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Anthony D. Barnosky, Marc A. Carrasco and Russell W. Graham

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Collateral mammal diversity loss associated with late Quaternary megafaunal extinctions and implications for the future

ANTHONY D. BARNOSKY[1,2]*, MARC A. CARRASCO[1] & RUSSELL W. GRAHAM[3]

[1]*Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, California 94720, USA*

[2]*Museum of Paleontology, University of California, Berkeley, California 94720, USA*

[3]*Department of Geosciences and Earth and Mineral Sciences Museum, The Pennsylvania State University, University Park, Pennsylvania, USA*

**Corresponding author (e-mail: barnosky@berkeley.edu)*

Abstract: Using data from two palaeontological databases, MIOMAP and FAUNMAP (now linked as NEOMAP), we explore how late Quaternary species loss compared in large and small mammals by determining palaeospecies-area relationships (PSARs) at 19 temporal intervals ranging from *c.* 30 million to 500 years ago in 10 different biogeographical provinces in the USA. We found that mammalian diversity of both large and small mammals remained relatively stable from 30 million years ago up until both crashed near the Pleistocene–Holocene transition. The diversity crash had two components: the well-known megafaunal extinction that amounted to *c.* 21% of the pre-crash species, and collateral biodiversity loss due to biogeographical range reductions. Collateral loss resulted in large mammal diversity regionally falling an additional 6–31% above extinction loss, and small mammal diversity falling 16–51%, even though very few small mammals suffered extinction. These results imply that collateral losses due to biogeographical range adjustments may effectively double the regional diversity loss during an extinction event, substantially magnifying the ecological ramifications of the extinctions themselves. This is of interest in forecasting future ecological impacts of mammal extinctions, given that *c.* 8% of USA mammal species, and 22% of mammal species worldwide, are now considered 'Threatened' by the IUCN.

Previously, we determined that throughout the Holocene (from *c.* 11 000 to 500 years ago) biodiversity of mammals in the USA has been 15–42% too low, depending on biogeographical province, with respect to the pre-Holocene baseline that had existed for millions of years (Carrasco *et al.* 2009). The Holocene biodiversity decline was associated with the widely-recognized Late Quaternary Extinction (LQE) event, which affected primarily mammals (and a few birds and reptiles) >44 kg in body weight and was globally time-transgressive. The LQE began in Australia some 50 000 years ago, became most intense in temperate (our study area) and high latitudes near the Pleistocene–Holocene boundary, and then diminished into the early, middle, and late Holocene (Martin 1966; Martin & Wright 1967; Martin & Klein 1984; Barnosky *et al.* 2004; Wroe *et al.* 2004; Koch & Barnosky 2006; Wroe & Field 2006; Brook *et al.* 2007; Barnosky & Lindsey 2010). Today extinction appears to be accelerating again, as indicated by elevated extinction rates over the past few centuries, and high numbers of species threatened with extinction due to human activities (Myers 1990; Leakey & Lewin 1992; May *et al.* 1995; Pimm *et al.* 1995; Dirzo & Raven 2003; Wake & Vredenburg 2008; Barnosky *et al.* 2011).

Whether or not humans were the primary cause of the onset of LQE in various regions still engenders debate, but recent treatments tend to recognize at least some role for *Homo sapiens* as a driver, with details of timing and intensity being controlled by complex synergies between human population sizes, timing and magnitude of climate change, and ecological attributes of species (Barnosky *et al.* 2004; Wroe *et al.* 2004; Koch & Barnosky 2006; Wroe & Field 2006; Brook *et al.* 2007, 2008; Barnosky 2008; Field *et al.* 2008; Barnosky & Lindsey 2010).

Whatever the ultimate cause of the LQE, it offers a natural experiment to assess ecological effects that result from extinction (Blois *et al.* 2010). Here we examine some of those effects, by using palaeospecies-area relationships to more fully characterize the diversity loss that occurred on a continental scale and at regional scales. Exploring these details is pertinent to understanding the biotic impacts that would ensue if currently threatened species (particularly mammals), as defined by the

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International Union for Conservation of Nature (IUCN) (Mace *et al.* 2008; IUCN 2010), in fact did go extinct.

