

Macroevolution and climate change influence phylogenetic community assembly of North American hoofed mammals

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Animal richness, community composition, and phylogenetic community structure (PCS) vary across the modern landscape. Animal communities vary from phylogenetically clustered (i.e. higher relatedness amongst co-occurring species than is expected by chance) to phylogenetically even (i.e. co-occurring taxa are more distantly related than expected by chance), which is explained by abiotic or climatic filtering and competitive exclusion, respectively. Under this model, the contribution of historical origination and extinction events to modern animal PCS remains relatively unknown. Because origination and extinction determine the make-up of the terrestrial community, the study of historical changes in animal PCS is tantamount to understanding formation of modern communities. In the present study, we test the effects of macroevolution and climate changes on 'hoofed mammals' (i.e. perissodactyl and artiodactyl) PCS from the late Cenozoic of North America because they experience large, phylogenetically dispersed extinctions of browsing species and phylogenetically dispersed originations of grazing species associated with the evolution of grassland ecosystems during the late Miocene. We show that the loss of numerically dominant nonhypsodont (putatively browsing and mixed feeding) clades and phylogenetically dispersed origination of less speciose clades following the mid Miocene climatic optimum led to an increase in phylogenetic evenness at the regional scale that is well explained by global climate changes. Phylogenetic evenness and a reduced richness during the late Cenozoic may have facilitated reduced niche overlap among co-occurring hoofed mammal species as global climates cooled. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **114**, 485–494.

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INTRODUCTION

The richness and composition of modern animal communities changes vastly across space, a phenomenon that is attributed to geographical variation in climate and topography (Rosenzweig, 1995). Spatial diversity patterns are also associated with changes in phylogenetic composition of communities; animal

communities vary across the landscape with respect to the degree of relatedness among species (Buckley & Jetz, 2008; Qian *et al.*, 2013). Studying the phylogenetic structure of modern communities is revealing the proximate factors that structure geographical diversity patterns (Hardy & Senterre, 2007; Kraft *et al.*, 2007; Emerson & Gillespie, 2008; Vamosi *et al.*, 2009; Swenson *et al.*, 2012). Most studies of modern phylogenetic community structure (PCS) invoke contemporary drivers such as abiotic or climatic filtering and competition (Vamosi *et al.*, 2009) to the exclusion

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of historical macroevolutionary events. However, understanding the contribution of macroevolution and historical factors to community assembly is required to test hypotheses about the formation of modern communities. Studying trends in PCS through time using the fossil record might reveal the effects of macroevolutionary processes on PCS, as well as the role of long-term climate changes in the formation of modern communities.

Modern species assemblages comprise populations of species drawn from the regional source pool (i.e. from the entire complement of species in a region). The identity and relatedness of species in a local assemblage are determined by a variety of factors, including but not limited to abiotic filtering, dispersal, and competition (Webb *et al.*, 2002; Kraft *et al.*, 2007; Emerson & Gillespie, 2008). Abiotic filtering is a process where species with different environmental tolerances are filtered out of terrestrial communities along environmental gradients (Swenson *et al.*, 2012). Assuming niche conservatism (closely-related species share similar niches), low rates of dispersal and abiotic filtering are associated with high phylogenetic relatedness among species or phylogenetic clustering. Conversely, competitive exclusion and high rates of dispersal can lead to phylogenetic evenness or species being less phylogenetically related than expected by chance (Cavender-Bares *et al.*, 2004; Losos, 2008). Thus, local species assemblages occupy a point on a spectrum between phylogenetically clustered and even. Note that myriad conditions such as low rates of phylogenetic niche conservatism and trait convergence can result in communities that show every condition from phylogenetic evenness to phylogenetic clustering (Cavender-Bares *et al.*, 2004; Kraft *et al.*, 2007). However, the theoretical framework outlined above generally excludes the fossil record and thus excludes the contribution of historical factors such as extinction events.

