

Geographic variability in North American mammal community richness during the terminal Pleistocene

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Abstract

In North America during the terminal Pleistocene (ca 15,000–10,000 BP), patterns of geographical variability in mammal community richness differed from those observed here today. This paper presents analyses of paleontological and archaeological faunal data from throughout the continental US, and these analyses control for factors that might confound paleontological measurement of past community richness. These analyses suggest that, in contrast to the present, and regardless of whether richness is measured at the local or the regional scale, terminal Pleistocene terrestrial mammal communities in the eastern portion of mid-latitude North America were richer than, or at least as rich as, communities in the west. In addition, the richness of large herbivores declined from south to north, in contrast to the current situation, in which large mammal richness increases with latitude across North America. The reversal in the north-south gradient in large mammal richness suggests that the richness of such taxa was determined primarily by available environmental energy during the terminal Pleistocene, whereas the modern pattern might be, at least in part, a result of the extinctions that occurred here near the end of the Pleistocene. The reversal in the east-west gradient indicates that two variables that have been proposed to be responsible for the gradient observed today—mean elevation and habitat heterogeneity associated with variability in elevation—could not have driven differences in richness between the east and the west during the terminal Pleistocene. Rather, these differences were likely the result of differences in energy and/or differences in habitat heterogeneity that were not related to elevational variability.

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1. Introduction

Much effort has been devoted to understanding how and why the richness of modern mammal communities varies over space on continental and subcontinental scales (e.g., Simpson, 1964; Wright, 1983; Currie, 1991; Rosenzweig and Abramsky, 1993; Wright et al., 1993; Kerr and Packer, 1997; Kaufman and Willig, 1998; Andrews and O'Brien, 2000; Badgely and Fox, 2000; Oindo, 2002). Much less effort has been devoted to understanding variability in richness on similar scales among communities that existed in the distant past, even though doing so might enhance our knowledge of the causes of contemporary patterning in mammalian richness (e.g., Badgely and Fox, 2000, p. 1463).

This paper presents the results of analyses of geographical variability in the richness of mid-latitude North American terrestrial mammal communities during the terminal Pleistocene (ca 15,000–10,000 radio-carbon years BP); I focus on this period in order to gain a better understanding of the environments occupied by the earliest human inhabitants of North America, which should, in turn, allow a better understanding of the foraging strategies that those early Americans pursued. This study employs the FAUNMAP database of paleontological and archaeological animal bone assemblages (FAUNMAP Working Group, 1994), and it suggests that the patterning of variability in mammalian richness across mid-latitude North America was quite different during the late Pleistocene than it is today. These results have implications both for our specific knowledge about North American environments during the terminal Pleistocene and for our general understanding of the causes of variability in mammal community richness.

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1.1. Mammal richness in contemporary North America

To understand how things were different during the terminal Pleistocene, it is necessary first to review briefly how and why mammal community richness varies across mid-latitude North America today. Two variables have been proposed to be particularly important causes of contemporary regional-scale variability in mammalian richness here: energy, or, more broadly, primary productivity, and habitat heterogeneity, especially as related to topographic relief.

Currie (1991) has tabulated the number of mammal species that occur in quadrats of 2.5° latitude by 2.5° longitude for North America north of Mexico, and he argues that available environmental energy, measured as annual potential evapotranspiration (PET), is the best statistical predictor of the richness of those quadrats. He suggests that this supports the hypothesis that richness is limited by energy, which is also the main variable that limits productivity in non-arid environments (see also Simpson, 1964; Wright, 1983; Rosenzweig and Abramsky, 1993; Wright et al., 1993; Grayson, 1998, 2000). Kerr and Packer (1997) have reexamined Currie's data, however, and they note that PET predicts mammalian richness well only where it is less than 1000 mm/yr, which is currently the case in North America only at latitudes above about 45° N. In the portion of the continent south of the 1000 mm/yr PET isocline but north of Mexico, they suggest that habitat heterogeneity, measured as within-region variability in both elevation and PET, is the best predictor of regional richness: they find that within-region variability in elevation alone explains 65% of the inter-regional variability in mammal richness here, while adding the variables of within-region PET variability and coastal location increases this somewhat to 77% (Kerr and Packer, 1997, Fig. 3). The proposed reason for the effect of topography on richness is that regions with higher degrees of relief will generally contain a wider variety of habitats suitable to a wider variety of taxa (Simpson, 1964).

More recently, Badgely and Fox (2000) have explored patterns in mammalian richness across all of North America, including Mexico and Central America. They counted numbers of species within the 150 mile × 150 mile quadrats originally used by Simpson (1964) in his pioneering work, but they used the current comprehensive mammalian taxonomy (Wilson and Reeder, 1993), which was updated after Currie collected his data (Badgely and Fox, 2000, pp. 1438–1439). The goal of their study was to evaluate how different size classes and trophic classes of mammals vary in richness in relation to several environmental variables. Among their results is the finding that many groups of small mammals, especially bats, decline substantially in richness as latitude increases, and they suggest that

these gradients are the result of latitudinal trends in variables related to temperature and moisture. On the other hand, they find that the largest size class, which consists of species with average body weights between 100 and 1000 kg, increases in richness as latitude increases. They also find that certain medium and large size classes increase in richness from east to west, as do the herbivore and granivore trophic classes, and they suggest that these gradients in richness are the result of longitudinal trends in PET and elevation.

Badgely and Fox (2000) note that their results are consistent with the energy hypothesis proposed by Currie (1991) because either PET or other measures of available energy, such as temperature or actual evapotranspiration (AET), have significant positive effects on richness in most of their analyses (e.g., Badgely and Fox, 2000, p. 1460). However, they find no significant effect of elevational variability on overall mammalian richness in the temperate zone of North America, which roughly corresponds to the part of the continent for which Kerr and Packer (1997) argue that this variable is the most important determinant of richness. This is seemingly inconsistent with the conclusions reached by Kerr and Packer (1997),¹ but the results of Badgely and Fox are not completely so: their analyses suggest that variables related to energy have a much stronger effect on mammalian richness north of 50° latitude than in the mid-latitude portion of North America (e.g., Badgely and Fox, 2000, Table 6a), which is entirely consistent with part of the argument that Kerr and Packer (1997) make. In addition, the absence of an effect of topographic relief on richness in mid-latitude North America would not necessarily imply the absence of an effect of habitat heterogeneity since there are factors other than elevational variability that might introduce heterogeneity into environments (e.g., Sousa, 1984).

Thus, in the low-energy far northern portion of North America, variability in regional-scale mammalian richness today appears to be driven primarily by variability in available energy, and richness here displays a striking latitudinal gradient (e.g., Currie, 1991, Fig. 1B; Badgely and Fox, 2000, Fig. 2). Further south, in the area that corresponds roughly to the continental US, modern mammal communities increase in richness from east to west, and it has been proposed that this longitudinal trend is driven by gradients either in elevational variability (Kerr and Packer, 1997) or in energy and mean elevation (Badgely and Fox, 2000). In addition, different size classes and trophic classes of mammals

¹The apparent discrepancy between the two studies may simply be due to the fact that they each involve slightly different portions of North America: the area between 30° and 50° north latitude in the case of the "temperate zone" used by Badgely and Fox (2000), and the narrower band between the 1000 mm/yr PET isocline and approximately the present US–Mexico border in the case of Kerr and Packer (1997).

exhibit different geographical patterns of variability in richness across North America, likely in response to different sets of environmental variables (Badgely and Fox, 2000; see also Andrews and O'Brien, 2000).

One goal of the analyses presented here is to evaluate whether terminal Pleistocene patterns in mammalian richness in mid-latitude North America—that is, in the portion of the continent south of the ice sheets but north of present-day Mexico—were similar to those that exist here today. Another goal is to determine what environmental variables might have caused mammalian richness to vary across this part of the continent during the terminal Pleistocene. To achieve these goals, I first consider differences among subsections of the continent in the average richness of local faunal communities, or the communities that existed in the areas immediately surrounding individual archaeological and paleontological sites. I then consider richness measured at a much larger regional scale.

2. Methods

2.1. Local-scale analysis

The first set of analyses that I present is based on numbers of mammal taxa reported for individual paleontological and archaeological faunal assemblages—or “faunules”—in the FAUNMAP database. The purpose of these analyses is to explore differences in the average richness of local-scale communities among three large subsections of the continent.

Of course, when using assemblages of animal bones to document variability in the richness of past communities, it is not appropriate simply to compare the raw numbers of taxa that are present in them because the richness observed for any assemblage is likely to be strongly influenced by its size (e.g., Grayson, 1984, pp. 131–167). It is necessary to employ a method that accounts for the effects of sample size on assemblage richness, and one such method, which I use here, involves comparing the slopes and elevations of regressions of numbers of taxa against sample size (e.g., Grayson, 1991, 1998; Grayson and Delpech, 1998). This method asks, in effect, whether taxa are added as sample size increases more quickly for one set of assemblages than for another (i.e., is the slope of the regression steeper for one set of assemblages than another?), and/or whether one set of assemblages contains more taxa at any given sample size than does another (i.e., is the elevation of the regression higher for one set than another?).

The “local communities” involved in these analyses consist of the taxa that were present within the area sampled by the taphonomic agent or agents responsible for the deposition of the bones in a given faunule;

among the faunules that I use, such agents include carnivores, raptors, rodents (e.g., packrats, genus *Neotoma*), humans, and geological processes, among others. The amount of terrain sampled by these different agents certainly varied, and the communities that I consider likely come from areas ranging in size from a few hundred square meters to a few dozen square kilometers. Depositional agents also undoubtedly varied in the subsets of taxa that they selected from the environments they sampled. Such variability among depositional agents in the size of the areas that they sampled and in the kinds of taxa that they collected is likely to be partially responsible for variability in the richness of the assemblages that I use. I control for the biases that this taphonomic variability may have introduced to the extent that it is both necessary and possible to do so.

To carry out these analyses, I have tallied the number of taxa present in each of the faunules that I use—following the protocol for counting “overlapping” taxa discussed by Grayson (1991, p. 490)—as well as the size of each faunule. I compare least-squares regression equations for different sets of faunules in which the sample size of individual faunules is the independent variable and the number of taxa in those faunules is the dependent variable. In order to meet the assumption of linear regression analysis that relationships be linear, I transform faunule sample sizes using the logarithmic transformation $x' = \text{Log}_{10}(x + 1)$ (Zar, 1999, p. 275); such semi-log relationships exhibit the best linear fit in all cases.

I use analysis of covariance techniques to compare regression coefficients following the procedures outlined by Zar (1999, pp. 360–376); if regression slopes are found to differ significantly, this is sufficient to conclude that the relationships are indeed different, but if no significant difference in slope is found, it is then appropriate to ask whether equations vary in elevation, or intercept. The tests for differences in slopes and intercepts that I use are analogous to *t*-tests or analyses of variance that test for differences in sample means in situations in which it is not necessary to consider a covariate such as sample size, and the test statistics generated are the familiar *t* and *F* statistics for two and more than two sets of faunules, respectively. In cases involving more than two sets of faunules, in which an analysis of covariance can indicate only whether there is some difference in slope or intercept among the sets, I use Tukey post hoc pairwise comparison tests to determine whether each regression differs significantly in slope from each of the others (Zar, 1999, pp. 210–214, 372–373).

Of course, only assemblages for which sample sizes are known can be included in analyses of this sort, and this information is not available for many FAUNMAP faunules. Moreover, among those for which it is

available, it is given in two incomparable ways: minimum numbers of individuals (MNI) per taxon are recorded for some faunules and numbers of identified specimens (NISP) per taxon are recorded for others, while both types of abundance values are provided for only a few faunules (see Grayson, 1984 for a detailed discussion of the definitions and characteristics of MNI and NISP). I therefore present two analyses for each of the groupings of faunules that I consider: one using all faunules for which MNI values are available and another using all faunules for which NISP values are available.

Finally, either numbers of genera or numbers of species per assemblage could be used in analyses of the sort that I present here, and each of these levels of taxonomic classification would seem to offer its own advantages and disadvantages. Analyses employing numbers of species might be more sensitive to differences in community richness than analyses based on numbers of genera, but they would likely also be more sensitive to variability in the ways in which different analysts assign bone specimens to taxonomic units: some researchers are certainly more conservative than others in identifying difficult specimens only to the generic level rather than to the specific level, and there is well-known disagreement over the validity of many of the nominal species within such ungulate genera as *Equus* (e.g., Graham and Semken, 1987; Harris, 1985, pp. 135–136; Semken and Graham, 1996). I have tabulated numbers of both species and genera for the faunules that I use, and the results of analyses based on one measure of richness are very consistent with those of analyses based on the other; below, I provide one example that demonstrates this. Because the results of analyses of numbers of genera do not differ substantially from the results of analyses that employ numbers of species, I focus on the genus-level analyses here. I also note that Grelle (2002) has found that, among modern mammal communities in Central and South America, richness measured at the generic level is a “useful surrogate” for species richness.

2.2. Regional-scale analysis

The second series of analyses presented in this paper explores variability in richness measured at spatial scales considerably larger than those involved in the first: rather than being based on the numbers of taxa present in individual faunal assemblages, they are based on the numbers of taxa that occur in the combined samples from all of the sites within geographic regions, most of which are thousands of square kilometers in area.

