

Predicting small-mammal responses to climatic warming: autecology, geographic range, and the Holocene fossil record

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Abstract

Forecasting how species will respond to climatic change requires knowledge of past community dynamics. Here we use time-series data from the small-mammal fossil records of two caves in the Great Basin of the American West to evaluate how contrasting and variable local paleoclimates have shaped small-mammal abundance dynamics over the last ~ 7500 years of climatic change. We then predict how species and communities will respond to future scenarios of increased warming and aridity coupled with continued spread of an invasive annual grass (*Bromus tectorum*). We find that most community-level responses to climatic change occur in the mammalian abundance structure at both sites; the dominance of the community by individuals from species with a southern geographic affinity increases with climatic warming. This suggests that responses occurred *in situ* rather than by the immigration of new taxa over this time interval. Despite predictability at the community-scale, species-level relationships between abundance and climate are variable and are not necessarily explained by a species' geographic affinity. Species present at both sites, however, exhibit remarkably similar responses to climate at each site, indicating that species autecology (specifically dietary functional group) is important in determining response to climatic warming. Regression-tree analyses show remarkable concordance between the two cave faunas and highlight the importance of a granivorous dietary strategy in this desert ecosystem. Under projections of increased temperature and decreased precipitation over the next 50 years, our results indicate that granivores should thrive as communities become more dominated by individuals with a southern geographic affinity. Granivores, however, are negatively impacted by the invasion of cheatgrass. The last century of anthropogenic impacts has thus placed granivores at a greater risk of extinction than predicted under climate-only scenarios.

Keywords: climate change, conservation paleobiology, functional group, geographic range, Great Basin, Holocene, paleoecology, small mammals

Received 15 October 2010 and accepted 19 March 2011

Introduction

Global temperatures and climatic variability are increasing at an alarming rate, with projections estimating an increase of 2.4–6.4 °C over the coming century (IPCC, 2007). Our ability to forecast how species and ecosystems will respond to future climate scenarios is a priority for multiple disciplines involved in conservation research (NRC, 2005, 2009; Hadly & Barnosky, 2009). This endeavor is complicated by two factors: (1) biotic responses to environmental change (including human impacts) unfold over timescales beyond those of direct ecological observation (Jablonski, 2002) and (2) the bulk of our knowledge on ecological dynamics comes from studies focused at annual to centennial

temporal scales (Blois & Hadly, 2009). Such studies are therefore unlikely to encompass the range of past environmental conditions that shaped the communities we see today, much less those envisioned in the future. Furthermore, the annual to centennial window of most prior studies captures systems already transformed by anthropogenic climate change and environmental degradation (Vitousek *et al.*, 1997), confounding our knowledge of how climate warming interacts with species biology at the most basic level (Dietl & Flessa, 2009). To better predict how extant species and their ecosystems will respond to future climatic change, we must expand our focus to include a multimillennial perspective – insights afforded only by examining the recent fossil record (Hadly & Barnosky, 2009).

It is well known that species abundances respond to climate. The carrying capacity of systems is linked to the availability of suitable habitat, thus changes in the environment are often manifest as changes in the

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abundances of species (del Monte-Luna *et al.*, 2004; Blois & Hadly, 2009). However, local interspecific interactions also play an important role in shaping the dynamics of species and their communities (May, 1984; Cooper, 2003), and these local interactions can be strongly influenced by processes working at larger spatiotemporal scales (e.g. the scale of the geographic range; Bruzgul & Hadly, 2006). The geographic range, the basic unit of biogeography (Brown *et al.*, 1996), integrates information about the evolutionary history, physiology, and dispersal ability of a species, as well as local interspecific interactions (Bruzgul & Hadly, 2006). We know that climate parameters play an important role in setting the boundaries of a species' geographic range, particularly poleward boundaries (Grinnell, 1917; Root, 1988; Graham *et al.*, 1996). Thus as climate has changed, we have observed many historical examples of ranges shifting across the landscape (reviewed in Parmesan, 2006). This phenomenon has also been well documented in the fossil record (e.g. Graham *et al.*, 1996; Lyons, 2003), with additional insights revealing that the size of the geographic range at both the species and genus levels has been relatively conserved through time (Lyons, 2003; Martinez-Meyer *et al.*, 2004; Hadly *et al.*, 2009). Thus, the geographic range has been a critical tool for elucidating how species respond in space to climatic change.

Far less is known about how communities at a fixed location have responded to climatic change through time (but see Hadly, 1996; Grayson, 2000a; Blois *et al.*, 2010), and whether patterns of response at both the species and community level are idiosyncratic across sites or influenced by a common suite of interacting factors. Yet the ability to make informed predictions about what will happen to local communities and their constituent species as climate changes into the future is important for conservation efforts. One expectation is that, as climate warms and dries, species will move poleward, manifesting as an increase in more equatorial species at a given point on the landscape through time (Root *et al.*, 2003; Myers *et al.*, 2009). Concomitantly, one might also expect an *in situ* increase in the abundances of species with environmental tolerances conducive to warming conditions (*sensu* Maurer & Taper, 2002).