Over long time scales of thousands to millions of years, origination and extinction are two of the dominant processes driving changes in organismal diversity (Benton & Pearson, 2001; Blois & Hadly, 2009; Dobrovolski *et al.*, 2012; Mayhew *et al.*, 2012; Price *et al.*, 2012). The composition of regional species pools and local assemblages through time are likely dependent upon numerous factors, including history of clades (e.g. species composition in preceding time intervals), patterns of origination and extinction across the phylogenetic tree (e.g. whether they are phylogenetically clumped or dispersed), climate, and tectonic changes. Whether extinction and origination are phylogenetically clumped or dispersed will largely depend on the distribution of ecologically relevant traits across the phylogenetic tree (i.e. whether those traits are conserved or convergent)

(Green *et al.*, 2011). Thus, both phylogenetically clumped and dispersed patterns of extinction and origination can result from abiotic filtering (Janis, Damuth & Theodor, 2000, 2004; Barnosky, 2005; Green *et al.*, 2011; Figueirido *et al.*, 2012). However, phylogenetically dispersed extinction should result in a trend of increasing phylogenetic evenness through time as the mean phylogenetic distance among surviving taxa increases. Conversely, if extinction is phylogenetically clumped, there should be a trend of increasing phylogenetic clustering through time as the mean phylogenetic distance between surviving taxa decreases. The effects of origination on PCS are more complex because they change throughout the history of a clade. For example, under an adaptive radiation model, early in the evolutionary history of a clade, the appearance of new species should result in increasing phylogenetic evenness as new branches are added to the phylogenetic tree. Later in the history of a clade, the origination of new species within well-established genera (i.e. adding new 'leaves' to the tree) should result in increasing phylogenetic clustering. Through time, local assemblages might mirror the changes in the regional species pool (i.e. follow the same trajectory) or show a different temporal trajectory related to more proximate drivers such as spatial abiotic filtering, dispersal, and competition. A comparison of PCS at regional and local scales might therefore reveal the extent to which local assemblages are influenced by macroevolutionary processes and changes in the regional species pool through time.

Over geological time, the diversity and composition of animal communities has changed dramatically, especially during the transition from the warm equitable climates of the early and mid Cenozoic to the cool temperate climates of the late Cenozoic (Alroy, Koch & Zachos, 2000; Janis *et al.*, 2000, 2004; Mayhew, Jenkins & Benton, 2008; Mayhew *et al.*, 2012; Fraser *et al.*, 2014). Therefore, the phylogenetic structure of regional species pools and local species assemblages has likely also been temporally variable. Evolution of late Cenozoic (Miocene to Pleistocene) North American ungulates is marked by a decline in richness, particularly of browsers (feeding on parts of woody plants, not herbaceous plants), associated with the expansion of open grassland habitats (Janis *et al.*, 2000, 2004; Fox & Koch, 2004; Fraser & Theodor, 2013). Furthermore, ecologically relevant traits such as tooth crown height and body size show significant changes among North American hoofed mammals as the ecosystems shifted away from woodland savannahs and primary productivity consequently declined (Janis *et al.*, 2000; Janis *et al.*, 2004; Smith *et al.*, 2010; Raia *et al.*, 2011; Cantalapiedra *et al.*, 2013). In the present study, we tested for effects of

late Cenozoic (15–0.01 Mya) extinction and global climate changes on North American ‘ungulate’ PCS at the regional and local-scales.

MATERIAL AND METHODS

We downloaded fossil occurrence data for the Miocene, Pliocene, and Pleistocene, which we partitioned by subdivisions of the North American Land Mammal Ages (NALMAs; see Supporting information, Table S1) because they delineate relatively stable community assemblages. The dates for all NALMA subdivisions are based on Woodburne (2004). Fossil ungulate (Perissodactyla and Artiodactyla) occurrence data for the Pliocene, and Pleistocene were downloaded from the Paleobiology Database (<http://paleodb.org/>) in July and August 2012, using the group name ‘mammalia’ and the parameters: time intervals = Cenozoic, region = North America, paleoenvironment = terrestrial. Miocene ungulate occurrence data were downloaded from the Miocene Mammal Mapping Project (Carrasco *et al.*, 2005) in March 2011 using the NALMA subdivision as our search criterion. We then created taxon-by-NALMA subdivision occurrence matrices for perissodactyls and artiodactyls separately at the species level (Davis, 2005; Atwater & Davis, 2011). We removed all taxa that had equivocal species identifications (e.g. *Equus* sp.) unless they were the only occurrence for a genus. We assumed all occurrences of open nomenclature (e.g. *Equus* cf. *simplicidens*) were correct identifications.