Studies of regional variability in richness among modern biotic communities typically employ areal units of fixed, or at least approximately equal, size (e.g.,

Andrews and O’Brien, 2000; Badgely and Fox, 2000; Currie, 1991; Simpson, 1964); this is desirable because observed richness is generally a function of the geographic scale at which richness is measured (e.g., Rosenzweig, 1995). When attempting to carry out such a study involving communities that existed in the past, however, the “equal-area” approach may not be ideal, given that the paleontological and archaeological sites that provide a window into those communities are distributed very unevenly across the landscape. If equal-area units were created, the number of sites within them would vary greatly (inevitably introducing severe effects related to the unequal sample sizes), and many or most would contain no sites at all. I therefore do not measure richness within spatial units of equal size, but instead do so within regions that are based in part on the empirical distribution of FAUNMAP Late Glacial period sites (see also, for example, Van Valkenburgh and Janis, 1993). I have attempted to define regions that are as equal as possible in both the number of assemblages that they contain and the amount of space that they cover, and although they do still vary considerably along these two dimensions, I control for this below.

The regions that I use are larger than those typically employed in studies of modern biotas (e.g., Rosenzweig, 1995; though again see Van Valkenburgh and Janis, 1993), but this is dictated by a need to incorporate enough sites into individual regions that taphonomic biases become at least partially “averaged out” among them (e.g., FAUNMAP Working Group, 1996, p. 1603; see also Badgely and Fox, 2000, p. 1438). This need for relatively large regions competes with another constraint, however, which is that there must be a large enough number of regions to allow meaningful analysis of correlations between regional richness and the variables that might affect it. The size of the regions that I use reflects an attempt to find an appropriate balance between these two competing requirements.

These regions are illustrated in Fig. 1 and listed in Table 1. There are 24 of these groups of sites, which are defined primarily according to the physiographic province in which sites are located, following Hunt (1967). Defining regions based on physiographic provinces provides a reasonably objective way of grouping sites, and it allows sites to be grouped in a manner that captures meaningful variability in degree of topographic relief. To obtain a useful number of regions of roughly equal size, I have secondarily subdivided many physiographic provinces along gaps that exist between clusters of sites, and in a few cases I have combined provinces or portions thereof.

I explore why richness varied among these regions during the terminal Pleistocene by examining the strength of relationships between richness and correlates of environmental variables that have been proposed to be determinants of mammalian richness in North

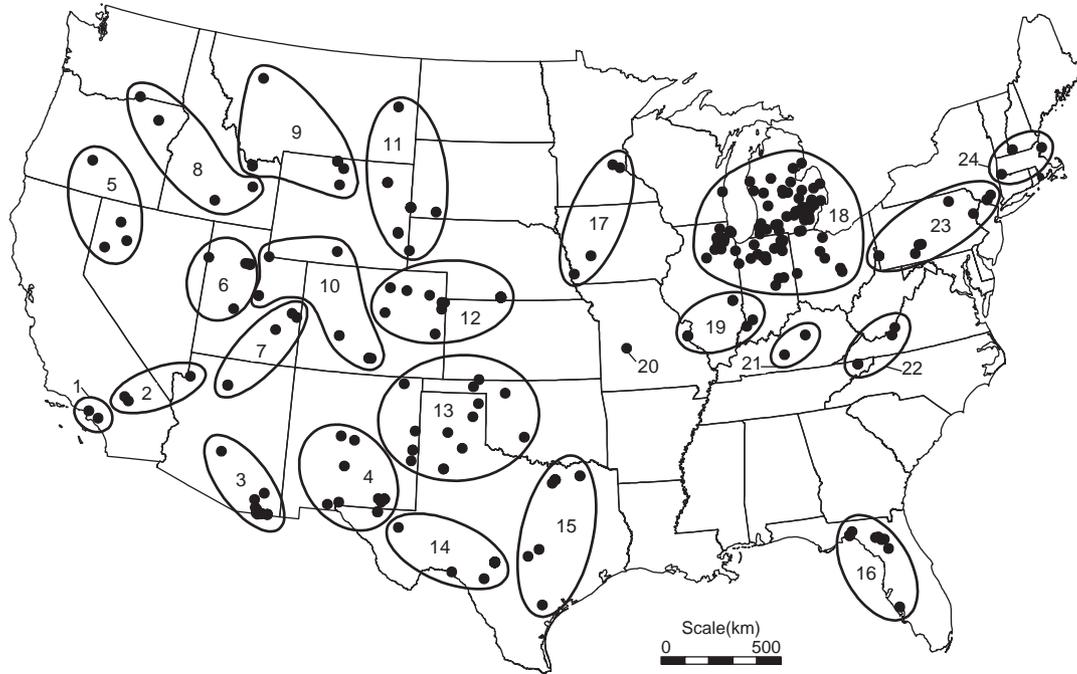


Fig. 1. Map showing the locations of FAUNMAP sites with Late Glacial age faunules, grouped by the regions defined for this study (numbers correspond to the regions listed in Table 1; this map excludes sites with “biological” faunules only).

Table 1
Regions defined for this analysis (see Fig. 1)

No.	Region	Group
1	Southern Pacific Border	West
2	West Southern Basin and Range	West
3	Central Southern Basin and Range	West
4	East Southern Basin and Range	West
5	Western Great Basin	West
6	Eastern Great Basin	West
7	Colorado Plateau	West
8	Columbia Plateau	West
9	Northern Rocky Mountains	West
10	Southern Rocky Mountains	West
11	Far Northern Great Plains	Plains
12	Central Northern Great Plains	Plains
13	Central Southern Great Plains	Plains
14	Far Southern Great Plains	Plains
15	Western Coastal Plain	East
16	Eastern Coastal Plain	East
17	Western Central Lowland	East
18	Eastern Central Lowland	East
19	Southern Central Lowland	East
20	Ozark Plateaus	East
21	Interior Low Plateaus	East
22	Southern Appalachian Plateaus/Valley and Ridge	East
23	Northern Appalachian Plateaus/Valley and Ridge	East
24	New England	East

America today (e.g., Simpson, 1964; Currie, 1991; Kerr and Packer, 1997; Badgely and Fox, 2000). I first consider the raw numbers of genera recorded per region, counting a taxon as present in a region if it occurs in any of the faunules from that region. I then present an

analysis of multiple regression residuals that controls for the effects of the size of regions, the number of assemblages that they contain, the average age of those assemblages, and their depositional context.

2.3. Assemblages and taxa included in analyses

My analyses employ faunules that FAUNMAP assigns to its “Late Glacial research age”, which spans the period between 15,000 and 10,000 radiocarbon years BP. Many of the sites included in FAUNMAP consist of multiple stratigraphic units, and some of these sites are represented in my analyses by multiple Late Glacial age faunules. I exclude from my analyses all faunules that are identified in the database as problematic due to the probable mixing of material of different ages. In addition, because the richness of island faunas is likely to be determined by factors different from those that affect continental faunas, I exclude faunules from islands (i.e., California’s Channel Islands). I also exclude faunules from the two Canadian sites in the database with Late Glacial age deposits: latitude and longitude, which are crucial for my analysis, are not provided for one of these, and the other is located much further north than any other site included in this study. Within faunules, I exclude taxa that are identified by FAUNMAP as likely being intrusive or redeposited, taxa for which FAUNMAP has determined the taxonomic identification to be “questionable” (though I include “cf.” identifications), and taxa for which specimens have been modified into tools or decorated by humans.

Table 2
Terrestrial mammal genera recorded in FAUNMAP Late Glacial research age non-biological faunules

Genus	Common name	Genus (continued)	Common name
Order Didelphimorphia		<i>Rangifer</i> ^a	Caribou
<i>Didelphis</i>	Large American Opossums	<i>Navahoceros</i> ^{a,b}	Mountain Deer
Order Xenarthra		<i>Cervalces</i> ^{a,b}	Stag-moose
<i>Holmesina</i> ^{a,b}	Northern Pamphateres	<i>Sangamona</i> ^{a,b}	Fugitive Deer
<i>Megalonyx</i> ^{a,b}	Jefferson's Ground Sloth	<i>Antilocapra</i> ^a	Pronghorn
<i>Nothrotheriops</i> ^{a,b}	Shasta Ground Sloth	<i>Capromeryx</i> ^{a,b}	Diminutive Pronghorn
<i>Glossotherium</i> ^{a,b}	Harlan's Ground Sloth	<i>Stockoceros</i> ^{a,b}	Stock's Pronghorn
<i>Dasyopus</i> ^{a,c}	Beautiful Armadillo	<i>Bison</i> ^a	Bison
Order Insectivora		<i>Ovis</i> ^a	Sheep
<i>Blarina</i>	American Short-tailed Shrews	<i>Euceratherium</i> ^{a,b}	Shrub Ox
<i>Cryptotis</i>	Small-eared Shrews	<i>Bootherium</i> ^{a,b}	Harlan's Musk Ox
<i>Notiosorex</i>	Desert Shrew	Order Rodentia	
<i>Sorex</i>	Holarctic Shrews	<i>Ammospermophilus</i>	Antelope Squirrels
<i>Condylura</i>	Star-nosed Mole	<i>Cynomys</i>	Prairie Dogs
<i>Parascalops</i>	Hairy-tailed Mole	<i>Marmota</i>	Marmots
<i>Scalopus</i>	Eastern Mole	<i>Sciurus</i>	Tree Squirrels
Order Carnivora		<i>Spermophilus</i>	Ground Squirrels
<i>Canis</i>	Wolves and Coyote	<i>Tamias</i>	Chipmunks
<i>Urocyon</i>	Gray Foxes	<i>Tamiasciurus</i>	Red Squirrels
<i>Vulpes</i>	Foxes	<i>Glaucomys</i>	New World Flying Squirrels
<i>Leopardus/Lynx/Puma/Panthera</i>	Cats	<i>Castor</i>	American Beaver
<i>Smilodon</i> ^b	Sabertooth Cat	<i>Castoroides</i> ^{a,b}	Giant Beaver
<i>Homotherium</i> ^b	Scimitar Cat	<i>Geomys</i>	Eastern Pocket Gophers
<i>Miracinonyx</i> ^b	American Cheetah	<i>Pappogeomys</i>	Mexican Pocket Gophers
<i>Lontra (= Lutra)</i>	New World River Otters	<i>Thomomys</i>	Western Pocket Gophers
<i>Conepatus</i>	Hog-nosed Skunks	<i>Dipodomys</i>	Kangaroo Rats
<i>Mephitis</i>	Striped Skunks	<i>Perognathus/Chaetodipus</i>	Pocket Mice
<i>Spilogale</i>	Spotted Skunks	<i>Napaeozapus</i>	Woodland Jumping Mouse
<i>Brachyprotoma</i> ^b	Short-faced Skunk	<i>Zapus</i>	Jumping Mice
<i>Martes</i>	Martens	<i>Clethrionomys</i>	Red-backed Voles
<i>Mustela</i>	Weasels	<i>Dicrostonyx</i>	Collared Lemmings
<i>Taxidea</i>	American Badger	<i>Lemmiscus</i>	Sagebrush Vole
<i>Bassariscus</i>	Ringtails	<i>Microtus</i>	Meadow Voles
<i>Procyon</i>	Raccoons	<i>Neofiber</i>	Round-tailed Muskrat
<i>Tremarctos</i> ^b	Florida Cave Bear	<i>Ondatra</i>	Muskrat
<i>Arctodus</i> ^b	Giant Short-faced Bear	<i>Phenacomys/Arborimus</i>	Heather and Tree Voles
<i>Ursus</i>	Black and Brown Bears	<i>Synaptomys</i>	Bog Lemmings
Order Proboscidea		<i>Baiomys</i>	American Pygmy Mice
<i>Mammuth</i> ^{a,b}	American Mastodon	<i>Neotoma</i>	Woodrats
<i>Mammuthus</i> ^{a,b}	Mammoths	<i>Ochrotomys</i>	Golden Mouse
Order Perissodactyla		<i>Onychomys</i>	Grasshopper Mice
<i>Equus</i> ^{a,b}	Horses	<i>Oryzomys</i>	Rice Rats
<i>Tapirus</i> ^{a,b}	Tapirs	<i>Peromyscus</i>	Deer Mice
Order Artiodactyla		<i>Podomys</i>	Florida Mouse
<i>Mylohyus</i> ^{a,b}	Long-nosed Peccary	<i>Reithrodontomys</i>	American Harvest Mice
<i>Platygonus</i> ^{a,b}	Flat-headed Peccary	<i>Sigmodon</i>	Cotton Rats
<i>Camelops</i> ^{a,b}	Yesterday's Camel	<i>Erethizon</i>	North American Porcupine
<i>Hemiauchenia</i> ^{a,b}	Large-headed Llama	Order Lagomorpha	
<i>Cervus</i> ^a	Red Deer (Elk)	<i>Ochotona</i>	Pikas
<i>Alces</i> ^a	Moose	<i>Lepus</i>	Hares and Jackrabbits
<i>Odocoileus</i> ^a	White-tailed and Mule Deer	<i>Sylvilagus</i>	Cottontails

Note: For extant taxa, genus and common names follow Wilson and Cole (2000), as does the order in which taxa are listed; designations for extinct taxa follow Grayson and Meltzer (2002) and FAUNMAP Working Group (1994).

^a Large herbivore.

^b Genus extinct in North America.

^c All *Dasyopus* specimens in the Late Glacial faunules used here are from the large, extinct *D. bellus*.

The terrestrial mammal genera that occur in the Late Glacial faunules that I use are listed in Table 2. The FAUNMAP working group standardized the taxonomic designations employed by the researchers who analyzed

the assemblages in the database into a set of “research identifications”, and these are the taxonomic units that I count in my richness analyses. These research identifications are based largely on the systematics presented by

Wilson and Reeder (1993), though the FAUNMAP working group used alternative classificatory schemes for a few taxa, and they employed designations for extinct taxa based on contemporary knowledge (see FAUNMAP Working Group, 1994, pp. 26, 27). There are a few instances, usually involving taxa that have undergone recent systematic revision, in which FAUNMAP combined two or more nominal genera into a single research identification (see Table 2), and I treat these research identifications as single genera here. My analyses are limited to non-domesticated terrestrial mammals; bats and marine mammals are excluded, as are dogs (*Canis familiaris*) and human remains.

