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The impact of taxonomic bias when comparing past and present species diversity

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ABSTRACT

It is becoming increasingly important to understand how present diversity patterns compare with past ones, in order to understand the extent of change that present faunas exhibit with respect to past baselines for such parameters as extinction rate and magnitude, ecological structure, and ecosystem function. However, these comparisons have been difficult to quantify because the modern and paleontological records are inherently different. This study examines how those differences affect comparisons of fossil and modern mammalian species diversity in the United States and suggests how the data can be treated to minimize their biases. I first compare extant mammalian species diversity to a paleo-baseline constructed from fossils covering the past 30 million years. Species–area relationships show that, contrary to expectations, today's mammalian diversity appears to have increased since the Holocene (11,500 to–500 years ago). This bump in diversity is the result of an increase in small mammal species in the modern dataset, in particular those that are the most difficult to identify and diagnose in the fossil record (e.g., Geomyidae and Heteromyidae). This increase results from neontological classifications of small mammal species that employ methodologies and characters (notably soft-tissue and molecular information) that cannot be used with fossils. One way to correct for these differences would be to reevaluate neontological species using the same morphological characters and species concept commonly used by paleontologists.

1. Introduction

Comparisons of modern and fossil data are becoming essential to understand the extent of human impacts on the biota (Hadly and Barnosky, 2009; Koch et al., 2009; Dietl and Flessa, 2011). However, adequate comparisons are difficult because modern and fossil data are so different (Barnosky et al., 2011a). The fossil record is an incomplete record of past species because of a rock record that varies in completeness through time and the highly variable preservation potential of different organisms based on the environment they live in (Peters and Heim, 2011). In addition, species are usually diagnosed using strictly morphological criteria, particularly of teeth. On the other hand, modern zoological data have different sampling biases, and species are more commonly diagnosed using a phylogenetic species concept that uses different character sets (e.g., molecular, soft part) (Barnosky et al., 2011a).

In order to judge current deviations from long-term ecological baselines, including the extent of diversity loss via extinction and biogeographic range changes (Barnosky et al., 2011b), and predict what to expect in the future, it is necessary to correct these differing biases as much as possible. North American mammals provide a unique opportunity to do this because they have a relatively robust and stable taxonomy, are well-sampled relative to other taxonomic groups, are cataloged in numerous large paleontological databases, and, among fossil taxa, are associated with good stratigraphic, chronologic, and geographic data (F.A.U.N.M.A.P. Working Group, 1994; Carrasco et al., 2005; Paleobiology Database, 2011). These characteristics help reduce the differences among time periods and datasets and, more importantly, can be adjusted for temporal and geographic inconsistencies using various methodologies.

Past work using species–area relationships has established that there was a diversity crash of mammals in central North America (i.e., the USA) in the Holocene with respect to earlier Cenozoic patterns, resulting in a “new normal” for local, regional, and continental biodiversity beginning in the Holocene (Carrasco et al., 2009; Barnosky et al., 2011b). However, it has not yet been possible to compare the Holocene fossil record with diversity patterns of the last century or so because of the disparity between the paleontological data used in previous studies and the modern data that are available. Therefore, this study applies the same species–area technique to the modern data, and then examines the results to identify where sampling biases are overriding the biological signal and discusses possible ways to overcome the biases.

2. Materials and methods

2.1. Data sources

Paleospecies occurrence data were extracted from NEOMAP (the Neogene Mammal Mapping Portal), a distributed database system

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that links three paleomammal databases: MIOMAP (Carrasco et al., 2005, 2007), FAUNMAP I (FAUNMAP Working Group, 1994), and FAUNMAP II (Graham and Lundelius, 2010). NEOMAP is housed at the University of California, Berkeley and can be accessed at http://www.ucmp.berkeley.edu/neomap/. The data for contemporary extant mammals was acquired from Arctos, a multi-institution, multi-collection museum database available online at http://arctos.database.museum/SpecimenSearch.cfm. This data acquisition was restricted (for reasons see Section 2.5) to the mammal collections from the Museum of Vertebrate Zoology at the University of California, Berkeley.

2.2. Mammal subgroups

The dataset was analyzed using three different groups: all mammals, large mammals, and small mammals. Small mammals included all taxa of the Rodentia, Insectivora (=Soricomorpha of Wilson and Reeder (2005)), and Lagomorpha following the reasoning of Liow et al. (2008) and Barnosky et al. (2011b). Essentially, these orders include those taxa that weigh less than approximately 2 kg. The large mammal group included all other non-volant terrestrial mammals. The modern dataset was further refined by removing taxa that were introduced by humans into the United States (e.g., horses, cows, domesticated ferrets). In addition, the extant taxonomy was verified and, when needed, modified to reflect the taxonomy of Wilson and Reeder (2005). For a complete list of the taxa analyzed in the Holocene and Modern time intervals, see Supplementary Table 1 (large mammals) and Supplementary Table 2 (small mammals).

2.3. Temporal bins

Occurrence data were placed into one of twenty different time intervals (Table 1) ranging in age from 30 million years ago through the Modern. Pre-Blancan (before 4.7 Ma) time periods were based on the subdivisions of the North American Land Mammal Ages (NALMAs) outlined by Tedford et al. (2004). Post-Blancan time intervals included the NALMAs used by the FAUNMAP Working Group (1994) as well as Holocene and Modern time intervals. Alternative binning methodologies have been employed (e.g., Alroy, 1998, 1999, 2003) that separate fossil occurrences into one million year intervals. However, these methods were not appropriate for this study because there would not have been enough data in many of the time slices to perform the analyses at the scale of single biogeographic provinces. As such, the temporal bins used are unequal in length, but, as discussed by previous authors (Barnosky et al., 2005; Carrasco et al., 2009; Barnosky et al., 2011b), it is unlikely that these differences would have significantly affected species diversity counts because no significant correlation exists between bin length and either number of localities or number of species, and the localities in each bin do not span the entire time represented by it.

Table 1
Temporal bins into which species occurrences were sorted. All values are given in years or millions of years (Ma).

Temporal division	Age boundaries	Interval length
Modern	~500–0	500
Holocene	11,500–~500	~11,000
Rancholabrean	0.15 Ma–11,500	~139,000
Irvingtonian	1.8–0.15 Ma	1.65 Ma
Blancan	4.7–1.8 Ma	2.7 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

2.4. Biogeographic provinces

The occurrence data were assessed across ten different biogeographic provinces (Fig. 1). These regions are considered biogeographically distinct from one another today (Hagmeier and Stults, 1964; Hagmeier, 1966), and it is likely that similar provinciality existed through the Oligocene (Storer, 1989; Janis et al., 1998; Barnosky and Carrasco, 2002; Tedford et al., 2004). This is particularly true in those provinces that have the most complete fossil record (e.g., Northern Great Plains, Southern Great Plains, and Gulf Coast) as they are also those that have undergone limited topographic change over the past 30 million years (Prothero, 1998; Condon, 2005).