We created composite phylogenies for fossil artiodactyls and perissodactyls primarily *sensu* Janis, Scott & Jacobs (1998) and Maguire & Stigall (2009). The backbone of the artiodactyl phylogeny is based on Price, Bininda-Emonds & Gittleman (2005). For comparison, we created two composite phylogenies each for the artiodactyls and perissodactyls, one better resolved tree based on published hypotheses (see Supporting information, Fig. S1) and one poorly resolved tree (see Supporting information, Fig. S2) where we assumed nothing about inter- and intra-generic relationships. For both sets of composite trees, we used taxonomy as a guide (i.e. we assumed species from the same genus were sister taxa with notable exceptions such as *Merychippus*, which is a known polyphyletic genus). Although fossil phylogenies inevitably include many polytomies, they are not problematic (Finarelli, 2007; Raia *et al.*, 2010). As such, our composite phylogenies may contain as yet unknown polyphyletic genera but reflect the current state of knowledge. Furthermore, all equivocal interfamilial and intergeneric relationships were represented by polytomies, and species that we could not place phylogenetically were removed from the analysis. We

created a third set of composite phylogenies for the artiodactyls from which we excluded the Bovidae and Cervidae, which comprise Eurasian immigrants. We used first and last occurrences of perissodactyl and artiodactyl taxa from the taxonomic range tool on the Paleobiology database with NALMAs as our time model and default settings to create dated composite phylogenies using the paleotree R package (Bapst, 2012).

We calculated the net relatedness index (NRI), which is a standardized measure of mean pairwise phylogenetic distance among co-occurring species, using the picante R package (Webb, 2000; Webb *et al.*, 2002; Kembel *et al.*, 2014). Positive values of NRI indicate that species in an assemblage (i.e. species that co-occur within a specific NALMA) are more closely related than expected by chance. Negative values of NRI indicate that species in an assemblage are more distantly related than expected by chance. NRI values of zero indicate phylogenetic randomness (Webb, 2000; Webb *et al.*, 2002; Raia, 2010). We calculated the NRI for each NALMA subdivision considered in the present study (see Supporting information, Table S1) at both the regional and locality scales. At the regional scale, we used the entire phylogeny (i.e. the total diversity of North American perissodactyls and artiodactyls) as the source pool from which communities (i.e. assemblages of species present in each NALMA subdivision) were drawn (Raia, 2010). At the locality scale, we calculated the mean NRI for all localities within each NALMA subdivision (i.e. assemblages of species present at each locality in each NALMA subdivision). Critically, we used a time slicing approach when analyzing locality scale NRI using the paleotree R package (Bapst, 2012). The time slice approach involves shortening the branch lengths to the youngest boundary for each NALMA subdivision to preclude overestimation of phylogenetic distance and thus to exclude species with temporal ranges outside the selected time interval.

To evaluate the relationship between dietary traits and extinction, we used stochastic character mapping to visualize the distribution of tooth crown traits (hypsodont, mesodont, submesodont, and brachyodont) across the artiodactyl and perissodactyl composite phylogenies (Huelsenbeck, Nielsen & Bollback, 2003; Paradis, Claude & Strimmer, 2004; Bollback, 2006; Revell, 2011). We assigned tooth crown types to fossil taxa using published sources (Janis *et al.*, 2004; Muhlbachler *et al.*, 2011). Where tooth crown types were unknown, we assumed similarity within genera. However, taxa for which tooth crown type is equivocal were excluded.

We tested for significant temporal trends in artiodactyl and perissodactyl NRI by regressing NRI