For the local-scale analyses that I present, I have calculated faunule sample sizes by summing the NISP or MNI values provided in FAUNMAP for those taxa that are included in the analyses. Counting numbers of taxa for these analyses is complicated somewhat by the fact that some faunules have abundance values recorded for only a portion of the taxa within them. In such cases, only taxa for which abundance values are provided are counted as “present” within a faunule in my local community analyses (though all taxa are counted as present in my regional-scale analyses): for example, if 10 genera are present in a faunule but MNI values are provided for only eight of them and NISP values are provided for only seven of them (there are cases of this sort in FAUNMAP), the number of genera that I use for this faunule in analyses based on MNI is eight and the number of genera that I use for this faunule in analyses based on NISP is seven.

3. Results: local-scale analysis

The analyses presented in this section use the richness-sample size regression method to explore spatial variability in the richness of local terrestrial mammal communities during the terminal Pleistocene. Before presenting the results of these analyses, however, I first show that the method used is capable of detecting a temporal decline in richness that is known to have occurred, and I then address potentially problematic taphonomic factors.

3.1. Late Pleistocene–early Holocene decline in richness

It is well-known that approximately 35 genera of mammals (27 of which occur in the Late Glacial faunules that I use), mostly large-bodied herbivores, went extinct in North America sometime before the end of the Pleistocene (see Grayson and Meltzer, 2003 for a discussion of terminal dates for individual taxa; also see McFarlane, 1999). These extinctions would certainly have reduced the richness of most local-scale mammalian communities. It is also known that many North

American late Pleistocene faunal communities included sets of taxa, primarily involving small-bodied rodents, whose ranges are today widely separated (e.g., Lundelius et al., 1983; Graham and Lundelius, 1984; Graham, 1985a, b; Stafford et al., 1999). The dissolution of these “non-analog” communities, which resulted from changes in the ranges of individual taxa, may also have led to a decline in local-scale richness (e.g., Graham, 1976, 1985a).

Table 3 lists the number of sites in FAUNMAP that contain faunules assigned to the Late Glacial research age, as well as the number of those faunules and the numbers of terrestrial mammal genera and species that occur in them; also given are the same data for FAUNMAP’s “Early Holocene” research age, which spans the period between 10,000 and 8000 radiocarbon years BP.² In addition to total numbers of genera, Table 3 provides numbers of “large herbivore” genera, which include all xenarthrans, proboscideans, perissodactyls and artiodactyls, as well as the large rodent *Castoroides* (Giant Beaver). There are 28 large herbivore genera in the Late Glacial faunules that I use (see Table 2). Of these, 21 went extinct in North America by the end of the Pleistocene, and the proportion of all genera that are large herbivores declines by approximately half between the Late Glacial research age and the Early Holocene (Table 3).

Overall, there are far fewer mammalian taxa reported for the Early Holocene than for the Late Glacial, which is consistent with a decline in mammalian richness between the two periods. However, there are also far fewer Early Holocene faunules than Late Glacial faunules, which may be at least partially responsible for the difference in numbers of taxa reported. This sample size difference can be controlled in an analysis such as the one presented in Fig. 2, in which the richness of individual faunules is plotted against their total MNI or NISP values.

The slopes of the Late Glacial richness-sample size relationships shown in this figure are steeper than those for the Early Holocene, both among faunules for which MNI values are available and among faunules with NISP values, and these differences in slope are statistically significant (see Table 4). Such differences in the rate at which genera are added as sample size increases are precisely what should be observed given the decline in mammalian richness that is known to have occurred in North America between the late Pleistocene and the early Holocene. That the richness-sample size regression method detects this temporal decline indicates that it should be equally sensitive to

²Table 3 excludes “biological” faunules because it is based on the same set of faunules that I used to derive Table 9, from which I exclude such faunules for purposes of my analysis of regional-scale richness; see discussion below.

Table 3
Numbers of sites, faunules, and taxa recorded in FAUNMAP per research age

Research age	<i>n</i> -Sites	<i>n</i> -Faunules	<i>n</i> -Genera	<i>n</i> -Species	<i>n</i> -Large herbivore genera	Proportion large herbivore genera
Early Holocene	67	92	64	107	10	0.16
Late Glacial	216	287	93	185	28	0.30

Table 4
Statistics for regression equations presented in Fig. 2 (“EH” = Early Holocene; “LG” = Late Glacial)

Regression	<i>n</i>	Slope	Intercept	r^2 (<i>p</i> -value)	Significance of difference between regression coefficients ^a
Fig. 2(a) EH	35	6.43	−1.50	0.72 (< 0.001)	Slopes: $t = 2.05$, $p = 0.021$
Fig. 2(a) LG	78	8.15	−1.91	0.83 (< 0.001)	
Fig. 2(b) EH	40	3.27	0.52	0.40 (< 0.001)	Slopes: $t = 2.01$, $p = 0.024$
Fig. 2(b) LG	55	4.89	−1.38	0.64 (< 0.001)	

^aSignificance values are for 1-tailed tests.

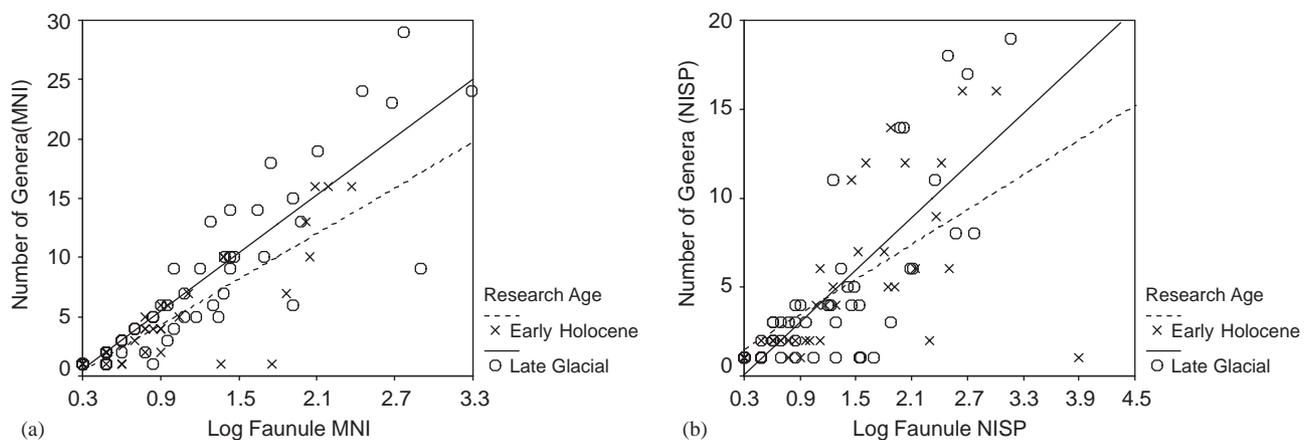


Fig. 2. Richness-sample size relationships for Late Glacial and Early Holocene faunules with abundance values, grouped by research age: (a) number of genera regressed against MNI for faunules with MNI values and (b) number of genera against NISP for faunules with NISP values. See Table 4 for regression statistics.

spatial differences in richness during the terminal Pleistocene.

3.2. Taphonomic factors

To the extent that assemblages from different regions have been subject to different taphonomic histories, observed differences in richness could be reflecting taphonomic variability rather than true geographical differences among past faunal communities (e.g., Graham and Semken, 1987; Semken and Graham, 1996). To determine whether such taphonomic variability might affect the method that I use for detecting differences in local-scale richness, I present Fig. 3, which groups Late Glacial age faunules according to three potentially problematic taphonomic factors.

The first of these factors, “deposit type”, should reflect variability in depositional and transformational processes among faunules. FAUNMAP classifies assem-

blages into a large number of depositional context categories (see FAUNMAP Working Group, 1994, pp. 16–18), but in the present analysis it is not feasible to control for depositional variability in as much detail as these fine-grained categories might permit because most would contain too few faunules to allow meaningful comparisons among them. I therefore assign faunules to three coarser-scale categories, which should still usefully capture variability among faunules in taphonomic processes that might affect the measurement of community richness. These categories include faunules from open sites, faunules from cave sites (including rock-shelters and sinkholes), and faunules classified by FAUNMAP as coming from “biological” depositional contexts. The majority of the biological faunules are from packrat middens, but a few comprise dung deposits preserved in dry caves; all of these biological faunules are limited in distribution to the arid west.

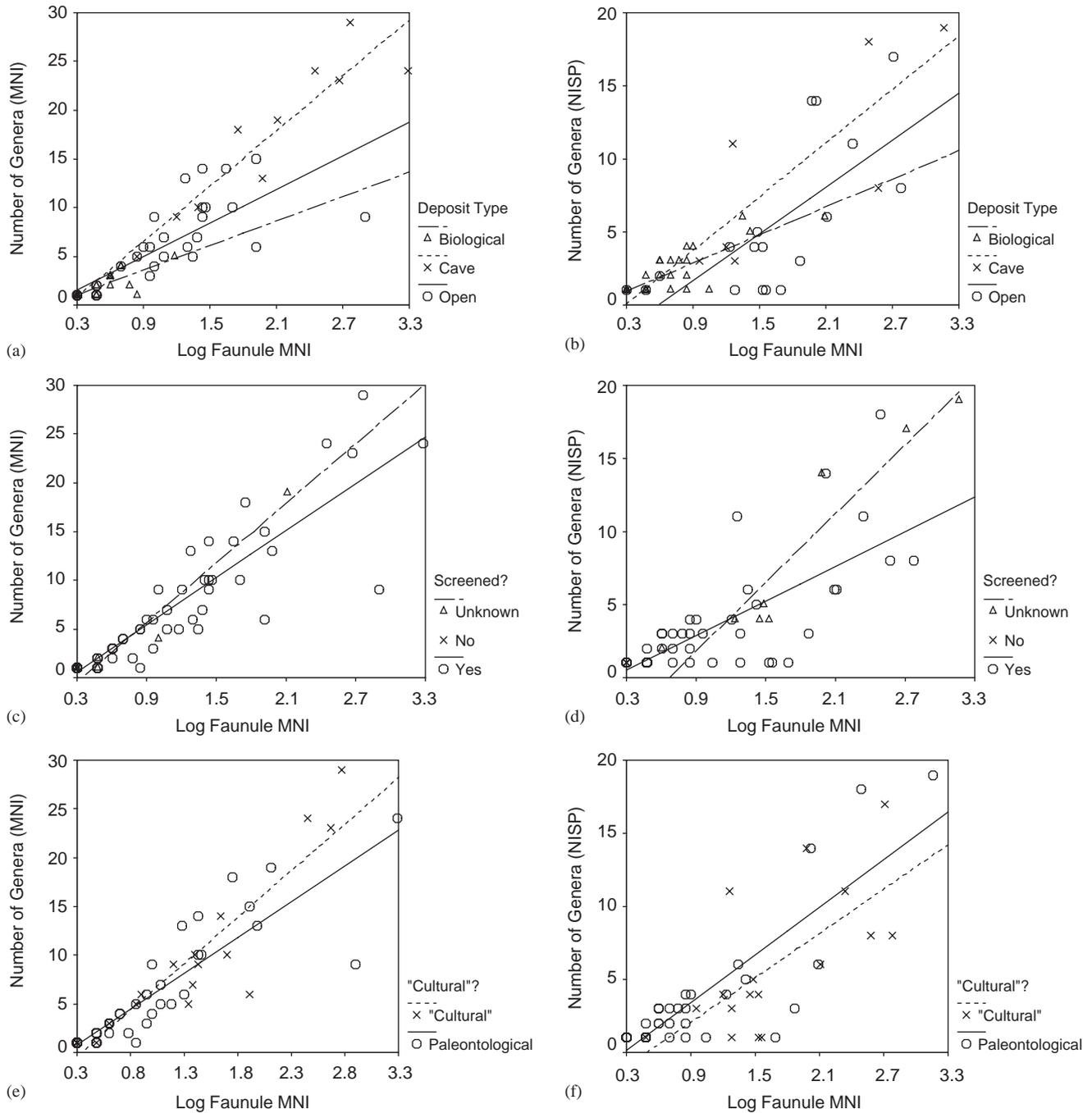


Fig. 3. Richness-sample size relationships for Late Glacial faunules with abundance values, grouped by taphonomic factors that might interfere with an analysis of regional differences in local community richness: (a) faunules with MNI values grouped by deposit type; (b) faunules with NISP values grouped by deposit type; (c) faunules with MNI values grouped according to whether screens were used in excavation; (d) faunules with NISP values grouped by use of screens; (e) faunules with MNI values grouped according to their classification in FAUNMAP as “cultural” or paleontological; (f) faunules with NISP values grouped by “cultural” vs. paleontological. See Table 5 for regression statistics.