We focus on mammals from the lower 48 states of the USA for several reasons. First, mammals were the primary victims at the LQE near the end of the Pleistocene, and once again are at risk of extinction in significant numbers: the IUCN has assessed all 5490 known species and classified *c.* 22% worldwide and *c.* 8% of the 439 USA species as threatened (Mace *et al.* 2008; IUCN 2010). For comparison, during the LQE *c.* 5% of species worldwide, and 19% of USA species, went extinct. Third, and critically for our purposes, there is a relatively good fossil record of mammals from the USA that is accessible through palaeobiological databases for past times up to 500 years ago, and which can be adjusted for spatial and temporal sampling inconsistencies (FAUNMAP Working Group 1994; MIOMAP 2010; NEOMAP 2010; NEOTOMA 2010; PaleoDB 2010). Finally, mammal taxonomy, both fossil and modern, has been relatively stable compared to many other kinds of organisms, and different species concepts produce broadly overlapping results, thus facilitating comparison of deep-time and near-time samples.

Methods

Our general approach was to construct palaeospecies-area relationships (PSARs) for a variety of time-intervals from *c.* 30 million to 500 years ago (Table 1) and biogeographical provinces (Fig. 1). We then compared the PSARs from the Holocene time interval ('anthropogenic' interval of Carrasco *et al.* 2009) to baseline PSARs derived from pre-Holocene time intervals ('pre-anthropogenic' of Carrasco *et al.* 2009, in the sense of lacking substantial numbers of humans in our study area). We did this for all mammals in the USA, for large mammals only (as defined below), and for small mammals only, using unnested PSARs that analyzed the data using methods detailed below.

Databases

Species occurrence data were extracted from three databases: MIOMAP (Carrasco *et al.* 2007; MIOMAP 2010), FAUNMAP I (FAUNMAP Working Group 1994), and FAUNMAP II (as of August, 2010) (NEOMAP 2010). MIOMAP spans the period from 5 to 30 million years ago, FAUNMAP II from 40 000 to 5 million years ago, and FAUNMAP I from 500 to 40 000 years ago. We combined FAUNMAP I and FAUNMAP II data into a single database and served it through the Neogene Mammal Mapping Portal (NEOMAP 2010), which we created to facilitate uniform searches and output from MIOMAP and FAUNMAP (http://ucmp.berkeley.edu/neomap/use.html). We used the online routines in NEOMAP to generate species counts and geographical areas that were ultimately used in the analysis (a slightly different version of the FAUNMAP data also is served online as part

Table 1. *Temporal bins into which species occurrences were sorted*

Time interval	Age boundaries	Interval duration
Holocene	*c.* 11 500–500	*c.* 11 000
Rancholabrean	0.15 Ma–*c.* 11 500	*c.* 140 000
Irvingtonian	1.8–0.15 Ma	1.65 Ma
Blancan	4.7–1.8 Ma	2.9 Ma
Late late Hemphillian	5.9–4.7 Ma	1.2 Ma
Early late Hemphillian	6.7–5.9 Ma	0.8 Ma
Late early Hemphillian	7.5–6.7 Ma	0.8 Ma
Early early Hemphillian	9–7.5 Ma	1.5 Ma
Late Clarendonian	10–9 Ma	1.0 Ma
Middle Clarendonian	12–10 Ma	2.0 Ma
Early Clarendonian	12.5–12 Ma	0.5 Ma
Late Barstovian	14.8–12.5 Ma	2.3 Ma
Early Barstovian	15.9–14.8 Ma	1.1 Ma
Late Hemingfordian	17.5–15.9 Ma	1.6 Ma
Early Hemingfordian	18.8–17.5 Ma	1.3 Ma
Late late Arikareean	19.5–18.8 Ma	0.7 Ma
Early late Arikareean	23.8–19.5 Ma	4.3 Ma
Late early Arikareean	27.9–23.8 Ma	4.1 Ma
Early early Arikareean	30–27.9 Ma	2.1 Ma

