat held constant between both time slices. The consistency of this relationship can be referred to as habitat tracking.

Projection of the GARP model for the Barstovian–Clarendonian time slice onto the environmental layers of the Hemphillian–Blancan time slice produced a distribution that covered 49% of the area originally predicted for the Hemphillian–Blancan time slice (Fig. 5B,C). This percentage of overlap suggests that *Cormohipparion occidentale* tracked its preferred habitat from the Barstovian–Clarendonian time slice into the Hemphillian–Blancan time slice. In addition, projection of the Hemphillian–Blancan time slice GARP model onto the Barstovian–Clarendonian time slice environmental layers produced a distribution that was 52% similar to the original distribution for the Barstovian–Clarendonian time slice (Fig. 5A,D). The predicted distribution maps show that during the Barstovian–Clarendonian time slice, the species' niche does not occupy the central region of the study area (Fig. 5A). In the Hemphillian–Blancan time slice, however, the predicted range does cover this central area, indicating that *C. occidentale* spread through this region as it tracked its habitat (Fig. 5D). Unlike other genera of Equinae, *Cormohipparion* migrated to the Old World during the Miocene (Skinner and MacFadden 1977; MacFadden 1992) possibly along with the genus *Hipparion* (but see Bernor and Armour-Chelu 1999). *Cormohippairon* was also one of the last genera remaining in North America at the end of the Miocene (*C. emsliei* survived in the coastal regions through the Blancan). The combination of its longevity and large range may be a result of its ability to track its preferred habitat when climate shifted.

Range Size versus Survival

A positive relationship between geographic range size and species longevity has been documented in many clades (Stanley 1979; Vrba 1987; Rode and Lieberman 2004; Hendricks et al. 2008). This relationship has not been quantitatively assessed in prior analyses of equid biogeography; however, this relationship can be analyzed statistically with the niche models constructed in this study. No significant relationship between predicted range size and longevity was recovered when all species ranges modeled from both time slices were combined in a single regression analysis ($p = 0.670$; Table 8). However, when the size of a species' geographic range was compared with survival or extinction across specific boundaries between NALMA divisions, a significant relationship emerged. The NALMA divisions (Alroy 2003) are based on first and last appearance data of all mammals in North America and are neither dependent on ''immigrant first appearance datum'' nor heavily dependent on geochronology data. Species living in the Barstovian that survived into the Clarendonian had statistically larger ranges than species that became extinct by the end of the Barstovian (Kruskal-Wallis test, $p = 0.013$; Table 9). Clarendonian species that survived into the Hemphillian did not have significantly larger ranges than species that became extinct (Kruskal-Wallis test, $p = 0.691$;

Table 10). Because only one species of Equinae modeled in this study had a stratigraphic range through the Miocene/Pliocene boundary, analysis of range size and survival from the Hemphillian to the Blancan was not possible.

The relationship between survival from one NALMA to another and species range size is likely related to changes in climate and vegetation during these intervals. During the Barstovian, temperatures dropped quickly from 13°C to 7.5–9.5°C (Zachos et al. 2001; Cooke et al. 2008). During this interval of climate change, vegetation cover was shifting and patchy. Under those conditions, the range size of individual species was related to survival into the Clarendonian. Range size is a function of ecological tolerance; consequently species with larger ranges were potentially more broadly adapted and better able to persist through the changing environmental conditions. The rapidly changing conditions, however, likely were too severe for those with smaller ranges and more restricted ecological tolerances to survive. During the late Miocene, however, species range size was irrelevant to survival. Temperatures continued to drop to approximately 2.3°C during the Clarendonian and Hemphillian, accompanied by decreasing MAP that reached 500 mm (Zachos et al. 2001; Retallack 2007; Cooke et al. 2008). Climatic deterioration became too severe even for those species with large ranges and broad ecological tolerances to survive.

Regional Trends

Although the Great Plains is analyzed as a case study for niche modeling because of its wealth of available data, equid species also inhabited other regions of North America during the Miocene. Dispersal between the Great Plains and other regions was frequent, and the resulting distribution patterns influenced speciation patterns within the clade (Maguire and Stigall 2008). One particular genus, *Pliohippus*, clearly demonstrates the relationship between regional patterns and local (ecological) patterns in the Great Plains region.

