Niche conservatism above the species level

Elizabeth A. Hadly[a,1], Paula A. Spaeth[b,2], and Cheng Li[a]

[a]Department of Biology, Stanford University, 371 Serra Mall, Stanford, CA 94305-5020; and [b]National Evolutionary Synthesis Center, 2024 West Main Street, Suite A200, Durham, NC 27705

Traits that enable species to persist in ecological environments are often maintained over time, a phenomenon known as niche conservatism. Here we argue that ecological niches function at levels above species, notably at the level of genus for mammals, and that niche conservatism is also evident above the species level. Using the proxy of geographic range size, we explore changes in the realized niche of North American mammalian genera and families across the major climatic transition represented by the last glacial–interglacial transition. We calculate the mean and variance of range size for extant mammalian genera and families, rank them by range size, and estimate the change in range size and rank during the late Pleistocene and late Holocene. We demonstrate that range size at the genus and family levels was surprisingly constant over this period despite range shifts and extinctions of species within the clades. We suggest that underlying controls on niche conservatism may be different at these higher taxonomic levels than at the species level. Niche conservatism at higher levels seems primarily controlled by intrinsic life history traits, whereas niche conservatism at the species level may reflect underlying environmental controls. These results highlight the critical importance of conserving the biodiversity of mammals at the genus level and of maintaining an adequate species pool within genera.

climate change | extinction | geographic range size | mammals | Pleistocene

The distributions of mammals are labile over ecological time and have been impacted by human activities, including climatic warming over the past century (1–6). Although humans are altering the distribution of Earth's species in our lifetimes (7), we have little information about how extant species and higher taxa altered their distributions in the past. Here we examine the fossil record for variation in the distribution of mammalian ranges at the level of genus and families in response to climatic change over an evolutionary and ecological relevant time scale (tens of thousands of years). The goal is to understand whether niche conservatism is evident at taxonomic levels higher than species and, if so, what actually underlies the conservation of a niche through long time periods.

Nearly all previous studies of niche conservatism have been at the level of species. The distribution of a species can be defined as the environmental space in which the species has a positive intrinsic growth rate (8). Predictions using the climatic envelope around this distribution are used to project species occurrence in geographic space into the future given modeled climates, typically over decades to centuries (i.e., ref 9). The models are based on the premise that niches are "conserved," or that species retain suites of inherited traits valuable for survival in the habitats in which they presently are found (10). Practically, these models thus presume that the distribution of a species today encompasses the entire potential range of environments in which it could survive and, by inference, that the species is close to occupying its fundamental niche (11). By using historic distribution data, climatic envelope models also may be used to hindcast niche occupancy to investigate whether the distribution of ranges has, in fact, varied through time (12). Hindcasting models have the possibility of independently verifying climatic

reconstructions with species occurrences and thus can be quite powerful (see ref. 12 for a recent summary).

Support for the conservation of niches comes from documented relationships between species distributions and environmental variables (13). Species distributions, or their geographic range boundaries, that change in response to environmental shifts represent one predictive outcome of niche conservatism (e.g., poleward expansion of species with warmer temperatures, ref. 14). Indeed, records of fossil mammal distributions show that ranges of individual species moved coincident with the timing of late Pleistocene (LP) warming (3, 4), and boundaries changed in the direction expected. Some extant species have shown rapid change in their range boundaries, depending on climate (e.g., refs. 5, 15), and invasive species can show continental-scale range expansions within decades [e.g., house sparrow (*Passer domesticus*, ref. 16) and cane toad (*Bufo marinus*, ref. 17)]. The geographic ranges of species today encompass a suite of environments that the species occupies now [the realized niche (18)] but not necessarily all environments that the species could potentially inhabit [the fundamental niche, (11)], as evidenced by the enormous number of invasive species, previously limited only by dispersal barriers. Despite much debate, it is unclear to what extent species generally occupy fundamental versus realized niches (8).

Ultimately, the assumption that underlies the concept of phylogenetic niche conservatism at the species level is that the geographic distribution is a proxy for the realized niche in a Grinnellian sense (8), and that it results from interactions between the (*i*) environment (both abiotic and biotic) and (*ii*) species-inherited traits [predominately physiological and morphological (19, 20)]. For clarity of discussion, in this article, we refer to these two types of niche-defining variables as "environment-based" and "trait-based," respectively. From a trait-based perspective, closely related species share more inherited traits than those more distantly related, so the controls on the geographic range of closely related species should be similar (21, 22). The same logic applies to environment-based controls. In fact, recent studies bear this out: Many traits, from body size to behavioral traits, show strong phylogenetic signal (24). Phylogenetic signal was also found in a study of range size in primates, carnivores, and artiodactyls (25).

Because of such geographic-range similarities between closely related species, it also follows that the aggregate ranges of congeneric species define the ecological niche of a genus (or any

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other monophyletic clade), and that these higher-level ecological niches may themselves be conserved through time. This is an important concept for two reasons: (*i*) it helps in sorting out at which levels in the biological hierarchy the controls on niche conservatism are more heavily weighted: Environment-based or trait-based; and (*ii*) it helps in recognizing the actual ecological consequences of losing some species within a genus. In other words, are the most important traits for persistence of ecological niches found at the species level or at some higher taxonomic rank, such as the genus level (19, 20, 26)?