2.5. Sampling biases

Fossil data are plagued by many well-documented sampling biases including an incomplete fossil record, varying preservation potential, and non-random collection methods. To account for these biases, species richness values per time slice and per biogeographic province were computed by rarefying the data using a richness value of 75 taxon occurrences (whether a taxon was present or absent at a given locality). The number of species per geographic area was calculated using minimum counts (Barnosky et al., 2005), where all specimens that were identified to only genus or a higher taxon were allocated to a species represented by more diagnostic material. This minimum count method reduces the potential of artificially inflating the number of species (i.e., double-counting by treating one species as two or more).

Because the paleo-time slices are similar subsets of the total fauna present at any particular time (i.e., they all have similar biases), rarefaction should account for the variability between very well-sampled temporal bins and those that are more poorly sampled (see Carrasco et al., 2009 for a more complete evaluation). However, neontological data does not suffer from the same rock record or preservational biases and is collected using different methods than those used by paleontologists. Because the intent of this study was to create a comparative modern dataset that most closely resembled the paleontological data, the modern dataset was culled only from the Museum of Vertebrate Zoology at the University of California, Berkeley even though a more accurate representation of abundance and diversity levels could have been acquired by combining data from many zoology museum collections. By doing this, some provinces (e.g., Central California) are very-well-sampled while others (e.g., Northern Great Plains) are poorly sampled just as we see in the fossil record. Nevertheless, because provincial sample sizes still varied greatly between the modern and fossil datasets, no attempt was made to compare diversity within a single province through time, but rather assess it across all provinces.

2.6. Geographic area bias

Geographic area biases were addressed by plotting the resulting rarefied diversities against geographic area to determine species–area relationships (SARs). SARs have been shown to be effective in evaluating paleodiversity (Barnosky et al., 2005; Carrasco et al., 2009; Barnosky et al., 2011b) because they allow paleontologists to compare diversity from areas of varying sizes from a single time period or across several time intervals. The relationships are generally

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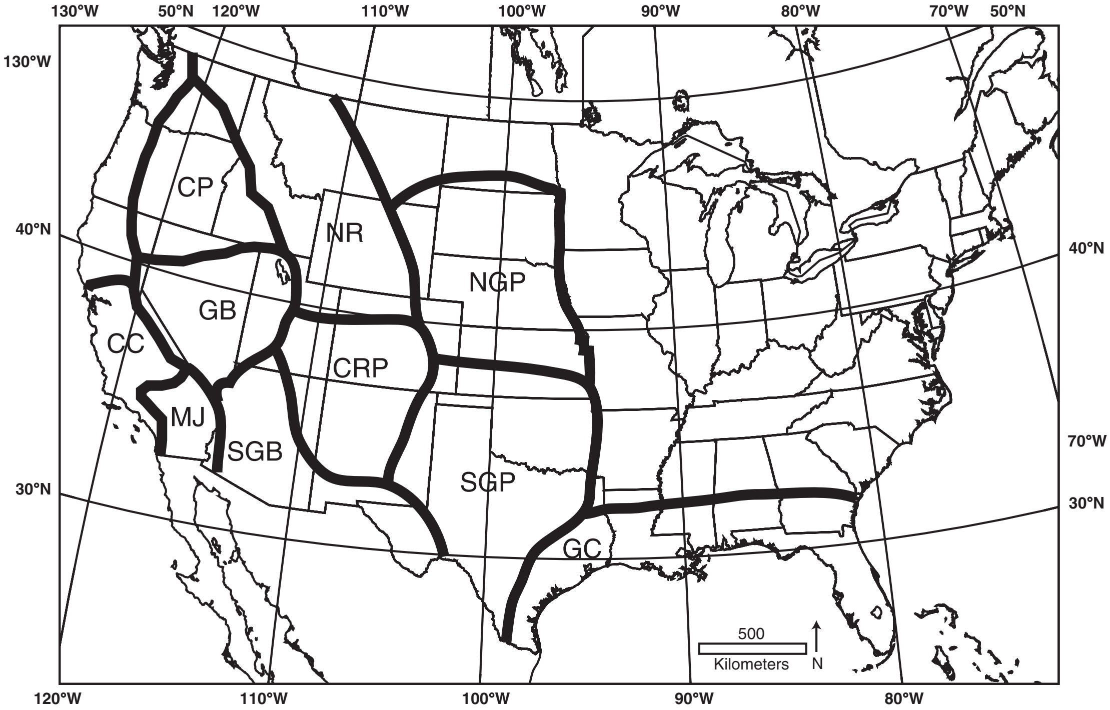

Fig. 1. Boundaries of the ten biogeographic provinces used. CC, Central California; MJ, Mojave; CP, Columbia Plateau; GB, Great Basin; SGB, Southern Great Basin; NR, Northern Rockies; CRP, Colorado Plateau; NGP, Northern Great Plains; SGP, Southern Great Plains; and GC, Gulf Coast.

expressed as $S = cA^z$, where S = the number of species, A = the area sampled, and z (the slope) and c are empirically derived constants. The geographic areas were calculated by querying the Berkeley Mapper mapping interface (http://berkeleymapper.berkeley.edu), tracing the minimum convex polygon of the relevant localities, and calculating the area enclosed by the polygon. The SARs were evaluated by constructing Type IV unnested species–area curves (Scheiner, 2003). In these curves, each point is simply the number of rarefied species in a given geographic area. This contrasts with nested Type I curves, which are species accumulation curves. As such, each point in a Type IV curve represents a distinct area (and/or time interval) with its own set of localities and species. Therefore, the slope of these curves does not necessarily need to be positive since points from depauperate, but large provinces (e.g., a big desert) will have lower diversity than a much smaller, but speciose province (e.g., rain forest). As such, the slopes of Type IV SARs are difficult to interpret and do not represent changes in beta diversity (differences between provinces) in a straightforward manner (Barnosky et al., 2011b). Therefore, the focus of the SARs presented here will be on the overall relative patterns of diversity.

2.7. Rarefaction methods

Rarefaction of the minimum species counts was done using S. Holland's Analytic Rarefaction v.1.3 software (2003, http://strata.uga.edu/software/). The data were rarefied by occurrences instead of the number of individual specimens to remove the effect of "high-graded" localities, those published localities that are based on only the best specimens in a museum's collection instead of all the specimens collected (Davis and Pyenson, 2003; Barnosky et al., 2005). The rarefaction occurrence value was set at 75 for all analyses (all mammals, large mammals, and small mammals) because that occurrence value provided the largest number of data points while at the same time eliminating points that were based on more suspect data (Barnosky et al., 2005).