against the midpoint age of each NALMA subdivision using generalized least squares (GLS) regression in R (Dornelas *et al.*, 2013; R Development Core Team, 2014). We also tested for a climatic filter by regressing NRI for both groups of hoofed mammals against stable oxygen isotopes from benthic foraminifera ($\delta^{18}\text{O}\text{‰}$) (Zachos, Dickens & Zeebe, 2008), atmospheric carbon dioxide (CO_2 ; Zhang *et al.*, 2013), and mean annual precipitation estimated from paleosols (as inferred from degree of weathering and depth of carbonate nodules; Retallack, 2007) using the GLS approach. We also included several proxies for sampling bias in our GLS models, including the number of localities, number of species, and length of the sampled interval (Myr) of the fossil localities. The number of localities broadly correlates with amount of available rock record and sampling effort. Similarly, the number of species accounts for sampling effort but may also represent true changes in richness (Benton *et al.*, 2011). The length of NALMA subdivisions is a metric for the amount of time averaging in each sample; sample species richness should tend to increase with higher time averaging. Best fit models were selected using an information theoretic approach in the MUMIN R package (Bartoń, 2013), which is superior to the commonly employed stepwise regression approach (Whittingham *et al.*, 2006). Furthermore, the multivariate approach used in the present study allows for the combination of climate proxies and taphonomic biases into a single model, thereby partitioning their explanatory power (Mannion *et al.*, 2011; Benson & Mannion, 2012; Dornelas *et al.*, 2013). We did not use detrending

methods such as first differences or extraction of residuals because the GLS method simultaneously deals with both temporal autocorrelation and bias.

RESULTS

Both artiodactyls and perissodactyls show phylogenetically dispersed extinction and origination through time (see Supporting information, Fig. S1, S2). Both clades also show dietary trait convergence (see Supporting information, Fig. S3). Furthermore, our composite phylogenies reflect declining browser (black) and mixed feeder (green and blue) diversity through time, in agreement with Janis *et al.* (2000, 2004) (see Supporting information, Fig. S3).

At the regional scale, both artiodactyls and perissodactyls show significant increases in phylogenetic evenness or decreases in the NRI through time when using both poorly resolved and better resolved composite phylogenies (Fig. 1B, Table 1; see also Supporting information, Fig. S3). Artiodactyl NRI shows a significant correlation with $\delta^{18}\text{O}\text{‰}$ from benthic foraminifera (Fig. 2A, B; Table 2). Perissodactyl NRI is best fit by models of NALMA length and $\delta^{18}\text{O}\text{‰}$ from foraminifera (Fig. 2C, D; Table 2).

Locality-scale NRI also shows a significant increase in phylogenetic evenness through time for artiodactyls (Fig. 1C; Table 1) when using both composite phylogenies, but shows strong dependence on the number of taxa in the sample (Table 2). Perissodactyl locality-scale NRI varies between phylogenetically even and clumped (Fig. 1C). There