Just as geographic range in species-level analyses is used as a proxy for the ecological niche, we use geographic ranges above the species level as a proxy for ecological niches at the generic and familial levels. We recognize that in some kinds of animals and many kinds of plants, the grouping of "genus" and "family" may not reflect monophyletic groups; thus, we confine our analysis to mammals, in which these ranks typically do reflect monophyly and aggregate similar evolutionary distances (27–29). We focus on mammals, because there is little disagreement that most genera are monophyletic and do in fact reflect a real evolutionary grouping, although we of course recognize some may object to even using the term "genus" in view of current phylogenetic practice. We also recognize that it will be important in the future, especially for groups where little consensus exists about phylogenetic relationships, to test the ideas we present here within a strict phylogenetic context. Given the rapid rate of global climate change today, the principal questions we address here are (*i*) how much the areal extent of higher-level ecological niches has been affected by past episodes of dramatic climate change, and (*ii*) whether pronounced changes in ecological niche-space, e.g., geographic range, of individual species percolate up to cause major changes in higher-level ecological-niche space, e.g., geographic ranges of entire genera and families.

We also explore what kinds of niche characteristics are being conserved in the face of climate change, especially above the species level: Those that relate more closely to environment-based constraints (e.g., thermal tolerance) vs. those that relate to trait-based constraints (e.g., intrinsic properties of individual taxa such as dispersal ability). This is important because, although most studies of niche conservatism focus on the distribution of species and links to climate, geographic ranges do reflect the entire suite of a taxon's ecological requirements and its interactions with other organisms (20). For example, the size, shape, and distribution of a geographic range results from a characteristic abundance distribution of individuals, which is determined by both intrinsic properties of the species, and extrinsic, or environmental, parameters (16, 30, 31). In theory, intrinsic properties such as population growth rates, dispersal ability, litter size, etc., as opposed to extrinsic factors such as climate alone, may heavily influence a species' realized niche. Empirical support for that view includes paleontological data, which have demonstrated that in some cases climate is only a weak predictor of species abundances and distributions, because some taxa have maintained consistent ranges and abundance distributions through thousands to millions of years that span major climatic change (26, 32, 33). In contrast, many species ranges do exhibit a startlingly rapid response to recent warming (5, 15). It may be that the resolution of this dichotomy can be explained if environment-based range controls are most important at the species level, and trait-based range controls are most important at higher taxonomic levels.

Thinking about niche conservatism in this way is consistent with prevailing wisdom in recognizing a relationship between species distributions and climate (9). However, it also acknowledges there is more to controlling species distributions than only climate-linked traits, and that the climate–geographic range relationship may actually be conserved above the species level. Further, maintenance of genus range sizes logically follows from processes of competitive release where congeners are the species most likely to expand their ranges in response to contraction or elimination of sister species, or to contract their ranges from the introduction of sister species not previously in the continental species pool. Thus, we also investigate whether extinction within a clade during a climatic transition (i.e., genus or family) influences range size of the clade.

Our approach is to use range size at varying taxonomic levels to investigate whether the range (as a proxy for higher-level ecological niches) is conserved over the past 130,000 years. Thus, we analyze the size of the geographic ranges of North American mammals through this time, independent of the particular spatial location of the ranges, and investigate how both absolute and relative size of these ranges responded to a major climatic change, the transition from the last glacial to the present interglacial. Future changes to North American environments include the immediate effects of global climatic change, habitat alteration, and extinctions. The dramatic climatic changes of the LP were chosen intentionally to similarly encompass large environmental changes and megafaunal extinction. Although the impending environmental changes are likely to unfold over decades to centuries, this glimpse into the legacy of the events of the LP will yield a baseline with which to measure the impacts of the future.

Although we investigate absolute range size, we also deem it important to look at the relative size of geographic ranges, in part because the maximum size of a terrestrial mammalian geographic range is obviously limited by the land area available on the continent. Over the past 130,000 years, terrestrial area in North America has almost doubled because of glacial melt. Further, fewer LP fossil localities relative to the more recent Holocene localities ($n = 427$ vs. $n = 1,588$, respectively) and differences in preservation environments also may bias raw range size measurements between taxa through time. By focusing on the relative size (i.e., rank) of geographic range of mammals for each temporal interval, we are, in effect, standardizing continental area, sampling effort and taphonomy for each time period, and searching for differences in relative-size patterns that would be meaningful in the context of understanding ecological niche conservation.

Specifically, we examine whether the relative and absolute sizes of geographic ranges of members of the North American fauna have remained similar despite the major climatic change that characterized the last glacial–interglacial transition. We are interested in how the climate of the past 130,000 years has influenced the continental pool of North American mammals and include genus- and family-level data in our analyses. Because we use data from genera and families, we also explicitly examine the influence of LP species extinctions on the range size patterns within genera and families for those groups for which we have species-level data.

