Niche modeling reveals lack of broad-scale habitat partitioning in extinct horses of North America

Abigail K. Parker[a,1,2,*], Brianna K. McHorse[a,b,2], and Stephanie E. Pierce[a,*]

[a]Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, 26 Oxford Street, Cambridge, MA, USA.

[b]Concord Field Station, Department of Organismic and Evolutionary Biology, Harvard University, Bedford, MA, USA

[1]Current address: Museum of Zoology and Department of Zoology, University of Cambridge, Downing Street, Cambridge, UK.

[2]Authors contributed equally

*Corresponding authors: Abigail K. Parker akp45@cam.ac.uk and Stephanie E. Pierce spierce@oeb.harvard.edu

Abstract

The classic traits of modern horses (Equidae) – large body size, high-crowned teeth (hypsodonty), and a single toe (monodactyly) – are often considered adaptations to grassland environments. However, extinct horses that varied in these three traits overlapped geographically for millions of years during the Miocene and Pliocene. It has been hypothesized that co-occurring horse species partitioned habitats, with large-bodied, hypsodont, and monodactyl equids dominating open grasslands, while equids with different combinations of traits lived in more wooded areas. We tested for the presence of broad-scale habitat partitioning by compiling a large database of North American horse fossil occurrences with data on trait state (body size, hypsodonty index, and toe number) and paleoenvironment (derived from paleovegetation records). Null modeling of niche overlap in each of the North American Land Mammal Ages of the Miocene and Pliocene revealed that taxonomic and trait-based groups show no differences in habitat occupancy. Cluster dendrograms visualizing niche overlap showed that some ecological guilds shared derived traits, but derived traits were not associated exclusively with grassland habitats. Trait values are not predicted by the proportion of grassland habitats in time bins. Further, the three traits show no co-evolution across the equid tree when corrected for phylogenetic relatedness. Together, these results suggest that the evolution of large body size, hypsodonty, and monodactyly in equids was not due to a shared selective regime in response to expanding grassland habitats; instead, these traits may have evolved separately, likely due to a variety of small-scale selective pressures acting across the variety of habitats present in the Miocene and Pliocene.

Keywords

- Equidae
- Paleoenvironment
- Monodactyly
- Hypsodonty
- Miocene
- Pliocene

1. Introduction

Extant horses (Equidae) are represented by a single genus of zebras, asses, and caballine horses. This lack of taxonomic diversity belies an evolutionary history that spans nearly 60 million years, a few hundred species, and nearly 50 genera (Prothero and Schoch, 1989; MacFadden, 1992). Equid evolution is historically explained by a shift from forests to grasslands over the course of the Miocene (approximately 23 – 5.3 Ma) that drove steady evolution of the hallmark traits of today’s horses: large bodies, high-crowned teeth for grazing (hyposdonty), and a single digit (monodactyly) on elongated legs (Marsh, 1873; Shotwell, 1961; Eronen et al., 2010; Orcutt and Hopkins, 2013). However, horse species that varied in these three traits overlapped geographically for millions of years (MacFadden, 1992). For example, the Bone Valley fauna of the late Hemphillian (approximately 5 Ma) had six sympatric horse species, four tridactyl (three-toed) and two monodactyl (MacFadden et al., 1999). The coexistence of sympatric horse species could have been supported by habitat partitioning, in which large-bodied, hypsodont, monodactyl equids dominated open grasslands, while equids with other combinations of traits lived in more wooded areas (MacFadden, 1992). Here, we test this hypothesis by quantifying niche overlap between trait groups to see if extinct horse species of North America partitioned habitats based on body size, tooth crown height, and digit state.

1.1 Derived horse traits

Increasing equid body size has been explained as a response to spreading grasslands because larger body sizes arose coincident with the expansion of grassland-savanna habitats (MacFadden, 1986). Grazing animals today often have larger body sizes than animals with other diets, possibly because grassy vegetation eaten by grazers has lower nutritional quality and takes longer to digest than leafy vegetation eaten by browsers (Gordon and Illius, 1994). As grassy vegetation spread in North America, competition with ruminant artiodactyls for higher-quality, more nutritionally-dense browse could have created a selective pressure for equids to increase in body size so that they could survive on grassy vegetation of lower nutritional quality (Janis et al., 2002). However, recent work has shown that selective pressure for larger body size may not have been necessary to produce the body size trends seen in Equidae. Shoemaker and Clauset (2013) found that over 90% of the changes in horse body size could be explained by diffusion-driven mechanisms of trait diversification, rather than by competition.

Hypsodonty is widespread and characteristic of horses since the Miocene, and their maximum hypsodonty level increased throughout the Miocene and Pliocene (Webb and Hulbert, 1986; Mihlbachler et al. 2011). Increased crown height has previously been seen as a response to the advent of grazing behavior in equids as grasslands began to spread in North America around the beginning of the Miocene (Stirton, 1947; MacFadden and Cerling, 1994). Grasses contain silica phytoliths that may abrade teeth, increasing wear and endangering individuals whose teeth have shorter crowns (McNaughton et al., 1985; Damuth and Janis, 2011). However, hypsodonty is not necessarily an indicator of a grazing diet; for example, analysis of carbon isotopes and tooth microwear of several species of hypsodont horses found evidence of grazing in small, tridactyl species, while monodactyl species of similar tooth morphology instead ate leafy browse (MacFadden et al., 1999). Additionally, it has not been shown that grass phytoliths abrade teeth; modern ungulates do not avoid eating grasses with phytoliths (Damuth and Janis, 2011). The idea that equid hypsodonty is an adaptation to grasslands is further undermined by the fact that the appearance of hypsodonty in North American equids lagged 4-10 million years behind the spread of grasslands inferred from phytolith data (Strömberg, 2006). A possible explanation for this observed lag comes from the "grit not grass" hypothesis, which argues that hypsodonty evolved later as aridity increased, leading to greater tooth wear as more gritty particles, such as dust, were ingested along with food (Jardine et al., 2012; Damuth and Janis, 2011; Strömberg et al., 2013).

Side toes in tridactyl horses have been hypothesized to confer stability on slippery or uneven substrates, prevent deep sinking in mud (Sondaar, 1968), or allow for agility in negotiating around obstacles in woodland or wooded savanna environments (Shotwell, 1961). Fossil tracks of *Hipparion* from the Pliocene of Tanzania show imprints of the side toes, supporting the hypothesis that the side toes acted to stabilize the foot when it was sliding in mud (Renders, 1984). The hoofs of reduced side toes would only touch the ground when the horse's full weight was on one foot, potentially giving it greater traction to maneuver around obstacles (Shotwell, 1961). In open grasslands, with fewer obstacles to dodge, the main requirement for locomotion has been hypothesized to be either for straight-line speed to escape predators (Shotwell, 1961; Simpson, 1961) or for increased efficiency in locomotion (Janis and Wilhelm, 1993). Because lower mass at the distal limb reduces inertial forces and allows for lower energy expenditure, elimination of the weight of the side toes could allow for faster and/or more economical running (Thomason, 1986). Reduced digits and an enlarged center metapodial may also have contributed to better resistance to the forces of locomotion at heavier body weights (Camp and Smith, 1942; McHorse et al., 2017). Shotwell (1961) suggested that the functional difference between tridactyl and monodactyl feet should lead to habitat partitioning in co-occurring horses with different toe numbers and that equids with more reduced toes lived in grassier habitats.

1.2 Study aim

Our primary aim was to characterize the environmental distributions of Miocene and Pliocene horses with different traits to determine if they lived in distinct habitats. If the expansion of grasslands drove the evolution of modern horse traits, including large body size, hypsodonty, and monodactyly, we hypothesized that horses with derived traits would be found in grasslands more frequently than contemporaneous horses with less-derived traits (i.e., evidence of habitat partitioning). To test this hypothesis, we used null modeling of ecological niche overlap between habitat types to test whether horses with more-derived and less-derived traits partitioned habitats. Further, we used visualizations of guild structure and trait evolution to examine the relationship among traits and between traits and the environment. If trait groups were living in different habitat distributions, we expected to see ecological guilds of equid genera with derived traits restricted to grassland habitats. At the spatial and temporal scale studied, our results question the assumption that equids with large body size, hypsodont teeth, or monodactyl limbs lived in grassier environments than their contemporaries.