Pliohippus mirabilis occupied a patchy distribution in the Great Plains during the Barstovian–Clarendonian time slice (Fig. 4F) that covered 24.3% of the study area. *Pliohippus pernix* has been hypothesized to have evolved from *P. mirabilis* via anagenetic speciation (Hulbert 1993). The patchy pattern of *P. mirabilis* supports the interpretation that vicariance following habitat fragmentation could have led to the speciation of *P. pernix* from an isolated population of *P. mirabilis*. During the Barstovian–Clarendonian time slice, *Pliohippus pernix* occupied a continuous range throughout the Great Plains that covered 43.4% of the study area (Fig. 4G). This range is larger and more continuous than other ranges modeled for middle Miocene equid species and suggests that *P. pernix* may have been an ecological generalist. In fact, *P. pernix* dispersed into the Gulf Coast in the Barstovian–Clarendonian time slice, which further supports a generalist interpretation (Maguire and Stigall 2008). The populations of *P. pernix* that remained in the Great Plains are hypothesized to have evolved anagenetically into *P. nobilis* (Hulbert 1993). *Pliohippus nobilis* occupied a patchy predicted distribution in the Great Plains that covered 28% of the total area (Fig. 4H). Although *P. nobilis* occupied a predominantly southern distribution in the Great Plains, this species remained in the Great Plains during the late Miocene and did not disperse to other regions of North America. The patchy geographic range of *P. nobilis* indicates the limited extent of suitable habitat for the species in the Great Plains, potentially an ecological specialist. This ecological restriction may have prevented *P. nobilis* from migrating to other regions of North America, for example the Gulf Coast, and resulted in its extinction when its preferred habitat disappeared in the Great Plains during the early Hemphillian (Fig. 1).

The combination of regional and local distribution patterns provides a more complete picture of the biogeography and evolution of Equinae during the Miocene than either does alone. Here, *Pliohippus* provides an example of how the local distribution pattern is consistent with the regional pattern. These five species that migrated into the

Great Plains from the southwest are another example of how the local pattern supports the regional pattern. Their predicted western distribution pattern in the Great Plains suggests (Fig. 4D,E) that they or their ancestors dispersed from the southwestern region of North America, which is consistent with interpretations based on phylogenetic biogeographic analyses (Maguire and Stigall 2008).

Conclusions

The geographic ranges of middle Miocene equid species comprised a higher number of discrete populations than late Miocene–early Pliocene species. Diversification of the Equinae occurred just prior to the middle Miocene, indicating that high rates of speciation coincided with the distribution of patchy habitats. Habitat fragmentation resulted from changes in vegetation within the Great Plains as the climate cooled and became more arid. Following dramatic cooling in the Barstovian, species with larger ranges survived into the Clarendonian better than species with smaller geographic distributions. During the late Miocene, however, when temperatures were even cooler and the climate more arid, species range size was irrelevant to survival. The dichotomy between these intervals may reflect differential response of species to rate of climatic deterioration (rapid versus gradual) or that a climatic threshold had been passed during the Clarendonian that affected ecological specialists and generalists equally. Some species, such as *Cormohipparion occidentale*, exhibited niche conservatism (habitat tracking) within the Great Plains as the climate deteriorated. Other species, such as *Dinohippus interpolatus* and *Astrohippus ansae*, tracked their preferred habitats from the southwestern region of North America to the Great Plains, while others, such as *Pliohippus pernix*, tracked their preferred habitats from the Great Plains to the Gulf Coast (Webb et al. 1995). Within the Great Plains region, distribution patterns show invasion of species from the southwest and an overall southward migration of taxa from the Great Plains toward the Gulf Coast.

Species ranges were more continuous during the late Miocene to early Pliocene than during the middle Miocene. Continuous ranges may have led to a decrease in speciation rate of the clade due to lack of subpopulation isolation. Low speciation rate coupled with increased extinction rate from the deteriorating climate resulted in the decline of Equinae in North America. While hipparion genera such as *Cormohipparion* and *Pseudhipparion* became extinct in the Great Plains, species of these two genera did survive in the coastal regions of North America until the Blancan and Irvingtonian, respectively. The genus *Equus*, however, did survive into the early Pliocene on the Great Plains and was represented by one dominant species, *Equus simplicidens*. Further diversification of *Equus* began only after the hipparion lineages became extinct later in the Pliocene (ca. 2 Ma) (MacFadden 1992).

Finally, niche modeling of horse species in this study has produced a quantitative, detailed framework in which to analyze further hypotheses about the relationship between morphology, ecology, and evolution. Niche modeling of species ranges in additional regions, such as the Gulf Coast, would provide further insight into the final decline of the clade. In addition, correlating morphological characteristics of individual species with the environmental parameters of their predicted niches would provide more detailed information about niche partitioning and habitat tracking during the Miocene. For example, examining the muzzle morphology of species in this study that showed significant migration southward versus those that did not may demonstrate whether all species migrated south or only those not specialized in open grassland grazing.

This study is the first quantitative analysis of ecological biogeography using ENM in a vertebrate fossil clade. The combination of a densely sampled fossil record of Miocene equids and detailed sedimentological information available for the Great Plains allowed detailed quantitative projections of individual species' geographic ranges not attainable through traditional historical biogeographic methods. Results of this study support ENM as both an effective tool for modeling the ranges of fossil vertebrate species and one that allows analysis of biogeographic patterns within a hypothesis-testing framework. Detailed range models provide a robust framework to interpret changes in geographic range size and distributional patterns across a significant climatic change and can potentially allow additional analyses of fine-scale patterns of ecological resource utilization. This study, combined with the successful results of Stigall Rode and Lieberman (2005) using ENM to model marine invertebrate taxa, suggests that ENM, and specifically the GARP method, offers great potential to investigate the relationship between abiotic and biotic controls on species distribution in the fossil record across many clades and geologic intervals.

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