Our temporal focus on the past 130,000 years covers a time spanning the latest glacial–interglacial transition in Earth's climate and encompasses climates not present today; however, it does not encompass an evolutionarily significant time period for mammals. Most mammal species in North America are significantly older than 130,000 years. In fact, the mean divergence between North American sister species (within genera) is at least an order of magnitude older (27, 28, 34). Thus, we predict that the intrinsic traits (e.g., trait-based controls on geographic range) that define range size in these animals evolved before the LP glacial–interglacial cycles and, accordingly, we anticipate that the relative range sizes will remain fairly constant, simply because North American mammalian species have witnessed repeated glacial–interglacial cycles in their lifespan (as many as 18 cycles; ref. 35), and presumably the species have inherited the ability to withstand these significant climatic transitions. Alternately, large fluctuations in relative range size would support the idea that range

boundaries of a clade are more tied to environment-based controls than to trait-based intrinsic properties of individual species within the clade.

Results

Genera. We compared the LP and late-Holocene (LH) geographic range sizes for 63 North American mammalian genera (Table 1; Fig. 1). Genera with the largest geographic ranges during the LP were *Sorex*, *Spermophilus*, *Bison*, *Rangifer*, and *Microtus*; those with the smallest ranges were *Aplodontia*, *Baiomys*, *Pappogeomys*, *Gulo*, and *Conepatus* (Fig. 2). During the LH, the genera with the largest ranges included *Procyon*, *Sylvilagus*, *Lynx*, *Odocoileus*, and *Canis*. Smallest LH ranges included *Aplodontia*, *Baiomys*, *Parascalops*, *Neofiber*, and *Oreamnos*.

LP and LH generic range sizes were significantly correlated ($R^2 = 0.62$, $P < 0.0001$; Fig. 3). In the LH, geographic ranges increased an average of 0.01 $\log_{10}$km^2; average absolute difference in size was 0.28 $\log_{10}$km^2. The maximum range increase was 1.60 $\log_{10}$ km^2, or an increase of 37% from the LP to the LH for *Pappogeomys*, which is represented by a single species, *Pappogeomys castanops*. The maximum decrease was a reduction in range size of 1.84 $\log_{10}$km^2, demonstrated by *Parascalops breweri*, a loss of 31% of the former species range.

Geographic range size and rank were significantly correlated (LP $R^2 = 0.53$, $P < 0.001$; LH $R^2 = 0.66$, $P < 0.001$). In the analysis of rank, we found that the taxon identity significantly influenced rank similarly for the LP and LH ($\chi^2 = 112.37$; $P < 0.001$). The majority of mammalian genera ($n = 40$ of 63 genera) show very little change in rank of geographic range size (mean absolute rank change = 8.35). The 23 genera that showed a greater-than-average change in rank (either increasing or decreasing >8 ranks) were not evenly distributed across body sizes ($P < 0.001$). Of the genera that show an increase in range size ranking, the majority are large mammals (>1,000 g) ($n = 11$ of 12 genera) and most were carnivores ($n = 7$ of 11 genera). Of the mammals that show a decrease in rank from the LP to the LH, most are small ($\leq1,000$ g) ($n = 9$ of 11 genera) (Table 1).

Differences in the number of species within a genus due to LP extinction did not significantly influence changes in geographic range rank between time intervals (Fig. 4). The change in range rank of the five genera that lost species due to extinctions at the end of the LP (average absolute change in ranks = 9.8) was not significantly different ($t = 1.607$; $P = 0.09$) from the change in rank of the genera that did not lose species (average absolute change in ranks = 6.2). The number of species per genus also did not unduly influence our results. Monotypic genera ($n = 8$) and multispecies genera ($n = 55$) were not statistically different ($t = 0.039$; $P = 0.48$). However, the genus with the largest number of modern species (*Sorex*; 26 species) did show one of the largest reductions in rank of any genus (−24 ranks and a loss of −0.28 $\log_{10}$ km^2); only *Synaptomys* (three species) showed a greater decline (−29 ranks and a loss of −0.47 $\log_{10}$km^2). Both genera, however, show a dramatic Holocene range expansion into previously glaciated North America, where we do not have fossil data. Additionally, the reduction in size of the geographic extent of these genera is counter to expectations based purely on taphonomic expectations, where younger deposits should contain more small specimens.

We investigated how differences in range size between species within a genus might influence the rank size change over the past 130,000 years. Variance in modern range sizes between species in a genus did not influence the change in rank size between LP and LH ($R^2 = 0.06$, $P = 0.19$). The number of species within a genus today has no significant effect on the change in rank size change between the LP and LH ($R^2 = 0.23$; $P = 0.199$). Thus, a genus generally retains the same rank regardless of the number and size of the geographic ranges of individual species in the genus.

