Spatial Response of Mammals to Late Quaternary Environmental Fluctuations

FAUNMAP Working Group: Russell W. Graham,*† Ernest L. Lundelius Jr.,† Mary Ann Graham, Erich K. Schroeder, Rickard S. Toomey III, Elaine Anderson, Anthony D. Barnosky, James A. Burns, Charles S. Churcher, Donald K. Grayson, R. Dale Guthrie, C. R. Harington, George T. Jefferson, Larry D. Martin, H. Gregory McDonald, Richard E. Morlan, Holmes A. Semken Jr., S. David Webb, Lars Werdelin, Michael C. Wilson

Analyses of fossil mammal faunas from 2945 localities in the United States demonstrate that the geographic ranges of individual species shifted at different times, in different directions, and at different rates in response to late Quaternary environmental fluctuations. The geographic pattern of faunal provinces was similar for the late Pleistocene and late Holocene, but differing environmental gradients resulted in dissimilar species composition for these biogeographic regions. Modern community patterns emerged only in the last few thousand years, and many late Pleistocene communities do not have modern analogs. Faunal heterogeneity was greater in the late Pleistocene.

Understanding the response of terrestrial biotic communities to environmental change is fundamental to modeling and planning for future climate change (*1*). The fossil record of Quaternary mammals provides a basis for understanding the ways communities have responded to rapid and repeated climatic fluctuations (*2*). These changes had dramatic effects on the terrestrial biota, especially the mammal fauna (*3*, *4*). During the late Pleistocene, tundra and boreal forest species like collared lemmings, muskox, and caribou (*5*) ranged as far south as southern Wisconsin, central Pennsylvania, central Illinois, and northern Alabama, respectively (*6*). Species that typically inhabit eastern deciduous forest environments today (for example, least shrew and eastern chipmunk) extended their distributions westward into the area of the Great Plains, and grassland species (for example, thirteen-lined ground squirrel and plains pocket gopher) ranged as far east as Pennsylvania, Tennessee, and Virginia (*6*). The late Pleistocene mammal fauna also contained a diverse megafauna (such as mastodons, mammoths, camels, horses, and ground sloths) that is now extinct.

There are two competing models of how communities may have responded to these environmental changes. In the Clementsian model (*7*), it is assumed that large groups of species are in equilibrium and that the organization of these groups is determined primarily by biological interactions, especially competition. This model suggests that communities are long-lived geologically (tens to hundreds of thousands of years) and that they can be tracked through time and space. Therefore, mammals in modern biomes (for example, tundra, boreal forest, and deciduous forest) would have moved successionally south and north as late Quaternary climates cooled and warmed, respectively (*8*). On the other hand, in the Gleasonian model (*9*) it is assumed that species respond in ecological time to environmental change in accordance with their individual tolerance limits, resulting in range shifts with varying rates, at different times, and in divergent directions. Extended into geological time, this model suggests that communities are continually emergent with a predictability of composition that decreases inversely with time.

Community Response to Environmental Change

These two models can be tested by examining the response of mammal communities to late Quaternary climate fluctuations that occurred rapidly and frequently but with an overall trend toward warming (*2*). During the full glacial, mean annual temperatures were as much as 5° to 7°C colder than today, but by about 14,500 years ago the climate began to warm and glacial ice ablated (*10*). There was a cold pulse at the end of the Pleistocene (~10,000 to 11,000 years ago) known as the Younger Dryas (*11*). Holocene climates were relatively stable, and by 4000 years ago, they were similar to the climate today (*2*, *10*). Under these warming conditions, a Clementsian model would predict a simple northward shift in life zones. Conversely, a Gleasonian model would suggest that individual species dispersed diachronically in different directions and at various rates.

To test these patterns of geographic range shifts predicted by the two models, we compiled an electronic relational database, FAUNMAP (*12*). These data consist, in part, of site location, species composition, geological and numeric ages, and stratigraphy for 2945 late Quaternary mammal localities for the 48 contiguous states of the United States (Fig. 1A). The database was interfaced with a Geographic Information System (GIS) to construct distribution maps for individual species at seven different time periods, although only three time periods are considered in these analyses [Full Glacial (15,000 to 20,000 years ago), Late Glacial (10,000 to 15,000 years ago), and Late Holocene (500 to 4000 years ago)].

Maps documenting changes in the distributions of individual mammal species (*12*) show that for the last 20,000 years mammals responded in a Gleasonian manner to late Quaternary climate warming (Fig. 1, B to F). Many species dispersed northward during this warming episode, but did so at different

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R. W. Graham, M. A. Graham, E. K. Schroeder, and R. S. Toomey III are at Research and Collections Center, Illinois State Museum, 1011 East Ash, Springfield, IL 62703, USA. E. L. Lundelius Jr., Department of Geological Sciences, University of Texas, Austin, TX 78712, USA. E. Anderson, Denver Museum of Natural History, Denver, CO 80205, USA. A. D. Barnosky, Mountain Research Center, Montana State University, Bozeman, MT 59715, USA. J. A. Burns, Provincial Museum of Alberta, Edmonton, Alberta, Canada T5N 0M6. C. S. Churcher, Department of Zoology, University of Toronto, Toronto, Ontario, Canada M5S 1A1. D. K. Grayson, Department of Anthropology, University of Washington, Seattle, WA 98195, USA. R. D. Guthrie, Department of Biology, University of Alaska, Fairbanks, AK 99701, USA. C. R. Harington, Earth Sciences Section (Paleobiology), Canadian Museum of Nature, Ottawa, Ontario, Canada K1P 6P4. G. T. Jefferson, Anza-Borrego Desert State Park, 200 Palm Canyon Drive, Borrego Springs, CA 92004, USA. L. D. Martin, Museum of Natural History, University of Kansas, Lawrence, KS 66045, USA. H. G. McDonald, Hagerman Fossil Beds National Monument, Post Office Box 570, Hagerman, ID 83332, USA. R. E. Morlan, Canadian Museum of Civilization, Post Office Box 3100 Station B, Hull, Quebec, Canada J8X 4H2. H. A. Semken Jr., Department of Geology, University of Iowa, Iowa City, IA 52242, USA. S. D. Webb, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA. L. Werdelin, Department of Paleozoology, Swedish Museum, Box 50007, S-104 05 Stockholm, Sweden. M. C. Wilson, Department of Archaeology, Simon Fraser University, Burnaby, BC, Canada V5A 1S6.