2. Materials and methods

2.1 Equid occurrence data

Our dataset includes 7673 occurrences of horse fossils (Family Equidae) from North America, most identified to the species level, ranging in age from 55.8 Ma to Recent. In total, our dataset includes 39 genera and 210 species that range across the Miocene and Pliocene. Occurrence data were obtained primarily from the Paleobiology Database (n = 3,445) from a search on 3 February, 2016 for Family Equidae in North America and from the Miocene Mammal Mapping Project ("MioMap," Carrasco et al. 2005) (n=3,820), with the remaining occurrences (n = 408) coming from the following literature sources: Fraser and Theodor (2013), MacFadden et al., (1999), Mihlbachler et al., (2011), and Voorhies (1990). We updated the taxonomical assignment of every fossil occurrence in our database to a currently accepted genus/species. To ensure that occurrences present in both the Paleobiology Database and MioMap database were not counted twice, we deleted occurrences from the MioMap data which overlapped with Paleobiology Database occurrences in county, formation, and genus and also those occurrences from the same genus from locations less than 10 kilometers apart. Each occurrence was identified in time to a North American Land Mammal Age (NALMA). Of the 7673 total occurrences in our dataset, 4879 were assigned to NALMA time bins in the Miocene and Pliocene and were used in subsequent analyses. In the NALMAs considered, 3518 occurrences were assigned to paleoenvironments for EcoSimR analysis (see section 2.4). The dataset we provide here includes all occurrences irrespective of time/environment assignment in hopes of providing a potential database for future studies.

2.2 Trait data

2.2.1 Body Size: Body size reconstructions came from literature sources (MacFadden 1986, MacFadden and Hulbert 1990, Damuth 1990, Scott 1990, Hulbert 1993, Alberdi et al. 1995, Robinson and Redford 1986, fossilworks.org). For species with no published estimated body size, we reconstructed body masses using the regression equations from tooth measurements in Janis (1990) and Damuth (1990). For most species, we used regressions based on the length, width, and area of the first lower molar (m1) taking the average of 5 regression outputs: m1 length and area from Janis (1990) and m1 length, width, and area from Damuth (1990). For species without m1 measurements, we reconstructed body mass using the regressions from Damuth (1990) for length and width of the upper premolar 4 (P4), upper premolar 3 (P3), and upper molar 1 (M1) and for area of P4 and M1, taking the average of regression outputs from teeth with measurements available. Body mass values for each species and average values for each genus can be found in Supplementary Data. Regression equations are available in Appendix 1. In figures where body mass is treated as categorical, we defined the categories as small (under 100 kg), medium (between 100 and 200 kg, inclusive), and large body (over 200 kg). These assignments were determined based on data distribution, with similar numbers of genera in each bin; such evenly-spaced body mass bins have been used in past studies such as Martin (2016) and Ahrestani et al. (2016). Analyses of habitat partitioning by body size also tested other bin divisions (see section 2.4).

2.2.2 Tooth Morphology: Hypsodonty index (HI) is a measure of relative tooth crown height calculated by dividing molar crown height by the occlusal width of that tooth. We collected HI values associated with specific specimens and species and calculated an average value for each genus, using data from MacFadden et al. (1999), Mendoza and Palmqvist (2007), Mihlbachler et al. (2011), Cantalapiedra et al. (2017), and Christine Janis (unpublished data). These sources measured HI on the most unworn teeth available to avoid underestimating original crown height due to wear, and on the third molar whenever possible. In figures where HI is treated as categorical, we defined categories as brachydont (HI under 1.1), mesodont (HI between 1.1 and 3, inclusive), or hypsodont (HI over 3). In comparison to previous categorizations of hypsodonty based on HI, these divisions give a wide range to the mesodont state, reserving the hypsodonty category for very high-crowned taxa (Janis, 2008; Jardine et al., 2012). However, our analyses of habitat partitioning by crown height also tested other divisions between these categories, including those used by Jardine et al. (2012); these divisions are listed in section 2.4. HI values for each species/genus can be found in Supplementary Data.

2.2.3 Digit State: We established the number of toes for each genus (and for each species in the genera *Pliohippus* and *Dinohippus,* which comprise both tridactyl and monodactyl species). Each species and genus was assigned to one of the following four categories: semi-tetradactyl (having four toes on the front limbs and three toes on the hind limbs), tridactyl, variable tridactyl/monodactyl (for species in which this trait varies), and monodactyl. While all four categories were used in phylomorphospace and trait correlation analyses (see sections 2.6 and 2.7), only three of these categories were used in our habitat partitioning analyses because all of the semi-tetradactyl species went extinct before the time period examined (Miocene-Pliocene). In addition to toe number classification, we calculated Toe Reduction Index (TRI) values for 27 genera. TRI quantifies the extent to which the side toes are reduced in tridactyl horses; it is the ratio of the proximal phalanx lengths of the central toe (digit III) to the side toes (digits II and

IV), ranging from 0 in monodactyl horses to 1 if the side toes are equal in size to the center toe (detailed in McHorse et al., 2017). Comparison between digit categorical and continuous TRI values across the horse phylogeny demonstrates how TRI captures a more nuanced picture of digit reduction (Fig. 1). Digit categories and TRI values for each species/genus can be found in Supplementary Data.

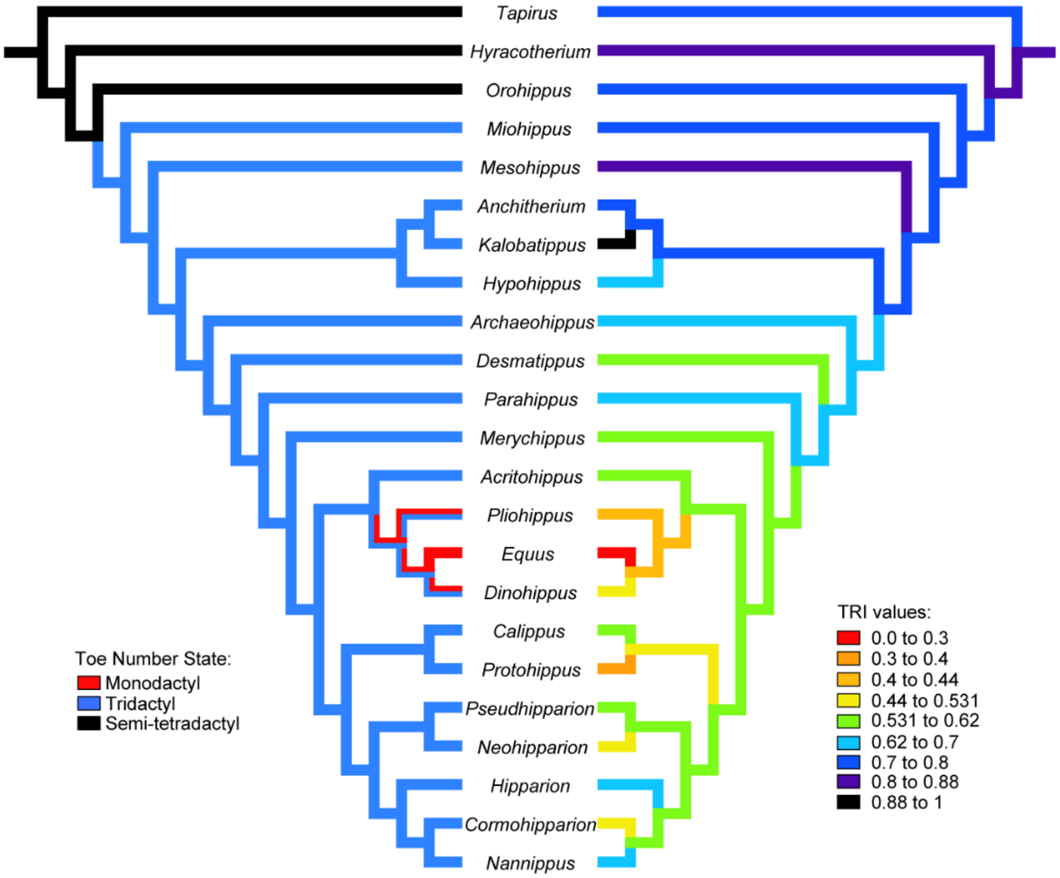

Figure 1: Phylogenetic distribution of digit stat vs. Toe Reduction Index (TRI). Left: a phylogeny of equids showing distribution of digit state (or number of toes). Right: the same phylogeny colored by TRI values, showing variation in side toe length. Cool colors indicate larger side toes, while warm colors indicate greater digit reduction with red denoting monodyactly. Phylogenetic topology adapted from Jones (2016) and Fraser et al. (2015). Traits mapped in Mesquite v.3.31 (Maddison and Maddison, 2017 using Parsimony Ancestral State reconstruction.