Families. We also compared LP and LH ranges for North American mammalian families ($n = 23$). As expected, given the results at the generic level, Aplodontidae (a monotypic family) had the smallest geographic ranges at both sampled time points (3.44 $\log_{10}$km in the LH and 3.11 $\log_{10}$km^2 in the LP). The Cervidae have the largest geographic range in the LP (6.84 $\log_{10}$ km^2), and the Canidae have the largest LH geographic distribution (6.93 $\log_{10}$km^2). Between the LP and the LH, family geographic range sizes were very stable, changing on average 0.04 ± 0.06 $\log_{10}$km^2. The Dasypodidae geographic range decreased by the largest amount (1.01 $\log_{10}$km^2) over time, whereas the geographic range of the Aplodontidae increased by the largest amount (0.33 $\log_{10}$km^2).
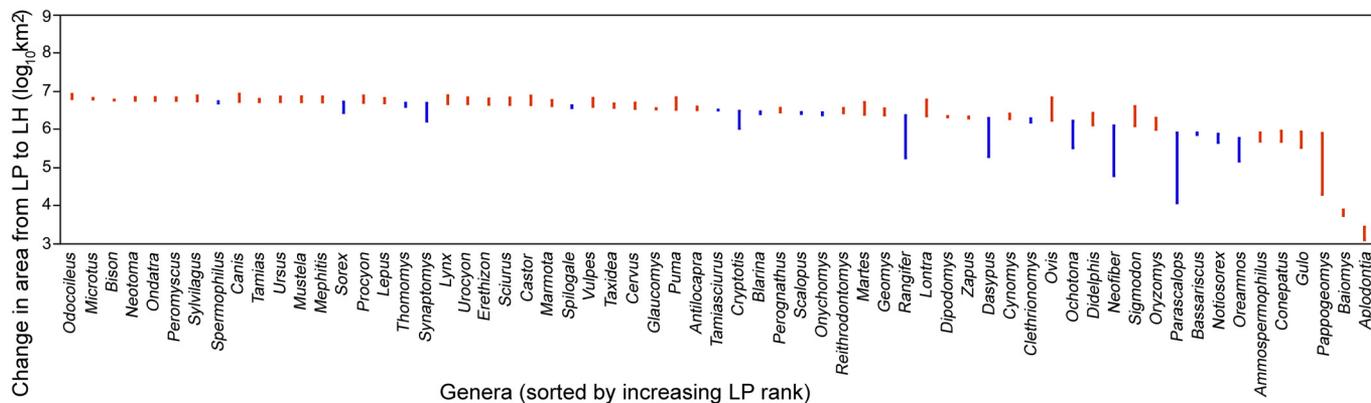
Within-family variance in geographic range size (as measured as the average variance in range sizes at both time points among the genera within a family) was not correlated with change in rank ($r^2 = 0.0186$; $P = 0.322$). Monotypic families (average change in rank was an increase of 1.25 ± 0.75 ranks; $n = 4$) and multispecies families (average change in rank was decline of 0.26 ± 0.96 ranks; $n = 19$) did not differ significantly in temporal range trends ($Z = 1.24$; $P = 0.11$). For the pooled dataset, the average absolute value of rank changes is 2.87 ± 0.52 ranks. Family identity significantly influenced rank across time intervals ($\chi^2 = 40.4$; $P < 0.001$).

Discussion

Our analyses of geographic range changes between the LP and LH demonstrate an increase in the distribution of most North American mammals (Fig. 1), consistent with reported patterns (3, 4). This demonstrates a change in the distribution of animals with respect to geography and melting of glaciers that extended south of the Canadian boundary; but the constancy of the relative range sizes (as seen in the rank analyses) at the genus and family levels suggests that ecological niches above the species level remained constant, i.e., they were conserved over the past 130,000 years. Although North America lost many large mammals at the terminal Pleistocene (36), the similarity of the relative geographic range sizes of the taxa composing the postextinction mammalian community remained constant relative to their preextinction condition, just as locally sampled faunas and relative abundances of taxa within local communities have been shown to exhibit conservatism over paleontological time scales (32). These data demonstrate that higher-level ecological niches in mammals, as defined by the size of the geographic ranges of genera and families, are conserved over at least 100 millennia.

Within-genus extinctions of species did not alter range patterns from the expectations of niche conservation at the genus level: the genera that lost species during the LP exhibited no differences in their LH range size. This pattern suggests that the other species in the genus expanded their ranges, occupying the niches that were vacated by their close relatives. Clearly, there is a role for the number of species in the genus, because those genera that became extinct in North America at the terminal Pleistocene were predominately represented by single species (79%; ref. 29). Similarly, species richness within genera did not significantly influence the size or rank of generic geographic range. In this respect, higher-level ecological niches appear relatively resistant to climatic change even as pronounced as glacial–interglacial transitions, so long as an adequate pool of species exists within higher-level clades. Although it is possible that novel physiological traits evolved in species over the past 130,000 years, these traits are less labile within mammals than are behavioral traits (24). Thus, ecological events that species experience and respond to over time scales shorter than evolutionary time in these mammalian lineages did not override the inherited life history traits that maintain geographic distributions at the genus level. These traits include life history attributes

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Table 1. List of North American mammalian genera used in our analyses