*To whom correspondence should be addressed at Earth Sciences, Denver Museum of Natural History, 2001 Colorado Boulevard, Denver, CO 80205, USA.

†These authors are codirectors of the FAUNMAP Working Group.

rates and times. Some species with northern distributions today, like the heather vole (Fig. 1B), reached their present southernmost limits in the eastern United States by the end of the Pleistocene. Others, like the southern red-backed vole (Fig. 1C), moved north more slowly and remained outside their modern ranges through the middle Holocene and into the late Holocene. The nine-banded armadillo, northern pygmy mouse, hispid cotton rat, meadow jumping mouse, and least weasel are still adjusting their distributions (*13*).

Some species dispersed in opposite directions in response to this postglacial warming. The least shrew and a suite of other species shifted eastward (Fig. 1D), whereas the northern pocket gopher and others retracted their distributions farther to the west (Fig. 1E). Species like the eastern woodrat, northern pygmy mouse, round-tailed muskrat, eastern mole, and woodland vole do not appear to exhibit any substantial changes in their geographic distributions throughout the last 20,000 years. Southern species (for example, eastern woodrat and northern pygmy mouse) maintained distributions as far north during the late Pleistocene as they do today (Fig. 1F). They were not displaced into southern refugia during cold climatic phases as would be predicted by the Clementsian model (8). These general patterns in distributional shifts, like those of late Quaternary plant dispersals (*14*), best fit predictions of the Gleasonian model. Modern (pre-European contact) community patterns appeared only in the last few thousand years because they have been assembled by the addition and subtraction of individual species throughout the late Quaternary (*15*).