*full color, 1.5 columns

2.3 Habitat classification

Paleoenvironments for each fossil occurrence were determined from literature data on plant fossils, grass phytoliths, and paleosols. A list of all literature sources consulted to classify habitats can be found in Appendix 2, and the Supplementary Data lists the source paper used to assign the paleoenvironment of each occurrence in our database. Each equid occurrence site was assigned to one of seven paleoenvironment categories: forest/swamp, forest, woodland, woodland-savanna, savanna, grassland-savanna, and grassland. In general, the resolution of habitat classification was at the level of sub-regions of states. We avoided assigning habitat types from evidence based on mammal fossils, such as the inferences of grasslands based on hypsodont teeth, which are common in the literature, as this would be circular logic. In total, we classified the habitat present at deposition of 5,605 of the 7,673 fossil occurrences (73%); only occurrences assigned to paleoenvironments were used in the EcoSimR (section 2.4) and guild clustering analyses (section 2.5). The distribution of habitat classifications for each NALMA considered is shown in Figure 2. A range of habitats were present at the fossil sites from all NALMAs, indicating that no specific habitat characterized a particular time bin.

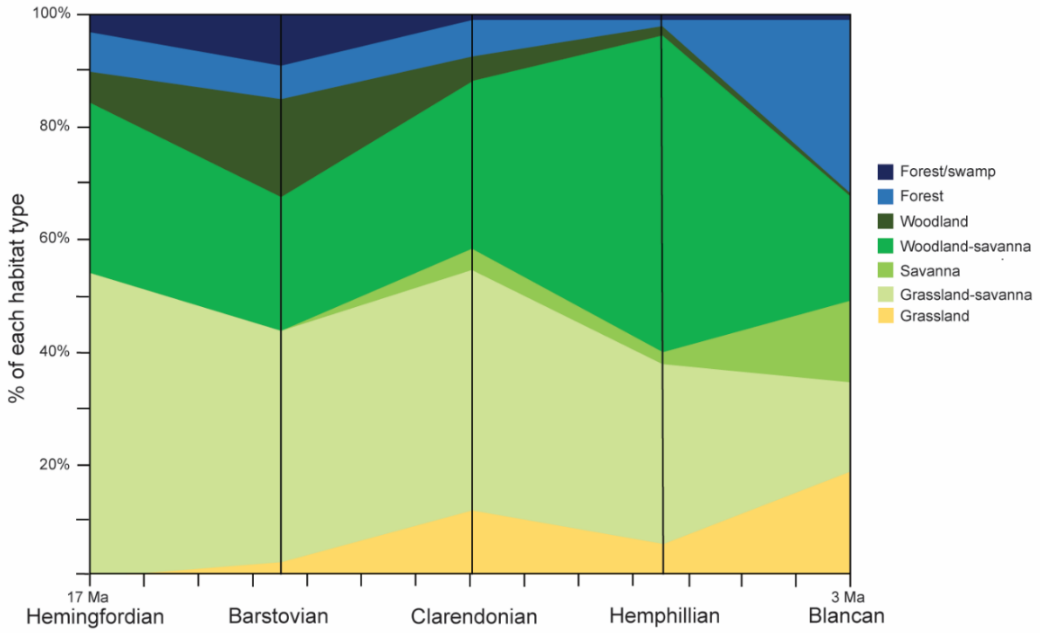

Figure 2: Paleoenvironment classifications of equid fossil sites through time. Stacked area graph showing the percentage of sites from our occurrence database classified into each habitat type for the five NALMAs analyzed.
*full color, 1 column

2.4 EcoSimR analysis

Habitat partitioning among extinct horses was assessed using the program EcoSimR (Gotelli et al. 2015). This program uses null modeling on an occurrence matrix to compare the average amount of niche overlap between pairs of taxa to the amount of overlap expected by random chance. The null model forms randomized matrices by shuffling the values in each row and calculates the niche overlap between rows. Comparing the average niche overlap between habitat categories of the randomly simulated matrices to the actual, observed overlap reveals whether the equids' community structure has more or less sharing of resource states than would be expected if each taxon used all resources randomly (i.e., no habitat partitioning). Here, niche overlap means the extent to which different groups share their distribution across the seven paleoenvironment types to which occurrences were assigned. It should be noted that we are not considering niche partitioning in the *sensu stricto* division of resources within a community, as equid groups across all of North America throughout entire NALMAs were not in direct competition with one another. Rather, our approach examines broad-scale habitat partitioning across NALMAs to better understand if equids with varying traits lived in similar or different habitat types across evolutionary time.

EcoSimR calculates the niche overlap between each pair of taxa or trait groups by using the Czekanowski Index. This index, formulated by Feinsinger et al. (1981), is calculated using the equation:

$$O_{12} = O_{21} = 1 - 0.5 \times \sum(P_{i1} - P_{i2}) \qquad (1)$$

where O_{12} is the overlap between taxa 1 and 2, O_{21} is the reciprocal overlap between taxa 2 and 1, P_{i1} is the fraction of occurrences of taxon 1 that occur in resource state i, and P_{i2} is the fraction of occurrences of taxon 2 that occur in resource state i. $\sum$ represents a sum of the calculation (P_{i1} - P_{i2}) for all resource states (Albrecht and Gotelli, 2001). In our analyses, the resource states are habitat categories. For taxa with identical resource utilization, the Czekanowski Index equals 1; for taxa that share no resources, the Czekanowski Index is 0. EcoSimR calculates the Czekanowski Index value for each pair of taxa and takes the average of all pairs to get the observed overlap value for the matrix. We used the randomization algorithm RA3, which retains niche breadth of each taxon.

We tested for niche overlap between genera and between species that varied in body size, degree of hypsodonty, and toe number. Trait data at the species level was used to assign occurrences to trait groups (defined below). North American Land Mammal Ages (NALMAs) were used as time slices; NALMAs are subdivisions of the Cenozoic based on mammal faunas of

North America (Wood et al., 1941; Barnosky et al., 2014). We created EcoSimR input matrices for the following NALMAs in the Miocene and Pliocene (the periods with the greatest diversity of extinct horses): Hemingfordian (approx. 18.5-16.3 Ma), Barstovian (approx.16.3-12.5 Ma), Clarendonian (approx. 12.5-9.4 Ma), Hemphillian (approx. 9.4-4.7 Ma), and Blancan (approx. 4.7-1.4 Ma).

For the continuous variables of body size and HI, we ran analyses with different numbers/sizes of bins to test the effect of how trait categories were divided. For body mass, we tested for niche overlap between 3 bins (under 100 kg, 100 to 200 kg, and over 200 kg), 5 bins (mass below 75 kg, 75 kg to 150 kg, 150 kg to 225 kg, 225 kg to 300 kg, and mass over 300 kg) and 7 bins (mass below 50 kg, 50 kg to 100 kg, 100 kg to 150 kg, 150 kg to 200 kg, 200 kg to 250 kg, 250 kg to 300 kg, and over 300 kg). In all cases the lower boundary is inclusive. For HI, we tested with our standard 3 bins ($HI < 1.1$, $1.1 \leq 3$, $HI \geq 3$), an alternate 3-bin division adapted from Jardine et al. (2012) ($HI<1.7$, $1.7 \leq 3.5$, $HI \geq 3.5$), a 2-bin division ($HI < 3$ and $HI \geq 3$), and a 5-bin division ($HI < 1$, $1 \leq HI < 2$, $2 \leq HI < 3$, $3 \leq HI < 4$, and $HI \geq 4$).

EcoSimR returns P statistics showing where in the range of simulated values the observed average overlap index value falls. It gives tail probabilities for the lower and higher end of the simulated distribution. Tail probabilities < .05 indicate that the observed niche overlap is lower or higher than random.

2.5 Visualization of niche overlap

We tested for the presence of ecological guilds − groups of taxa with high niche overlap within the guild group and low niche overlap among groups − by creating cluster dendrograms nesting together equid genera based on similarity of their habitat category distributions (i.e., proportion of occurrences in each of our seven habitat types) using PRIMER 7 software (Clarke and Gorley, 2015). Czekanowski Index of overlap between pairs of genera was calculated for each NALMA and across the Miocene and Pliocene using EcoSim Professional (Entsminger). Genera were clustered by their niche overlap using the single linkage agglomeration method with the pairwise Czekanowski Index values (Clarke and Gorley, 2015, Martínez-Falcón et al. 2011). Trait-based guild structure could then be detected by inspecting the trait states of genera clustered together in the dendrograms.

2.6 Correlation of trait values to habitat type

To further explore the relationship between derived equid traits and grassland environments, we ran ordinary least squares regression (OLS) analyses. These analyses used the percentage of habitats from each NALMA that were classified as grassland or grassland-savanna as a predictor variable for the average value of each trait considered across the NALMAs. Regressions were performed in R version 3.3.2 (R Core Team, 2016).

2.7 Phylogenetic structure

To consider the phylogenetic signal present in the evolution of equid body size, hypsodonty, and toe number, we created trait-based phylomorphospaces in R using the package ‘phytools’ (Revell, 2017). Each morphospace is defined by two of the three traits, with genera plotted as points and the third trait indicated by their color. Points on the morphospace are linked by their phylogenetic relationships, allowing identification of clades with unique or constrained traits and indicating how traits have evolved together across the phylogeny. The phylogeny used is a composite, following the topology of the time-scaled trees in Fraser et al. (2015) and Jones (2016).