Genus	No. species per genus	Range size of LH, $\log_{10}\text{km}^2$	Rank of LH range	Range size of LP, $\log_{10}\text{km}^2$	Rank of LP range	Average body size, $\log_{10}\text{g}$
Ammospermophilus	4	5.91182	52	5.68897	58	2.08782
Antilocapra	1	6.58796	31	6.51571	31	4.66000
Aplodontia	1	3.44241	63	3.10925	63	3.00000
Baiomys	1	3.88874	62	3.74539	62	0.92867
Bassariscus	1	5.86469	54	5.90816	55	3.05000
Bison	1	6.77274	22	6.76833	3	5.73092
Blarina	3	6.41277	41	6.46045	34	1.22710
Canis	3	6.92863	1	6.73048	9	4.17088
Castor	1	6.87595	6	6.64837	23	4.30000
Cervus	1	6.69202	26	6.54707	28	5.06848
Clethrionomys	3	6.18860	48	6.28079	47	1.41493
Conepatus	1	5.95480	50	5.68177	59	3.13404
Cryptotis	1	6.02595	49	6.47873	33	0.94472
Cynomys	4	6.40554	42	6.28087	46	2.99355
Dasypus	1	5.28401	57	6.29049	45	3.47049
Didelphis	1	6.42364	39	6.11604	50	3.08789
Dipodomys	18	6.34047	44	6.32683	43	1.83460
Erethizon	1	6.80227	20	6.65392	21	3.85036
Geomys	9	6.54015	36	6.37752	40	2.33905
Glaucomys	2	6.54783	35	6.53484	29	2.01269
Gulo	1	5.93441	51	5.52535	60	4.22608
Lepus	7	6.81499	19	6.69689	16	3.39847
Lontra	1	6.77221	23	6.35438	42	3.80077
Lynx	2	6.88675	3	6.67459	19	4.03717
Marmota	6	6.76450	24	6.62354	24	3.64350
Martes	2	6.70980	25	6.39687	39	3.18395
Mephitis	2	6.85429	8	6.71997	13	3.11144
Microtus	17	6.81770	18	6.79439	2	1.50751
Mustela	5	6.85765	7	6.72448	12	2.42000
Neofiber	1	4.78354	60	6.09602	51	2.42488
Neotoma	10	6.83954	10	6.76132	4	2.31807
Notiosorex	2	5.65324	55	5.87558	56	0.64279
Ochotona	2	5.51427	56	6.21950	49	2.20000
Odocoileus	2	6.92118	2	6.80703	1	4.74094
Ondatra	1	6.83709	11	6.76063	5	2.99189
Onychomys	3	6.38068	43	6.44092	37	1.44016
Oreamnos	1	5.16692	59	5.76559	57	4.86034
Oryzomys	2	6.29540	46	6.00022	53	1.77817
Ovis	2	6.82784	15	6.23562	48	4.88418
Pappogeomys	1	5.89914	53	4.29415	61	2.34212
Parascalops	1	4.07132	61	5.90832	54	1.70757
Perognathus	9	6.55718	33	6.45506	35	1.08153
Peromyscus	15	6.83034	13	6.76046	6	1.52735
Procyon	3	6.87925	5	6.70451	15	3.66075
Puma	2	6.83135	12	6.52585	30	4.71265
Rangifer	1	5.25103	58	6.36416	41	4.93467
Reithrodontomys	5	6.55405	34	6.43478	38	1.11370
Scalopus	1	6.41516	40	6.44468	36	1.96027
Sciurus	8	6.82605	16	6.65174	22	2.66398
Sigmodon	4	6.60125	29	6.09589	52	2.10021
Sorex	27	6.44049	38	6.71939	14	0.78454
Spermophilus	21	6.69090	27	6.73134	8	2.36922
Spilogale	2	6.56828	32	6.62337	25	2.45191
Sylvilagus	8	6.88060	4	6.74538	7	3.07622
Synaptomys	2	6.21533	47	6.68814	18	1.41626
Tamias	24	6.79027	21	6.72761	10	1.86028
Tamiasciurus	2	6.50694	37	6.50974	32	2.32787
Taxidea	1	6.67014	28	6.57658	27	3.85172
Thomomys	9	6.60011	30	6.68861	17	2.16414
Urocyon	2	6.82990	14	6.67385	20	3.48169
Ursus	3	6.85249	9	6.72636	11	5.25381
Vulpes	3	6.81797	17	6.60137	26	3.48642
Zapus	4	6.33000	45	6.29745	44	1.37845

Genus names follow Wilson and Reeder (48). Genera are listed in alphabetical order, with number of species, late-Holocene range size and rank, late-Pleistocene range size and rank, and average body size (for North American species within the genus). Body sizes are taken from ref. 29. The list of genera and the number of species per genus is calculated from the North American mammalian database (52).

such as dispersal ability, body size, potential population growth rates, population density, and degree of ecological specialization. The constancy in relative size and rank of geographic ranges

indicates that important ecological traits are conserved above the species level. We speculate that this constancy in geographic range size and rank also implies constancy in how species within

Fig. 1. Change in log₁₀ area from late Pleistocene (LP) to late Holocene (LH) for North American genera. Genera listed left to right from highest LP rank to lowest LP rank. Bars shows difference in geographic range area between the two periods: blue indicates that genus range decreased in LH, red indicates genus range increased in LH. Note that most genera increased in range size in the LH.

genera (of mammals, at least) interact with species of sympatric genera, but we recognize that rigorous tests of this idea have yet to be performed. We also recognize that our results so far apply only to mammals, and that it will be of great interest to see whether analyses of other kinds of organisms demonstrate similar results. Because the size of the geographic ranges of genera remains constant even when species are deleted, geographic range appears to be an emergent property (in the sense of ref. 37) of mammalian genera.