3. Results

3.1. Total mammal analyses

When all mammals were plotted together for each temporal bin across all biogeographic provinces combined (Fig. 2), the Holocene showed significantly reduced species diversity relative to the baseline (30 Ma to 11,500 years ago), concordant with previous work (Carrasco et al., 2009). Another way to assess this drop in diversity is to compare the actual diversity level for a time period to the expected diversity based on a baseline SAR's equation (Carrasco et al., 2009; Barnosky et al., 2011b). Using the equation shown in Fig. 2, this decline in Holocene diversity is estimated to be about 19.5% relative to the expected

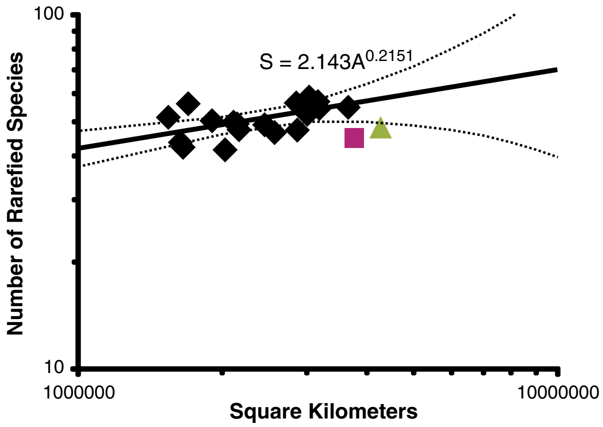

Fig. 2. Number of rarefied species plotted versus total geographic area for each temporal bin. Each data point represents the cumulative data from a single time interval (see Table 1 for the time bins) for all ten biogeographic provinces combined. The black diamonds represent each of the time slices from 30 Ma to 10,000 years ago, the pink square the Holocene time slice, and the green triangle the Modern time interval. The black line is the best fit line for the black diamonds, and the dashed lines represent its 95% confidence intervals. In the equation, S = Species and A = Area.

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diversity. However, diversity appears to have stayed relatively flat or even slightly increased (only a 15.9% reduction relative to the baseline) from the Holocene to the Modern.

3.2. Large/small mammal analyses

Evaluating the data by individual time slices across all ten biogeographic provinces combined, large mammal diversity appears to have decreased markedly (a 45% drop relative to the expected diversity) in the Holocene (Fig. 3A), as anticipated given the end-Pleistocene megafaunal extinction (Barnosky et al., 2004; Koch and Barnosky, 2006; Carrasco et al., 2009). Diversity is comparable or slightly reduced (a 49% decline) in the Modern temporal bin relative to the Holocene. However, a different picture emerges when one views the small mammal results (Fig. 3B). Both Holocene and Modern diversity fall well within the 95% confidence intervals of the baseline. Holocene diversity is reduced 11.7% relative to the baseline while diversity during the Modern temporal bin shows a slight increase relative to the Holocene (only a 2.4% drop relative to the expected diversity). These results suggest that small mammal diversity over large geographic regions (all ten biogeographic provinces combined) has changed little over the past 30 Ma in North America, and may have actually increased recently.

More differences emerge when one plots the large and small mammal data by individual province and time period (e.g., the late Barstovian of the Northern Great Plains). The number of large mammal rarefied species significantly declines in the Holocene and continues to decline in the Modern temporal bin (Fig. 4A). This again agrees with previous work that has documented a large megafaunal extinction at the end of the Pleistocene (Barnosky et al., 2004; Koch and Barnosky, 2006; Carrasco et al., 2009) — a trend that appears to have continued into the Modern. However, small mammal diversity reveals a drastically different view (Fig. 4B). First, at this provincial level, it appears that small mammal diversity significantly decreased during the Holocene contrary to the results found across all provinces combined. This result can best be explained if beta diversity (differences between provinces) increased in the Holocene, likely the result of range contractions and/or shifts, which has been documented in previous studies (Carrasco et al., 2009; Hadly et al., 2009; Blois et al., 2010; Barnosky et al., 2011b). It is possible that additional factors may be affecting this decline in Holocene diversity, such as sampling biases unique to the Holocene. However, as discussed in the Materials and Methods, all paleo-time slices appear to have similar collecting and sampling biases, and evaluation of rarefied species diversity and SARs should minimize any sampling differences among them. In addition, if sampling biases were the driving force, similar patterns should be seen in Figs. 3B and 4B, but the opposite situation occurs. Second,

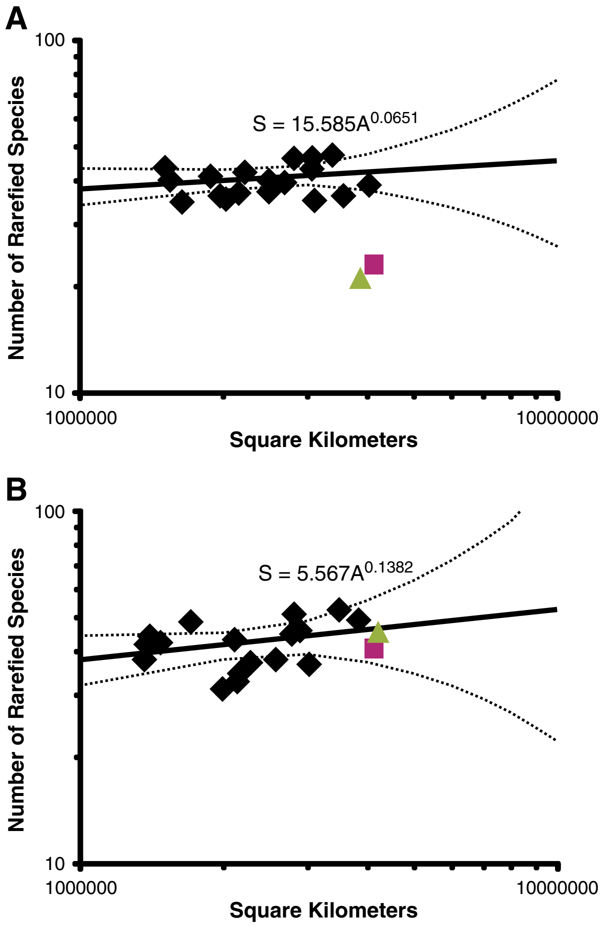

Fig. 3. Number of rarefied species plotted versus total geographic area for each temporal bin for large (A) and small (B) mammals. As in Fig. 2, each data point represents the cumulative data from a single time interval (see Table 1 for the time bins) for all ten biogeographic provinces combined. The black diamonds represent each of the time slices from 30 Ma to 10,000 years ago, the pink squares the Holocene time slice, and the green triangles the Modern time interval. The black lines are the best fit lines for each set of black diamonds, and the dashed lines are the 95% confidence intervals of these lines. In the equations, S = Species and A = Area.