As Figs. 3(a) and (b) show, there does appear to be considerable variability in average richness among these three categories. The slope of the richness-sample size regression is steepest for cave sites, and least steep for biological deposits, among both faunules with MNI values and faunules with NISP values. Among the MNI

faunules, an analysis of covariance indicates that the regression slopes for the three site type categories differ significantly, and pairwise comparisons indicate that the slope for the cave site group is significantly different from the slopes for both other groups (Table 5). The overall differences in slope and intercept among the

Table 5
Statistics for regression equations presented in Fig. 3

Regression	<i>n</i>	Slope	Intercept	<i>r</i> ² (<i>p</i> -value)	Significance of difference between regression coefficients ^a
Fig. 3(a) Biological	28	4.21	−0.22	0.64 (< 0.001)	Slopes: <i>F</i> = 11.14, <i>p</i> < 0.001 ^b
Fig. 3(a) Cave	14	9.47	−1.99	0.93 (< 0.001)	
Fig. 3(a) Open	36	5.75	−0.21	0.64 (< 0.001)	
Fig. 3(b) Biological	28	3.21	−0.02	0.67 (< 0.001)	Slopes: <i>F</i> = 1.68, <i>p</i> = 0.197 ^c Intercepts: <i>F</i> = 2.85, <i>p</i> = 0.067
Fig. 3(b) Cave	9	6.11	−1.74	0.75 (0.003)	
Fig. 3(b) Open	18	5.34	−3.13	0.50 (0.001)	
Fig. 3(c) Unknown	5	10.19	−3.49	0.95 (0.004)	Slopes: <i>t</i> = 1.12, <i>p</i> = 0.268 Intercepts: <i>t</i> = 0.19, <i>p</i> = 0.846
Fig. 3(c) Yes	69	8.06	−1.87	0.82 (< 0.001)	
Fig. 3(d) Unknown	8	7.83	−5.22	0.89 (< 0.001)	Slopes: <i>t</i> = 2.94, <i>p</i> = 0.005
Fig. 3(d) Yes	45	3.93	−0.66	0.52 (< 0.001)	
Fig. 3(e) “Cultural”	20	9.53	−3.25	0.86 (< 0.001)	Slopes: <i>t</i> = 2.46, <i>p</i> = 0.016
Fig. 3(e) Paleontological	58	7.33	−1.38	0.81 (< 0.001)	
Fig. 3(f) “Cultural”	17	5.06	−2.48	0.45 (0.003)	Slopes: <i>t</i> = 0.32, <i>p</i> = 0.752 Intercepts: <i>t</i> = 1.68, <i>p</i> = 0.099
Fig. 3(f) Paleontological	38	5.46	−1.52	0.73 (< 0.001)	

^aSignificance values for *t*-tests are 2-tailed.

^bPost hoc pairwise comparisons indicate that the slope of the cave site regression is significantly different from the slopes of both the open site and the biological faunule regressions (*p* < 0.005 in both cases), while the open site and biological faunule slopes do not differ significantly (*p* > 0.5).

^cPost hoc pairwise comparisons indicate that the slope of the cave site regression is significantly different from the slope of the biological faunule regression (*p* < 0.05), while the open site slope does not differ significantly from either the biological faunule slope (*p* > 0.2) or the cave site slope (*p* > 0.5).

NISP faunules are not significant at the 0.05 level, but a pairwise comparison of slopes does give a significant result for the difference between the NISP biological and cave site groups. Because these results clearly show that biological faunules of a given size are less rich, on average, than faunules from other contexts, and because they also show a consistent tendency for cave site faunules to be richer than open site faunules, I control for deposit type in the analyses of spatial variability in richness that I present here.

A second factor that might affect richness-sample size relationships involves the recovery methods used in the excavation of individual assemblages (e.g., Nagaoka, 1994; Semken and Graham, 1996). FAUNMAP classifies faunules into a large number of recovery method categories (see FAUNMAP Working Group, 1994, p. 16), and, as with depositional context categories, these fine-grained categories are not particularly useful for present purposes. I therefore again assign faunules to three coarser-scale categories: the first includes faunules for which any type of screening was employed, the second includes faunules for which no screens were used, and the third includes faunules for which it is unknown whether screens were used (see Figs. 3(c) and (d)).

Few faunules with abundance values are known to have been collected without the use of screens, and all of these contain only one specimen from a single taxon (for

which reason it is not possible to compute regression equations for them). These few small unscreened faunules should have little effect on the analysis of spatial variability in richness that I present here. There are many more faunules for which it is unknown whether screens were used, but these do not appear to pose a problem either: although the difference in regression slopes is significant for the faunules with NISP values (Table 5), among both the MNI faunules and the NISP faunules it is the unknown-screen group that appears to be the richest. Because this is the opposite of what would be expected to occur if these unknown-screen faunules had not been screened, I do not consider the recovery method issue further here.

The final potential confounding factor that I evaluate involves humans as agents of deposition. FAUNMAP classifies faunules as either paleontological or “cultural”, with the latter designation given to faunules from deposits containing archaeological materials and/or for which humans have been proposed to be depositional agents (see FAUNMAP Working Group, 1994, pp. 25, 26). Of course, the assignment of an assemblage to this “cultural” category does not mean that a strong case can be made for human involvement in the taphonomic history of all, or even any, of the bones in that assemblage (see Grayson and Meltzer, 2002 for a detailed discussion of this issue regarding extinct taxa),

and I do not assume that this is the case. It can be shown, however, that faunules classified by FAUNMAP as “cultural” do not differ systematically in richness from faunules that are purely paleontological (cf. Semken and Graham, 1996).

Regressions for faunules grouped by this factor are shown in Figs. 3(e) and (f). There is a significant difference in slope among the faunules with MNI values, and while the faunules with NISP values show no significant difference in slope, they do show a difference in intercept that is significant at $\alpha = 0.1$ (Table 5). Perhaps most important, however, is that the MNI faunules and the NISP faunules present contradictory pictures of the effect of classification as “cultural”: the “cultural” slope is higher among the MNI faunules, but the “cultural” intercept is lower among the NISP faunules. Because the direction of the difference between “cultural” and paleontological assemblages is inconsistent among these two sets of faunules, and because humans may not have deposited many of the bones in many of the “cultural” faunules in the first place (e.g., Grayson and Meltzer, 2002), I do not consider this factor any further.³

3.3. Geographic variability in terminal Pleistocene local-scale richness

To determine how the richness of local-scale mammal communities varied across North America during the terminal Pleistocene, I aggregate faunules into three groups that each represent a large subsection of the continent: a “plains” group consisting of all faunules from the Great Plains physiographic province, an “east” group consisting of all faunules from sites located to the east of this province, and a “west” group consisting of all faunules from west of the plains (see Table 1 and Fig. 1). There are too few faunules with taxonomic abundance values in FAUNMAP to allow exploration of finer-grained spatial variability in local community richness, but I do consider finer-grained spatial variability in the regional-scale analyses presented below. Fig. 4 shows richness-sample size relationships for all

Late Glacial age faunules with abundance values from each of these three “region groups”.

Figs. 4(a) and (b) present analyses of numbers of genera, and the differences among the regression slopes in these graphs suggest that local-scale mammal communities were richer, on average, in eastern North America than in either the plains or the west during the terminal Pleistocene. For the faunules with MNI values, an analysis of covariance indicates that there are significant differences in slope among the three groups, and pairwise comparisons show significant differences between the east group and the west group (Table 6). The difference between the east and west groups is also significant among the faunules with NISP values (there are no faunules in the plains group with NISP values).

Figs. 4(c) and (d) present analyses based on numbers of species, and these illustrate how such analyses produce results that are entirely consistent with those of analyses conducted at the genus level (see Table 6). In other words, the average richness of local-scale terrestrial mammal communities appears to have been higher in the east than in the west regardless of whether richness is counted as numbers of genera or as numbers of species.

Because biological faunules tend to contain fewer taxa than do similarly sized faunules from either open sites or cave sites, and because all biological faunules come from western North America, it is possible that the differences illustrated in Fig. 4 are reflecting variability in deposit type rather than true geographic variability in the richness of past communities. However, Fig. 5, which presents faunules from open sites and cave sites separately, shows that the differences illustrated in Fig. 4 are not being driven by biological faunules. For open sites, the differences that occur among groups are entirely consistent with those observed when faunules from all site types are combined, and the differences between the east and west groups remain statistically significant (Table 6). Such differences between east and west are not evident, though, among cave sites. These results suggest that the differences shown in Fig. 4 are being driven primarily by open sites.

The differences between subsections of the continent that are apparent among open sites are important because they suggest that the situation in North America during the terminal Pleistocene was quite unlike the situation today, in which western faunas tend to be much richer than eastern ones, at least when measured on a regional scale. However, even if the picture presented by cave sites is more accurate (e.g., Hadly, 1999), it would suggest at the very least that eastern faunas were about as rich as western ones, on average, and this would still be very different from the way things are today. I consider this apparent difference between the terminal Pleistocene situation and the modern one further after I present my analysis of variability in regional-scale richness, which also suggests

³These three taphonomic factors do not pose problems for the analysis of temporal change in local community richness presented above. Biological faunules are slightly more common in the Late Glacial research age than the Early Holocene (Late Glacial=19.4%, Early Holocene=14.0%), while cave site faunules are much less common (Late Glacial=23.3%, Early Holocene=43.0%): because cave site faunules tend to be the richest and biological faunules tend to be the least rich, it would seem that, if anything, the declines in local community richness apparent in Fig. 2 may be under-representing the reductions that actually occurred. The percentage of no/unknown screen faunules varies somewhat between research ages (Late Glacial=40.4%, Early Holocene=20.6%), as does the percentage of “cultural” faunules (Late Glacial=34.8%, Early Holocene=72.0%), but these factors do not appear to have any important effect on richness-sample size relationships.

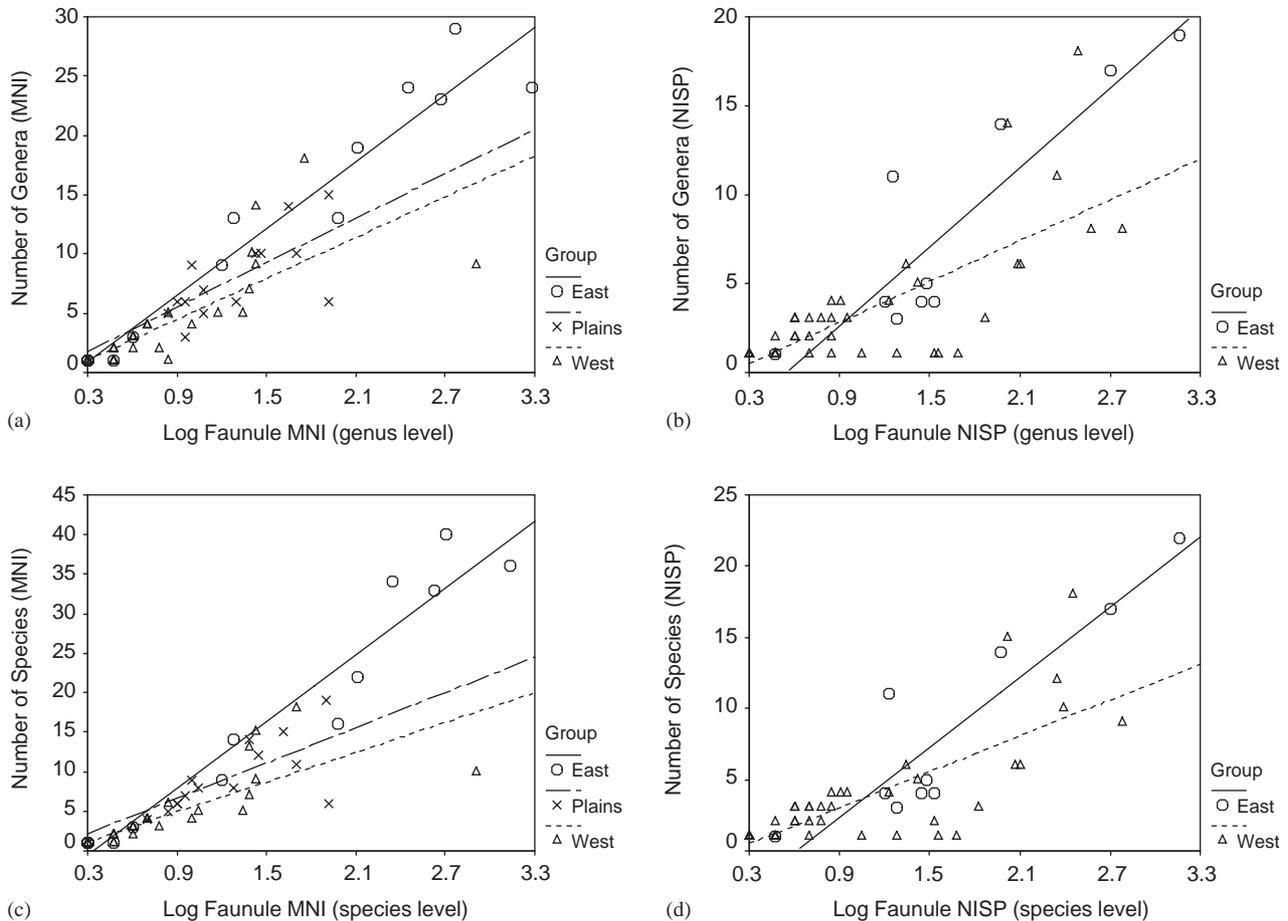


Fig. 4. Richness-sample size relationships for Late Glacial faunules with abundance values, aggregated by “region group” (NISP values are not available for any plains faunules): (a) number of genera against MNI; (b) number of genera against NISP; (c) number of species against MNI; (d) number of species against NISP. See Table 6 for regression statistics.

that eastern communities were richer than western ones during the late Pleistocene.

4. Results: regional-scale analysis

Numbers of sites, faunules and taxa for each of the 24 regions that I have defined are listed in Table 7; this table and all subsequent analyses exclude biological faunules, which, as I noted, contain relatively few taxa for their sizes and are found only in the west. To evaluate why richness varied among these regions during the terminal Pleistocene, I first present relationships between raw numbers of genera per region and geographical variables that might be expected to have some effect on mammalian richness. I then consider factors that could interfere with the use of animal bone assemblages to measure regional-scale richness in the past, and I conclude by presenting an analysis of multiple regression residuals that controls for these factors.