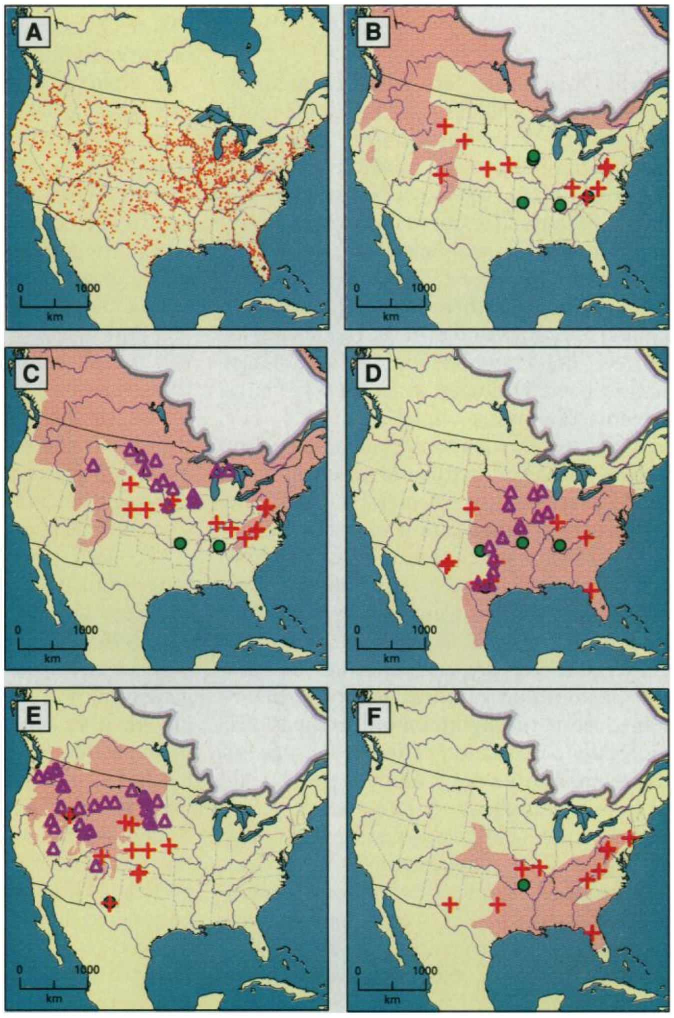


Fig. 1. Maps showing the geographic distribution of all mammal sites in the FAUNMAP database (**A**) and shifts in the geographic distributions of individual species during the late Quaternary (**B** to **F**). For (B) to (F), time intervals (FG, LG, and LH) are defined in (*12*); modern mammal species distributions are shaded; fossil distributions are represented by symbols [(●) FG, (+) LG, (△) LH]; position of the Laurentide Ice Sheet (white) is for 10,000 years ago; binomial latinized names for all mammal species are given in (*15*); and *n* equals the number of localities for a specific taxon at a given interval of time. (B) Distributions of the heather vole for FG (*n* = 5) and LG (*n* = 10) times. This species and others (collared lemming, meadow jumping mouse, Franklin's ground squirrel, water shrew, and masked shrew) document "rapid" northward dispersal. (C) Distributions of the southern red-backed vole for FG (*n* = 2), LG (*n* = 13), and LH (*n* = 15). This species and others (American pika, prairie vole, meadow vole, and southern bog lemming) record "slow" northward dispersal. (D) Distributions of the least shrew for FG (*n* = 4), LG (*n* = 10), and LH (*n* = 18). This species and others (eastern chipmunk, short-tailed shrew, and marsh rice rat) show eastward shifts. (E) Distributions of the northern pocket gopher for FG (*n* = 2), LG (*n* = 10), and LH (*n* = 53). This species and others (montane vole, long-tailed vole, black-tailed prairie dog, and plains pocket gopher) exemplify westward retraction of geographic range. (F) Distributions of the eastern woodrat for FG (*n* = 1) and LG (*n* = 10). This species and the northern pygmy mouse exemplify southern species not significantly displaced southward during cold phases of the late Pleistocene.

Provinciality

To investigate provinciality of late Quaternary mammals, we grouped FAUNMAP data to average the biases of taphonomy so that they are more or less constant between the samples compared (*16*). The grouped data were then analyzed with a two-way indicator species, hierarchical, divisive clustering technique known as TWINSPAN (*17*). The data were analyzed for two time intervals, late Wisconsin and late Holocene.

Three hierarchical levels of clustering were performed. At the first level of clustering, TWINSPAN split both late Wisconsin and late Holocene faunas into eastern and western components along the 100°W longitude (Figs. 2 and 3) (*18*). This meridian also marks a major biogeographic boundary in the modern fauna, separating the grasslands and forests of the east from the deserts and forests of the west. At the second level of clustering, the faunas are divided primarily along latitudinal boundaries for the entire United States in the late Wisconsin. For the late Holocene, the latitudinal division occurs only in the west, whereas in the eastern United States, the faunal division is primarily along the forest-prairie border, a predominantly east-west moisture gradient. A slight eastern bulge forms the Prairie Peninsula (*19*) of central Illinois. TWINSPAN divisions were stopped at the third level. The resulting clusters are mapped for both the late Holocene (Fig. 2) and late Pleistocene (Fig. 3).

Because distributions of most mammal species have changed little since the late Holocene (*12*), this map (Fig. 2) is comparable to modern faunal provinces. Faunas in cluster 8, for the late Holocene, occur in the northeast (Fig. 2) and contain species that today are generally indicative of the southern boreal forest and the northern mixed coniferous-deciduous forest (*20*). Mammals in the southeastern province (cluster 9) are generally characteristic of a mixture of deciduous forest and southern coniferous forest. Faunas of clusters 10, 11, and 12 occur in regions occupied today by tall grass and mixed grass prairies and contain species that prefer open habitat. The late Holocene mammals in the southwest (cluster 13) are a mixture of species associated with modern alpine forest and lowland deserts. Another biogeographic region (cluster 14) in the northern plains and the northwestern United States is defined primarily by boreo-montane species. In the central northern plains, cluster 15 is weakly differentiated from cluster 14, and both can be combined to form a single category of boreo-montane and grassland species.

The geographic distribution of the eight late Pleistocene clusters is similar to those of the late Holocene, but there are significant differences. In the eastern United States, the late Pleistocene faunas are divided into northern and southern components. Species characteristic of the modern boreal forest (yellow-cheeked vole, northern bog lemming, and arctic shrew) were intermingled with species indicative of deciduous forest (eastern chipmunk and short-tailed shrew) and grassland (thirteen-lined ground squirrel) in cluster 9. Many of these species do not occur together today, a common situation for late Pleistocene animal and plant communities (*21*, *22*). These faunas extend farther west along the middle latitudes from Maryland to central Nebraska and western Oklahoma than do any of the eastern divisions of the late Holocene (Fig. 3). This suite of species likely thrived in open parkland containing some boreal forest species. Farther to the south, Florida (cluster 11) is distinct from the rest of the southeast, but during the late Holocene, Florida's faunas clustered with others from the southeast.

In the plains region, the late Pleistocene (Fig. 3) supported a more heterogeneous mammal fauna (clusters 9 and 10) than did the late Holocene (Fig. 2) and lacked the tall grass prairie of the late Holocene. The southern plains and intermontane west faunas (clusters 12 and 13) are not strongly differentiated by species composition. Mammals in these faunas generally prefer dry, open habitats (pocket gopher, desert shrew, and black-tailed jackrabbit). Faunas from the northwest and northern plains (cluster 14) are characterized by a mixture of species indicative of northern grassland (northern pocket gopher, Richardson's ground squirrel, and sagebrush vole), alpine tundra (American pika), and coniferous forest (yellow-bellied marmot, heather vole, and bushy-tailed woodrat). The differentiation of cluster 15, a single grid cell in northern Indiana, appears to be driven primarily by taphonomic factors (*23*).

Previous attempts to identify late Pleistocene mammal provinces (*24*, *25*) have relied on the distributions of a few mammal genera, rather than inclusion of most mammalian species within a region. These earlier maps exhibit some general similarities with our distributions, but there are interesting differences. For example, our maps show greater regional differentiation, especially in the western United States and central Great Plains. The *Camelops* province of earlier maps (*25*) incorporated the entire western United States. Our analyses subdivided the *Camelops* province into at least four regions (clusters 12, 13, and 14, and parts of clusters 9 and 10). East of the Mississippi River, our map combines the *Symbos-Cervalces* and *Odocoileus-Pitymys* provinces into one province (clusters 8 and 9, with some of cluster 10). Florida makes up most of cluster 11, which corresponds with the Chlamythere-Glyptodont province. Our late Pleistocene map lacks data for most of the Gulf Coastal Plain, which is also included in the Chlamythere-Glyptodont province. This map does not have a *Dicrostonyx-Ovibos* province because of the absence of faunas for the glaciated regions of the north in our grouped data.