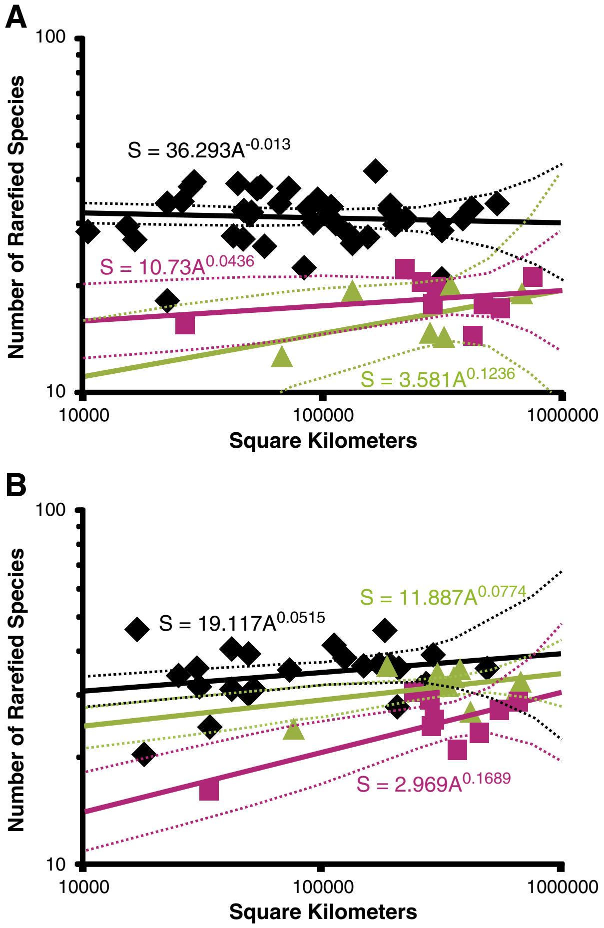

Fig. 4. Number of rarefied species plotted versus total geographic area for large (A) and small (B) mammals. Each data point represents the data from a single biogeographic province (e.g., Gulf Coast) for a single temporal bin (e.g., early Barstovian). The black diamonds represent individual provinces for each of the time slices from 30 Ma to 10,000 years ago, the pink squares the provinces from the Holocene time slice, and the green triangles the provinces from the Modern time interval. The black lines are the best fit lines for each set of black diamonds, the pink lines the best fit lines for each set of pink squares, and the green lines the best fit lines for each set of green triangles. The dashed lines (black, green, and pink) represent the 95% confidence intervals for each of the best fit lines. In the equations, S = Species and A = Area.

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diversity unexpectedly appears to have increased during the Modern time slice relative to the Holocene, although it remains depressed relative to the 30 Ma baseline. This difference between the Holocene and Modern time intervals appears robust given little overlap (except at large areas) of the 95% confidence intervals of the two respective trend lines.

4. Discussion

While most of the analyses are consistent with the conclusions of previous workers, the apparent increase in small mammal diversity in the Modern time slice relative to the Holocene is unexpected (Fig. 4B). It is this small mammal diversity increase that also mainly explains the overall slight increase in total mammalian diversity seen in Fig. 2. This apparent increase in small mammal species in the Modern temporal bin may stem from one of several possibilities. First, the bump in diversity may represent a real increase in small mammal diversity at the provincial level. However, previous work suggests that current rates of mammalian extinction are higher than those seen in the past and are expected to rise in the future (Pimm et al., 1995; Pereira et al., 2010; Barnosky et al., 2011a; IUCN, 2011). Currently, 25% of mammal species are considered threatened (IUCN, 2011), a number that has only increased over the past fifteen years (Hoffmann et al., 2010; IUCN, 2011). In addition, a real increase in small mammal diversity seems unlikely given the extent of habitat destruction (Ellis, 2011; Foley et al., 2011) and documented reduction of many species' ranges in the past century (Ceballos and Ehrlich, 2002).

A second possibility is that the increase is the result of better sampling in the Modern temporal bin relative to the Holocene time period. This also seems unlikely to be the dominant signal for two reasons. First, while some regions (e.g., Central California) are better sampled in the Modern temporal bin, several others are more poorly sampled (e.g., Northern Great Plains) (Table 2)—the result of building the Modern dataset from only the Museum of Vertebrate Zoology collections. Nevertheless, in every biogeographic province, diversity is greater in the Modern than in the Holocene. Second, correlation analyses reveal no significant relationship between the number of rarefied species and the number of occurrences of small mammals in the Modern ($r = 0.490$; $p = 0.151$) or across all temporal bins ($r = 0.110$; $p = 0.467$) by province.

A third explanation is that extant species numbers are inflated due to a taxonomic artifact. Living species are diagnosed using different criteria than those used to diagnose paleospecies. Paleontologists generally employ a morphological species concept when diagnosing taxa because of their reliance on hard parts, primarily teeth. On the other hand, extant species are commonly diagnosed using a biological or phylogenetic species concept and rely more on soft part and/or genetic data. The ability to use soft-tissue and molecular data can lead to recognizing more species within a given genus for extant taxa (Purvis et al., 2000; Agapow et al., 2004; Barnosky et al., 2011a). If modern diversity is inflated because of different classification criteria, we would expect to see this inflation among 1) the most speciose families and genera, 2) groups that have small ranges with many areas of sympatric congeners, and 3) families that have the most conservative dental morphology and which are correspondingly difficult to diagnose in the fossil record. In addition, the "new" species in the Modern temporal bin should predominantly be those that have been diagnosed today using non-morphological criteria.

All of the above features are found more commonly in small mammals as opposed to large mammals, consistent with observing relatively higher species numbers only among smaller taxa. Comparisons between the small mammals found in the Holocene and those in the Modern temporal bin reveal which families have the largest increases (Table 3). Among those families with more than 10 species, the highest percentages are found in the Sciuridae (35.7%), Geomyidae (46.2%), and Heteromyidae (47.2%) (see Supplementary Table 2 for a complete list of taxa). In addition, among these three families the most speciose genus in each (*Tamias*, *Thomomys*, and *Dipodomys*) is the taxon with the largest discrepancy between the Modern and Holocene temporal bins.

In the genus *Tamias*, the chipmunk, 12 of 18 species are known only from the Modern. As predicted, the generic designation of this taxon continues to be problematic (Piaggio and Spicer, 2000, 2001; Wilson and Reeder, 2005), and specific designations have been hampered by a lack of diagnostic external or more traditional morphological characters forcing neontologists to rely on bacular, karyotypic, immunological, and molecular features (e.g., Callahan, 1975; Levenson and Hoffmann, 1984; Patterson, 1984; Levenson et al., 1985; Piaggio and Spicer, 2000, 2001). In addition, the majority of the species of *Tamias* found only in the Modern temporal bin live in sympatry or parapatry with up to eight other species of the genus (Best, 1993a, b; Best and Granai, 1994; Best et al., 1994a, b; Clawson et al., 1994). Lastly, fossil sciurids have often presented problems for diagnoses given their simple conservative dentition (Black, 1963; Korth, 1994; Thorington et al., 2005).

Species designations within *Thomomys* and *Geomys*, members of the Geomyidae, also rely heavily on non-morphological characters (Patton and Smith, 1989, 1994; Jolley et al., 2000; Wilson and Reeder, 2005). Of the six species of geomyids found only in the modern sample, four (*Geomys arenarius*, *Thomomys clusius*, *T. idahoensis*, and *T. mazama*) were formerly considered subspecies of other species of geomyids in Hall (1981) until additional diagnostic molecular characters were discovered (Wilson and Reeder, 2005), while *Geomys personatus* had been suggested to be conspecific with *G. pinetis* (Martin, 1974a, b) until it was shown to be karyologically distinct by Williams and Genoways (1975). In the Geomyidae, paleontologists have commonly relied on size differences because of a general lack of diagnostic dental features (Rensberger, 1971, 1973; Korth, 2008).