To quantify the extent to which each pair of the three traits varies together, we employed both OLS and phylogenetic generalized least squares (PGLS) models. PGLS modelling takes into account the expectation that more closely-related taxa will have more similar traits and shows whether traits are correlated despite that effect of relatedness. These correlation analyses were also run in R using the package 'caper' v.0.5.2; the PGLS used a branch length transformation for Pagel's Delta, which was found to indicate accelerating rates of trait evolution in the equid tree (Orme et al., 2013).

3. Results

3.1 Body size

High niche overlap was found among body size bins in all NALMAs (Table 1). In the Barstovian, Clarendonian, and Hemphillian, the observed average overlap index values were significantly above the simulated distributions for all bin divisions. In the Hemingfordian, only the 5 bin trial had a significantly higher overlap values than the simulations. In the Blancan, the 3 and 7 bin trials had significantly higher overlap than random. None of the NALMAs show lower-than random niche overlap, so no habitat partitioning by body size is detected.

Table 1: Niche overlap by body size categories.

NALMA	Tail	3 Bins P statistic	5 Bins P statistic	7 Bins P statistic
Hemingfordian	Upper	.088	.0124*	.0702
Barstovian	Upper	.0002*	.0004*	.0002*
Clarendonian	Upper	.0002*	.0002*	.0002*
Hemphillian	Upper	.0002*	.0002*	.0002*
Blancan	Upper	.0184*	.1224	.0222*

Upper tail indicates which tail the overlap index falls towards; in this case, the upper corresponds to higher-than-random overlap. Statistics marked with * are significant below .05.

3.2 Hypsodonty index:

High niche overlap was also found among brachydont, mesodont, and hypsodont horses using a variety of hypsodonty index binning methods (Table 2). In the Barstovian, Clarendonian, and Hemphillian, observed niche overlap was significantly higher than random for all trait bin divisions. In the Hemingfordian, the average niche overlap between these groupings, while high, fell within the range of average values for the null model of random overlap except in our first 3-bin trial, where overlap was significantly higher than simulated. In the 2- and 3-bin trials, only equids defined as hypsodont occurred in the Blancan; niche overlap between the 5 bin divisions was calculated, but the relative scarcity of occurrences in the lower HI categories (10 and 19 occurrences vs. 368 in the HI > 4 category) means that the low side of random niche overlap value calculated is likely an inaccurate representation of how the habitat distributions of crown height categories in the Blancan compare.

Table 2: Niche overlap by hypsodonty categories.

NALMA	**Tail**	**2 Bins P statistic**	**3 Bins P statistic**	**Jardine et al. (2012) 3-bin P statistic**	**5 Bins P statistic**
Hemingfordian	Upper	N/A	.0204*	.1002	.0622
Barstovian	Upper	.014*	.0006*	.002*	.0068*
Clarendonian	Upper	.0324*	.0128*	.0034*	.0006*
Hemphillian	Upper	.033*	.0364*	.0078*	.0006*
Blancan	Lower	N/A	N/A	N/A	.3344

Statistics marked with * are significant below .05. N/A indicates NALMAs where there were insufficient occurrences in more than one hypsodonty category to run analyses.

3.3 Toe number:

The three toe number categories tested for habitat partitioning – tridactyl, variable monodactyl/tridactyl, and monodactyl – had high niche overlap (Table 3). This result was found in all NALMAs. In the Barstovian and Hemphillian, the average niche overlap was significantly greater than in the random simulations, but the other NALMAs also had average niche overlap values on the high end of the range found in the simulations. Since habitat partitioning requires significantly lower than random niche overlap, none of the NALMAs show habitat partitioning by toe number.

Table 3: Niche overlap by toe number.

NALMA	**Tail**	**P statistic**
Barstovian	Upper	.005*
Clarendonian	Upper	.1442
Hemphillian	Upper	.0004*
Blancan	Upper	.0544

Statistics marked with * are significant, below .05.

3.4 Taxonomic overlap

High niche overlap was found among genera in each NALMA. For all NALMAs except the Blancan, the average overlap index was significantly higher than the distribution of overlap index values in the null model (Fig. 2). In the Blancan, the observed niche overlap was still on the high end of the distribution (p value for Czekanowski index value ≥ simulated = 0.058); no evidence for habitat partitioning between genera was found.

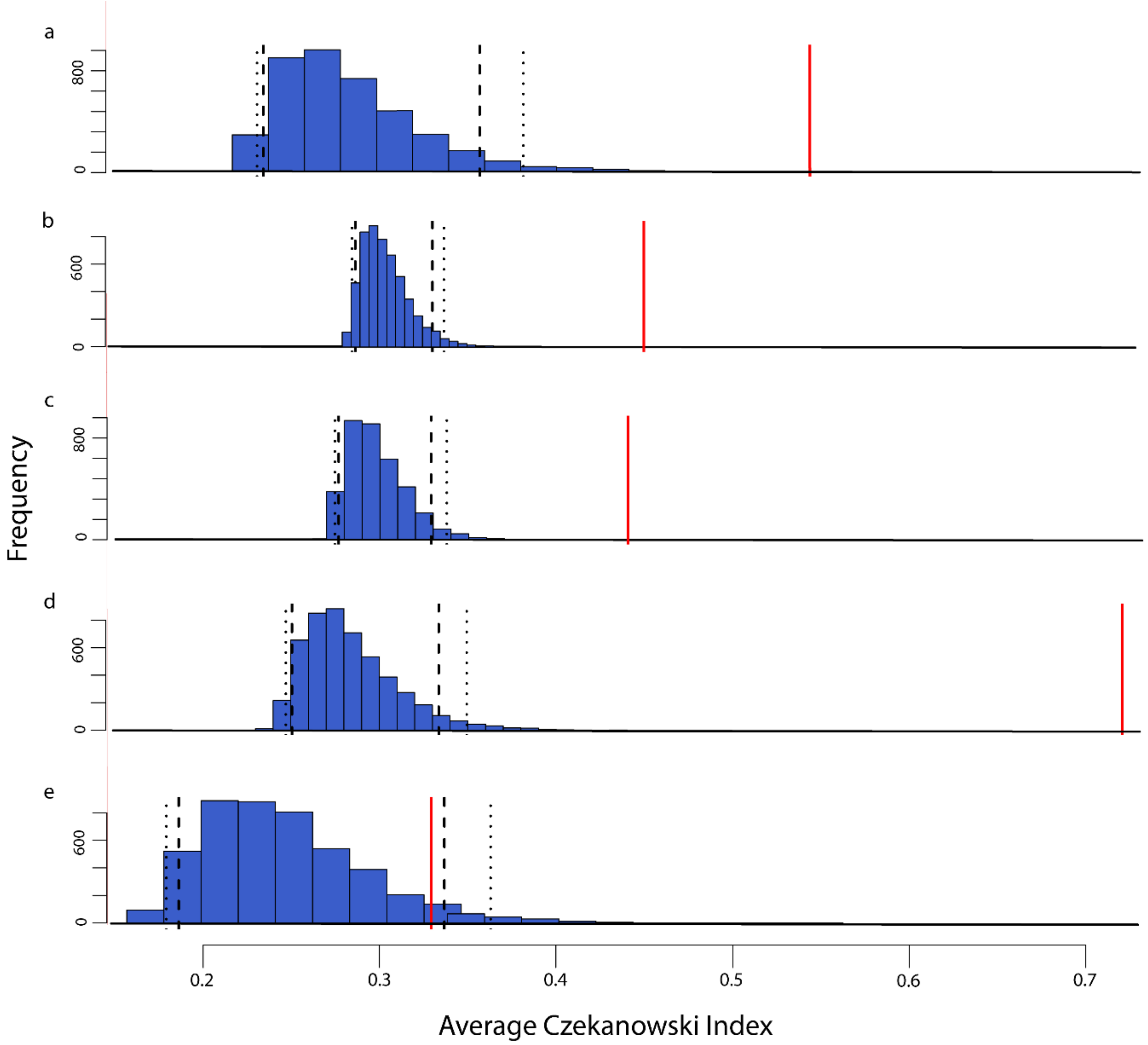

Figure 3: Taxonomic (genera) niche overlap vs. null model distribution. Average overlap index values from EcoSimR randomized simulations (i.e., null model; blue bars) and observed index values (red lines) for a) Hemingfordian, b) Barstovian, c) Clarendonian, d) Hemphillian, and e) Blancan. The thin-dashed and thick-dashed lines show the one-tailed and two-tailed 95% confidence intervals of the simulated index values, respectively.