4.1. Numbers of genera per region

As discussed above, two variables have been proposed to be particularly important causes of variability in regional-scale mammalian richness in North America north of Mexico today. Energy appears to have a very strong effect on richness at high latitudes, but it seems to have less of an effect at middle-latitudes, or in roughly that part of the continent in which the late Pleistocene FAUNMAP sites that I use are located (Kerr and Packer, 1997; Badgely and Fox, 2000). In these middle-latitudes, Kerr and Packer (1997) have argued that habitat heterogeneity, especially as related to elevational variability, is the primary determinant of mammalian richness, while Badgely and Fox (2000) have suggested that, at least for certain size and trophic classes, variability in richness is associated with longitudinal gradients in energy and elevation.

Here, I evaluate the roles that energy and elevational variability played in structuring the richness of mammal communities in mid-latitude North America during the terminal Pleistocene. While other environmental

Table 6
Statistics for regression equations presented in Figs. 4 and 5

Regression	<i>n</i>	Slope	Intercept	<i>r</i> ² (<i>p</i> -value)	Significance of differences among regression coefficients ^a
Fig. 4(a) East	13	9.41	−1.90	0.94 (< 0.001)	Slopes: <i>F</i> = 16.23, <i>p</i> < 0.001 ^b
Fig. 4(a) Plains	14	6.26	−0.13	0.46 (0.007)	
Fig. 4(a) West	51	5.75	−0.70	0.67 (< 0.001)	
Fig. 4(b) East	10	7.43	−4.07	0.80 (< 0.001)	Slopes: <i>t</i> = 2.96, <i>p</i> = 0.005
Fig. 4(b) West	45	3.84	−0.64	0.56 (< 0.001)	
Fig. 4(c) East	13	14.08	−4.75	0.94 (< 0.001)	Slopes: <i>F</i> = 28.58, <i>p</i> < 0.001 ^c
Fig. 4(c) Plains	14	7.44	−0.06	0.48 (0.006)	
Fig. 4(c) West	51	6.28	−0.73	0.70 (< 0.001)	
Fig. 4(d) East	10	8.22	−5.05	0.82 (< 0.001)	Slopes: <i>t</i> = 3.26, <i>p</i> = 0.002
Fig. 4(d) West	45	4.20	−0.75	0.60 (< 0.001)	
Fig. 5(a) East	5	12.44	−3.21	0.97 (0.002)	Slopes: <i>F</i> = 3.74, <i>p</i> = 0.035 ^d
Fig. 5(a) Plains	14	6.26	−0.13	0.46 (0.007)	
Fig. 5(a) West	17	4.45	0.08	0.63 (< 0.001)	
Fig. 5(b) East	5	10.93	−11.18	0.89 (0.017)	Slopes: <i>t</i> = 2.15, <i>p</i> = 0.049
Fig. 5(b) West	13	3.85	−1.71	0.43 (0.015)	
Fig. 5(c) East	8	9.44	−2.14	0.87 (0.001)	Slopes: <i>t</i> = 0.47, <i>p</i> = 0.645 Intercepts: <i>t</i> = 0.42, <i>p</i> = 0.683
Fig. 5(c) West	6	10.58	−2.63	0.95 (0.001)	
Fig. 5(d) East	5	6.73	−2.33	0.83 (0.032)	Slopes: <i>t</i> = 0.39, <i>p</i> = 0.709 Intercepts: <i>t</i> = 0.27, <i>p</i> = 0.795
Fig. 5(d) West	4	5.51	−1.20	0.67 (0.179)	

^aSignificance values for *t*-tests are 2-tailed.

^bPost hoc pairwise comparisons indicate that the slope of the east regression is significantly different from the slope of the west regression (*p* < 0.001), while the plains slope does not differ significantly from either the east slope (*p* > 0.2) or the west slope (*p* > 0.5).

^cPost hoc pairwise comparisons indicate that the slope of the east regression is significantly different from the slopes of both the west regression (*p* < 0.001) and the plains regression (*p* < 0.05), while the plains slope does not differ significantly from the west slope (*p* > 0.5).

^dPost hoc pairwise comparisons indicate that the slope of the east regression is significantly different from the slope of the west regression (*p* < 0.025), while the plains slope does not differ significantly from either the east slope (*p* > 0.1) or the west slope (*p* > 0.5).

variables certainly may also have been important in this regard (e.g., Andrews and O'Brien, 2000; Badgely and Fox, 2000), I focus on these two because they are easily measured for periods in the distant past. In addition, since the richness of different mammalian size or trophic classes may be driven by different environmental factors (e.g., Andrews and O'Brien, 2000; Badgely and Fox, 2000), I examine the richness of large herbivores alone in addition to total terrestrial mammal richness.

Available environmental energy might be measured as either annual potential evapotranspiration or as temperature, the two of which are generally strongly and positively correlated with each other (e.g., Wright et al., 1993; Pianka, 1994, pp. 65, 66). These two variables should further correlate negatively with both latitude and elevation (e.g., Bartlein et al., 1998, Fig. 5). Thus, if mammalian richness was limited by energy during the terminal Pleistocene, it should display negative relationships with latitude and elevation. The mean latitude of the sites within each of the regions that I use and the

mean elevation of those sites are listed in Table 8. Relationships between these two variables and both total mammalian richness and large herbivore richness are shown in Fig. 6, and regression and partial correlation statistics for these relationships are provided in Table 9. Negative partial correlations with mean latitude and mean elevation do occur here, though they are fairly weak and insignificant.

Within-region variability in elevation (i.e., the variable that Badgely and Fox, 2000 refer to as "relief") can be measured directly for this analysis because elevations are provided for most of the sites in FAUNMAP. I use the range of site elevations as a measure of this, calculated as the difference in elevation between the highest and the lowest site within each region; these elevation ranges are listed in Table 8. This measure is not perfect because elevations are not provided for all sites (Table 8), nor is it possible to calculate an elevation range for some regions. However, a measure that is based on the actual elevations of the sites included in my sample is preferable to the alternative, which would be a

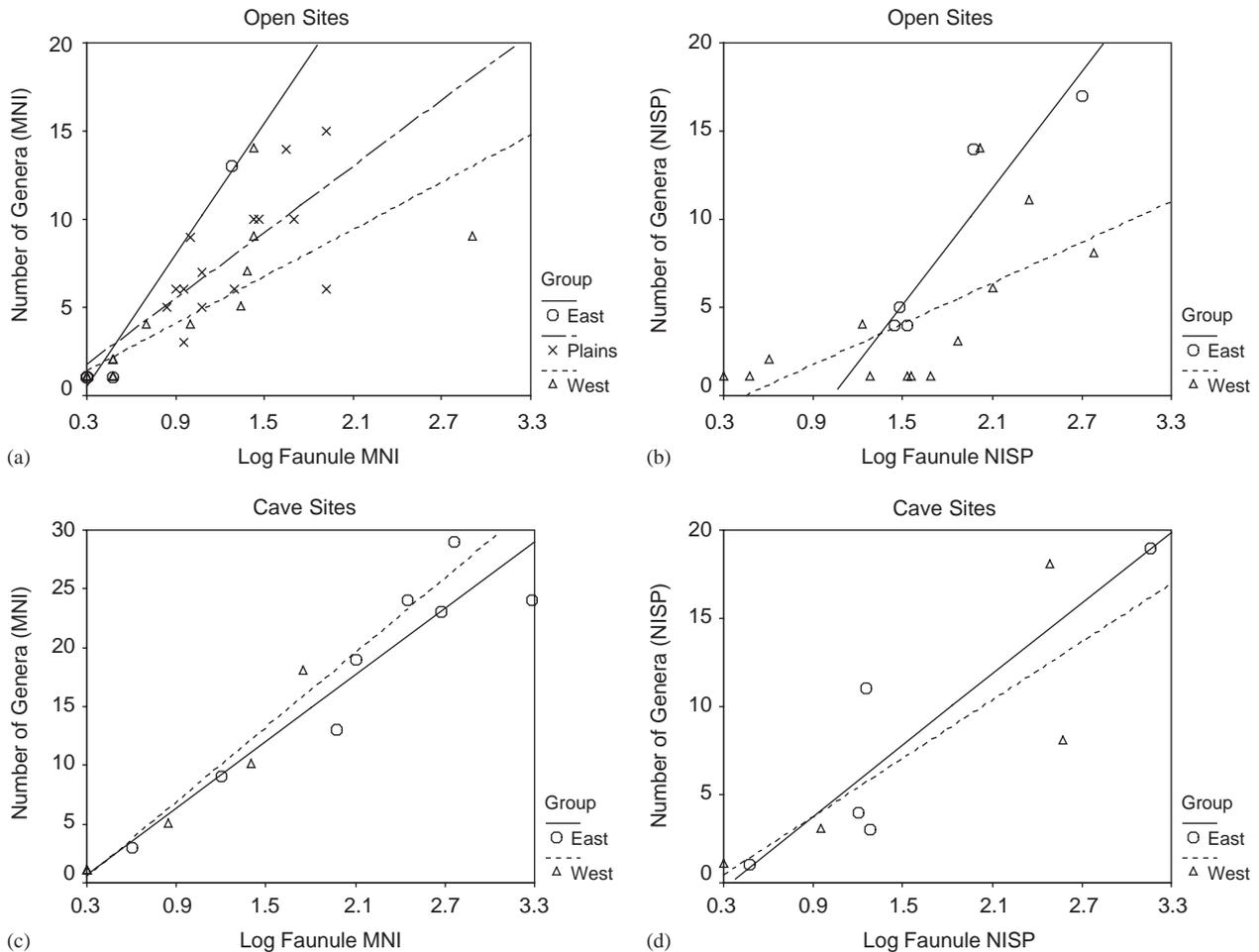


Fig. 5. Richness-sample size relationships for Late Glacial open site and cave site faunules with abundance values, aggregated by “region group” (NISP values are not available for any plains faunules, and there are no plains cave sites with MNI values): (a) number of genera against MNI for open sites; (b) number of genera against NISP for open sites; (c) number of genera against MNI for cave sites; (d) number of genera against NISP for cave sites. See Table 6 for regression statistics.

measure based on the entire range of elevations that occurs within regions: the sites that I use are surely located within only a portion of the range in elevation that occurs in the regions circumscribed by them, and those sites thus do not sample the all of the habitats that might exist at different elevations within their respective regions. Relationships between numbers of genera per region and elevation range are illustrated in Fig. 6; the partial correlations for elevation range are slightly stronger than those for mean latitude and elevation (Table 9), though they are still fairly weak and insignificant.

That the relationships between numbers of genera and the three independent variables considered here are weak may, of course, indicate that there are other variables affecting observed regional richness. If this is the case, then controlling for these other variables should cause the relationships presented in Fig. 6 and Table 9 to become stronger. I next consider such variables, and I then show that controlling for

them does help to clarify the causes of variability in regional-scale mammalian richness during the terminal Pleistocene.

4.2. Covariates of regional richness

Four variables are likely to have particularly important effects on the paleontological measurement of regional-scale faunal community richness. These include regional sample size, the amount of space covered by each region, the age of the assemblages from each region, and the depositional context of those assemblages. Fig. 7 presents relationships between numbers of genera per region and measures of these four variables, and I discuss each of these in turn (see Table 10 for regression and partial correlation statistics).

Just as the number of taxa found in an individual assemblage should be a function of the size of that assemblage, the number of taxa recorded for a region

Table 7

Numbers of sites, faunules, and taxa recorded in Late Glacial samples from each of the regions defined for this analysis (biological faunules excluded); values in parentheses are standardized residuals from multiple regression models incorporating *n*-taxa (genera, species or large herbivore genera) as the dependent variable and log *n*-faunules, maximum linear distance, mean date midpoint, and percentage of faunules from cave sites as independent variables

Region	<i>n</i> -Sites	<i>n</i> -Faunules	<i>n</i> -Genera	<i>n</i> -Species	<i>n</i> -Large herbivore genera
1	2	2	23 (1.16)	25 (0.85)	9 (1.92)
2	3	3	10 (−0.90)	11 (−0.80)	4 (−0.52)
3	11	13	15 (−1.05)	17 (−0.86)	6 (−0.67)
4	9	14	45 (1.05)	79 (2.11)	13 (1.63)
5	4	4	9 (−0.99)	11 (−0.79)	5 (−0.27)
6	6	6	15 (−0.98)	17 (−0.81)	6 (−0.42)
7	5	5	9 (−1.60)	9 (−1.37)	4 (−1.21)
8	4	4	20 (−0.52)	24 (−0.39)	8 (0.02)
9	6	8	33 (0.34)	40 (0.17)	8 (−0.17)
10	8	8	25 (0.02)	26 (−0.26)	8 (0.03)
11	8	11	21 (−0.19)	25 (−0.17)	5 (−1.06)
12	9	23	43 (0.43)	59 (0.79)	10 (−0.54)
13	13	15	34 (0.82)	43 (0.71)	8 (−0.09)
14	4	35	46 (−0.43)	48 (−1.02)	11 (−0.59)
15	7	11	40 (1.24)	47 (0.83)	13 (1.69)
16	11	13	41 (1.17)	47 (0.70)	11 (0.93)
17	4	4	24 (0.11)	29 (0.24)	8 (0.06)
18	79	79	31 (−1.46)	32 (−1.52)	12 (−0.43)
19	5	7	28 (0.50)	33 (0.39)	6 (−0.45)
20	1	1	8 (0.19)	8 (−0.09)	1 (0.00)
21	2	2	20 (−0.33)	23 (−0.38)	3 (−1.01)
22	3	5	36 (0.94)	49 (0.87)	7 (0.25)
23	9	11	48 (1.30)	66 (1.38)	14 (1.65)
24	3	3	2 (−0.81)	2 (−0.56)	2 (−0.74)