Table 2
Comparison of small mammal samples and rarefied species diversity (based on 75 occurrences) in the Holocene and Modern temporal bins by biogeographic province. For province abbreviations, see Fig. 1.

	Holocene		Modern	
Province	Occurrences	Rarefied species	Occurrences	Rarefied species
CC	125	16.1	9763	36.5
CP	1014	25.5	735	34.7
CRP	307	24.4	2472	33.7
GB	513	29.3	3857	33.6
GC	329	21	128	27
MJ	52	N/A	1497	24.1
NGP	447	23.5	87	31.8
NR	737	28.8	1049	32.6
SGB	284	30.5	1434	35.6
SGP	556	27.2	182	29.6

Table 3
The number of new species of small mammals (listed by family) found in the Modern time slice relative to the Holocene time slice.

Family	Number of new species	Total modern species	Percentage of new species (%)
Soricidae	5	18	27.8
Talpidae	2	4	50.0
Leporidae	2	12	16.7
Ochotonidae	0	1	0
Aplodontidae	1	1	100
Castoridae	0	1	0
Dipodidae	1	3	33.3
Erethizontidae	0	1	0
Geomyidae	6	13	46.2
Heteromyidae	17	36	47.2
Muridae	14	57	24.6
Sciuridae	20	56	35.7

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The Heteromyidae are perhaps the best example of a group whose fossil record is composed almost entirely of isolated teeth that lack qualitative characters with which to diagnose species (Wahlert, 1993; Carrasco, 2000a). Therefore, quantitative characters tend to be used to diagnose taxa (e.g., Lindsay, 1972; Martin, 1984; Barnosky, 1986; Carrasco, 1998). Because of this, extant heteromyids have been diagnosed based on non-dental characters including cranial, bacular, karyotypic, and genic features (e.g., Stock, 1974; Williams, 1978; Hafner et al., 1979; Best et al., 1986; Best, 1993c; Williams et al., 1993). In addition, heteromyids are noted for their high degree of sympatry and/or parapatry within genera (Schmidly et al., 1993).

Of particular note is the genus *Dipodomys*, the kangaroo rat, which has a dental morphology that lacks almost any cusp morphology (Fig. 5) and is subject to large amounts of geographic and age variation (Carrasco, 2000b). Eight of the fifteen species found in the MVZ collections are not found in the Holocene record. Of those fifteen species, the same eight taxa (*Dipodomys agilis*, *D. californicus*, *D. compactus*, *D. ingens*, *D. nitratoides*, *D. panamintinus*, *D. stephensi*, and *D. venustus*) were those most frequently misdiagnosed based on dental measurements in a previous study (Carrasco, 2000b) - an expected result if extant species are not equivalent to those found in the fossil record. In addition, the majority of these eight taxa have generally been considered to be subspecies of other species of the genus at some period in their taxonomic history (Williams et al., 1993; Wilson and Reeder, 2005).

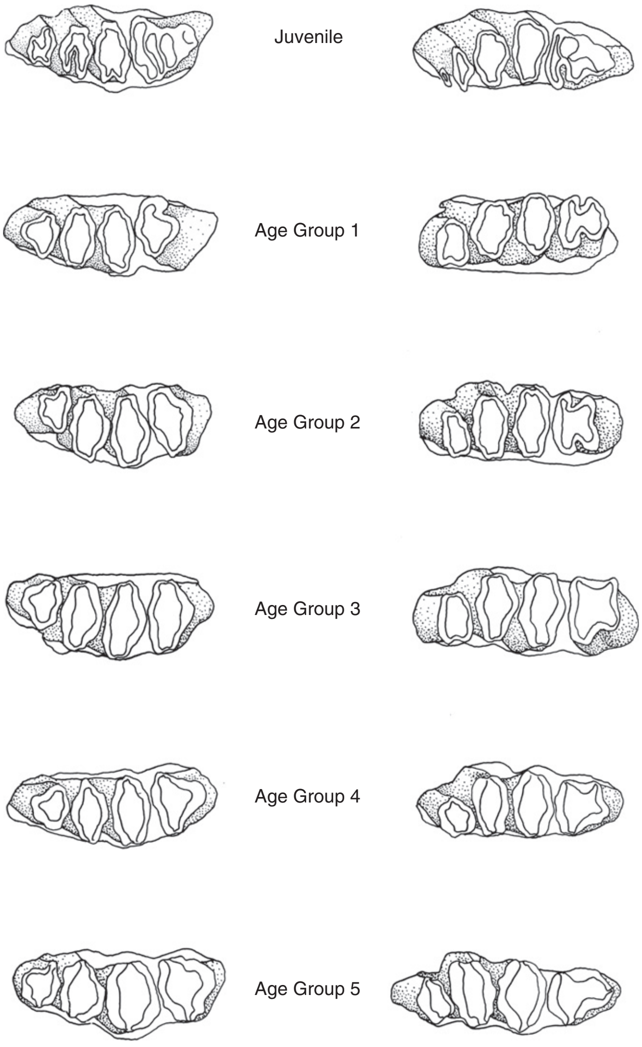

Fig. 5. Occlusal views of the left dentition of six age groups (Juvenile through Age Group 5) of kangaroo rats (genus *Dipodomys*). The left column contains upper dentitions while the right column shows lower dentitions. Note the limited cusp morphology of the teeth throughout the life of the organism.

5. Conclusions and recommendations

Species–area relationships found in the Holocene and Modern temporal bins are lower than the baseline diversity found during the previous 30 million years. While most of this decline is found among large mammals, it also appears that at a provincial level, but not at larger scales, small mammal diversity declined, confirming the results of previous workers (Blois et al, 2010; Barnosky et al., 2011b). However, small mammals in the Modern temporal bin unexpectedly show an increase in diversity relative to the Holocene, particularly at the provincial level, despite recent studies that suggest diversity loss is likely to have been increasing over the past few centuries (Hoffmann et al., 2010; Pereira et al., 2010; Barnosky et al., 2011a; IUCN, 2011). The most probable explanation for the apparent elevation of Modern diversity with respect to the Holocene levels stems from the different classification methods used by paleontologists, who rely on morphological criteria, and neontologists, who often rely on soft part and molecular characters for species diagnoses. As predicted, inspection of the taxa with the greatest increase in small mammal diversity (sciurids, geomyids, and heteromyids) are those that are among the most difficult to diagnose using only traditional morphological criteria, particularly of the dentition.