*full color, 1.5 columns

3.5 Clustering by niche overlap

Cluster analysis shows which genera had the most similar habitat distributions, grouping them into ecological guilds. Figure 4 shows all genera with more than 5 occurrences in the Miocene and Pliocene clustered by their pairwise Czekanowski indices. While genera with large body size are scattered across the tree, the hypsodont and monodactyl genera fall in some apparent clusters sharing habitat distributions. The nodes labelled 2 and 4 on Figure 4 are potential guilds of horses with derived traits. Guild 4 stands out from the others in living in less wooded habitats; less than 1% of these genera's occurrences are in woodlands, forests, or forest/swamp. Guild 2, however, shows quite an average habitat distribution, which is very similar to that of guild 5, except that guild 5 was found in slightly more grassland-savannas, while guild 2 was found in more woodland-savannas. Guild 1 was overwhelmingly found in woodland-savanna habitats (67.6% of occurrences). Guild 3, which is plesiomorphic in containing brachydont and tridactyl genera, was found more in woodlands and less in woodland-savannas than the other guilds, though it still occurred frequently in grassland-savannas. It is important to note the y axis scale of Figure 4; the "similarity" values of 75% and above mean that each genus had a Czekanowski Index value of over 0.75 with another genus or guild of genera. The habitat distributions of all genera are very similar, as confirmed in Figure 3, though this cluster dendrogram allows us to parse out which are the most similar.

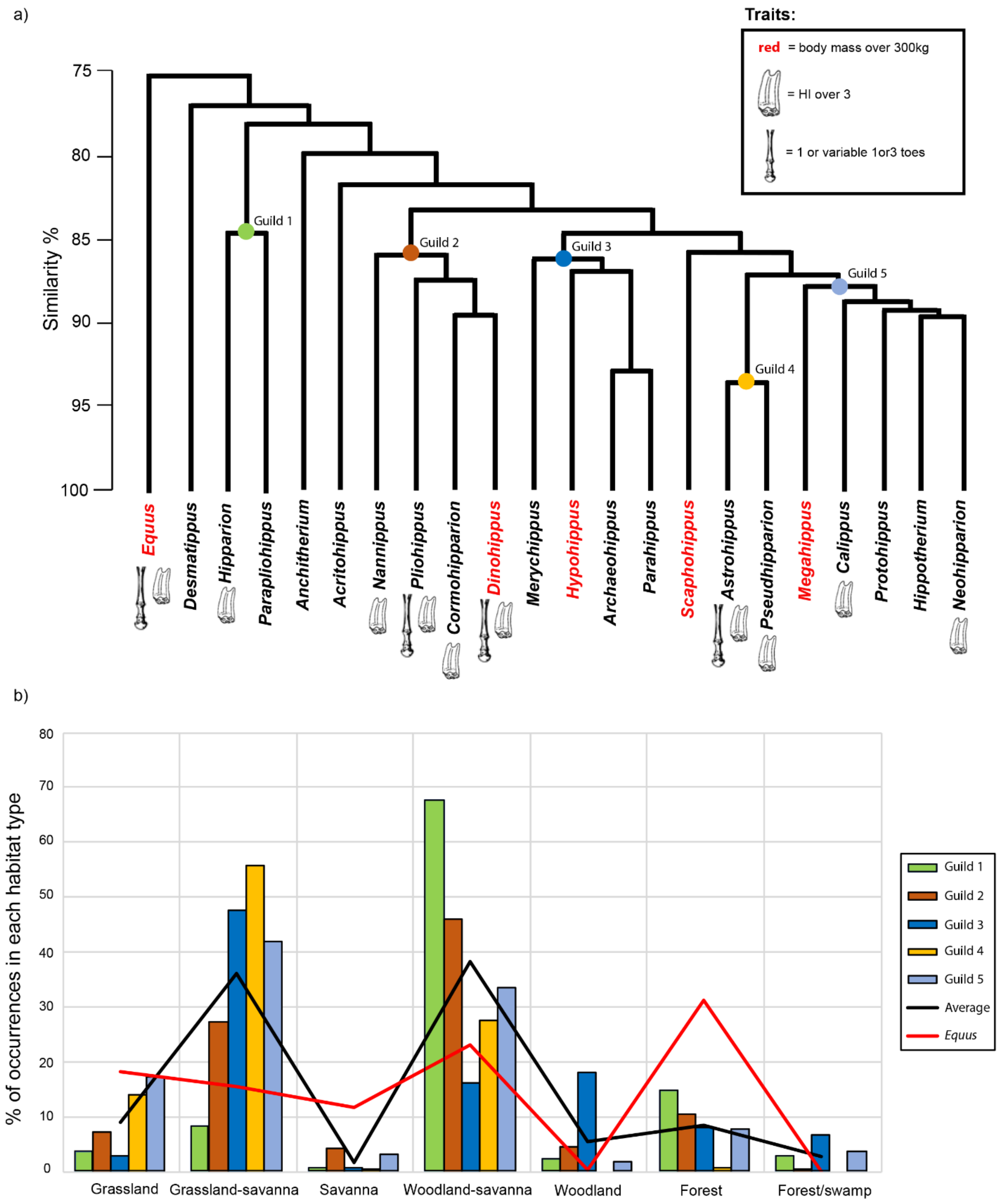

Figure 4: Clustering by niche overlap. a) Cluster dendrogram nesting all equid genera from the Miocene and Pliocene based on similarity of their habitat distributions. Genera with the traits of large body size, hypsodonty, and monodactyly are marked, and selected guilds labelled. b) Bar graph showing the percentage habitat occupancy of selected guilds, with the average habitat distribution and that of *Equus* marked as lines.

*full color, 2 columns

3.6 Correlation of traits and habitat

There was no relationship found between derived traits and the prevalence of grassland habitats across the NALMAs (Table 4). Although a significant relationship between TRI and both body size and HI was recovered, after correcting for phylogenetic relatedness, no pairs of traits showed a significant relationship (Table 5).

Table 4: Linear models of the relationships between trait values and percent grasslands.

Comparison	Equation from GLM	R^2	P value
log(m_b) ~ % grassy	log(m_b) = 500.171 -7.193*(% grassy)	0.3359	0.1805
HI ~ % grassy	HI = 7.72458 -0.10175*(% grassy)	0.3479	0.1748
TRI ~ % grassy	TRI = -0.26685 + 0.01631*(% grassy)	0.2583	0.2196

Best-fit equations describing the relationships between the average values of each trait per NALMA and the proportion of sites with grassland habitats, with their R^2 values. m_b = body mass, % grassy = percentage of equid fossil sites whose paleoenvironments are classified as grassland or grassland-savanna. The p values show the significance of the relationship; significance is defined as below .05.

Table 5: Models of trait correlation.

Comparison	Equation from non-phylogenetic GLM	R^2	P value	Equation from PGLS	R^2	P value
TRI ~ log(m_b)	TRI = 1.085 - 0.239(log(m_b))	0.324	0.0019*	TRI = 1.035 - 0.149(log(m_b))	0.092	0.159
TRI ~ HI	TRI = 0.79642 - 0.0826(HI)	0.413	0.0007*	TRI = 0.866 - 0.0459(HI)	0.076	0.205
HI ~ log(m_b)	TRI + 1.5086 - 0.718(log(m_b))	0.124	0.0662	HI = 0.832 + 0.146(log(m_b))	0.002	0.81

Best-fit equations describing the relationships between pairs of trait values (m_b = body mass), with their R^2 values. The p values show the significance of the relationship; those marked with * are significant below .05.

3.7 Phylomorphospaces

Phylomorphospaces reveal how traits are distributed across the horse phylogeny. We included pre-Miocene semi-tetradactyl horses in these analyses to track the evolution of digit reduction. In general, phylogenetic structure is low. The modern tapir, used as an outgroup, is clearly demarcated by its large body size but low-crowned teeth and minimal toe reduction (Figs.

5-7); however, its location in trait space is very similar to *Hypohippus*, a pony-sized, tridactyl horse. In Figure 5, the earliest-branching semi-tetradactyl equids are clustered in the small body size and low-crowned teeth area of morphospace, while a clade of monodactyl equids dominate the morphospace of highest body size and hypsodonty. However, the tridactyl genera that make up most of the equids' diversity span a wide range of trait values.

Phylomorphospaces based on Toe Reduction Index are more suggestive of linked trait evolution (Figs. 6 and 7). In Figure 6, the most basal brachydont equids are clustered with low body size and high TRI values (indicating minimal toe reduction), while the latest-branching genera are the largest with the most reduced toes. The genera in between (excluding the tapir) are clustered loosely around a line of negative slope, representative of trait correlation. However, the taxa in each crown height category scatter widely across the TRI-body size space. The TRI-HI phylomorphospace in Figure 7 shows a similar linear trend with limited phylogenetic control over where genera fall in the morphospace. Beyond clustering apparent in the earliest equids (with high TRI and low HI), the branches of the phylogeny scatter widely, showing high levels of trait evolution between some closely-related taxa.