Environmental Heterogeneity

Environmental or faunal heterogeneity is strongly dependent on scale (*26*) and can be measured by either overall dissimilarity of faunal composition over arbitrarily defined distances or by the rate of change of similarity of composition with distance. We measured faunal heterogeneity as overall dissimilarity of composition. We also assume that faunal heterogeneity is a reflection of environmental heterogeneity. Different taphonomic pathways may lead to greater heterogeneity for fossil faunas (*27*), but taphonomy does not appear to account for most of the differences between the late Pleistocene and late Holocene data sets because many of the faunas share similar taphonomic pathways. Furthermore, grouping of data helped average taphonomic biases.

Reductions in the heterogeneity or patchiness of the environment at the end of the Pleistocene may have caused the evolution of new biomes and mammal communities (*21*, *24*, *28*, *29*), and perhaps even extinctions (*29*). Decreasing heterogeneity would suggest that the Holocene would have larger coarse-grained patches of similar conditions in comparison to the more fine-grained environments of the late Pleistocene. Under this model, faunal similarity across a landscape should be higher in the Holocene than in the Pleistocene.

To test the hypothesis that late Pleistocene faunal and environmental heterogeneity was greater than that of the Holocene, we calculated Dice faunal similarity indices (DFSIs) (*30*) and the distances between grid cell centers for all pairs of grid cells for the late Pleistocene (Fig. 4A) and late Ho-

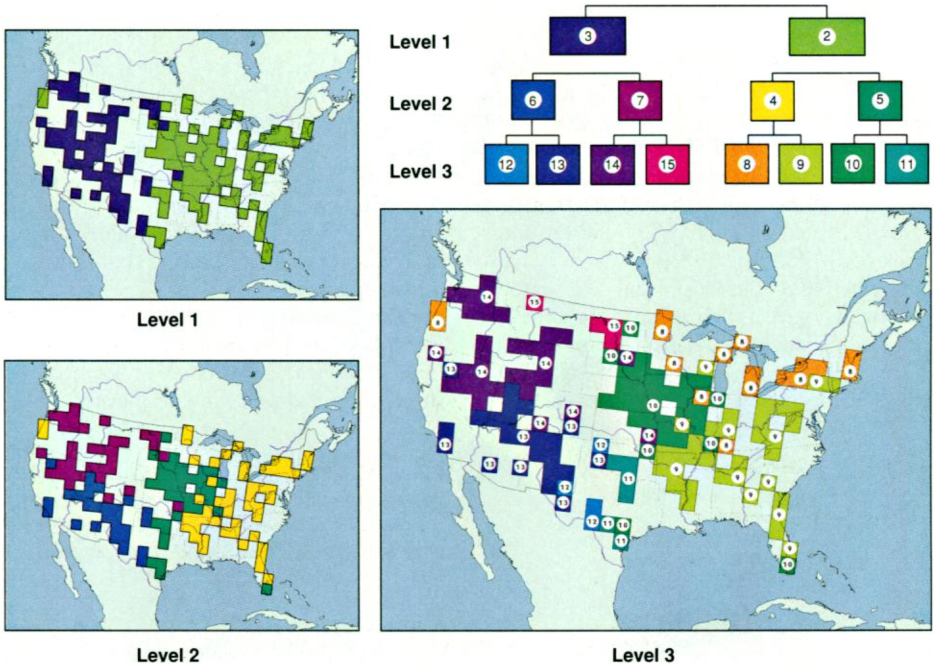


Fig. 2. Map of TWINSPAN clusters for late Holocene faunas. Levels represent steps in divisions shown in the division tree. Cluster numbers are those assigned by the TWINSPAN program. Indicator species for clusters are as follows: cluster 8: moose, American marten, common porcupine, and red squirrel; cluster 9: eastern gray squirrel, common opossum, marsh rice rat, swamp rabbit, and eastern woodrat; cluster 10: short-tailed shrew, Franklin's ground squirrel, thirteen-lined ground squirrel, prairie vole, meadow vole, southern bog lemming, meadow jumping mouse, eastern chipmunk, and woodchuck; cluster 11: hispid cotton rat and black-tailed jackrabbit; cluster 12: hispid pocket mouse, hispid cotton rat, and plains pocket gopher. Clusters 10, 11, and 12 can be grouped into a single category characteristic of tall grass and mixed grass prairies (plains pocket gopher, least shrew, prairie vole, hispid pocket mouse, northern grasshopper mouse, Franklin's ground squirrel, thirteen-lined ground squirrel, and southern bog lemming); cluster 13: mule deer, bighorn sheep, Botta's pocket gopher, mountain cottontail, prairie dog, and kangaroo rat; cluster 14: yellow-bellied marmot, montane vole, mule deer, bighorn sheep, and snowshoe hare; cluster 15: prairie vole, Richardson's ground squirrel, meadow vole, meadow jumping mouse, and thirteen-lined ground squirrel.