Based on these results, the next step in comparing modern diversity to long-term baselines needs to be the equilibration of fossil and modern taxonomic classifications among small mammals. One possible solution is to reevaluate fossil species using additional techniques. Paleontologists have tended to rely on simple length and width measurements for taxonomic diagnoses of small mammal taxa (e.g., Rensberger, 1971; Martin, 1984; Barnosky, 1986), but multivariate analyses of dental characters have been shown to have higher discriminatory power (Carrasco, 2000a; McGuire, 2010). While this may uncover some formerly cryptic species, a more promising approach would be to carefully collapse modern taxa into groupings that would mimic fossil taxa by using a morphological species concept and employing only paleontological characters, primarily of the dentition. In the end, such revised taxonomies would provide a feasible way to more accurately gauge whether current mammalian species diversity, extinction, and biogeographic range adjustments deviate significantly from the long-term patterns that have characterized most of the Holocene and earlier paleo-time intervals.

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References

Agapow, P.-M., Bininda-Emonds, O.R.P., Crandall, K.A., Gittleman, J.L., Mace, G.M., Marshall, J.C., Purvis, A., 2004. The impact of species concept on biodiversity studies. The Quarterly Review of Biology 792, 161–179.

Alroy, J., 1998. Equilibrial diversity dynamics in North American mammals. In: McKinney, M.L., Drake, J.A. (Eds.), Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities. Columbia University Press, New York, pp. 232–287.

Alroy, J., 1999. The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. Systematic Biology 48, 107–118.

Alroy, J., 2003. Taxonomic inflation and body mass distributions in North American fossil mammals. Journal of Mammalogy 84, 431–443.

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Barnosky, A.D., 1986. New species of the Miocene rodent Cupidinimus (Heteromyidae) and some evolutionary relationships within the genus. Journal of Vertebrate Paleontology 6, 46–64.

Barnosky, A.D., Carrasco, M.A., 2002. Effects of Oligo-Miocene global climate changes on mammalian species richness in the northwestern quarter of the USA. Evolutionary Ecology Research 4, 811–841.

Barnosky, A.D., Koch, P.L., Feranec, R.S., Wing, S.L., Shabel, A.B., 2004. Assessing the causes of late Pleistocene extinctions on the continents. Science 306, 70–75.

Barnosky, A.D., Carrasco, M.A., Davis, E.B., 2005. The impact of the species–area relationship on estimates of paleodiversity. PLoS Biology 3, 1356–1361.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B., Ferrer, E.A., 2011a. Has the Earth's sixth mass extinction already arrived? Nature 471, 51–57.

Barnosky, A.D., Carrasco, M.A., Graham, R.W., 2011b. Collateral mammal diversity loss associated with late Quaternary megafaunal extinctions and implications for the future. In: McGowan, A.J., Smith, A.B. (Eds.), Comparing the Geological and Fossil Records: Implications for Biodiversity Studies: The Geological Society of London, Special Publication, London, pp. 179–189.

Best, T.L., 1993a. *Tamias ruficaudus*. Mammalian Species 452, 1–7.

Best, T.L., 1993b. *Tamias sonomae*. Mammalian Species 444, 1–5.

Best, T.L., 1993c. Patterns of morphologic and morphometric variation in heteromyid rodents. In: Genoways, H.H., Brown, J.H. (Eds.), Biology of the Heteromyidae: American Society of Mammalogists, Special Publication, pp. 197–235.

Best, T.L., Granai, N.J., 1994. *Tamias merriami*. Mammalian Species 476, 1–9.

Best, T.L., Sullivan, R.M., Cook, J.A., Yates, T.L., 1986. Chromosomal, genic, and morphologic variation in the agile kangaroo rat, *Dipodomys agilis* (Rodentia: Heteromyidae). Systematic Zoology 35, 311–324.

Best, T.L., Clawson, R.G., Clawson, J.A., 1994a. *Tamias panamintinus*. Mammalian Species 468, 1–7.

Best, T.L., Clawson, R.G., Clawson, J.A., 1994b. *Tamias speciosus*. Mammalian Species 478, 1–9.

Black, C.C., 1963. A review of the North American Tertiary Sciuridae. Bulletin of the Museum of Comparative Zoology 130, 109–248.

Blois, J.L., McGuire, J.L., Hadly, E.A., 2010. Small mammal diversity loss in response to late-Pleistocene climatic change. Nature 465, 771–774.

Callahan, J.R., 1975. Status of the Peninsula chipmunk. Journal of Mammalogy 56, 266–269.

Carrasco, M.A., 1998. Variation and its implications in a population of *Cupidinimus* (Heteromyidae) from Hepburn's Mesa, Montana. Journal of Vertebrate Paleontology 18, 391–402.

Carrasco, M.A., 2000a. Species discrimination and morphological relationships of kangaroo rats (*Dipodomys*) based on their dentition. Journal of Mammalogy 81, 107–122.

Carrasco, M.A., 2000b. Variation in the dentition of kangaroo rats (genus *Dipodomys*) and its implications for the fossil record. The Southwestern Naturalist 45, 490–507.

Carrasco, M.A., Kraatz, B.P., Davis, E.B., Barnosky, A.D., 2005. Miocene Mammal Mapping Project (MIOMAP). University of California Museum of Paleontology, http://www.ucmp.berkeley.edu/miomap.

Carrasco, M.A., Barnosky, A.D., Kraatz, B.P., Davis, E.B., 2007. The Miocene Mammal Mapping Project (MIOMAP): an online database of Arikareean through Hemphillian fossil mammals. Bulletin of the Carnegie Museum of Natural History 39, 183–188.

Carrasco, M.A., Barnosky, A.D., Graham, R.W., 2009. Quantifying the extent of North American mammal extinction relative to the pre-anthropogenic baseline. PLoS One 4, e8331, http://dx.doi.org/10.1371/journal.pone.0008331.

Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. Science 296, 904–907.

Clawson, R.G., Clawson, J.A., Best, T.L., 1994. *Tamias alpinus*. Mammalian Species 461, 1–6.

Condon, S.M., 2005. Geological studies of the Platte River, south-central Nebraska and adjacent areas—geologic maps, subsurface study, and geologic history. Geological Survey Professional Paper 1706, 1–63.

Davis, E.B., Pyenson, N.D., 2003. Assessing mammalian paleofaunal diversity: discrepancies between published and museum collection data for the Miocene of northwestern Nevada, USA. Geological Society of America 35, 498 (Abstracts with Programs).

Dietl, G.P., Flessa, K.W., 2011. Conservation paleobiology: putting the dead to work. Trends in Ecology & Evolution 26, 30–37.

Ellis, E.C., 2011. Anthropogenic transformation of the terrestrial biosphere. Philosophical Transactions of the Royal Society A 369, 1010–1035.

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., Tilman, D., Zaks, D.P.M., 2011. Solutions for a cultivated planet. Nature 478, 337–342.

Graham, R.W., Lundelius Jr., E.L., 2010. FAUNMAP II: new data for North America with a temporal extension for the Blancan. Irvingtonian and early Rancholabrean. FAUNMAP II Database, version 1.0 , http://www.ucmp.berkeley.edu/faunmap/index.html.