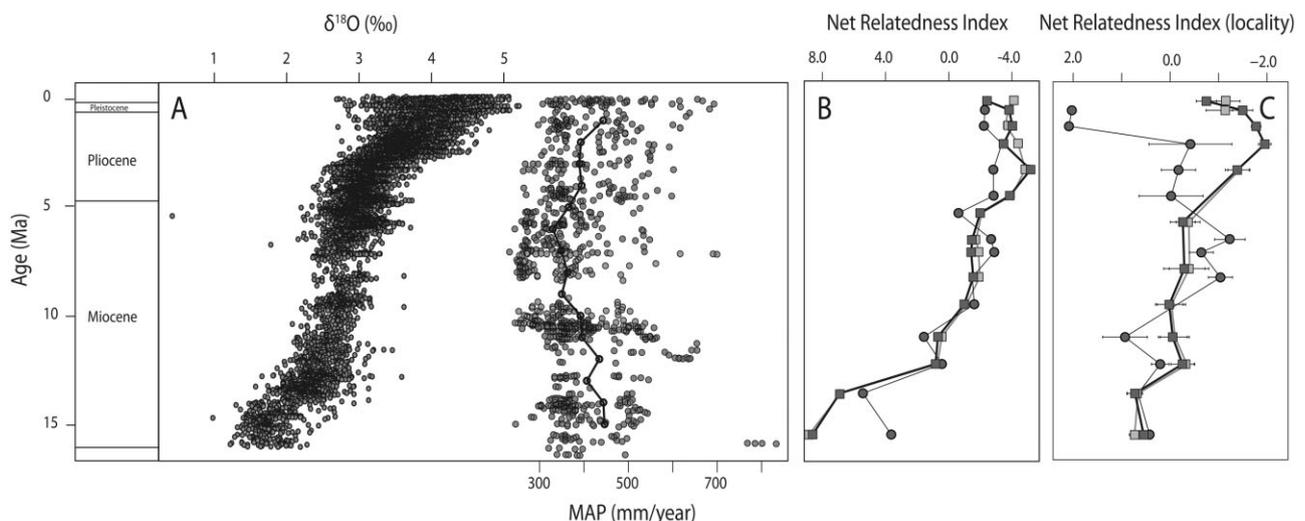


Figure 1. Relationships of artiodactyl (squares; black with immigrants and grey without immigrants) and perissodactyl (circles) phylogenetic community structure (PCS) (net relatedness index; NRI) with (A) $\delta^{18}\text{O}\text{‰}$ from benthic foraminifera (Zachos *et al.*, 2008) and mean annual precipitation (MAP) from paleosols (Retallack, 2007) at the (B) regional scale and (C) local-scale calculated from the well resolved artiodactyl and perissodactyl phylogenies.

Table 1. Generalized least squares regression of phylogenetic community structure against North American Land Mammal Age subdivision midpoint age

Order	Dependent variable	<i>t</i> -value	<i>P</i> -value
Artiodactyla	NRI (resolved)	4.98	< 0.001
	NRI (unresolved)	2.63	0.020
	NRI without immigrants (resolved)	3.60	0.003
	NRI without immigrants (unresolved)	3.38	0.005
	NRI local scale (resolved)	3.29	0.008
	NRI local scale (unresolved)	3.23	0.009
	NRI local scale without immigrants (resolved)	5.50	< 0.001
	NRI local scale without immigrants (unresolved)	7.29	< 0.001
Perissodactyla	NRI (resolved)	4.06	0.001
	NRI (unresolved)	4.23	0.001
	NRI local scale (resolved)	-0.59	0.570
	NRI local scale (unresolved)	-0.35	0.730

NRI, net relatedness index.

were no significant regression coefficients for perissodactyl locality-scale NRI (Tables 1, 2).

At the regional and local scales, artiodactyls still show increasing phylogenetic evenness through time after the removal immigrant taxa; with and without immigrant taxa artiodactyl PCS show an almost identical trend (Fig. 1B; see also Supporting information, Fig. S4). We have not analyzed these data further as a result of model nonconvergence, although we are confident that our interpretations will remain unaffected.

DISCUSSION

Neontological studies of PCS often invoke the proximate processes of abiotic filtering and competition to explain phylogenetic clustering and evenness, respectively (Webb, 2000; Losos, 2008; Vamوسي *et al.*, 2009). However, there has been limited focus on how historical events have influenced the PCS of modern communities, even though macroevolutionary events determine the number and identity of taxa in regional source pools from which local assemblages are drawn (McPeck, 2008). We therefore specifically test for the effects of North American ‘ungulate’ macroevolution on PCS because ungulate extinction rates are high after the warm mid Miocene climatic optimum (Janis *et al.*, 2000, 2004).

At the regional scale, assemblages of species emerge from the cumulative effects of origination, extinction, immigration, and emigration (McPeck, 2008). Thus, climatic filtering, insofar as climate influences patterns and rates of extinction and origination (Mayhew *et al.*, 2008), are more likely to explain long-term temporal changes in the regional pool than competition. We made two predictions about the PCS of

regional species pools based on the distribution of extinction events throughout the phylogenetic tree: (1) phylogenetically dispersed extinction and origination should result in a trend toward phylogenetic evenness and (2) phylogenetically clumped extinction and origination should lead to increased phylogenetic clustering through time. We also suggest that (3) local assemblages might follow the same trajectory as the regional species pool if they are drawn at random from the regional pool or, alternatively, that changes in local assemblages might diverge from the regional pattern as a result of other proximate mechanisms (e.g. abiotic filtering, dispersal, competition).

The evolution of late Cenozoic North American ungulates is typified by both a dramatic decline in richness and a dramatic loss of browsing species (i.e. woody plant specialists) within both the artiodactyl and perissodactyl clades (Janis *et al.*, 2000, 2004). Large, dominant clades of browsers were replaced by comparatively depauperate faunas comprised primarily of larger bodied grazers and mixed feeders (Janis *et al.*, 2004). One of the drivers of declining browser richness may have been the mid latitude transition from productive woodland savannah during the mid Miocene to grassland savannah from the latest Miocene through the Pliocene that was facilitated by climatic cooling and declining atmospheric CO₂ (Jacobs, Kingston & Jacobs, 1999; Janis *et al.*, 2000, 2004; McInerney, Strömberg & White, 2011; Strömberg & McInerney, 2011; Fox *et al.*, 2012; Fraser & Theodor, 2013; Zhang *et al.*, 2013). We showed that, contemporaneous with declining browser richness, regional ungulate PCS increased in phylogenetic evenness through time (Fig. 1B). At the regional scale, artiodactyls and perissodactyls show