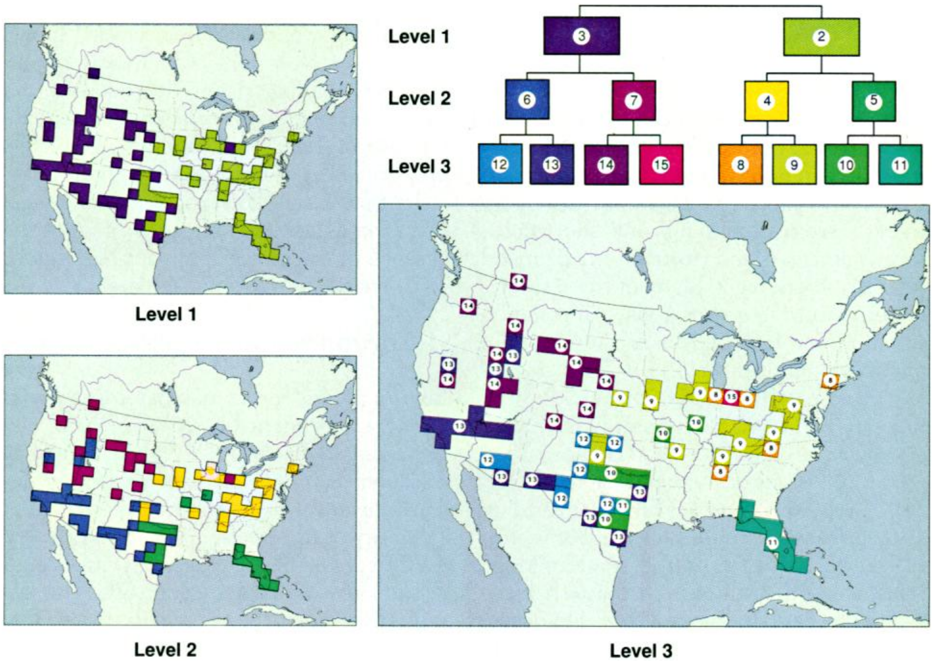


Fig. 3. Map of TWINSPAN clusters for late Pleistocene faunas. Levels represent steps in divisions shown in the division tree. Cluster numbers are those assigned by the TWINSPAN program. Indicator species for clusters are as follows: cluster 8: deer is the only indicator species (all other species in this cluster also occur in cluster 9); cluster 9: short-tailed shrew, southern bog lemming, northern bog lemming, thirteen-lined ground squirrel, eastern chipmunk, southern red-backed vole, heather vole, yellow-cheeked vole, masked shrew, arctic shrew, northern pygmy shrew, water shrew, meadow jumping mouse, and eastern chipmunk; cluster 10: pronghorn, masked shrew, northern grasshopper mouse, harvest mouse, black-tailed jackrabbit, southern bog lemming, and plains pocket gopher; cluster 11: common opossum, common raccoon, eastern gray squirrel, common gray fox, flat-headed peccary, and tapir; cluster 12: There are no strong indicator species unique to this group (see text); cluster 13: Shasta ground sloth, camel, badger, pronghorn, desert woodrat, pocket gopher, and yellow-bellied marmot; cluster 14: northern pocket gopher, bushy-tailed woodrat, sagebrush vole, and American pika; cluster 15: caribou, stag-moose, woodland muskox, and giant short-faced bear.

locene (Fig. 4B). Although there is wide variability, both generally show a decrease in DFSIs with distance, which is expected and has been documented by similar studies for different time periods and organisms (*31*). Results for both late Pleistocene and late Holocene faunas have nonlinear trends, and the DFSIs become relatively constant after a distance of about 2000 km.

To further explore these relations, we grouped the data in "bins" of 250-km intervals (*32*). The mean DFSIs decrease with distance (bin number), and the rate of change (slope) is slightly greater for the late Holocene data set and flattens after 3000 km (bin 12) (Fig. 5). The rate of change for Pleistocene faunas decreases after 2250 km (bin 9) and then increases slightly between 3000 and 4000 km (bins 12 and 16). These trends are consistent with those observed in the plot of the DFSIs versus distance between grid cell centers (Fig. 4, A and B). However, the grouped data show that for distances up to 3000 km (bin 12), the late Pleistocene DFSIs are consistently and significantly (no overlap of the 95% confidence intervals) lower than those of the late Holocene. The higher DFSI values for the late Holocene faunas indicate that they were more alike over short distances than were the late Pleistocene faunas. This pattern suggests that late Holocene faunas, and by inference environments, were more homogeneous than those of the late Pleistocene.

The possibility that some of the observed differences might be the result of chance was tested by a series of Monte Carlo faunas created from the species pools for the late Holocene and late Pleistocene data sets (*33*). There is no decrease in the DFSI values with distance for either of the late Pleistocene or late Holocene Monte Carlo faunas (Fig. 5). The DFSIs for the Monte Carlo faunas vary around 0.33 and increase slightly with distance. Also, unlike the DFSIs for the actual data, there is overlap of the 95% confidence limits for all late Pleistocene and late Holocene Monte Carlo fauna bins. These analyses indicate that the actual faunal data are significantly different from those due to chance, which supports