Table 8

Geographical and chronological characteristics of the Late Glacial period sites within each region (biological faunules excluded)

Region	Mean site latitude (° North)	<i>n</i> -Sites with elevation (% of total)	Mean site elevation (m asl)	Range of site elevations (m)	Maximum linear distance (km)	Mean faunule date midpoint (¹⁴ C yr BP)
1	33.97	2 (100.0)	65	30	50	12,250
2	35.24	3 (100.0)	619	195	296	11,500
3	31.72	9 (81.8)	1287	261	326	11,622
4	32.84	5 (55.6)	1550	720	352	11,776
5	41.33	4 (100.0)	1273	154	371	11,183
6	40.33	5 (83.3)	1384	136	240	12,261
7	37.64	1 (20.0)	1770	—	408	11,773
8	44.39	2 (50.0)	1437	294	618	11,806
9	45.04	5 (83.3)	1603	914	555	11,519
10	39.09	4 (50.0)	2743	531	597	11,162
11	43.49	4 (50.0)	1305	319	604	10,749
12	39.80	2 (22.2)	1269	22	489	12,868
13	35.37	3 (23.1)	1233	569	549	10,928
14	30.17	0 (0.0)	—	—	429	12,982
15	31.80	0 (0.0)	—	—	583	11,323
16	29.65	4 (36.4)	15	24	388	11,884
17	43.11	0 (0.0)	—	—	485	12,468
18	42.06	9 (11.4)	227	136	605	12,152
19	38.93	1 (20.0)	127	—	282	12,116
20	38.09	0 (0.0)	—	—	0	10,750
21	37.56	1 (50.0)	264	—	121	12,725
22	37.09	3 (100.0)	562	282	220	11,740
23	40.89	3 (33.3)	300	288	552	12,023
24	42.54	2 (66.7)	80	136	213	11,112

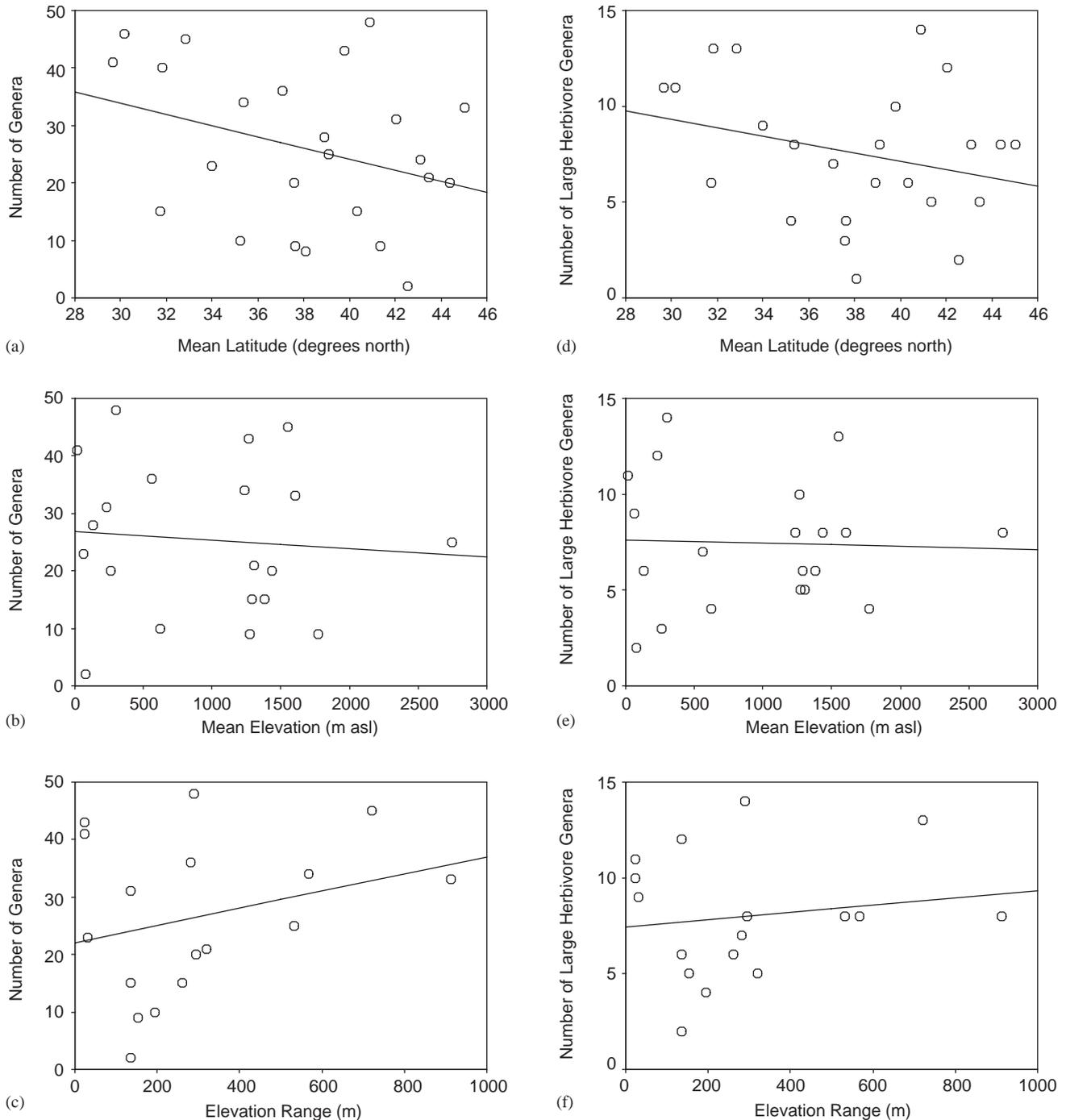


Fig. 6. Relationships between the number of genera recorded in FAUNMAP for each region and geographical correlates of variables that might cause regional-scale mammalian community richness to vary (this and all subsequent figures are based on non-biological Late Glacial age faunules): (a) number of genera against mean site latitude; (b) number of genera against mean site elevation; (c) number of genera against range of site elevations; (d) number of large herbivore genera against mean latitude; (e) number of large herbivore genera against mean elevation; (f) number of large herbivore genera against elevation range. See Table 9 for regression and partial correlation statistics.

should be a function of the number and/or size of assemblages from that region. Fig. 7(a) plots the total number of genera present in each of the regions that I use against the number of faunules from each region. This relationship is highly significant ($r^2 = 0.42$, $p = 0.001$; see Table 10), as is the equivalent relationship

for large herbivores alone ($r^2 = 0.48$, $p < 0.001$). Thus, some of the variability in regional richness that is apparent in the plots shown in Fig. 6 is surely due to variability in the number of assemblages per region rather than to the geographical variables that are considered in that figure. The number of faunules is a

Table 9

Regression r^2 values and partial correlation coefficients for the relationships presented in Fig. 6 (“LH” = large herbivore); significance values are in parentheses

Relationship	r^2	Partial correlation coefficient ^a
<i>n</i> -Genera–mean latitude (Fig. 6(a))	0.11 (0.121)	–0.25 (0.184)
<i>n</i> -Genera–mean elevation (Fig. 6(b))	0.01 (0.733)	–0.21 (0.228)
<i>n</i> -Genera–elevation range (Fig. 6(c))	0.08 (0.288)	0.38 (0.084)
<i>n</i> -Genera multiple regression	0.18 (0.436)	
<i>n</i> -LH genera–mean latitude (Fig. 6(d))	0.08 (0.187)	–0.21 (0.223)
<i>n</i> -LH genera–mean elevation (Fig. 6(e))	0.00 (0.884)	–0.19 (0.245)
<i>n</i> -LH genera–elevation range (Fig. 6(f))	0.02 (0.575)	0.26 (0.173)
<i>n</i> -LH genera multiple regression	0.11 (0.659)	

Note: Multiple regression r^2 values are for models incorporating all three of the independent variables. In the partial correlations with each independent variable, the effects of the other two are controlled.

^aPartial correlation significance values are for 1-tailed tests.

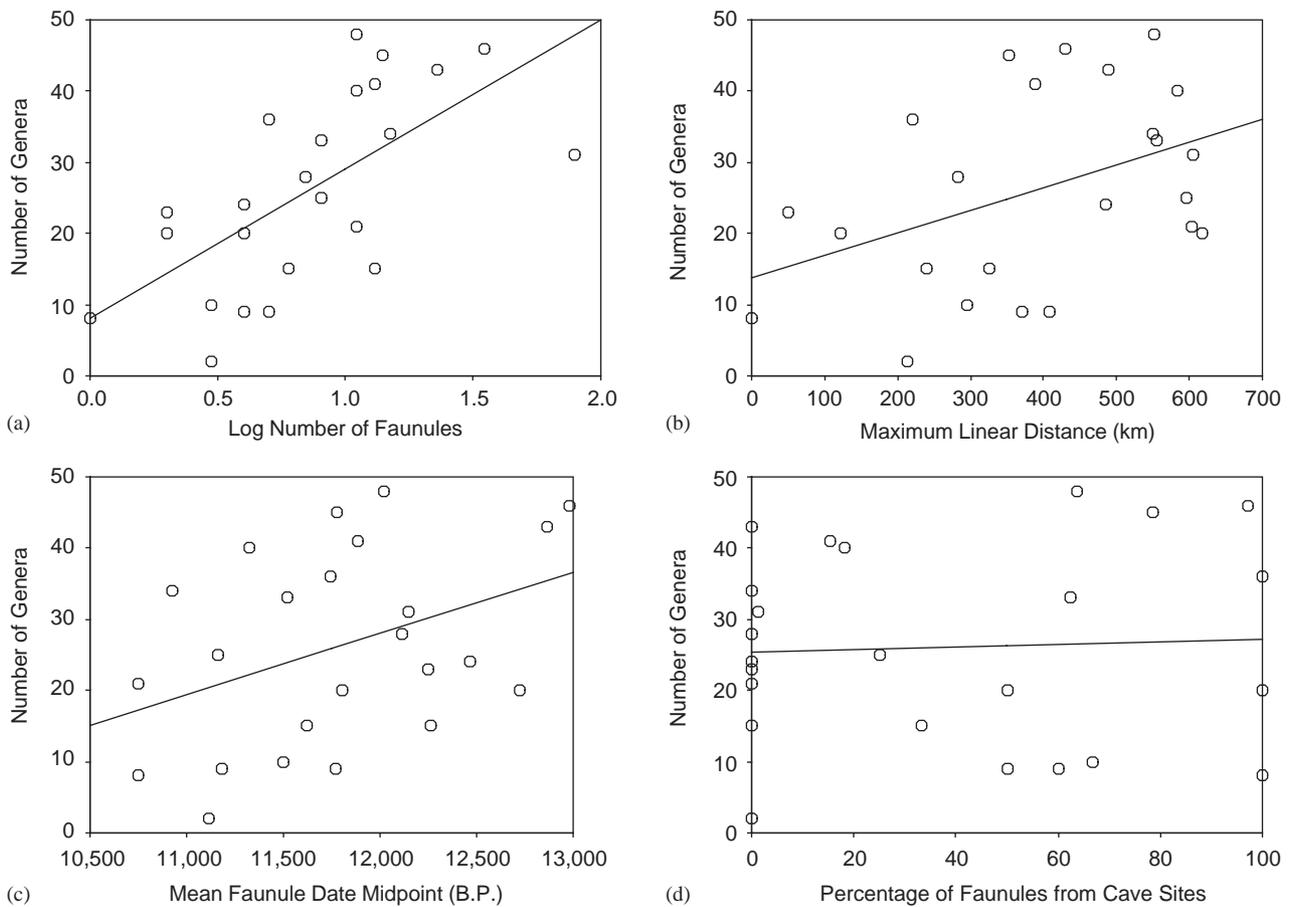


Fig. 7. Relationships between the number of genera recorded for each region and covariates of regional-scale paleontological/archaeological richness: (a) number of genera against log number of faunules; (b) number of genera against region size measured as the maximum linear distance between sites; (c) number of genera against mean faunule age measured as the mean of the “date midpoints” for the faunules from each region (note that time proceeds from right to left); (d) number of genera against the percentage of faunules from cave sites. See Table 10 for regression and partial correlation statistics.

much better predictor of the total number of genera per region than is number of sites ($r^2 = 0.18$, $p = 0.037$) or the average size of the assemblages per region as

determined by either mean MNI ($r^2 = 0.20$, $p = 0.075$) or mean NISP ($r^2 = 0.06$, $p = 0.511$; see Table 11 for mean taxonomic abundance values), and for this reason

Table 10

Regression r^2 values and partial correlation coefficients for relationships between numbers of genera per region and log number of faunules, maximum linear distance, mean date midpoint, and the percentage of faunules from cave sites (see Fig. 7); significance values are in parentheses

Relationship	r^2	Partial correlation coefficient ^a
<i>n</i> -Genera–log <i>n</i> -faunules (Fig. 7(a))	0.42 (0.001)	0.48 (0.013)
<i>n</i> -Genera–max. linear distance (Fig. 7(b))	0.18 (0.038)	0.16 (0.245)
<i>n</i> -Genera–mean date midpoint (Fig. 7(c))	0.16 (0.053)	0.31 (0.086)
<i>n</i> -Genera–% from cave sites (Fig. 7(d))	0.00 (0.799)	0.32 (0.078)
<i>n</i> -Genera multiple regression model	0.54 (0.004)	
<i>n</i> -LH genera–log <i>n</i> -faunules	0.48 (< 0.001)	0.42 (0.028)
<i>n</i> -LH genera–max. linear distance	0.30 (0.006)	0.28 (0.107)
<i>n</i> -LH genera–mean date midpoint	0.13 (0.089)	0.32 (0.078)
<i>n</i> -LH genera–% from cave sites	0.02 (0.522)	0.09 (0.346)
<i>n</i> -LH genera multiple regression model	0.56 (0.003)	

^aPartial correlation significance values are for 1-tailed tests.