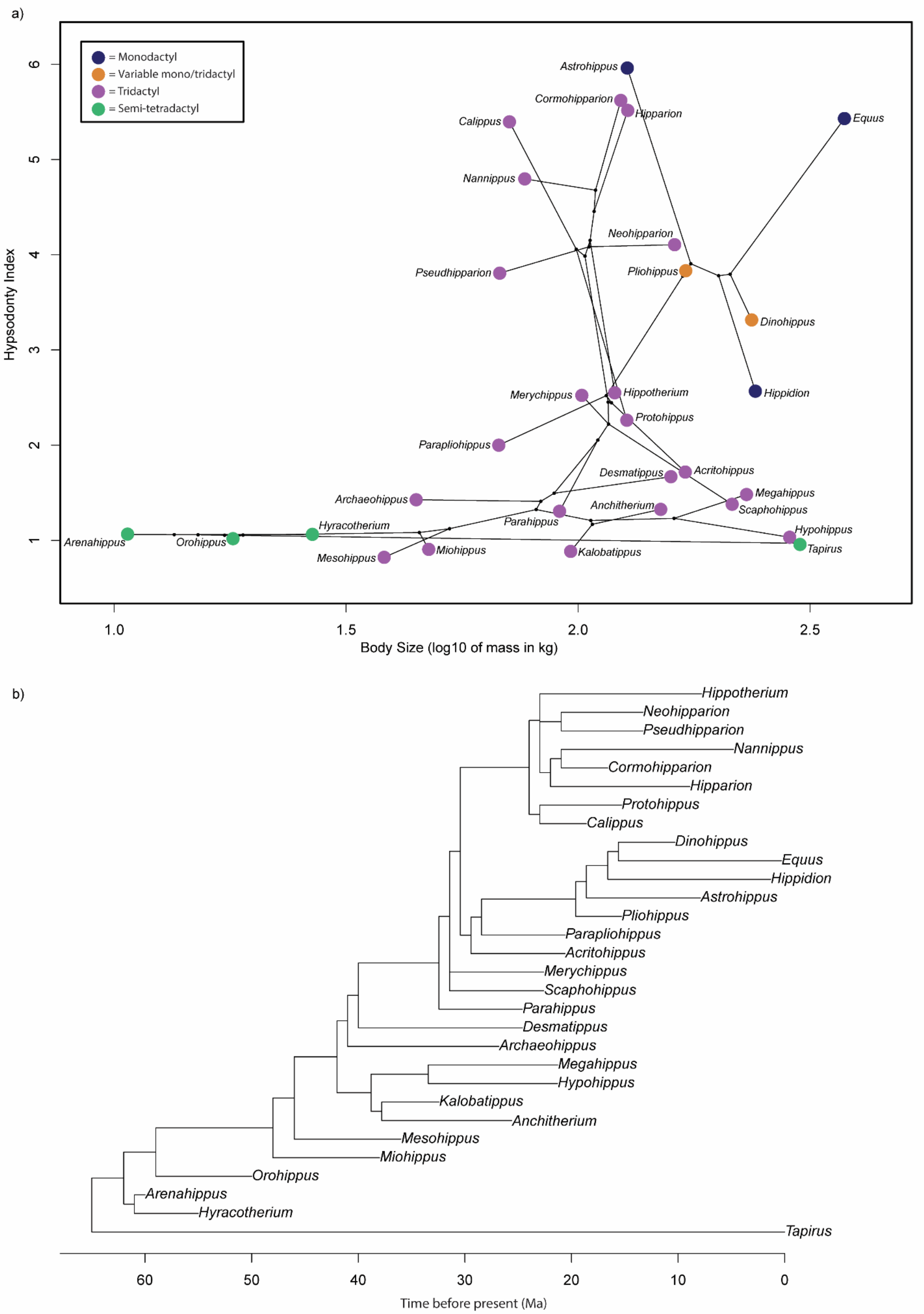
a)
= Monodactyl
= Variable mono/tridactyl
= Tridactyl
= Semi-tetradactyl
Hypsodonty Index
1
2
3
4
5
6
Body Size (log10 of mass in kg)
1.0
1.5
2.0
2.5
Astrohippus
Cormohipparion
Hipparion
Calippus
Equus
Nannippus
Neohipparion
Pseudhipparion
Pliohippus
Dinohippus
Merychippus
Hippotherium
Hippidion
Protohippus
Parapliohippus
Desmatippus
Acritohippus
Archaeohippus
Megahippus
Anchitherium
Scaphohippus
Parahippus
Hyracotherium
Hypohippus
Arenahippus
Orohippus
Mesohippus
Miohippus
Kalobatippus
Tapirus
b)
Hippotherium
Neohipparion
Pseudhipparion
Nannippus
Cormohipparion
Hipparion
Protohippus
Calippus
Dinohippus
Equus
Hippidion
Astrohippus
Pliohippus
Parapliohippus
Acritohippus
Merychippus
Scaphohippus
Parahippus
Desmatippus
Archaeohippus
Megahippus
Hypohippus
Kalobatippus
Anchitherium
Mesohippus
Miohippus
Orohippus
Arenahippus
Hyracotherium
Tapirus
60
50
40
30
20
10
0
Time before present (Ma)

Figure 5: Phylomorphospace showing evolutionary relationships between body size, HI, and toe number. a) Phylomorphospace with axes of reconstructed body size and hypsodonty index plotting 29 genera of equids and the outgroup *Tapirus*. Colors mark the toe number of each genus. Black lines and nodes connecting taxa represent the phylogenetic tree of these genera. b) Time-calibrated phylogeny used to construct the phylomorphospace (Fraser et al., 2015 and Jones, 2016). A subset of this phylogeny is used in Figures 6 and 7.
* Full color, 2 columns

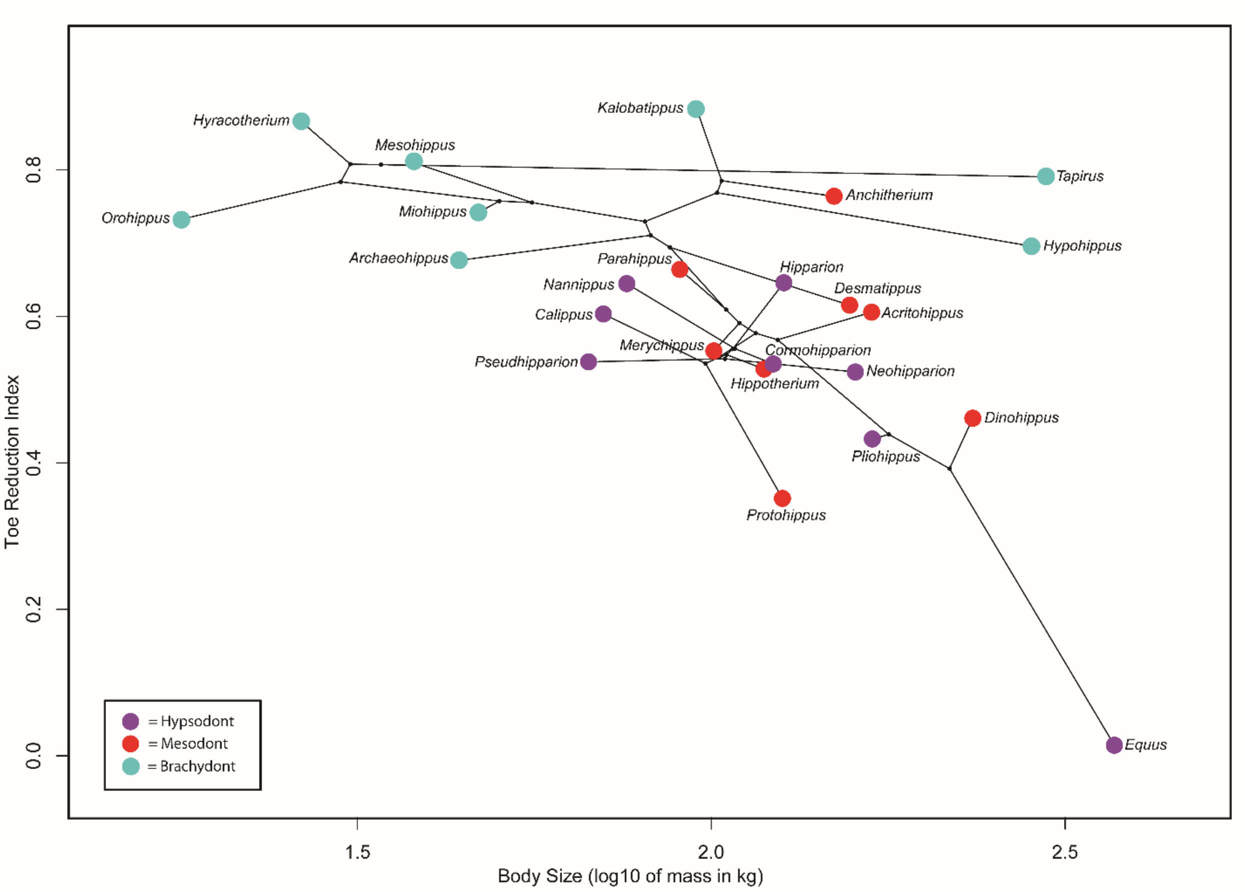

Figure 6: Phylomorphospace showing evolutionary relationships between body size and TRI. Colors mark the hypsodonty categories of each genus. Black lines and nodes connecting taxa represent the phylogenetic tree of these genera with reconstructed ancestral nodes.
* Full color, 2 columns