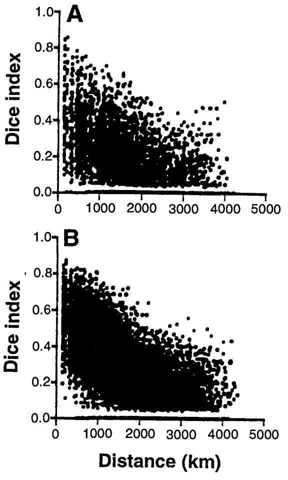
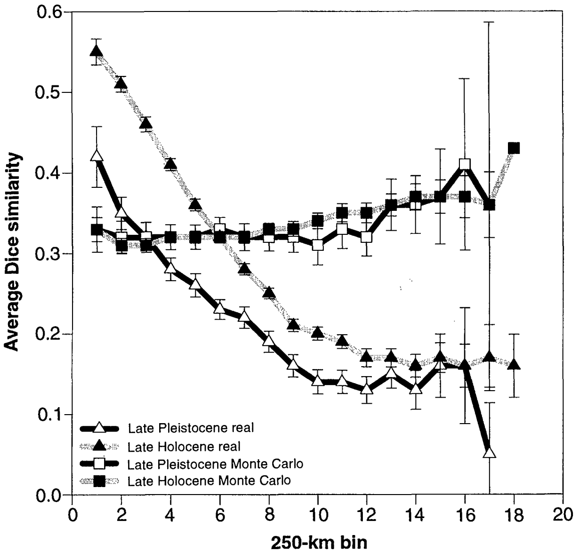


Fig. 4. Bivariate plots of DFSI against geographic distance for grouped late Pleistocene (**A**) and late Holocene (**B**) faunal data.

Fig. 5. Mean DFSIs and 95% confidence intervals for actual faunal data and Monte Carlo faunal data against bin distance (one bin = 250 km). For the first five bins (1250 km), late Holocene DFSIs are above the Monte Carlo values and overlap with the Monte Carlo values only at bin 6 (1500 km). In contrast, for the late Pleistocene, only for bins 1 and 2 (250 to 500 km) are the DFSIs above the Monte Carlo values, and they overlap with them in bins 2 and 3 (500 to 750 km). The 95% confidence intervals for both the late Pleistocene and late Holocene do not overlap until bin 13 (3250 km).



the contention that late Pleistocene environments were responsible for maintaining more heterogeneous mammal faunas.

Conclusions

Species that make up mammal communities in the contiguous United States have responded to late Quaternary environmental fluctuations in a Gleasonian manner. Although these changes in mammal communities were caused by the direct effects of climate, other factors like habitat reorganization, biological interactions, and stochastic events must also have played a role. Species dispersed diachronically, in divergent directions, and at variable rates. Mammal communities are continually, and unpredictably, emergent. Therefore, many late Pleistocene communities do not have modern analogs. Although late Pleistocene communities differed from Holocene ones, they were organized into similar biogeographic patterns (faunal provinces). These similarities reflect east-west moisture and north-south temperature gradients. However, dissimilarities in species composition for these provinces indicate different gradients for these two time periods as well as continual change in fluctuating environments. Late Pleistocene faunas tended to be more variable in composition. Some of this variability may be attributed to taphonomic factors but results largely from greater environmental heterogeneity. It is, therefore, important to consider individualistic shifts in species distributions, nonanalog composition of communities, and changes in environmental heterogeneity in modeling the responses of mammal communities to past and future climatic and environmental changes. Models for future change must rely increasingly on individual species and their requirements, rather than species associations.