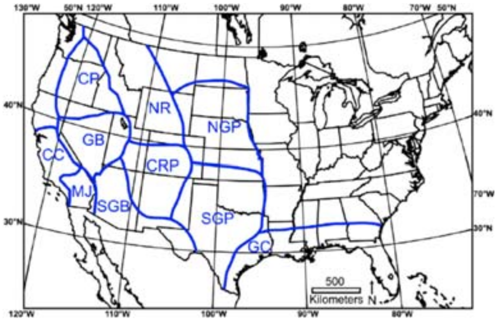

Fig. 1. Biogeographical provinces used in this study. Central California (CC); Columbia Plateau (CP); Colorado Plateau (CRP); Great Basin (GB); Gulf Coast (GC); Mojave (MJ); Northern Great Plains (NGP); Northern Rockies (NR); Southern Great Basin (SGB); Southern Great Plains (SGP).

of the NEOTOMA database effort (NEOTOMA 2010), which combines several Quaternary fossil databases).

Biogeographical provinces

Although Quaternary mammal fossils are distributed essentially continent-wide, most of the Cenozoic North American mammalian fossil record is best represented in the USA west of the Mississippi River (Tedford *et al.* 1987, 2004). Therefore, we concentrated on this region, dividing it into 10 biogeographical provinces (Fig. 1). Today, these provinces are considered biogeographically distinct from one another (Hagmeier & Stults 1964; Hagmeier 1966; Janis *et al.* 1998; Lugo *et al.* 1999), and it is likely that the same held true back through the Oligocene (Tedford *et al.* 1987; Storer 1989; FAUNMAP Working Group 1996; Barnosky & Carrasco 2002; Tedford *et al.* 2004). This is especially true in those provinces with the most complete fossil record (e.g. Northern Great Plains), as they have undergone limited topographic change over the past 30 million years (Prothero 1998; Condon 2005).

Large v. small mammal samples

The species data from each time interval and biogeographical province were divided into two separate groups: large mammals and small mammals (Table 2). Small mammals included all members of the mammalian orders Rodentia, Insectivora, and Lagomorpha, that is, animals with body mass generally <2 kg (though a few rodents and lagomorphs exceed 2 kg). Large mammals comprised all other non-volant, terrestrial mammalian orders. Because of their limited representation in the databases, Chiropterans were eliminated from the analysis. For counts of extant species in the USA, we used IUCN data (IUCN 2010) as summarized in Table 2. Counts of extinct species and their approximate

Table 2. *Extant USA species per clade and total extinct USA species since 50 thousand years ago*

Size	Clade	Species	
Large extant	Carnivora	53	
Large extant	Cetartiodactyla	62	
Large extant	Cingulata	1	
Large extant	Didelphimorpha	1	
Small extant	Eulipotyphla	43	
Small extant	Lagomorpha	19	
Small extant	Rodentia	211	
Not included	Chiroptera	49	
Totals			
Extant	Minus Chiroptera	390	
Large extant	Minus Chiroptera	117	
Small extant	Minus Chiroptera	273	
Extant	With Chiroptera	439	
Large extant	With Chiroptera	117	
Small extant	With Chiroptera	322	
Extinct	Minus Chiroptera	106	
Large extinct	Minus Chiroptera	100	
Small extinct	Minus Chiroptera	6	
% Extinct			
Extant + extinct	With Chiroptera	545	19.45
Large extant + extinct	With Chiroptera	217	46.08
Small extant + extinct	With Chiroptera	328	1.83
Extant + extinct	Minus Chiroptera	496	21.37
Large extant + extinct	Minus Chiroptera	217	46.08
Small extant + extinct	Minus Chiroptera	279	2.15

Small 1/4 less than *c.* 2 kg body mass; Large 1/4 greater than *c.* 2 kg.
Data for extant mammals are from the IUCN Red List of Threatened Species, Version 2010.4, www.iucnredlist.org, downloaded 13 Dec. 2010 (IUCN, 2010). Not included in this table are Sirenia (2 spp.) and Primates (1 sp.). The IUCN lists 37 (includes chiropterans) or 32 (excludes chiropterans) USA species as Threatened.
Data for extinct species primarily from references in Barnosky *et al.* (2011) and Smith *et al.* (2003). The IUCN lists 2 spp. extinct in historic times; these are included in the totals, of extinct species.

body sizes were compiled from references detailed in previous publications (Smith *et al.* 2003; Barnosky *et al.* 2011).