These observations lead us to suggest that disparities in the geographic ranges of species within genera thus may be inferred to be due more to competitive interactions between species in the genus and less strictly to the abiotic environment. This conclusion is consistent with rules of community assembly, which proceeds first by adding taxa that are overdispersed after which close relatives are included (38, 39). Additionally, there is strong evidence showing higher taxonomic affinity for biogeographic region in North America through the Pleistocene, such that genera found, for example, in montane or desert regions have persisted there regardless of movements of individual species (32, 40). Further, the assemblage of North American taxa has remained relatively stable at the genus level over the past million years, with obvious exceptions (i.e., *Bison*, *Microtus*, *Mammuthus*) due to immigration events through Beringia (41). Because genera with one species behave in a similar fashion as genera with multiple species, we propose that the genus is an ecologically important clade to recognize for mammals. In essence, genera form the continental pool from which species are derived and are thus the backbone of the ecological communities over long evolutionary periods. Geographic ranges are also conserved at the family level as well. That we observe these patterns at both the generic and familial levels in mammals raises the interesting possibility that niche conservatism is expressed at different levels of the taxonomic hierarchy, that is to say, at different nodes in the phylogeny, and perhaps are even controlled by different evolutionary or ecological factors at each. Testing that intriguing possibility is beyond the scope of the present article but in theory should be possible by focusing on
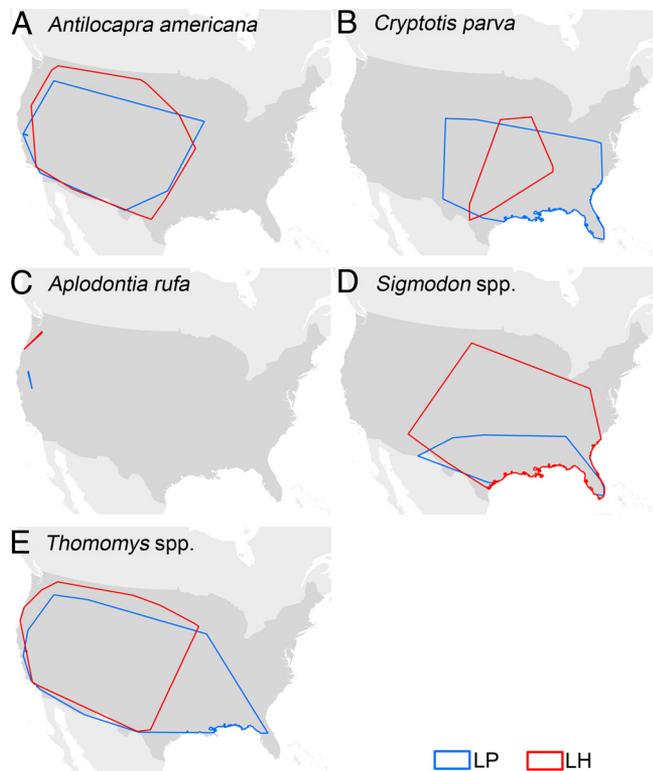
Fig. 2. Examples of the LP and LH geographic range sizes for North American mammalian genera. Included are differences in late-Pleistocene to LH range sizes for (*A*) monotypic genus *Antilocapra americana* (0 ranks changed), (*B*) monotypic genus *Cryptotis parva* (reduction in two orders of rank), (*C*) the smallest range *Aplodontia rufa* (0 ranks changed), (*D*) the largest range expansion *Sigmodon* spp. (increase in 23 ranks), and (*E*) the largest range contraction *Thomomys* spp. (decrease in 13 ranks).
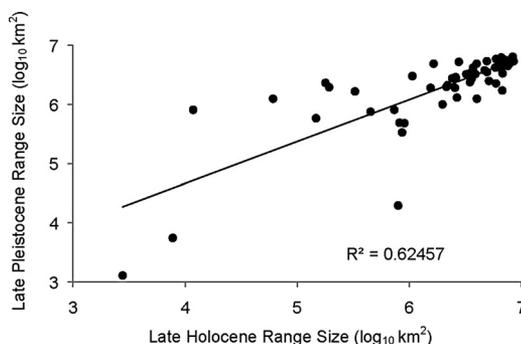
Fig. 3. Correlation between North American LP and LH generic range sizes ($R^2 = 0.6246$).