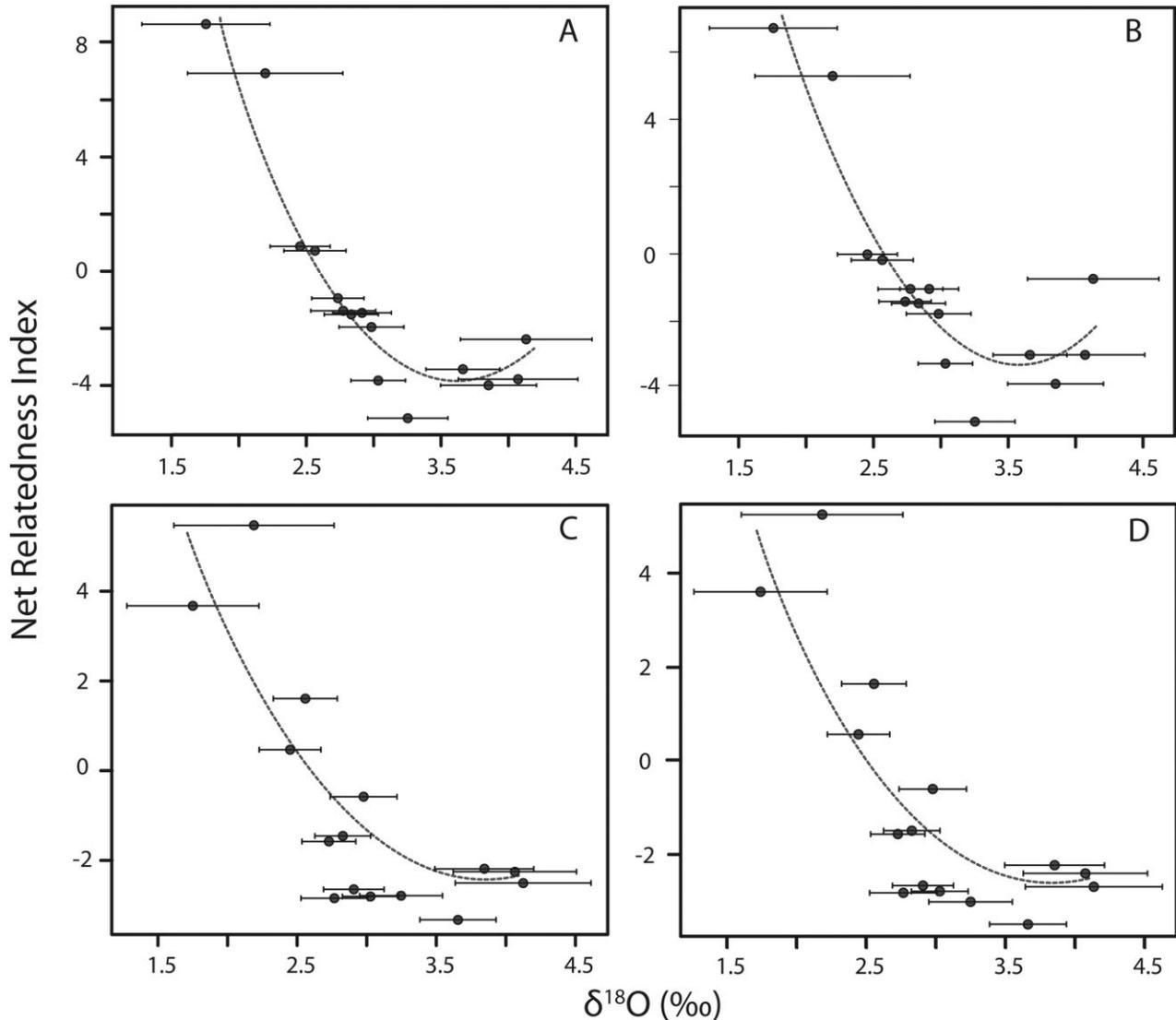


Figure 2. Relationship of $\delta^{18}\text{O}$ (‰) from benthic foraminifera with (A) artiodactyl regional phylogenetic community structure (PCS) (net relatedness index; NRI) calculated from the resolved, (B) unresolved composite phylogeny, (C) perissodactyl regional NRI calculated from the resolved, and (D) unresolved composite phylogeny.