Species counts

Species data were tabulated using the MIOMAP EstimateS (Colwell 2009) web service function via the Berkeley Mapper (http://berkeleymapper.berkeley.edu), which produced a table of the minimum number of individuals (MNI) for each taxon by locality. After exporting the EstimateS table to Microsoft Excel, the MNI data were adjusted to occurrence (presence/absence) data. Within individual localities, generic or higher level occurrences were eliminated when a more precise taxonomic assignment in that locality was present (e.g. the occurrence *Canis* sp. would be eliminated from a locality if *Canis dirus* was known from the same locality). Thus we used minimum counts of species. Occurrence data were then added across all localities for the given time period and geographical province. Only minimum counts as opposed to maximum counts (all specimens identified to genus or higher taxon assigned to a new species) were employed here as previous work showed little difference among these two counting methods (Barnosky *et al.* 2005).

Geographical area calculation

For each time interval, the geographical area encompassed by the sample was determined by using the routines in NEOMAP to zoom in to a scale that included all pertinent localities, trace the minimum convex polygon that would include all the localities of interest, and calculate the area enclosed by the polygon. Geographical areas were calculated using the Berkeley Mapper mapping interface.

Temporal binning

Methods based on taxon co-occurrences have been developed to sort fossil occurrences into one million year intervals (Alroy 1992, 1996, 1998, 1999, 2003). However, these methods were not appropriate for our study because they reduce the number of localities per time slice such that not enough data exists for many time slices when dividing the record into discrete biogeographical regions, and also can introduce false precision for localities that are not well dated and that have few taxa. Therefore, we assigned fossil occurrences to one of 19 subdivisions of the North American Land Mammal Ages (Table 2) as specified in Tedford *et al.* (2004) for pre-Blancan time intervals and FAUNMAP I (FAUNMAP Working Group 1994) for post-Blancan temporal bins.

Durations of temporal bins are not equal, but we determined this has little influence on diversity counts per time period because (i) there is no correlation between bin length and number of localities (Barnosky *et al.* 2005) or species richness (Carrasco *et al.* 2009); (ii) the localities do not span the entire time represented by each bin but instead subsample discrete times within bins, thus correcting for number of localities as described below also to some extent corrects for temporal variations; and (iii) bins of the sort used here, based on maximum taxon associations, are best suited to comparisons of diversity through time, as they produce a series of biologically meaningful groupings that do not change much within each bin (Tedford *et al.* 2004).

We limited our Holocene sample to contain localities older than 500 years, in order to use only fossil data and therefore make the Holocene sample comparable to the pre-Holocene sample. Therefore, both Holocene and pre-Holocene data were assembled in the same way: primarily through fossils reported over the past century by scientists employing similar collecting methodologies. Nevertheless, Holocene samples were often larger, which would be expected to result in a greater number of total species in each biogeographical province. Because prior statistical analyses have demonstrated a significant correlation within each temporal bin between the total number of species and the rarefied species richness as well as the total number of occurrences (Carrasco *et al.* 2009), the palaeospecies-area relationships from the Holocene bin should have higher diversity if this bias were present. Therefore, any results that reveal a *reduction* in species diversity during the Holocene should be particularly robust.

Sampling biases and sample standardization

There are well-recognized sampling problems that must be adjusted for when using fossil data to assess diversity, including differences in sampling intensity and geographical areas sampled for each time slice (Barnosky *et al.* 2005). To standardize samples, we computed species richness values per time slice and per geographical area (for both small and large mammals) by rarefaction using a richness value of 75 taxon occurrences. Rarefaction of the raw minimum species counts was accomplished with S. Holland's analytical rarefaction software (http://www.uga.edu/~strata/software/). A review of the development of rarefaction methodology can be found in Tipper (1979) while the programs we used were ultimately based on the rarefaction work of (Raup 1975), and originally derived by Hurlbert (1971) and Heck *et al.* (1975). The data was rarefied by occurrences instead of the number of individual specimens to remove the effect of high-graded localities and missing data (Barnosky *et al.* 2005). We set the rarefaction occurrence value at 75 because that value provided an adequate number of data points while at the same time eliminating samples that were based on spotty data.