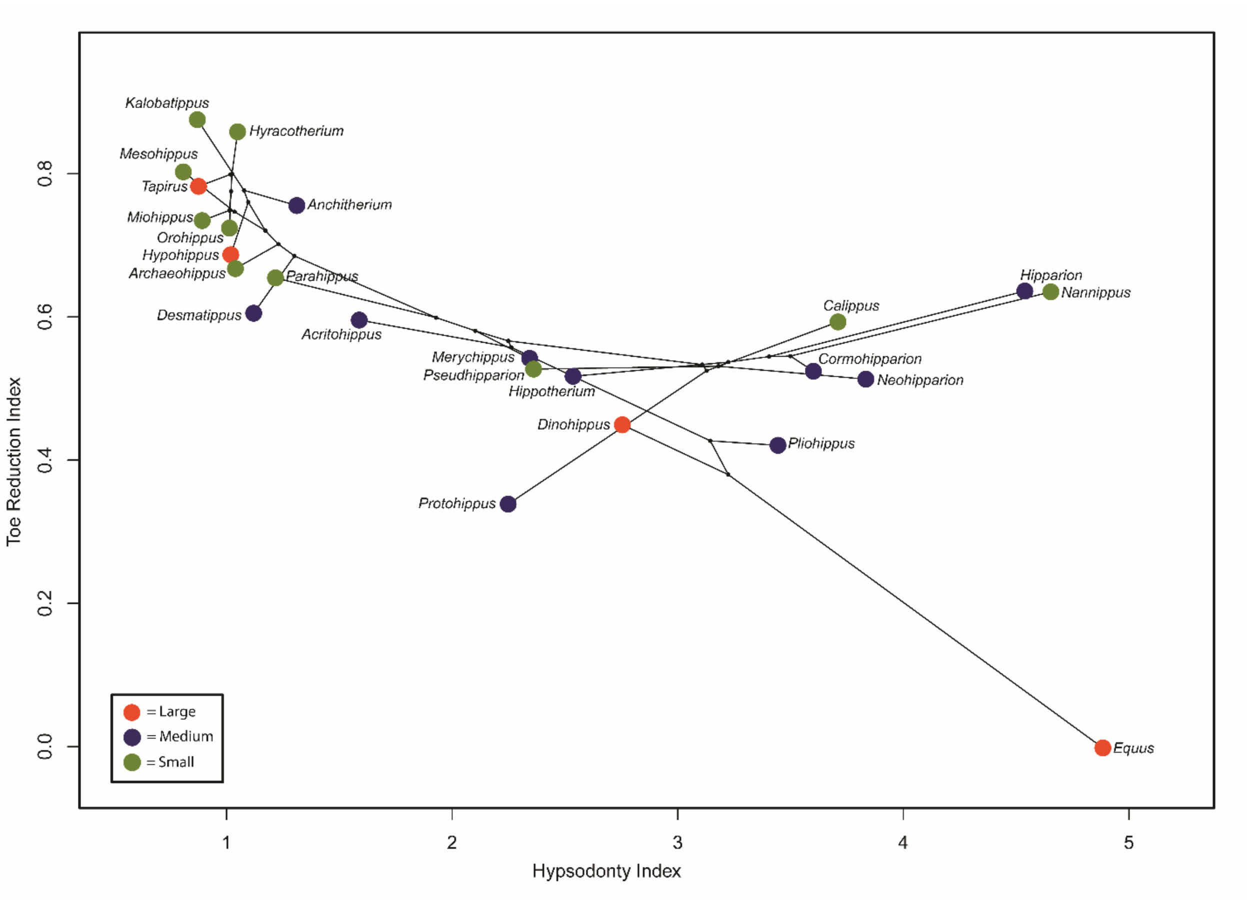

Figure 7: Phylomorphospace showing evolutionary relationships between HI and TRI. Colors mark the category of reconstructed body size for each genus. Black lines and nodes connecting taxa represent the phylogenetic tree of these genera with reconstructed ancestral nodes.
* Full color, 2 columns

4. Discussion

4.1 Lack of habitat partitioning among trait groups

Our EcoSimR analyses find no support for habitat partitioning in extinct horses with different traits at the spatial and temporal scale of this study. This result holds across all NALMAs and traits considered, regardless of bin size. While not all results showed significantly higher overlap than random, those that fell within the range of the null model had P statistics indicating niche overlap at the higher end of random. In no case was there statistical support for habitat partitioning. This finding is inconsistent with the hypothesis that derived equid traits – large body size, high-crowned teeth, a single toe – arose as adaptations to grassland habitats (Shotwell, 1961; Eronen et al., 2010; Orcutt and Hopkins, 2013). Equids with these derived traits were not found in grasslands more often than those without the derived traits. In fact, our results show that the diverse, morphologically varying horse taxa of the Miocene and Pliocene had similar distributions across habitat types. This overlap in habitat occupation suggests that the evolution of new equid traits in some taxa was not due to exposure to different broad-scale environmental conditions.

Our cluster analyses, which visualize guild structure by showing which genera overlap most in their habitat distributions, show some grouping in the habitat preferences of genera with derived traits. Specifically, the guilds labelled 2 and 4 in Figure 4a contain monodactyl and hypsodont genera. However, only guild 4 shows a habitat distribution skewed away from closed forests relative to the other guilds. The guilds including genera with more mixed and plesiomorphic traits still occur frequently in grassland-savanna sites, with the exception of guild 1 which is found almost exclusively in woodland-savannas. While this clustering suggests that some hypsodont and monodactyl equids shared habitat distributions to the exclusion of less-derived taxa, the habitat distributions of all guilds are generally similar, as visualized by their proximity to the average line on Figure 4b. This finding of trait-based guild structure is not accompanied by clear differential grassland occupation by derived genera, as would be expected if selective pressures in open habitats were crucial to the evolution of these traits. Modelling of the influence of grassland habitats at equid sites on trait values confirms that grassy habitats are not linked to derived traits (Table 4). Across the NALMAs considered, changes in the proportion of equid fossil sites classified as grasslands do not correlate to changes in trait values, further challenging the hypothesis that the spread of grasslands lead to trait evolution.

An important limitation of this study is the resolution of the paleoenvironment data currently available. The paleobotanical, phytolith, and paleosol sources used in this study (Appendix 2) provide habitat designations for areas generally several counties in size and in time slices the length of North American Land Mammal Ages. This level of resolution (spatial or temporal) may not be fine enough to reveal smaller-scale (e.g. functional and/or behavioral) habitat partitioning, if it did occur. Modern grazing ungulates have been observed sharing home ranges and habitats, but exhibiting different patterns of foraging area use such as moving between vegetated areas at different rates (Owen-Smith et al. 2015), which could allow for division of resources between groups that would certainly be assigned to the same habitat at the spatial scale of our data. Shotwell (1961) proposed that monodactyl and tridactyl horses living together in savanna environments partitioned within the habitat such that monodactyl taxa utilized the more open areas in the savanna, while tridactyl ones lived amongst more dense trees and shrubs. If such small-scale environmental patchiness was the true level at which horses were partitioning habitats, our analyses based on classifications of larger areas may have been unable to detect it. Given the number of equid species living in sympatry in this period, some form of temporal or behavioral partitioning of resources may have occurred at a finer scale. What our broad-scale data does show is that equids grouped by body size, hypsodonty, and toe number categories were not living in significantly different habitat types in any NALMA.