Hadly, E.A., Barnosky, A.D., 2009. Vertebrate fossils and the future of conservation biology. In: Dietl, G.P., Flessa, K.W. (Eds.), Conservation Paleobiology: Using the Past to Manage the Future. The Paleontological Society, Boulder, CO, pp. 39–60.

Hadly, E.A., Spaeth, P.A., Li, C., 2009. Niche conservation above the species level. Proceedings of the National Academy of Sciences of the United States of America 106, 19707–19714.

Hafner, D.J., Hafner, J.C., Hafner, M.S., 1979. Systematic status of kangaroo mice, genus *Microdipodops*: morphometric, chromosomal, and protein analyses. Journal of Mammalogy 60, 1–10.

Hagmeier, E.M., 1966. A numerical analysis of the distributional patterns of North American mammals. II. Re-evaluation of the provinces. Systematic Zoology 15, 279–299.

Hagmeier, E.M., Stults, C.D., 1964. A numerical analysis of the distributional patterns of North American mammals. Systematic Zoology 13, 125–155.

Hall, E.R., 1981. The Mammals of North America, 2nd ed. John Wiley and Sons, New York.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T.M., Butchart, S.H.M., Carpenter, K.E., Chanson, J., Collen, B., Cox, N.A., Darwall, W.R.T., Dulvy, N.K., Harrison, L.R., Katariya, V., Pollock, C.M., Quader, S., Richman, N.I., Rodrigues, A.S.L., Tognelli, M.F., Vié, J.-C., Aguiar, J.M., Allen, D.J., Allen, G.R., Amori, G., Ananjeva, N.B., Andreone, F., Andrew, P., Ortiz, A.L.A., Baillie, J.E.M., Baldi, R., Bell, B.D., Biju, S.D., Bird, J.P., Black-Decima, P., Blanc, J.J., Bolaños, F., Bolivar-G, W., Burfield, I.J., Burton, J.A., Capper, D.R., Castro, F., Catullo, G., Cavanagh, R.D., Channing, A., Chao, N.L., Chenery, A.M., Chiozza, F., Clausnitzer, V., Collar, N.J., Collett, L.C., Collette, B.B., Fernandez, C.F.C., Craig, M.T., Crosby, M.J., Cumberlidge, N., Cuttelod, A., Derocher, A.E., Diesmos, A.C., Donaldson, J.S., Duckworth, J.W., Dutson, G., Dutta, S.K., Emslie, R.H., Farjon, A., Fowler, S., Freyhof, J., Garshelis, D.L., Gerlach, J., Gower, D.J., Grant, T.D., Hammerson, G.A., Harris, R.B., Heaney, L.R., Hedges, S.B., Hero, J.-M., Hughes, B., Hussain, S.A., Icochea, M.J., Inger, R.F., Ishii, N., Iskandar, D.T., Jenkins, R.K.B., Kaneko, Y., Kottelat, M., Kovacs, K.M., Kuzmin, S.L., La Marca, E., Lamoreux, J.F., Lau, M.W.N., Lavilla, E.O., Leus, K., Lewison, R.L., Lichtenstein, G., Livingstone, S.R., Lukoschek, V., Mallon, D.P., McGowan, P.J.K., McIvor, A., Moehlman, P.D., Molur, S., Alonso, A.M., Musick, J.A., Nowell, K., Nussbaum, R.A., Olech, W., Orlov, N.L., Papenfuss, T.J., Parra-Olea, G., Perrin, W.F., Polidoro, B.A., Pourkazemi, M., Racey, P.A., Ragle, J.S., Ram, M., Rathbun, G., Reynolds, R.P., Rhodin, A.G.J., Richards, S.J., Rodríguez, L.O., Ron, S.R., Rondinini, C., Rylands, A.B., Sadovy de Mitcheson, Y., Sanciangco, J.C., Sanders, K.L., Santos-Barrera, G., Schipper, J., Self-Sullivan, C., Shi, Y., Shoemaker, A., Short, F.T., Sillero-Zubiri, C., Silvano, D.L., Smith, K.G., Smith, A.T., Snoeks, J., Stattersfield, A.J., Symes, A.J., Taber, A.B., Talukdar, B.K., Temple, H.J., Timmins, R., Tobias, J.A., Tsytsulina, K., Tweddle, D., Ubeda, C., Valenti, S.V., Paul van Dijk, P., Veiga, L.M., Veloso, A., Wege, D.C., Wilkinson, M., Williamson, E.A., Xie, F., Young, B.E., Akçakaya, H.R., Bennun, L., Blackburn, T.M., Boitani, L., Dublin, H.T., da Fonseca, G.A.B., Gascon, C., Lacher, T.E., Mace, G.M., Mainka, S.A., McNeely, J.A., Mittermeier, R.A., Reid, G.M., Rodriguez, J.P., Rosenberg, A.A., Samways, M.J., Smart, J., Stein, B.A., Stuart, S.N., 2010. The impact of conservation on the status of the world's vertebrates. Science 330, 1503–1509.

Holland, S.M., 2003. Analytic Rarefaction, version 1.3, http://strata.uga.edu/software/2003.

IUCN, 2011. IUCN Red List of Threatened Species. Version 2011.2. International Union for Conservation of Nature, http://www/iucnredlist.org.

Janis, C.M., Scott, K.M., Jacobs, L.L., 1998. Evolution of Tertiary mammals of North America. Terrestrial Carnivores. : Ungulates, and Ungulatelike Mammals, Vol. 1. Cambridge University Press, Cambridge, p. 691.

Jolley, T.W., Honeycutt, R.L., Bradley, R.D., 2000. Phylogenetic relationships of pocket gophers (genus *Geomys*) based on the mitochondrial 12S rRNA gene. Journal of Mammalogy 81, 1025–1034.

Koch, P.L., Barnosky, A.D., 2006. Late Quaternary extinctions: state of the debate. Annual Review of Ecology, Evolution, and Systematics 37, 215–250.

Koch, P.L., Fox-Dobbs, K., Newsome, S.D., 2009. The isotopic ecology of fossil vertebrates and conservation paleobiology. In: Dietl, G.P., Flessa, K.W. (Eds.), Conservation Paleobiology: Using the Past to Manage the Future. The Paleontological Society, Boulder, CO, pp. 95–112.

Korth, W.W., 1994. The Tertiary Record of Rodents in North America. Plenum Press, New York.

Korth, W.W., 2008. Mammals from the Blue Ash local fauna (late Oligocene), South Dakota. Rodentia, part 2: families Florentiamyidae and Geomyidae. Paludicola 7, 14–25.

Levenson, H., Hoffmann, R.S., 1984. Systematic relationships among taxa in the Townsend chipmunk group. The Southwestern Naturalist 29, 157–168.

Levenson, H., Hoffmann, R.S., Nadler, C.F., Deutsch, L., Freeman, S.D., 1985. Systematics of the holarctic chipmunk (*Tamias*). Journal of Mammalogy 66, 219–242.