Constructing palaeospecies-area Relationships (PSARs)

The rarefied species richness data were plotted against sampled area to determine palaeospecies-area relationships (PSARS) (Barnosky *et al.* 2005). PSARs were determined at two different geographical scales: continental and provincial. The continental analysis plots continental species richness per time interval against area per time interval for all intervals for which data existed (Figs 2–4). The provincial analysis plots species richness per biogeographical province against sampled area within the province for each time interval for which data were available (Figs 5 & 6). Thus each data point in the graphs represents a single time slice for either all 10 provinces combined (Figs 2–4) or for individual provinces (Figs 5 & 6).

PSARs in this paper correspond to Type IV unnested species-area relationships (SARs) (Scheiner 2003). They simply plot species richness against geographical area for each area sampled. These differ from nested Type I SARs, in that they do not represent species accumulation curves, an important distinction in interpreting the data. In a nested Type I SAR, the expectation is that adding more area will always result in adding more species, because as new species are encountered as one expands the sampling into new habitats, the species are added to the list that has already accumulated by previous sampling efforts. Thus, as beta diversity (the difference in species composition between sites) increases, so does the slope of the nested SAR. In contrast, in unnested Type IV curves, which we use here, the relationship shows how many species are in a given sampling area, but the species in one area may be entirely the same as those in another, entirely different, or somewhere in between. Therefore the slope of an unnested Type IV curve does not reflect beta diversity in a straightforward way, because there is no embedded information about species identity. Likewise, the slope of the unnested SAR may deviate from positive, if, for example, different biogeographical provinces are being compared, and diversity is markedly different within each because of provincial environmental constraints. One might imagine, for example, equally sized areas, one in a productive, topographically diverse mountainous area

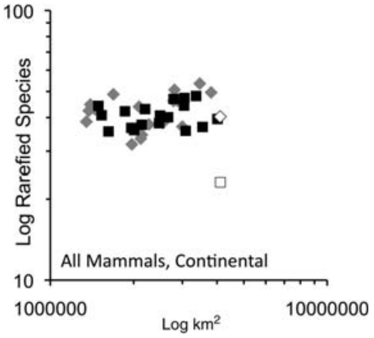

Fig. 2. Type IV palaeospecies-area relationship for all mammals at the continental scale. Squares = large mammals, black from pre-Holocene time intervals, white from Holocene. Diamonds = small mammals, grey from pre-Holocene time intervals, white from Holocene. Each point represents one time interval and encompasses all fossil localities known from that time interval.

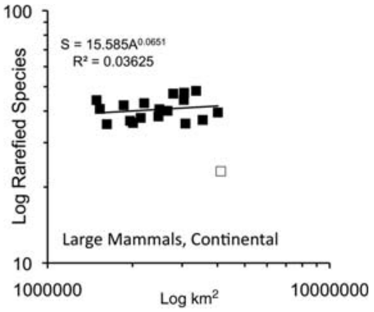

Fig. 3. Type IV palaeospecies-area relationship for large mammals at the continental scale. Black symbols are pre-Holocene time intervals, white symbol is Holocene. Each point represents one time interval and encompasses all fossil localities known from that time interval.

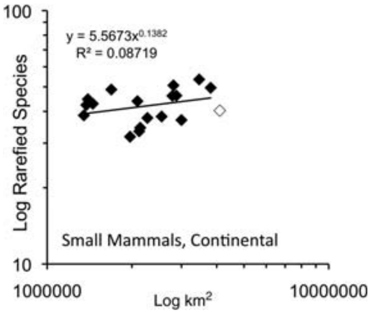

Fig. 4. Type IV palaeospecies-area relationship for small mammals at the continental scale. Black symbols are pre-Holocene time intervals, white symbol is Holocene. Each point represents one time interval and encompasses all fossil localities known from that time interval.

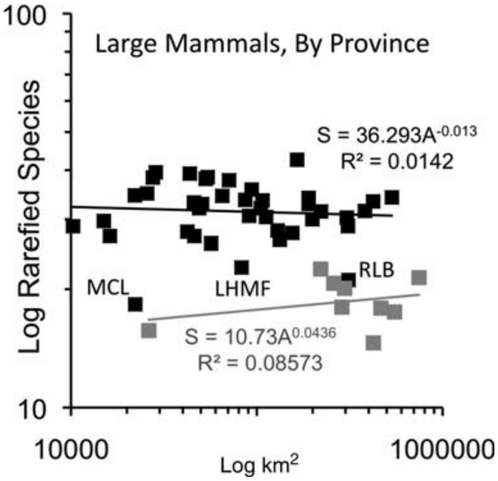

Fig. 5. Type IV palaeospecies-area relationship for large mammals per biogeographical province. Black symbols are pre-Holocene time intervals, grey symbols are Holocene. Each point represents one species richness value from a single time interval within a single biogeographical province. MCL, Middle Clarendonian from Central California; LHMF, Late Hemingfordian from the Northern Rocky Mountains; RLB, Rancholabraean from the Colorado Plateau.