To learn more about how the specific niches occupied by species differed, further examination of habitat partitioning using paleoenvironment data at finer spatial and temporal scales is required. Fieldwork in regions with many horse fossils from a series of sites would allow future analyses of plant fossils, phytoliths, and/or paleosols to show fine-scale differences in the habitats occupied by different equids. Assumptions that sites yielding large, hypsodont, or monodactyl horses represent open paleoenvironments are common in the literature (e.g., Fraser and Theodor, 2013), but to establish an unbiased connection between horse traits and habitat type, descriptions of heterogenous plant assemblages from equid-bearing localities must be made.

4.2 Correlation of traits across the phylogeny

The phylomorphospaces illustrate little phylogenetic constraint on body size, tooth morphology, or digit state (Figs. 5-7). This result is in accord with Cantalapiedra et al. (2017), who found considerable overlap among equid clades when their phylogeny was plotted on the axes of body size and hypsodonty index. Use of the Toe Reduction Index (TRI), which captures more subtle differences in digit morphology, allowed us to parse out how increased reduction of the side digits relates to the other traits (Figs. 5-6); standard OLS modeling confirms that TRI is significantly related to both body size and HI (Table 5). However, PGLS analysis reveals that when expected trait similarity between closely-related taxa is taken into account, the potential co-evolutionary relationships between TRI and the other two traits are not significant (Table 5). Such a result is indicative of a situation where the trait similarity between closely-related taxa accounts for the observed relationship between traits; at the scale of the whole tree, the traits appear correlated, but within subclades they do not evolve together (Cantalapiedra et al. 2014). These non-significant PGLS regressions show that large body size, hypsodonty, and toe reduction did not evolve as a linked suite of characters, as would be expected according to the hypothesis that all three were progressive adaptations to grassier environments.

4.3 Selective pressures on equids ranging across habitat types

Given the lack of habitat partitioning between trait groups found here, alternative drivers for the evolution of large body size, hypsodonty, and monodactyly should be considered. Body mass evolution may have been influenced by evolutionary dynamics other than environmental adaptation. For instance, increase in equid body size could have been driven by competition within habitats, either between horse species or with other herbivores. Finer-scale habitat partitioning based on differential spatiotemporal resource use, like that found in modern grazers by Owen-Smith et al. (2015), could have created localized selection on the body size of sympatric equids. Ruminant artiodactyls, which rose in abundance through the Miocene, would have competed with equids for browse; since these other herbivores came to dominate the middle body sizes at the same time as equid body size increased, competitive displacement could explain the pattern (Janis et al. 2002). Though equids across trait groups shared habitats, habitat partitioning between equids and artiodactyls, whose different foregut-fermenting digestive strategy allows for superior processing of higher-quality leaves, could have pressed equids into new environmental conditions (Janis 2008). Alternatively, increase in body size could be due to random increase in trait variation over evolutionary time. Evolutionary diffusion within the equid lineage, which started with species of small size, would lead the maximum and average body size to increase over time (Gould, 1988). Shoemaker and Clauset (2013) found that 92% of the increase in horse body mass could be explained by random diffusion; they propose that short term selective effects on specific populations' body size caused size increases and decreases, fueling this diffusion. In this case, small-scale trait changes in populations could occur across groups sharing overall habitat distributions and sum up over time to create the larger trait changes previously attributed to differential environmental selection.

The "grit not grass" hypothesis provides a viable alternative explanation for the evolution of hypsodonty. High-crowned teeth could have evolved not in equids sequestered in grassy habitats but in equids eating a variety of types of vegetation covered in grit or ash from arid surrounding environments (Jardine et al., 2012; Strömberg et al., 2013). Mihlbachler et al. (2011) found a wide range of mesowear scores within most fossil horse species. This result supports a lack of habitat partitioning because it shows that all individuals within each species or genus were not necessarily eating the same foods. Selection for increased crown height due to high levels of tooth wear was not constant; as wear varied between populations, selection for hypsodonty would have been episodic, resulting in evolution of higher crowns in specific environments with high levels of exogenous grit or abrasive vegetation (Mihlbachler et al., 2011). Furthermore, tooth wear analyses show that equids were eating grass long before they evolved high levels of hypsodonty (Semprebon et al., 2016). Without habitat partitioning, hypsodonty may have been selected for in varying degrees as species ranged across environments, perhaps due to wear by grit in areas of decreased precipitation.

Evolutionary mechanisms for changes in toe number have not been tested as thoroughly as the other two major traits. The reasoning of Shotwell (1961) and Renders (1984), that tridactyly was advantageous for traction in dodging maneuvers and stability in muddy substrates, has not been tested. The advantage of toe reduction for running speed or locomotor efficiency based on decreased limb inertia has gained some support, and having a single robust digit rather than several smaller ones may be advantageous for resisting bending forces − particularly as body mass increases (Thomason, 1986; McHorse et al., 2017). It is possible that reduction in toe number was adaptive not just in the context of running through open grasslands but that other selective pressures, which would apply across the range of habitats shown to be inhabited by most equids, were involved. Given the increase in aridity that occurred in the Miocene, the advantage of having three toes in wet substrates may have decreased in importance (Polly and Head, 2015). As with hypsodonty and body size, it is possible that changes in digit state could have been selected for in small-scale, specific contexts within the range of habitats occupied by each equid group.

5. Conclusions

Our results challenge the long-standing hypothesis that derived equid traits – large body size, high-crowned teeth (hyposonty), and a single toe (monodactyly) – evolved as a suite of adaptations to the spread of grassland environments in North America. At the spatial and temporal scale analyzed here, we find no evidence for long-term differentiation in habitat use between equids with more- or less-derived traits. Although equid species living in sympatry during the Miocene and Pliocene may have utilized different resources at finer spatial and temporal scales (e.g. specific dietary/ behavioral adaptations), our results indicate that horses with derived traits were not found differentially in grassland habitats. This indicates that the selective pressures leading to the evolution of derived horse traits did not exclusively arise due to changes in broad-scale habitat use. While cluster analyses show some ecological guilds sharing derived traits, the habitat distributions of those guilds are broadly similar to those of guilds containing equids with fewer derived traits. Furthermore, models correcting for phylogenetic relatedness show that the evolution of large body size, hypsodonty, and monodactyly is not correlated. The lack of habitat partitioning found here suggests that these equid traits did not evolve within a single strict selective regime in newly-opened grasslands; instead, they were the product of a complex set of heterogeneous selective pressures encountered in the various habitats shared by Miocene-Pliocene equids.

Acknowledgments We would like to thank Christine Janis for use of unpublished data and all the contributors of the PBDB for inputting occurrence data. We are also grateful to Lars Schmidt for the phylomorphospace code, which was part of the workshop "Paleobiological and phylogenetics approaches to Macroevolution" at NESCent Academy (supported by the National Evolutionary Synthesis Center, NSF #EF-0423641) and to Juan Cantalapiedra for the code used for PGLS, which was part of the workshop "Introduction to macroevolutionary analyses using phylogenies" (Transmitting Science). AKP submitted a version of this study as an undergraduate thesis in Integrative Biology, Department of Organismic and Evolutionary Biology, Harvard University. Further, we thank three anonymous reviewers for their feedback which greatly enhanced the quality and clarity of the manuscript.

Funding AKP received funding for this project from the Harvard Herchel Smith Summer Undergraduate Research Fellowship. BKM was supported by a NSF Graduate Research Fellowship (#DGE1144152) while this work was conducted. Data collection was supported by an NSF Doctoral Dissertation Improvement Grant to BKM and SEP (#DEB-1701656).

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Appendix 1: Body Mass Regressions. The following regression equations were used to reconstruct body mass for equid species based on dental measurements.

Measurement for x	Regression Equation	Source of Equation
m1length	log(body mass)= 3.268*log(x) + 1.337	Janis, 1990
m1 area	log(body mass)= 1.663*log(x) + 1.701	Janis, 1990
m1length	log(body mass)= 3.17*log(x) + 1.04	Damuth, 1990
m1width	log(body mass)= 2.79*log(x) + 1.88	Damuth, 1990
m1area	log(body mass)= 1.51*log(x) + 1.44	Damuth, 1990
P3 length	log(body mass)= 2.93*log(x) + 1.43	Damuth, 1990
P3 width	log(body mass)= 2.72*log(x) + 1.66	Damuth, 1990
P4 lenght	log(body mass)= 3.13*log(x) + 1.16	Damuth, 1990
P4 width	log(body mass)= 2.81*log(x) + 1.41	Damuth, 1990
P4 area	log(body mass)= 1.46*log(x) + 1.33	Damuth, 1990
M1 length	log(body mass)= 3.11*log(x) + 1.11	Damuth, 1990
M1 width	log(body mass)= 2.86*log(x) + 1.3	Damuth, 1990
M1 area	log(body mass)= 1.48*log(x) + 1.22	Damuth, 1990

Appendix 2: Sources for Paleoenvironment Classifications

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