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5. Latinized binomial names for all taxa discussed in the text or figures are listed here in alphabetical order under their vernacular names, and extinct taxa are marked with an asterisk: American marten (*Martes americana*), American pika (*Ochotona princeps*), arctic shrew (*Sorex arcticus*), bighorn sheep (*Ovis canadensis*), black-tailed jackrabbit (*Lepus californicus*), black-tailed prairie dog (*Cynomys ludovicianus*), Botta's pocket gopher (*Thomomys bottae*), bushy-tailed woodrat (*Neotoma cinerea*), *camel (*Camelops* spp.), caribou (*Rangifer tarandus*), *chlamythere [*Holmesina* spp. (*Chlamytherium* spp.)], collared lemming (*Dicrostonyx* spp.), common porcupine (*Erethizon dorsatum*), common raccoon (*Procyon lotor*), desert shrew (*Notiosorex crawfordi*), desert woodrat (*Neotoma lepida*), eastern chipmunk (*Tamias striatus*), eastern gray squirrel (*Sciurus carolinensis*), eastern mole (*Scalopus aquaticus*), eastern woodrat (*Neotoma floridana*), *flat-headed peccary (*Platygonus compressus*), Franklin's ground squirrel (*Spermophilus franklinii*), *giant short-faced bear (*Arctodus simus*), *glyptodont (*Glyptotherium* spp.), common gray fox (*Urocyon cinereoargenteus*), *Harlan's ground sloth (*Glossotherium harlani*), harvest mouse (*Reithrodontomys* spp.), heather vole (*Phenacomys intermedius*), hispid cotton rat (*Sigmodon hispidus*), hispid pocket mouse (*Chaetodipus hispidus*), *Jefferson's ground sloth (*Megalonyx jeffersonii*), kangaroo rat (*Dipodomys* spp.), least shrew (*Cryptotis parva*), least weasel (*Mustela nivalis*), long-tailed vole (*Microtus longicaudus*), marsh rice rat (*Oryzomys palustris*), masked shrew (*Sorex cinereus*), meadow jumping mouse (*Zapus hudsonius*), meadow vole (*Microtus pennsylvanicus*), moose (*Alces alces*), mountain cottontail (*Sylvilagus nuttalii*), mountain lion (*Felis concolor*), montane vole (*Microtus montanus*), mule deer (*Odocoileus hemionus*), muskox (*Ovibos moschatus*), nine-banded armadillo (*Dasypus novemcinctus*), northern bog lemming (*Mictomys borealis*), northern grasshopper mouse (*Onychomys leucogaster*), northern pocket gopher (*Thomomys talpoides*), northern pygmy mouse (*Baiomys taylori*), plains pocket gopher (*Geomys bursarius*), pocket gopher (*Thomomys* spp.), prairie dog (*Cynomys* spp.), prairie vole [*Microtus* (*Pedomys*) *ochrogaster*], pronghorn (*Antilocapra americana*), pygmy shrew (*Sorex hoyi*), red squirrel (*Tamiasciurus hudsonicus*), Richardson's ground squirrel (*Spermophilus richardsonii*), *river cat (*Felis amnicola*), round-tailed muskrat (*Neofiber alleni*), sagebrush vole (*Lemmiscus curtatus*), *Shasta ground sloth (*Nothrotheriops shastensis*), short-tailed shrew (*Blarina* spp.), snowshoe hare (*Lepus americanus*), southern bog lemming (*Synaptomys cooperi*), southern red-backed vole (*Clethrionomys gapperi*), eastern spotted skunk (*Spilogale putorius*), *stag-moose (*Cervalces scotti*), swamp rabbit (*Sylvilagus aquaticus*), tapir (*Tapirus* spp.), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*), Virginia opossum (*Didelphis virginianus*), water shrew (*Sorex palustris*), woodchuck (*Marmota monax*), *woodland muskox [*Bootherium bombifrons* (*Symbos cavifrons*)], woodland vole [*Microtus* (*Pitymys*) *pinetorum*], yellow-bellied marmot (*Marmota flaviventris*), and yellow-cheeked vole (*Microtus xanthognathus*). Vernacular names for extant species follow J. K. Jones Jr., R. S. Hoffmann, D. W. Rice, C. Jones, R. J. Baker, and M. D. Egan [*Occas. Pap. Mus. Tex. Tech. Univ.* **146**, 1 (1992)] and for extinct species follow B. Kurtén and E. Anderson [*Pleistocene Mammals of North America* (Columbia Univ. Press, New York, 1980)]. Systematic latinized names follow (*6*).
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16. Grid cells 150 km by 150 km were created on the base map of the United States. Individual faunas were placed in grid cells on the basis of their geographic location (for example, latitude and longitude). All faunas in a grid cell were combined to form a faunal list for each grid cell. Only grid cells with nine or more taxa were selected, and separately only taxa that occurred in nine or more grid cells were used. Therefore, some grid cells in this analysis may have less than nine taxa, and some taxa could occur in less than nine grid cells.
17. M. O. Hill, *TWINSPAN—A FORTRAN Program for Arranging Multivariate Data in a Two-way Table by Classification of Individuals and Attributes* (Cornell Univ., Ithaca, NY, 1979). There were four separate TWINSPAN analyses, three of which excluded superabundant taxa from the grid cell faunas of (*14*). For the late Pleistocene sample, the 13 taxa that occurred in 35 or more grid cells were eliminated, and for the late Holocene sample, the 13 taxa that occurred in more than 66 grid cells were eliminated. Separate TWINSPAN analyses were run for these late Pleistocene and the late Holocene samples.
18. Two grid cells in Oregon are misclassified with the eastern group in the late Holocene because of an artifact of data grouping. These two cells contain five taxa of marine mammals that were eliminated from the analysis; they also contained a number of superabundant and rare taxa that were eliminated. Finally, some taxa were identified only to genus, and the remaining taxa (grid cell 21 = 2 and grid cell 40 = 4) are generally widespread and related to eastern taxa. Because these cells did not contribute to any other divisions, we have excluded them from the analysis.
19. The Prairie Peninsula is a wedge of grassland that extends eastward through Iowa, northern Missouri and southern Minnesota and into northern and central Illinois, and northwestern Indiana [H. A. Gleason, *Ann. Assoc. Am. Geogr.* **12**, 39 (1922); E. N. Transeau, *Ecology* **16**, 422 (1935); J. E. King, *ibid.* **51**, 43 (1981).
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22. J. T. Overpeck *et al.*, *Geology* **20**, 1071 (1992). Terms like "disharmonious" and "intermingled" have also been used to characterize these same nonanalog assemblages.
23. This grid cell is composed solely of large mammals that frequently occur as isolated fossils in bogs. However, these taxa are also indicative of cool, open woodlands, which were the predominant late Pleistocene environment of this area.
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117 (1978); L. D. Martin and R. S. Hoffmann, in *Quaternary Environments of Kansas*, W. C. Johnson, Ed. (Kansas Geological Survey Guidebook Series 5, Lawrence, KS, 1987), pp. 159–165; L. D. Martin *et al.*, in *Environment and Extinctions: Man in Late Glacial North America*, J. I. Mead and D. Meltzer, Eds. (Center for the Study of Early Man, Orono, ME, 1985), pp. 15–30; R. A. Rogers *et al.*, *J. Biogeogr.* **17**, 131 (1990). Specifically, a map by Rogers *et al.* illustrates five provinces in the coterminous United States that are named after characteristic genera (*14*). Three latitudinally distributed provinces are identified in the eastern United States with *Odocoileus-Pitymys* located between the northern *Symbos-Cervalces* and the southern Chlamythere-Glyptodont (*Holmesina-Glyptotherium*). The *Dicrostonyx-Ovibos* province occupied a narrow area along the glacial ice front in the northwestern United States. Most of the western United States is grouped into a single *Camelops* province.