significant decreases in the NRI when using the poorly resolved and better resolved phylogenies (Fig. 1B; Table 1). A declining ungulate NRI is explained by changes in global temperatures ($\delta^{18}\text{O}$ from benthic foraminifera) (Fig. 2; Table 2). However, perissodactyl NRI does show dependence on the length of the NALMA subdivision (Table 2), which might reflect a lack of precision in first and last occurrence dates used to timescale the composite phylogeny; some first and last occurrences correspond to NALMA boundaries in the absence of chemical dating.

Among North American ungulates, increased tooth crown height (i.e. hypsodonty) or a tendency toward open habitat living and consumption of herbaceous

plants has evolved multiple times (see Supporting information, Fig. S3) (i.e. feeding specialization is phylogenetically dispersed). We show that the loss of numerically dominant nonhypsodont (putatively browsing and mixed feeding) clades and phylogenetically dispersed origination of less speciose clades following the mid Miocene climatic optimum led to an increase in phylogenetic evenness at the regional scale. Strong correlation with global climate proxies ($\delta^{18}\text{O}$ from benthic foraminifera and mean annual precipitation; Fig. 2; Table 2) is likely indirectly driven by the effects of declining global temperatures and possibly declining atmospheric CO_2 on the evolution of grassland ecosystems (Zachos *et al.*, 2001, 2008; Zhang *et al.*, 2013), consistent with the

Table 2. Results of best fit generalized linear models relating phylogenetic community structure to mean annual precipitation (MAP) from paleosols (Retallack, 2007), $\delta^{18}\text{O}$ (‰) from benthic forams (mm year⁻¹; Zachos *et al.*, 2008), length of North American Land Mammal Age subdivision, number of taxa sampled, and number of fossil localities

Order	Dependent variable	Best fitted model	Pseudo r^2	Independent variable	t -value	P -value
Artiodactyla	NRI (resolved)	$\delta^{18}\text{O}$ (‰) (quadratic)	0.93	$(\delta^{18}\text{O})^2$	6.11	< 0.001
				$\delta^{18}\text{O}$	-7.43	< 0.001
	NRI (unresolved)	$\delta^{18}\text{O}$ (‰) (quadratic)	0.88	$(\delta^{18}\text{O})^2$	4.99	< 0.001
				$\delta^{18}\text{O}$	-6.02	< 0.001
	NRI local scale (resolved)	Number of taxa	0.43	–	3.33	0.008
	NRI local scale (unresolved)	Number of taxa	0.51	–	3.23	0.009
Perissodactyla	NRI (resolved)	$\delta^{18}\text{O}$ (‰) (quadratic), length of NALMA subdivision	0.88	$(\delta^{18}\text{O})^2$ $\delta^{18}\text{O}$ Length of NALMA	3.57 -4.18 4.53	0.002 0.004 0.001
	NRI (unresolved)	$\delta^{18}\text{O}$ (‰) (quadratic), length of NALMA subdivision	0.87	$(\delta^{18}\text{O})^2$ $\delta^{18}\text{O}$ Length of NALMA	3.35 -3.96 4.20	0.007 0.002 0.002
	NRI local scale (resolved)	Null	–	Intercept	0.68	0.51
	NRI local scale (unresolved)	Null	–	Intercept	2.21	0.049

NALMA, North American Land Mammal Age; NRI, net relatedness index.

proposition of Janis *et al.* (2000, 2004). Our analysis therefore adds a phylogenetic component to the findings of Janis *et al.* (2000, 2004), revealing that loss of diversity during the late Miocene resulted in phylogenetic evenness and probably reduced niche overlap, as had been suggested.