with overall high species richness, and the other in an adjacent flat desert, with overall low species richness. In that case, a larger area in the desert may still sample fewer species than a smaller area in the mountains. For that reason the key information in unnested analyses that compare different provinces, as we do in some cases, is not the slope of the SAR, but whether the diversity values per area for a given time slice are higher or lower than for comparative time slices.

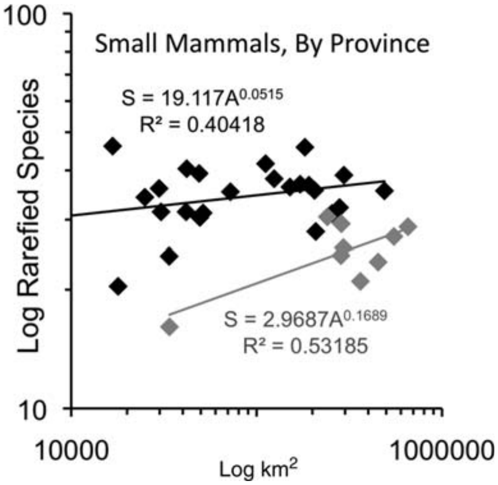

Fig. 6. Type IV palaeospecies-area relationship for small mammals per biogeographical province. Black symbols are pre-Holocene time intervals, grey symbols are Holocene. Each point represents one species richness value from a single time interval within a single biogeographical province.

For Type IV SARS within a biogeographical province, one would expect an increase of species with an increase of area, up until a large enough part of the province was sampled to include most species, at which point adding area no longer adds species and the curve flattens. Therefore, a series of samples all from areas that are larger than that critical value, even within a province, would be expected to produce a flat SAR, even if there was variation in sampling area.

We plotted separate PSARs for the Holocene data; these are the PSARs that characterize the time humans were abundant in our study area. We then compared the Holocene PSARs to corresponding ones for pre-Holocene (pre-anthropogenic) times. This separation of the data is justified by previous work (Carrasco *et al.* 2009), which through analysis of nested Type I and unnested Type IV PSARS demonstrated that PSARs for various pre-Holocene time intervals did not differ significantly from one another, but Holocene PSARs plotted significantly lower than pre-Holocene PSARs.

Results

The continental-scale analysis highlights that prior to the Holocene, PSARS for both small and large mammals were similar (Figs 2–4). However, while Holocene large mammals demonstrate a prominent diversity crash (Fig. 3) at this scale, the small mammals maintain diversity similar to that predicted from pre-Holocene PSARs (Fig. 4). This is consistent with previous knowledge about the LQE, long recognized to have caused extinctions primarily of the megafauna (Martin 1966; Martin & Wright 1967; Martin & Klein 1984; Barnosky *et al.* 2004, 2008; Koch & Barnosky 2006; Barnosky & Lindsey 2010).

The LQE worldwide took place largely between *c.* 50 000 and 8000 years ago and in our study area seems concentrated mostly between 13 500–11 000 years ago. During the LQE the USA lost *c.* 106 of *c.* 545 total species (*c.* 19%) estimated to have inhabited the continent prior to the extinction episode (Table 2). This estimation of total species is simply 106 extinct by the Pleistocene–Holocene transition (*c.* 11 000 years ago), plus 439 extant today (including Chiropterans), which are presumed also to have been on the continent during the late Pleistocene. However, the fossil sample excludes Chiropterans; extracting them from the extant sample as well results in an extinction percentage of *c.* 21% (Table 2).