Table 11

Numbers of faunules with MNI and NISP values per region and mean MNI and NISP for each region; also provided are the percentage of faunules from each region that are from cave sites, the percentage for which screens were not used or for which it is unknown whether screens were used, and the percentage classified as “cultural” (biological faunules excluded)

Region	<i>n</i> -Faunules with MNI (% of Total)	Mean MNI	<i>n</i> -Faunules with NISP (% of Total)	Mean NISP	% Cave site faunules	% No or unknown screen faunules	% “Cultural” faunules
1	2 (100.0)	412.0	1 (50.0)	103.0	0.0	0.0	0.0
2	1 (33.3)	1.0	1 (33.3)	73.0	66.7	0.0	0.0
3	6 (46.2)	8.8	6 (46.2)	158.7	0.0	7.7	46.2
4	0 (0.0)	—	0 (0.0)	—	78.6	35.7	35.7
5	1 (25.0)	1.0	1 (25.0)	8.0	50.0	0.0	75.0
6	5 (83.3)	2.8	5 (83.3)	79.2	33.3	66.7	16.7
7	0 (0.0)	—	0 (0.0)	—	60.0	80.0	20.0
8	2 (50.0)	2.5	0 (0.0)	—	50.0	50.0	25.0
9	2 (25.0)	15.0	0 (0.0)	—	62.5	12.5	50.0
10	4 (50.0)	20.5	3 (37.5)	145.0	25.0	25.0	62.5
11	4 (36.4)	45.0	0 (0.0)	—	0.0	18.2	100.0
12	10 (43.5)	20.7	0 (0.0)	—	0.0	17.4	30.4
13	0 (0.0)	—	0 (0.0)	—	0.0	60.0	73.3
14	0 (0.0)	—	0 (0.0)	—	97.1	5.7	94.3
15	1 (9.1)	15.0	5 (45.5)	138.0	18.2	63.6	63.6
16	3 (23.1)	1.7	1 (7.7)	18.0	15.4	7.7	84.6
17	1 (25.0)	18.0	0 (0.0)	—	0.0	50.0	0.0
18	2 (2.5)	1.5	0 (0.0)	—	1.3	96.2	1.3
19	0 (0.0)	—	0 (0.0)	—	0.0	42.9	42.9
20	0 (0.0)	—	0 (0.0)	—	100.0	0.0	100.0
21	1 (50.0)	127.0	1 (50.0)	1455.0	100.0	100.0	0.0
22	4 (80.0)	357.0	0 (0.0)	—	100.0	20.0	60.0
23	1 (9.1)	1931.0	3 (27.3)	11.3	63.6	63.6	36.4
24	0 (0.0)	—	0 (0.0)	—	0.0	100.0	66.7

I use number of faunules to control for regional sample size in what follows.⁴

The second variable that may be introducing noise into the relationships shown in Fig. 6 is the geographic

size of the regions that I use, which, as I have noted, are not equal in area. As a measure of geographic size, I employ the maximum linear distance between sites, or the distance between the two sites within each region that are located the furthest from each other.⁵ These distances are provided in Table 8, and the relationship

⁴For the regressions discussed here, I have logarithmically-transformed numbers of faunules and numbers of sites by the equation $x' = \text{Log}_{10}(x)$. This produces a better linear fit than the transformation $x' = \text{Log}_{10}(x + 1)$, which I use for all measures of sample size involving MNI or NISP, including mean faunule MNI and NISP per region.

⁵These distances were calculated using the “Latitude/Longitude Distance Calculation” website (<http://jan.ucc.nau.edu/~cvm/latlong-dist.html>).

between this variable and the number of genera per region is illustrated in Fig. 7(b). Since the areas of these regions are two-dimensional, maximum linear distance is not a perfect measure of regional size, but it does scale well with regional area (compare the sizes of the clusters of sites shown in Fig. 1 and the distance values listed in Table 8). Because maximum linear distance explains a portion of the variability in richness among regions (all genera: $r^2 = 0.18$, $p = 0.038$), I control for it in what follows as well. I also note that the geographic size of regions appears to have a somewhat greater effect on the richness of large herbivores than it does on overall terrestrial mammal richness (large herbivores only: $r^2 = 0.30$, $p = 0.006$).

The third variable that must be considered is the age of the faunules from each region. FAUNMAP's Late Glacial research age spans 5000 radiocarbon years, and the considerable changes in climate that occurred during this period likely reduced faunal richness within it, just as richness declined between the terminal Pleistocene and the early Holocene. As a measure of average faunule age, I use "mean date midpoints" for the faunules from each region. FAUNMAP provides a minimum age and a maximum age for all faunules (see FAUNMAP Working Group, 1994, pp. 20, 21), and I have averaged these two dates for each Late Glacial faunule in order to derive a "date midpoint" for it. These are not "mean dates", as might be calculated, for example, by averaging all of the radiocarbon dates that exist for a faunule, but they should provide a useful measure of faunule age. I have averaged the date midpoints for all of the faunules within each region, and these mean date midpoints are listed in Table 8. As Fig. 7(c) shows, richness does seem to have declined during the Late Glacial period, and relationships between regional richness and age are nearly significant at $\alpha = 0.05$ (all genera: $r^2 = 0.16$, $p = 0.053$; large herbivores only: $r^2 = 0.13$, $p = 0.089$). I therefore control for faunule age here.

A final factor to take into account is variability among regions in faunule depositional context. I showed above that cave site assemblages tend to be richer than those from open sites, and regions in which most faunules come from caves might appear to be richer than others for this reason. The percentage of the faunules from each region that are from cave sites is given in Table 11 (since biological faunules are excluded from this analysis, the remainder of these faunules are from open sites), and the number of genera per region is plotted against this variable in Fig. 7(d). Bivariate relationships between this variable and both the number of genera and the number of large herbivore genera are practically non-existent (all genera: $r^2 = 0.00$, $p = 0.799$; large herbivores only: $r^2 = 0.01$, $p = 0.522$), but the partial correlation with total number of genera, in which the effects of the other independent variables are

controlled, is reasonably strong ($r_{\text{partial}} = 0.32$, $p = 0.078$). Because of this, I control for the percentage of faunules from cave sites here. I note, however, that the percentage of cave site faunules appears to have little effect on large herbivore richness ($r_{\text{partial}} = 0.09$, $p = 0.346$), even though it does seem to affect overall mammalian richness.

To control for the effects of these four factors on the paleontological measurement of regional richness, I have computed multiple regression equations in which numbers of taxa are dependent variables and in which log number of faunules, maximum linear distance, mean date midpoint, and percentage of cave site faunules are all independent variables. Table 10 provides r^2 values for these multiple regression models, and these r^2 values can, of course, be interpreted as reflecting the proportion of the variability in richness among regions that is explained by the four independent variables (54% for all genera and 56% for large herbivores only).

The remainder of the variability—the residual variability—is what might be explained by geographical variables such as latitude or elevation range, and this is captured in the regression model standardized residuals for each region. A standardized residual with a value greater than zero indicates that a region contains more taxa than is to be expected given the sample size, geographic size, average faunule age, and percentage of cave site faunules for that region, and a standardized residual less than zero indicates that a region is less rich than is to be expected. The absolute value of a standardized residual reflects the degree to which a region deviates from its expected level of richness, expressed in units of standard deviation. The standardized residuals from the models shown in Table 10, which are provided in Table 7, can be used as dependent variables in analyses such as those presented in Fig. 6, and the four covariates of regional richness will effectively be controlled.

Though not presented in Table 10, I have computed an analogous model for numbers of species, and the residuals from this model are also given in Table 7. The residuals for numbers of species are highly correlated with those for numbers of genera ($r = 0.93$, 1-tailed $p < 0.001$), which again indicates that results should not vary substantially with the taxonomic level at which richness is counted. On the other hand, the correlation between the total number of genera residuals and the residuals for large herbivores alone is weaker ($r = 0.77$, 1-tailed $p < 0.001$), which suggests that geographic patterns of large herbivore richness differed somewhat from patterns of overall terrestrial mammal richness during the terminal Pleistocene.

These residuals do not appear to be greatly affected by either faunule recovery method or classification as "cultural", which suggests that these two taphonomic factors pose little problem for the analysis that I present

next. Table 11 lists the percentage of faunules from each region that were not screened during excavation or for which it is unknown whether screens were used, as well as the percentage that are classified as “cultural” as opposed to paleontological. Partial correlations in which the effect of one of these variables is evaluated while the effect of the other is controlled are weak and insignificant, both for the total number of genera residuals (% no/unknown screen: $r_{\text{partial}} = -0.18$, $p = 0.206$; % “cultural”: $r_{\text{partial}} = 0.14$, $p = 0.265$) and for the number of large herbivore genera residuals (% no/unknown screen: $r_{\text{partial}} = -0.20$, $p = 0.186$; % “cultural”: $r_{\text{partial}} = 0.11$, $p = 0.313$).

4.3. Analysis of residuals

Having controlled for variables that affect the paleontological measurement of past faunal community richness, and having shown that other taphonomic variables do not appear to be problematic, it is now possible to better evaluate the causes of variability in regional-scale mammalian richness during the terminal Pleistocene. Fig. 8 is analogous to Fig. 6 except that it employs the multiple regression standardized residuals in place of raw numbers of genera, and Table 12 presents regression and partial correlation statistics comparable to those in Table 9. After accounting for the effects of the four covariates of regional richness, all of the relationships between richness and the three geographical variables considered here become somewhat stronger, both for overall mammalian richness and for the richness of large herbivores alone.

Of the three geographical variables, latitude and elevation range appear to have the strongest effects on overall terrestrial mammal richness, and the partial correlations with these two variables are approximately equal in strength (-0.41 and 0.43 , respectively). The positive correlation with elevation range suggests that, during the terminal Pleistocene, habitat heterogeneity related to elevational variability was an important determinant of mammalian richness in mid-latitude North America, just as Kerr and Packer (1997) have suggested is the case in this part of the continent today. However, the equally strong negative correlation with latitude suggests that energy was about as important to richness as elevational variability was during the terminal Pleistocene, and the weaker negative correlation with mean elevation ($r_{\text{partial}} = -0.31$) is also consistent with the hypothesis that richness was limited by energy during that period.

For large herbivores alone, elevation range has the weakest effect of the three variables (0.34 , vs. -0.43 for mean latitude and -0.36 for mean elevation), which suggests that energy was the most important determi-

nant of large herbivore richness in mid-latitude North America during the terminal Pleistocene. This result is consistent with the observation made by Andrews and O'Brien (2000) that large mammal richness in contemporary southern Africa is strongly correlated with average annual temperature, even though the richness of smaller mammals there appears to be driven by other factors. On the other hand, the negative correlation found in this analysis between large herbivore richness and latitude during the terminal Pleistocene is inconsistent with the results of Badgely and Fox (2000), who have shown that large mammal richness increases with latitude in North America today. I discuss this difference between the present and the late Pleistocene further below.

The correlations between richness and latitude that lead to the conclusion that richness was limited by energy in North America during the late Pleistocene could, of course, be the result of some other causal variable. In particular, some of the eastern regions used here lie partially or entirely north of the maximum southern extent of the Laurentide ice sheet, and Graham (1985a) has argued that such areas might have been less rich than others during the terminal Pleistocene due to colonization lags following deglaciation. However, a negative relationship between richness and latitude occurs even if the regions that were at least partially glaciated (regions 17, 18, 23 and 24) are excluded from consideration. If these regions are dropped from the analyses presented in Table 12, the partial correlation between the number of genera residuals and mean latitude remains negative (-0.26 , $p = 0.206$), and the partial correlation for the number of large herbivore residuals changes little (-0.41 , $p = 0.092$). It thus appears that the latitudinal gradients in richness documented here for the terminal Pleistocene were indeed driven by variability in available energy, rather than by colonization lags in the far north.

Finally, this analysis of regional-scale richness supports the main result of my local-scale analysis, which was that, in contrast to the modern situation in North America, mammal communities were richer in the east than in the west during the terminal Pleistocene. A similar east-west difference in overall richness is evident in the number of genera multiple regression model residuals shown in Table 7: the mean of these residuals for the eastern and plains regions combined is 0.25 , while it is -0.35 for the western regions ($t = 1.64$, 1-tailed $p = 0.058$). On the other hand, when only large herbivores are considered, as opposed to all terrestrial mammals, there is practically no difference in richness between east and west: the mean of the large herbivore residuals for the western regions is 0.03 , while the mean for the eastern and plains regions is -0.02 ($t = 0.15$, 1-tailed $p = 0.441$).