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A Late Pleistocene

B Late Holocene

▲ *Canis lupus*   ✕ *Canis dirus*   • *Canis latrans*
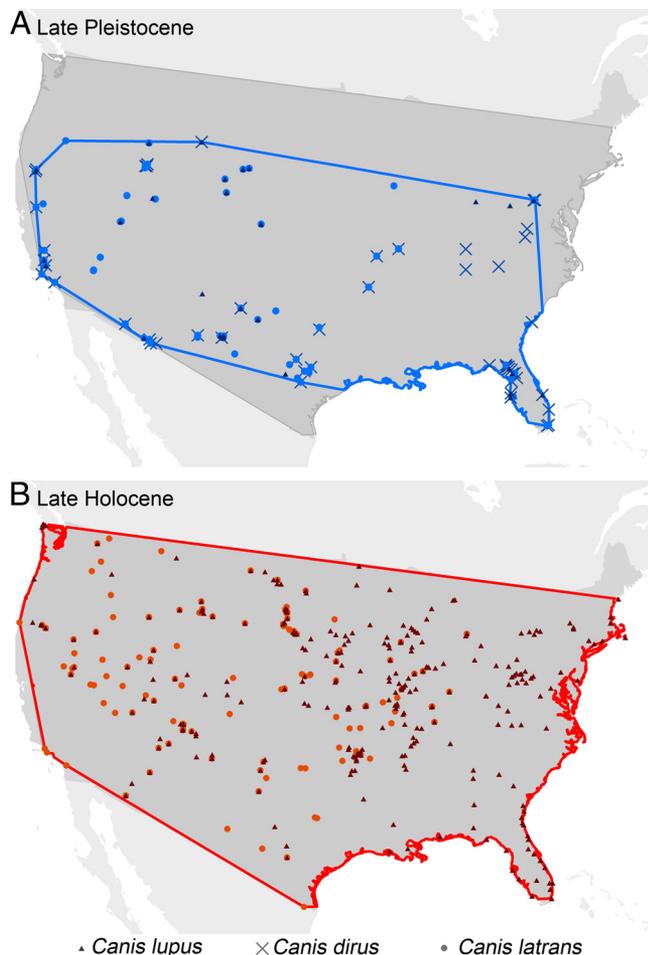
Fig. 4. Differences in the number of species within a genus due to late-Pleistocene extinction did not significantly influence changes in geographic range rank between time intervals. Example shown is genus *Canis*, which ranked second in range size in LP and seventh in LH. (*A*) LP *Canis* species, (*B*) LH *Canis* species. Note that *Canis dirus* became extinct at the end of the Pleistocene.

groups in which phylogenetic and distributional relationships are relatively well understood.

Our data also demonstrate details about community interactions. The large mammal community, which was the most severely impacted by extinction in the LP, shows evidence of competitive release. Of the mammals exhibiting the largest increases in range size ranks, 92% were >1,000 g. This suggests that mammals larger than 1,000 g were responding to the loss of megafaunal species (>4,400 g), notably 22 megafaunal genera and families with no extant species remaining in North America (i.e., *Mammuthus*, *Smilodon*, etc.; ref. 36). In contrast, 82% of the mammals showing the largest reduction in the relative geographic range ranking were mammals <1,000 g, which may signify heightened competition through the Holocene in this community.

In summary, we have used the fossil record to expand the theory of niche conservatism in an innovative way, using actual data on generic response to past periods of climatic change to assess conservation of ecological properties above the species level. This study enabled us to use a traditional "limitation" of the fossil record (the incomplete taxonomic resolution below the generic level) as an asset for visualizing an ecological process at higher evolutionary levels. We note that our data are only for a single clade of organisms, Mammalia, and that other groups may

exhibit different patterns. Nevertheless, our results reveal two insights for a major group of animals that figure prominently in ecological, evolutionary, and conservation research. The first is that there are ecological niches and corresponding niche conservatism above the species level. The second is the importance of intrinsic traits manifested at the level of genera in defining and maintaining higher-level niches, e.g., conservation of niches primarily by trait-based controls. This explains why higher-level ranges seem to change so little in response to a major climate change of the past. We suspect that the markedly different observations for many species during both the Pleistocene–Holocene transition and today's global warming—shifting ranges during climatic change—indicate that species-level niches are influenced more by environment-based controls such as biotic interactions. We have not tested that proposition explicitly but suggest the test is needed. We think species within a genus divide up niche space through competition for resources and thus their ranges correspondingly fluctuate as changing climate influences the resources, but the aggregation of several different species, each with slightly different resource preferences, buffers change in range size at the generic level. Thus, higher-level niches are less affected by environmental changes than are species-level niches. Thus it may be informative and powerful to model the ecological effects of climate change at the range of the genus in mammals, as opposed to the range of the species, to reveal the significance and magnitude of range changes into the future.

However, the same geographic ranges that have been conserved over the last several thousand years have begun to disappear rapidly over the past century. By focusing on the LH instead of the present, we do not account for recent changes in geographic range due to historic human impacts such as agricultural modification of the landscape and hunting, such as the reduction in range of the bison (*Bison bison*) or grizzly bear (*Ursus arctos*). Although we do not have data for every North American mammal species, range changes over the past century may be of significantly greater magnitude than those of the previous 130,000 years; the immediate future may be greater still (42, 43). How do we reconcile stability in range sizes through millennia with the rapid contractions of species ranges today? What has maintained constancy in areal extent of higher-level niches in the past is an adequate pool of species within genera. The trajectory of future change is toward conditions—both climatic and otherwise—that species have not experienced in their existence (43). Ongoing habitat degradation, population loss, and human population growth (44, 45) may signify an altered continental state such that the North American species pool will contain fewer species overall (45, 46), and both environmental change and species loss may occur at rates too fast for species interactions, dispersal, and competitive release to compensate (47). Our results also indicate that perhaps the best and most tractable predictor of mammal response to environmental change lies at the genus level (as a convenient clade for representing deeper evolutionary units). Further, species that are the sole representative of a genus, or indeed a family, may represent the evolutionary manifestation of a truly novel ecological niche. Thus it may be informative and powerful to model the ecological effects of climate change at the range of the genus in mammals, as opposed to the range of the species, to reveal the significance and magnitude of range changes into the future. On this landscape, our data indicate that conservation of the "generic pool," perhaps even more so than conservation of the "species pool," is critically important for continuity of North American mammalian community function into the future.