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32. In the case of the analysis of environmental heterogeneity, we calculated DFSIs for each pair of grid cells using the data set from (*16*) and the Monte Carlo data sets. The distance from the centers of these grid cells was also calculated. These data were then plotted on a graph showing DFSIs and the distance between grid cell centers. DFSIs were grouped in "bins" of 250 km (for example, distance between cell centers 0 to 250 km and 250 to 500 km). This allowed for horizontally and vertically adjacent grid cells (center distance, 150 km) and diagonally adjacent grid cells (center distance ~212 km) to be combined. Means, standard deviations, and 95% confidence intervals of DFSIs were calculated for each bin.
33. The following steps were followed separately to construct Monte Carlo faunas for the late Pleistocene and late Holocene. The underlying probability distributions of fauna sizes and taxon occurrences were determined from the actual data. These probability distributions were used to build "random" grid-cell faunas. These grid-cell faunas were randomly assigned to cells matching those present in the same time period. This procedure resulted in a set of Monte Carlo faunas comparable to the real faunas of the late Pleistocene and late Holocene.
34. We thank E. C. Grimm for discussions of TWINSPAN and late Quaternary paleoecology. We also thank R. F. Stearley and M. Kelly for assistance in the compilation of the database. We are indebted to A. Weil, B. Styles, R. B. McMillan, J. Lundelius, R. L. Lyman, and an anonymous reviewer for comments. We thank J. Ferguson and R. Warren for assistance with Figs. 4 and 5, respectively. The Illinois State Museum Society, Geology Foundation of the Department of Geological Sciences of the University of Texas at Austin, and National Science Foundation grant BSR-9005144 provided funds for this project and publication.

RESEARCH ARTICLES

Structural Analysis of Substrate Binding by the Molecular Chaperone DnaK

Xiaotian Zhu,* Xun Zhao,* William F. Burkholder,
Alexander Gragerov,† Craig M. Ogata, Max E. Gottesman,
Wayne A. Hendrickson

DnaK and other members of the 70-kilodalton heat-shock protein (hsp70) family promote protein folding, interaction, and translocation, both constitutively and in response to stress, by binding to unfolded polypeptide segments. These proteins have two functional units: a substrate-binding portion binds the polypeptide, and an adenosine triphosphatase portion facilitates substrate exchange. The crystal structure of a peptide complex with the substrate-binding unit of DnaK has now been determined at 2.0 Å resolution. The structure consists of a β-sandwich subdomain followed by α-helical segments. The peptide is bound to DnaK in an extended conformation through a channel defined by loops from the β sandwich. An α-helical domain stabilizes the complex, but does not contact the peptide directly. This domain is rotated in the molecules of a second crystal lattice, which suggests a model of conformation-dependent substrate binding that features a latch mechanism for maintaining long lifetime complexes.

Molecular chaperones of the 70-kD heat shock protein (hsp70) family are present in the cells of all organisms, and in eukaryotes they occur in all major cellular compartments. They are named for their selective expression in response to metabolic stress, but they are also expressed normally and participate in various cellular processes, including the folding of nascent polypeptides, assembly and disassembly of multimeric protein structures, membrane translocation of secreted proteins, and protein degradation (*1*). Current understanding of hsp70 function follows from the initial suggestion by Pelham (*2*) that they bind to aggregation-prone exposed hydrophobic surfaces that may be induced by stress and from Rothman's extension (*3*) that both the response to stress and other functions such as translocation and nascent chain folding involve the antifolding activity of polypeptide binding to prevent aggregation. DnaK, originally identified for its DNA replication by bacteriophage λ in *Escherichia coli* (*4*) is the bacterial hsp70 chaperone with both constitutive and stress-induced functions (*5*). It shares about 40 to 50 percent sequence identity with its eukaryotic homologs.

Polypeptide substrate binding and release by hsp70s is facilitated by adenosine triphosphate (ATP) binding. DnaK and other hsp70s have relatively strong binding affinity for ATP but are slow adenosine triphosphatase (ATPases) (*6*). Binding of ATP to DnaK leads to the release of substrates and possible rebinding of others (*7–12*). With the hydrolysis of ATP, DnaK is switched back into the ADP-bound form, which exchanges substrates slowly. The ATPase and substrate-binding activities of DnaK and other hsp70s are divided into two separable functional units: the NH_2-terminal half (~44 kD) has ATPase activity but no peptide affinity, and the COOH-terminal half (~27 kD) binds polypeptide substrates (*13–15*). Genetic data and in vitro studies suggest that DnaK acts together with two other heat-shock proteins, DnaJ and GrpE (*5*, *10*). GrpE is a nucleotide-exchange factor that binds sub-stoichiometrically to the ATPase unit (*16*, *17*), and DnaJ binds both to denatured and to certain native proteins and probably to the substrate-binding unit (*18*, *19*).

The crystal structure of the ATPase unit of bovine hsc70, the constitutively present

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X. Zhu, X. Zhao, W. F. Burkholder, A. Gragerov, M. E. Gottesman, and W. A. Hendrickson are in the Department of Biochemistry and Molecular Biophysics, College of Physicians and Surgeons, Columbia University, New York, NY 10032, USA. X. Zhu and W. A. Hendrickson are also with the Howard Hughes Medical Institute, Columbia University. W. F. Burkholder and M. E. Gottesman are also in the Institute of Cancer Research, Columbia University, New York, NY 10032, USA. C. M. Ogata is with the Howard Hughes Medical Institute, National Synchrotron Light Source, Brookhaven National Laboratory, Stony Brook, New York, USA.

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*The contributions of X. Zhu and X. Zhao were of equivalent importance.

†Present address: ABL Basic Research Program, NCI-FCRDC, Post Office Box B, Building 539, Frederick, MD 21702, USA.