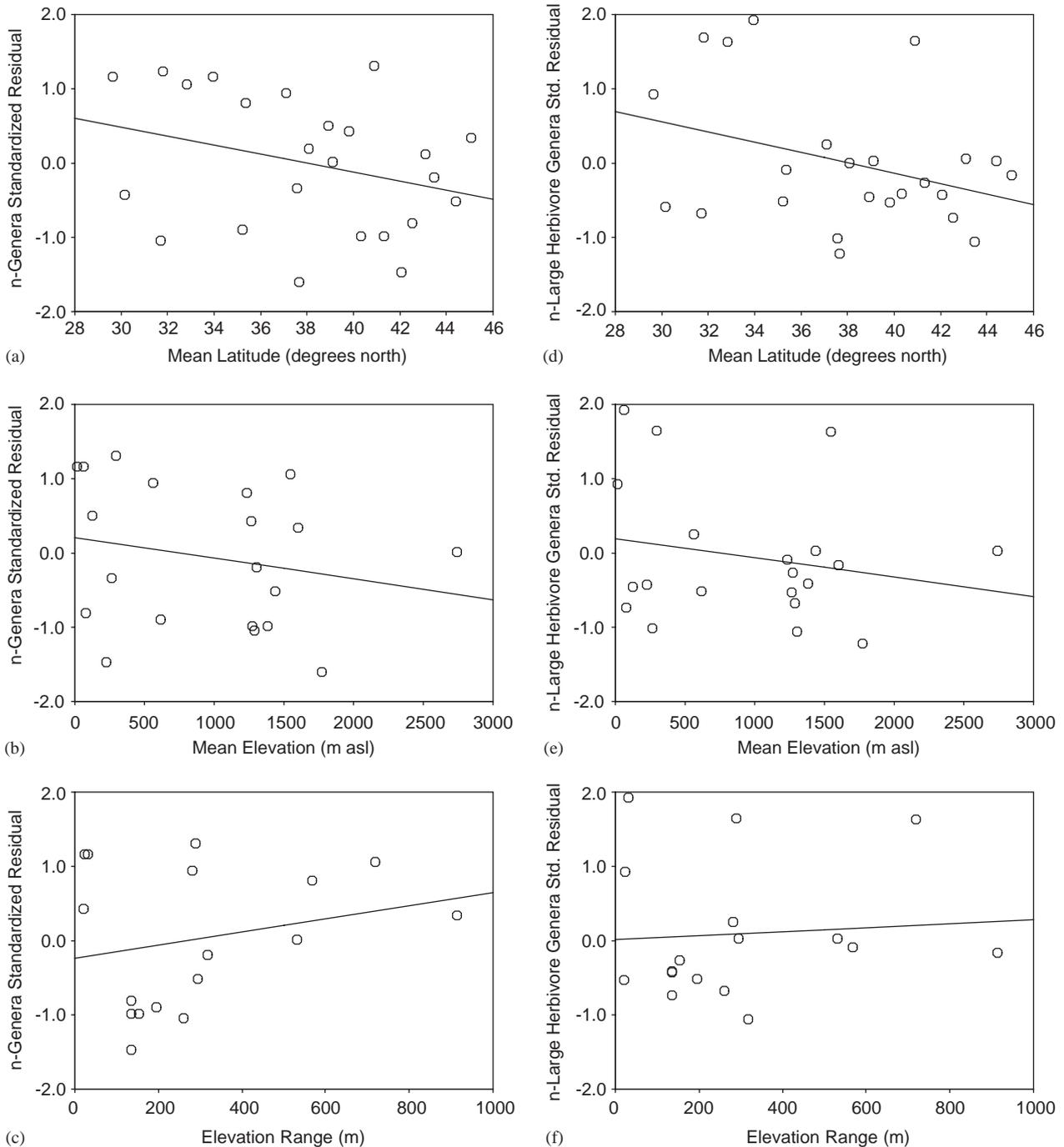


Fig. 8. Relationships between the multiple regression model standardized residuals for each region and geographical correlates of variables that might cause regional-scale mammalian community richness to vary: (a) *n*-genera residuals against mean site latitude; (b) *n*-genera residuals against mean site elevation; (c) *n*-genera residuals against range of site elevations; (d) *n*-large herbivore genera residuals against mean latitude; (e) *n*-large herbivore residuals against mean elevation; (f) *n*-large herbivore genera residuals against elevation range. See Table 12 for regression and partial correlation statistics.

5. Discussion

The analyses presented in this paper suggest that gradients in mammalian richness across North America were quite different during the terminal Pleistocene than

they are today. The two most striking differences involve gradients in the richness of the largest mammals from north to south and gradients in overall mammalian richness from east to west. I discuss each of these differences in turn.

Table 12

Regression r^2 values and partial correlation coefficients for the relationships presented in Fig. 8 (“SR” = standardized residual); significance values are in parentheses

Relationship	r^2	Partial correlation coefficient ^a
<i>n</i> -Genera SR–mean latitude (Fig. 8(a))	0.09 (0.151)	–0.41 (0.067)
<i>n</i> -Genera SR–mean elevation (Fig. 8(b))	0.05 (0.355)	–0.31 (0.129)
<i>n</i> -Genera SR–elevation range (Fig. 8(c))	0.06 (0.361)	0.43 (0.053)
<i>n</i> -Genera SR multiple regression	0.31 (0.180)	
<i>n</i> -LH genera SR–mean latitude (Fig. 8(d))	0.12 (0.096)	–0.43 (0.056)
<i>n</i> -LH genera SR–mean elevation (Fig. 8(e))	0.04 (0.375)	–0.36 (0.092)
<i>n</i> -LH genera SR–elevation range (Fig. 8(f))	0.01 (0.771)	0.34 (0.105)
<i>n</i> -LH genera SR multiple regression	0.31 (0.172)	

^aPartial correlation significance values are for 1-tailed tests.

5.1. Large mammal richness, latitude, and extinctions

In contemporary North America, mammal communities generally become less rich from south to north (e.g. Simpson, 1964; Currie, 1991; Kerr and Packer, 1997; Badgely and Fox, 2000). Badgely and Fox (2000) have suggested that this trend in overall richness is primarily the result of gradients in the richness of the smallest mammals, especially bats, which exhibit the steepest declines in richness with latitude. At the other end of the size spectrum, Badgely and Fox (2000) have shown that the largest mammals today increase in richness as latitude increases. The analyses presented here exclude bats, but they nonetheless show a declining trend in overall richness from south to north across mid-latitude North America during the terminal Pleistocene. More important, they indicate that the richness of large herbivores also declined with latitude across this part of the continent during the terminal Pleistocene, which stands in direct contrast to the way in which large mammal richness varies with latitude across North America today.

Badgely and Fox (2000) point out that the richness of the largest mammals was likely higher at lower latitudes during the late Pleistocene than is the case today, and the results presented here provide strong support for their suggestion that latitudinal gradients in richness may have differed during that period as a result of this (Badgely and Fox, 2000, p. 1462). They make this suggestion in the context of a discussion about the role that extinctions, rather than environmental variables, might have played in structuring modern richness gradients in North America, noting that hypotheses about the effects of extinctions on modern patterns of richness can be tested by considering paleontological data (Badgely and Fox, 2000, pp. 1462, 1463). While the analyses of such data presented here by no means provide a full test of the hypothesis that modern patterns of richness are, at least in part, due to patterns of extinction, they do suggest that richness gradients were quite different in North America prior to the late Pleistocene extinctions, which would suggest, in turn, that richness gradients changed as a result of those extinctions.

In support of this I note that North America during the terminal Pleistocene appears to have been much like the modern situation in southern Africa studied by Andrews and O'Brien (2000), in which large mammal richness is positively correlated with a measure of available energy. However, the pattern that occurs in North America today—of increasing large mammal richness with latitude—is quite unlike either the pattern that seems to have occurred here during late Pleistocene or the pattern seen in contemporary southern Africa in that it equates to a negative correlation between large mammal richness and energy. The apparent uniqueness of this modern North American gradient in large mammal richness begs for an explanation. The hypothesis that it is, at least in part, a result of the extinctions that occurred in North America during the late Pleistocene (Badgely and Fox, 2000) is a reasonable one, and it finds some support in the results presented here. This, however, only raises another question to be addressed by future research: why did large mammal extinctions in mid-latitude North America apparently affect southern faunal communities to a greater degree than northern ones?

5.2. Overall richness, longitude, and habitat heterogeneity

In mid-latitude North America today, western regions tend to contain many more mammal taxa than do eastern regions (e.g. Simpson, 1964; Currie, 1991; Kerr and Packer, 1997; Badgely and Fox, 2000). Badgely and Fox (2000) have found that this longitudinal gradient in richness is most pronounced for certain medium and large size classes and for herbivores and granivores, and they suggest that it is the result of increasing trends from east to west in energy and elevation. Kerr and Packer (1997), on the other hand, propose that the east-west difference in mammalian richness is due to greater degrees of topographic relief in the west.

The analyses presented here suggest that, in contrast to the present, mammal communities in the east were richer than (or at least as rich as) those in the west. This is the case regardless of whether overall richness is

measured at the local or the regional scale. A difference in longitudinal patterns between past and present also appears in the richness of large mammals alone: the richness of large herbivores, which are among the taxa that contribute the most to the east-west differences observed today (Badgely and Fox, 2000), seems to have varied little between east and west during the terminal Pleistocene.

What might have caused mammal communities in the east to have been richer than those of the west during the terminal Pleistocene? Regardless of whether it provides an adequate explanation for the contemporary east-west difference in mammalian richness (Badgely and Fox, 2000), habitat heterogeneity associated with elevational variability (Kerr and Packer, 1997) clearly cannot explain the late Pleistocene situation: the east-west difference in richness seems to have been reversed during that period in comparison to the present, while east-west differences in topographic relief, of course, were not. For the same reason, longitudinal gradients in richness during the terminal Pleistocene cannot be attributed to differences in mean elevation (e.g., Badgely and Fox, 2000). On the other hand, the east-west difference in richness may have been the result, at least in part, of an energy difference between east and west: climate simulations suggest that late Pleistocene temperatures were lower in the high-elevation west than they were in much of the east, particularly during the summer (e.g., Bartlein et al., 1998, Fig. 5).

Alternatively, or perhaps in addition, this east-west difference in richness may have been due to an east-west difference in habitat heterogeneity that was unrelated to any difference in topography. An easy answer to the question of why eastern communities were richer than western ones during the terminal Pleistocene may relate to the fact that nearly all of the sets of “non-analog” mammalian taxa that have been reported for this period in North America come from sites located to the east of the Rocky Mountains (e.g., Lundelius et al., 1983; Graham, 1985b; Lundelius, 1989; Stafford et al., 1999). While such sets of taxa are certainly not unknown from the west (e.g., Wood and Barnosky, 1994), the majority of them by far come from the east and the midwest (e.g., Lundelius et al., 1983, p. 346). Thus, the finding of this study that eastern communities were richer than western ones may just be another way of showing that non-analog communities were primarily a feature of the east.⁶ However, this answer is something that itself

requires explanation: why do most of these sets of “intermingled” mammals occur in the east?

The explanation that is most commonly given for these sets of taxa is that they were the result of reduced seasonal variation in climate during the late Pleistocene, which is argued to have produced greater heterogeneity in habitats (e.g., Graham, 1985a, b; Graham and Mead, 1987; Lundelius, 1989). The spatial dissimilarity analysis conducted by the FAUNMAP Working Group (1996) supports this by showing that habitats of this time were likely more heterogeneous than habitats of the late Holocene. Although the explanation that has been offered for this increased heterogeneity—that it reflects greater climatic equability—has recently been questioned (Williams et al., 2001), the existence of the increased heterogeneity has not. To the extent that these non-analog sets of mammals reflect environments that were more heterogeneous than modern ones, that most of them come from the east suggests that increased heterogeneity was primarily a feature of this part of the continent. In support of this, I note that late Pleistocene vegetation communities in the east were changing very rapidly (e.g., Williams et al., 2001), and this may have introduced a great deal of habitat heterogeneity to this part of the continent (e.g., Sousa, 1984). On the other hand, habitat heterogeneity in much of the west may have been somewhat reduced during this time, relative to the present, due to a reduction in the elevational zonation of vegetation (e.g., see papers in Betancourt et al., 1990).

Thus, habitat heterogeneity may have played an important role after all in structuring longitudinal gradients in overall terrestrial mammal richness during the terminal Pleistocene, even though such gradients could not have been determined primarily by elevational variability.

6. Conclusions

Because gradients in mammalian richness across mid-latitude North America appear to have been much different during the terminal Pleistocene than they are today, it would also seem that the causes of variability in richness have changed somewhat since that time. The reversal in the north-south gradient in large mammal richness suggests that the richness of such taxa was determined primarily by energy during the terminal Pleistocene, as is also the case in southern Africa today (Andrews and O'Brien, 2000), whereas the modern pattern might be, at least in part, a result of the extinctions that occurred here near the end of the Pleistocene (Badgely and Fox, 2000). Likewise, the changes that have apparently occurred in east-west richness gradients indicate that two variables that have been proposed to be responsible for such gradients

⁶The higher richness of eastern communities relative to western ones cannot be explained by greater numbers of now-extinct taxa in the east. Of the 27 extinct genera in the Late Glacial faunules that I use, 22 have been found in the east and/or the plains and 22 have been found in the west. Of those that are not known to have occurred across the continent, six are known only from the east and/or the plains and six are known only from the west (see maps in FAUNMAP Working Group, 1994).

today—elevational variability (Kerr and Packer, 1997) and mean elevation (Badgely and Fox, 2000)—could not have driven them during the terminal Pleistocene. Rather, differences between the east and the west during that time were likely the result of differences in available energy and/or differences in habitat heterogeneity that were not related to elevational variability.

Because they suggest that patterns of variability in richness, as well as the causal variables underlying such patterns, have changed over time in North America, the analyses presented in this paper should have important implications for our general understanding of geographical variability in mammalian richness. The long-term perspective provided by these analyses makes it clear that, just as patterns and causes have changed during the late Quaternary, they may well continue to change with future changes in the continent's climate and vegetation.

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