Looking only at the large mammal subset of our data (that is, larger than rabbits) there are 100 species that went extinct during the LQE out of 217 total species (extinct plus extant). Thus, *c.* 46% of large mammal species suffered extinction during the LQE. The PSARs for the large mammal subset of the total data indicates that diversity dropped by 45% then (Table 3; this is the percentage difference between the species richness value expected from the pre-Holocene PSAR v. the observed Holocene value). These two different ways of calculating extinction intensity agree well, and indicate that essentially all of the diversity drop recognized from the large-mammal PSAR analysis can be accounted for by actual extinction of large mammals during the LQE.

However, the large-mammal PSARs constructed at the provincial level (Fig. 5) suggest loss by extinction did not evenly affect biogeographic provinces across the continent. Depending on the province, large mammal diversity is 27% to 52% (average 39%) lower than one would expect based on the pre-Holocene PSARs (Table 3). This is 6–31% more reduction, depending on province, than the loss predicted by extinction alone.

The pre-Holocene large-mammal PSAR at this scale exhibits flattening, probably for reasons elaborated in the Methods section. It is also notable that points for the MCL (see Fig. 5 for abbreviations) in Central California, the RLB in the Colorado Plateau, and to a lesser extent the LHMF in the Northern Rockies are more characteristic of the Holocene PSAR than the pre-Holocene PSAR. The LHMF previously was shown to have both a relatively small sampling area, and low overall diversity, in both the Northern Rockies and Great Plains (Barnosky *et al.* 2005). Also the boundary between the LHMF and the preceding Early Hemingfordian marks one of the most impressive faunal turnover events in the northern Rockies in the last 30 million years, including high extinction, immigration, and emigration (Barnosky 2001). It is unclear whether the LHMF decline in large mammal diversity is related to this faunal turnover event, or to the small sampling area. Sampling area cannot account for the low large-mammal diversity in the

Table 3. *Expected v. observed rarefied species richness values for large and small mammals per province and for the continent*

Province	Expected	Actual	% Decline
Small mammals			
CC	32.7	16.1	50.8
Colorado	36.6	25.5	30.3
CP	36.5	24.4	33.2
GB	36.5	29.3	19.8
GC	37.0	21.0	43.2
NGP	37.4	23.5	37.1
NR	38.1	28.8	24.4
SGB	36.2	30.5	15.7
SGP	37.8	27.2	28.0
Continental	45.7	40.3	11.8
Province average			31.4
Province regression	$S = 19.117A^{0.0515}$		
Continental regression	$S = 5.5673A^{0.1382}$		
Large mammals			
CC	31.8	15.7	50.6
Colorado	30.8	18.0	41.6
CP	30.8	20.1	34.8
GB	30.9	20.7	32.9
GC	30.7	14.6	52.4
NGP	30.6	17.9	41.6
NR	30.4	21.4	29.7
SGB	30.9	22.5	27.3
SGP	30.6	17.5	42.7
Continental	42.0	23.1	45.0
Province average			39.3
Province regression	$S = 36.293A^{-0.013}$		
Continental regression	$S = 15.585A^{0.0651}$		

MCL of Central California, because this time is characterized by one of the largest sampling areas, yet one of the lowest diversity values. Whether this anomalously low point indicates a real, biologically significant provincial diversity decline, or some sort of taphonomic bias, remains to be determined. While the RLB low point could indicate that large mammal diversity declined in the Colorado Plateau slightly earlier than the Holocene decline elsewhere, it is more likely due to an anomalous sampling situation, in which many localities consist of a single occurrence, generally of a large mammal such as *Bison* or *Mammuthus* (Carrasco *et al.* 2009).

Only six small mammal species went extinct during the LQE (1.1% of the small plus large species and 2.2% of the small species subset). The loss by extinction is so small that in the PSARs a diversity drop is barely apparent (and not statistically below expectations) at the continental scale (Figs 2 & 4), yet the diversity drop at the provincial level is dramatic, between 16% and 51% (average 31%), depending on province (Fig. 6, Table 3). This suggests that geographical range changes accompanying extinction episodes may dramatically reduce biodiversity provincially even in mammal groups that are little culled by extinction itself, as anticipated from\ previous studies (Graham 1976, 1985).