At the local scale, trends in artiodactyl and perissodactyl phylogenetic community structures are divergent (Fig. 1C). Artiodactyl PCS shows a similar, albeit dampened, increase in phylogenetic evenness, as is also the case at the regional scale (Fig. 1C; Table 1), suggesting that local assemblages are partly reflecting macroevolutionary dynamics rather than other proximate processes (e.g. competition and dispersal limitation) (Raia *et al.*, 2012), at least at this scale of analysis. However, local artiodactyl PCS is not well explained by global climate ($\delta^{18}\text{O}$ from benthic foraminifera) (Table 2) but rather by the number of taxa in the sample. Artiodactyl local-scale PCS might therefore reflect the combined effects of phylogenetically dispersed extinctions and originations, as well as sampling effort. Even with the possible influence of sampling bias, our result is significant because we show that the extinctions noted by Janis *et al.* (2000, 2004) resulted in larger phylogenetic distances amongst surviving species, lending circumstantial support to their model of reduced niche overlap among late Cenozoic ungulates.

Perissodactyl locality-scale PCS shows a contrasting pattern to the regional-scale, cycling between phylogenetic clustering and evenness throughout the late Cenozoic (Fig. 1C). There are two periods of large PCS changes among late Cenozoic perissodactyls: late Miocene and late Pliocene (Fig. 1C; see also Supporting information, Fig. S4C; circles). The late Miocene increase in phylogenetic evenness (i.e. decrease in NRI) is coincident with the loss of small-bodied, nongrazing species from within *Merychippus*, *Archaeohippus*, and *Hypohippus* (see Supporting information, Fig. S3B) associated with the opening of grassland ecosystems and loss of woodland savannah in North America (Janis *et al.*, 2000, 2004). The late Pliocene increase in phylogenetic clustering is coincident with a loss of most perissodactyl diversity in North America, with the exception of a few grazing equid genera including *Equus* and *Nannippus*, as well as *Tapirus* (see Supporting information, Fig. S3B). Changes in perissodactyl locality-scale PCS therefore appear to have resulted from stepped extinction and origination events that were coincident with the closure of the Panama seaway, with consequent changes in the distribution of oceanic heat, declining atmospheric CO_2 , and the intensification of Northern Hemispheric glaciation (Zachos *et al.*, 2001, 2008; Ballantyne *et al.*, 2006, 2010; Csank *et al.*, 2011; Zhang *et al.*, 2013).

CONCLUSIONS

The role of macroevolution in shaping the phylogenetic structure of animal communities is poorly known. We show that North American perissodactyl and artiodactyl communities increased in phylogenetic evenness at the regional scale, coincident with large extinctions of woody dicot specialists or browsers and their replacement by depauperate faunas of grazers and mixed feeders following the mid Miocene climatic optimum. We suggest that the phylogenetic community structure of both clades reflects the loss of speciose nongrazing clades because of climatic filtering as a result of global cooling trends and the encroachment of grasslands during the late Cenozoic of North America. Artiodactyl phylogenetic community structure following the mid Miocene climatic optimum is also explained by phylogenetically dispersed origination of large bodied, grazing species. Patterns of perissodactyl community structure diverge, particularly at the locality scale, because origination is confined primarily to *Equus* during the late Cenozoic. Our results lend further support to studies of North American hoofed mammal richness, showing the effects of climatic filtering on ungulate phylogenetic community structure in North America.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. Well-resolved phylogenies for North American (A) Artiodactyla and (B) Perissodactyla.

Figure S2. Poorly-resolved phylogenies for North American (A) Artiodactyla and (B) Perissodactyla.

Figure S3. Character maps of tooth crown height conditions in North American (A) Artiodactyla and (B) Perissodactyla. Black lines show the brachydont or low crowned tooth conditions, green shows the mesodont condition, blue shows the submesodont condition, and red shows the hypsodont or high crowned tooth condition.

Figure S4. Relationships of artiodactyl (squares) and perissodactyl (circles) PCS (NRI) with (A) $\delta^{18}\text{O}$ (‰) from benthic foraminifera (Zachos *et al.*, 2008) and mean annual precipitation (MAP) from paleosols (Retallack, 2007) at the (B) regional scale and (C) local-scale calculated from the poorly resolved artiodactyl and perissodactyl phylogenies. PCS, phylogenetic community structure; NRI, net relatedness index.

Table S1. Summary of North American Land Mammal Age subdivisions and associated sample sizes.