Materials and Methods

Taxonomy. Genus and family names follow Wilson and Reeder (48). Use of the genus level provides the largest sampling of the fossil record, because many fossils are not identifiable to species but can be assigned to genus. Further,

rules of mammalian community assembly demonstrate that life history, demography, and body size (refs. 29 and 49, but see refs. 50 and 51), all of which influence geographic range size, are most similar among congeneric species. Despite significant environmental change over the past 1 million years, the available species pool (at least for small mammals) has remained generally constant (32). Thus, the intrinsic factors that define the extant North American species and the extrinsic factors involved in their distributions have not been altered to such an extent that there has been complete turnover of the American fauna. Part of our objective was to understand how taxa responded to range size or extinction of closely related congeners, a pattern perhaps best captured by the behavior of generic range size. Of the 63 genera and 23 families we analyze, nine genera and three families are represented by a single species. Thus, our analyses also include comparisons between monotypic and multispecies higher-order taxa.

List of Genera. We compiled a database of 63 North American mammalian genera with living representatives for the LP and the LH (Table 1). A comprehensive fossil database is not yet available for Mexico, Asia, or Canada. Thus, to maximize our temporal comparisons, we excluded primarily Holarctic genera and those that maintain the majority of their ranges south of the U.S. border or north in Canada and Alaska, focusing instead on the lower 48 states. Our use of ranks is an attempt to resolve the issue of missing distribution data from the rest of North America. We also excluded mammalian genera that were present in the LP but went extinct before the LH. However, extinct species within extant genera were deliberately included to investigate the role of potential range expansion from competitive release ($n = 5$). We did not use modern generic ranges because we wanted to standardize our data collection methods, and fossil sampling is performed very differently than is modern mammal sampling. However, we did calculate the modern ranges of all species in each genus in our database using modern range data (1), so that we could determine the variance of species range sizes within genera. A list of genera of from the contiguous U.S. and the numbers of species per genus were taken from the North American mammalian database (52); body sizes are from ref. 29.

List of Families. We assigned all of the taxa used in the generic-level analyses to families ($n = 23$; ref. 48). For the LP [11,800–130,000 years before the present (ybp)] and LH time periods (0–4,500 ybp), we used all available datapoints from the NEOTOMA Paleoecology Database (53) to assess geographic range for each family. For those families that encompassed more than one genus ($n = 14$), we calculated the within-family variance in geographic range change and rank of geographic range change between periods. We calculated the correlation between the variance within a family and the rank changes.

Geographic Range Size Calculations. For our paleo-range study, we used data points from the NEOTOMA Paleoecology Database (53). We focused on data points within the contiguous U.S., because there were a limited number of Canadian sites in the database. Our final dataset focused on two time periods: the LP (defined in the NEOTOMA database as 11,800–130,000 ybp) and the LH (0–4,500 ybp). These two time periods have thousands of specimens identified within localities (LP: $n = 5,108$; LH: $n = 17,436$) and encompass the greatest environmental changes of the last 130,000 years. More precise dating is possible for only a subset of these data. Thus, we used all of the data for the LP as defined in the NEOTOMA database.

We used the Geographic Information System (GIS) to estimate genus or family range (54) and used only genera with more than two data points in each time bin to estimate area. We converted all data to a USA Contiguous Albers Equal Area Conic USGS projection, created minimum convex polygons around the data points of each genus or species (55), clipped these polygons to the lower 48 states in North America, removed oceanic coverage, and calculated the area of each polygon in square kilometers (56). We used minimum convex polygons to estimate taxa range, because it provides a way to consistently calculate range across time and taxa.

Analyses of Geographic Range-Size Rank. Our method of calculating geographic-range area may overestimate the true geographic ranges of taxa that are patchily distributed and are restricted to specific habitats [i.e., range of American pika (*Ochotona princeps*) in the LH]. Furthermore, the area estimations are affected by factors such as taphonomy, the completeness of fossil records, and the total available space in a given time period because of the presence of continental glaciers. Additionally, our geographic ranges are limited by continental area. Thus, variance decreases with increasing size in log space, violating assumptions of continuous data in a linear regression. Therefore, we needed also to use a nonparametric approach. Thus, we used ranks of log area for our statistical analyses to standardize range sizes for the LP and LH. We evaluated differences in the rank of geographic range between periods using Friedman's test (23). We examined the effects of late-Pleistocene extinctions on the range-size rank by comparing average rank changes of genera that lost species at the Pleistocene–Holocene transition ($n = 5$) to genera that did not ($n = 58$). This comparison was performed using Student's t test. We also address the influence of intragenus species richness by comparing average rank changes of monotypic genera ($n = 9$) with the remaining genera ($n = 54$), using Student's t test. We further examined the influence of body size on larger than average changes in geographic range rank by performing a χ^2 test.

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