Discussion

Spurious results introduced by sampling problems are always an issue in using palaeontological data as we have. In our study, perhaps the largest red flag is that most of the pre-Holocene time intervals are so much longer than the Holocene one. If species were accumulating through evolutionary replacement in the time averaged by the samples, one might expect higher diversity in the longer time intervals. For reasons outlined in the methods, this does not seem to be the case for the composite large-mammal plus small-mammal sample (Carrasco *et al.* 2009). To further explore this possibility for the separated large- and small-mammal samples, we examined the correlation between temporal duration and diversity for the non-Holocene continental sample and for the provincial sample in each of the two body-size classes, using a power function (given the order-of-magnitude differences in lengths of time bins), for time intervals ranging from 4.3 million to 140 000 years. We found no significant correlation between diversity and bin length for either large or small mammals at the continental or provincial scale, with P-values of 0.12 and 0.28 for large mammals (continental and provincial scales, respectively) and 0.99 (continental) and 0.49 (provincial) for small mammals. Further verifying that temporal interval is not the best explanation for our results is the much more comprehensive sample and more highly resolved taxonomy for Holocene mammals; as noted in the Methods section, one would expect this to elevate Holocene diversity, so depressed Holocene diversity is a particularly robust result.

Given these considerations, it seems likely that geographical range shifts, especially contractions, explain most of the apparent diversity crash of small mammals at the provincial scale. In effect, the diversity loss becomes apparent at the provincial scale because even relatively small range shifts (relative to the continental scale) can retract a species distribution outside the province. This finding is consistent with other studies that have demonstrated dramatic geographical-range shifts of mammals at the Pleistocene–Holocene transition (Graham 1976; Graham & Grimm 1990; Graham 1997; Lyons 2003, 2005; Lyons *et al.* 2010), and Holocene diversity declines in small mammals at the local scale (Blois *et al.* 2010) and continental scale (FAUNMAP Working Group 1996). At the local scale, such declines have been related to abundance increases in 'weedy' species as ecologically restricted species move out of a given area (Blois *et al.* 2010), whereas at the continental scale, the explanations have revolved around decreasing environmental heterogeneity (Graham & Lundelius 1984; Guthrie 1984). It is also tempting to speculate a feedback between the removal of large mammals and the distributional patterns of small mammals, because large mammals act as ecosystem engineers to help maintain mosaic habitats in landscapes where they are abundant (Owen-Smith 1987).

Conclusions

Previous work (Carrasco *et al.* 2009) showed that observed Holocene mammalian diversity (e.g. the diversity baseline traditionally assumed to be the 'normal' one) in the USA is actually between 15% and 42% too low, depending on biogeographical province, with respect to diversity expected from PSARs. That study did not differentiate how much of the diversity decline was due to actual extinction, and how much resulted from reducing the average size of geographical ranges such that intra-provincial diversity fell even though species may have survived. Our results shed light on that distinction through separating the diversity reductions by body size and by looking at them on both a continental and provincial biogeographical scale.

Our analyses suggest that at extinction events such as those that took place during the LQE, diversity declines in two ways. There is loss by extinction itself, but there also is collateral diversity loss within biogeographical provinces as the surviving fauna rearrange their geographical ranges. For small mammals, that collateral diversity loss reduced modern mammalian diversity in every biogeographical province we analyzed to levels far below the pre-Holocene baseline, coincident with the late Pleistocene megafaunal extinctions, even though very few small mammals went extinct. The result is that contemporary mammal communities have between 16 and 51% fewer small-bodied species than was typical before the large-mammal extinction event (Table 3), as well as 6–31% fewer large-mammal species than can be accounted for by extinction alone.

Besides shedding light on how mammalian diversity reduced in the USA during the LQE, our data suggest that similar collateral biodiversity loss should probably be anticipated as a by-product of future mammal extinctions – a very real possibility inasmuch as 8% of USA species and 22% of species worldwide are currently regarded as threatened. Should these species actually be lost, the diversity decline at the scale of biogeographical provinces might well be much more than the percentage of species-reduction caused by the extinctions themselves, if the LQE is any guide. The fact that future extinctions will take place on a landscape much more fragmented by human modifications than was the case at the LQE would probably exacerbate collateral losses on local and regional scales. We qualify our conclusions by noting they are based on a single large clade, mammals, from a single large geographical region, the lower 48 states of the USA. It will be of interest to learn whether these inferences from our data agree with future studies on other taxa from other regions.

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