Lindsay, E.H., 1972. Small mammal fossils from the Barstow Formation, California. University of California. Publications in Geological Science 93, 1–104.

Liow, L.H., Fortelius, M., Bingham, E., Lintulaakso, K., Mannila, H., Flynn, L., Stenseth, N.C., 2008. Higher origination and extinction rates in larger mammals. Proceedings of the National Academy of Sciences of the United States of America 105, 6097–6102.

Martin, R.A., 1974a. Fossil mammals from the Coleman IIA Fauna, Sumter County. In: Webb, S.D. (Ed.), Pleistocene Mammals of Florida. University Presses of Florida, Gainesville, pp. 35–99.

Martin, R.A., 1974b. Fossil vertebrates from the Haile XIVA Fauna, Alachua County. In: Webb, S.D. (Ed.), Pleistocene Mammals of Florida. University Presses of Florida, Gainesville, pp. 100–113.

Martin, J.E., 1984. A survey of Tertiary species of Perognathus (Perognathinae) and a description of a new genus of Heteromyinae. Carnegie Museum of Natural History, Special Publication, 9, pp. 90–121.

McGuire, J.L., 2010. Geometric morphometrics of vole (*Microtus californicus*) dentition as a new paleoclimate proxy: shape change along geographic and climatic clines. Quaternary International 212, 198–205.

Paleobiology Database. The Paleobiology Database, http://paleodb.org/cgi-bin/bridge.pl.

Patterson, B.D., 1984. Geographic variation and taxonomy of Colorado and Hopi chipmunks (genus *Eutamias*). Journal of Mammalogy 65, 442–456.

Patton, J.L., Smith, M.F., 1989. Population structure and the genetic and morphologic divergence among pocket gopher species (genus *Thomomys*). In: Otte, D., Endler, J.A. (Eds.), Speciation and its Consequences. Sinauer Associates Inc., Sunderland, MA, pp. 284–304.

Patton, J.L., Smith, M.F., 1994. Paraphyly, polyphyly, and the nature of species boundaries in pocket gophers (genus *Thomomys*). Systematic Biology 43, 11–26.

Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., Araújo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guénette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R., Walpole, M., 2010. Scenarios for global biodiversity in the 21st century. Science 330, 1496–1501.

Peters, S.E., Heim, N.A., 2011. Macrostratigraphy and macroevolution in marine environments: testing the common-cause hypothesis. In: McGowan, A.J., Smith,

Please cite this article as: Carrasco, M.A., The impact of taxonomic bias when comparing past and present species diversity, Palaeogeogr. Palaeoclimatol. Palaeoecol. (2012), doi:10.1016/j.palaeo.2012.06.010

A.B. (Eds.), Comparing the Geological and Fossil Records: Implications for Biodiversity Studies: The Geological Society of London, Special Publication, London, pp. 95–104.

Piaggio, A.J., Spicer, G.S., 2000. Molecular phylogeny of the chipmunk genus *Tamias* based on the mitochondrial cytochrome oxidase subunit II gene. Journal of Mammalian Evolution 7, 147–166.

Piaggio, A.J., Spicer, G.S., 2001. Molecular phylogeny of the chipmunks inferred from mitochondrial cytochrome b and cytochrome oxidase II gene sequences. Molecular Phylogenetics and Evolution 20, 335–350.

Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., 1995. The future of biodiversity. Science 269, 347–350.

Prothero, D.R., 1998. The chronological, climatic, and paleogeographic background to North American mammalian evolution. In: Janis, C.M., Scott, K.M., Jacobs, L.L. (Eds.), Evolution of Tertiary Mammals of North America. Terrestrial Carnivores, Ungulates, and Ungulatelike Mammals, 1. Cambridge University Press, Cambridge, pp. 9–36.

Purvis, A., Jones, K.E., Mace, G.M., 2000. Extinction. BioEssays 22, 1123–1133.

Rensberger, J.M., 1971. Entoptychine pocket gophers (Mammalia, Geomyoidea) of the early Miocene John Day Formation, Oregon. University of California. Publications in Geological Science 90, 1–209.

Rensberger, J.M., 1973. Pleurolicine rodents (Geomyoidea) of the John Day Formation, Oregon and their relationships to taxa from the early and middle Miocene, South Dakota. University of California. Publications in Geological Science 102, 1–131.

Scheiner, S.M., 2003. Six types of species–area curves. Global Ecology and Biogeography 12, 441–447.

Schmidly, D.J., Wilkins, K.T., Derr, J.N., 1993. Biogeography. In: Genoways, H.H., Brown, J.H. (Eds.), Biology of the Heteromyidae. Special Publication. American Society of Mammalogists, pp. 319–356.

Stock, A.D., 1974. Chromosome evolution in the genus *Dipodomys* and its taxonomic and phylogenetic implications. Journal of Mammalogy 55, 505–526.

Storer, J.E., 1989. Rodent faunal provinces, Paleocene–Miocene of North America. In: Black, C.C., Dawson, M.R. (Eds.), Papers on Fossil Rodents in Honor of Albert Elmer Wood. Natural History Museum of Los Angeles County, Los Angeles, pp. 17–29.

Tedford, R.H., Albright III, L.B., Barnosky, A.D., Ferrusquia-Villafranca, I., Hunt Jr., R.M., Storer, J.E., Swisher III, C.C., Voorhies, M.R., Webb, S.D., Whistler, D.P., 2004. Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene through early Pliocene epochs). In: Woodburne, M.O. (Ed.), Late Cretaceous and Cenozoic Mammals of North America. Columbia University Press, New York, pp. 169–231.

Thorington Jr., R.W., Schennum, C.E., Pappas, L.A., Pitassy, D., 2005. The difficulties of identifying flying squirrels (Sciuridae: Pteromyini) in the fossil record. Journal of Vertebrate Paleontology 25, 950–961.

Wahlert, J.H., 1993. The Fossil Record. In: Genoways, H.H., Brown, J.H. (Eds.), Biology of the Heteromyidae. Special Publication. American Society of Mammalogists, pp. 1–37.

Williams, D.F., 1978. Systematics and ecogeographic variation of the apache pocket mouse (Rodentia: Heteromyidae). Bulletin of Carnegie Museum of Natural History 10, 1–57.

Williams, S.L., Genoways, H.H., 1975. Karyotype of *Geomys pinetis* (Mammalia: Geomyidae), with a discussion of the chromosomal relationships within the genus. Experientia 31, 1141–1143.

Williams, D.F., Genoways, H.H., Braun, J.K., 1993. Taxonomy. In: Genoways, H.H., Brown, J.H. (Eds.), Biology of the Heteromyidae. Special Publication. American Society of Mammalogists, pp. 38–196.

Wilson, D.E., Reeder, D.M., 2005. Mammal Species of the World, A Taxonomic and Geographic Reference, 3rd ed. Johns Hopkins University Press, Baltimore, p. 2142.

FAUNMAP Working Group, 1994. FAUNMAP: a database documenting late quaternary distributions of mammal species in the United States. Illinois State Museum Scientific Papers 25, 690.

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