To test these hypotheses, we evaluated how suites of interacting small-mammal species have responded to the last ~7500 years of climatic change at two independent fossil localities in the northern Great Basin of the American West. More specifically, we compared independent local paleoclimate proxies with reconstructed species abundance dynamics at each site, focusing our analysis on both species- and community-level patterns. We used the broad species descriptors of geographic affinity and functional group association to

link these two ecological scales of response to climate; hindcasting the past to better predict the impacts of future climatic warming on small-mammal biodiversity in the Great Basin.

Methods

Study system – Great Basin

Two Ledges Chamber (TLC) and Homestead Cave (HC) are two exceptionally rich Holocene small-mammal fossil localities in a region of great importance to biodiversity conservation: the high deserts of the Great Basin, western United States (Fig. 1, Plate 1). The Great Basin has become one of the most threatened of North America's ecosystems, as climatic change, land use, and invasive species continue to alter the structure

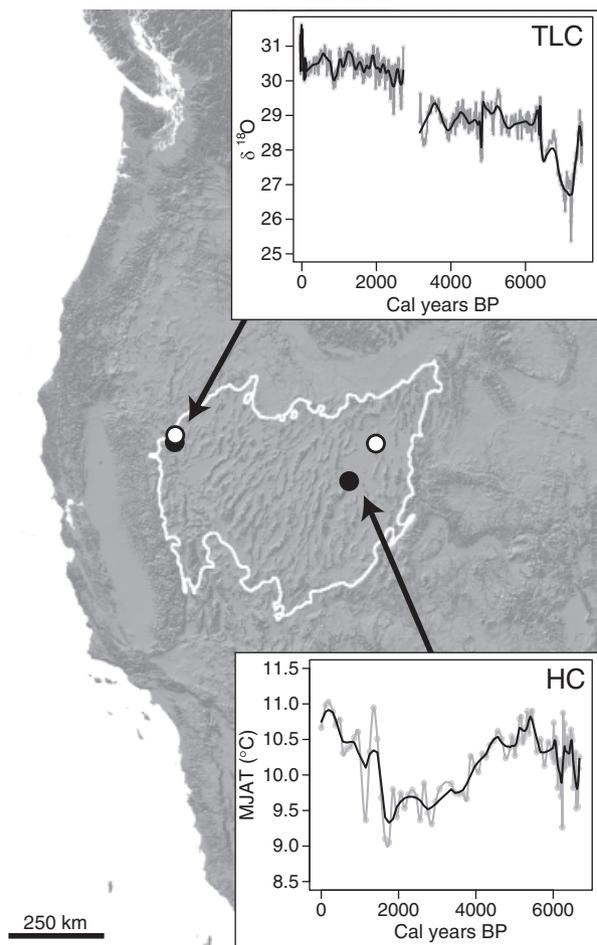


Fig. 1 Map of study area and cave locations. The boundary of the Great Basin is highlighted in white. White circles denote cave localities. Black circles denote locations of the associated paleoclimate reconstructions used in this study. TLC, Two Ledges Chamber; paleoclimate data from Benson *et al.* (2002); HC, Homestead Cave; paleoclimate data from Reinemann *et al.* (2009).



Plate 1

and dynamics of native communities (Miller & Wigand, 1994; Noss *et al.*, 1995; Knapp, 1996; Rowe, 2007). Often considered bellwethers of environmental change, the strong habitat affinities of small mammals make them a powerful group in which to study the effects of climatic change on biotic systems (Hadly & Barnosky, 2009).

TLC (located in the Smoke Creek Desert of northwestern Nevada, elevation 1244 m) and HC (located at the northern end of the Lakeside Mountains west of the Great Salt Lake, UT, elevation 1406 m) represent similar taphonomic and geomorphological contexts and share a high proportion of their modern small-mammal fauna (~70% of species and 86% of genera; NatureServe Database; Fig. 1). Both caves were formed through wave action of Pleistocene pluvial lakes. As the lakes receded in the early Holocene, both caves became long-term roosts for large-bodied owls (Hockett, 1993; Grayson, 2000a). While characterized by similar desert shrub habitats over the last 7500 years (Nowak *et al.*, 1994; Rhode, 2000), the land-use histories of these two sites have diverged markedly in the last half-century. Today, the habitat surrounding TLC is a diverse sagebrush steppe community with limited anthropogenic activity (Terry, 2010a). In contrast, the area surrounding HC has been used by the military as a weapons test and training range since the mid-1960s (Powell, 1994). It thus shows high levels of landscape disturbance and has a plant community dominated by the invasive cheatgrass (*Bromus tectorum*) (Terry, 2010b). TLC was excavated in 1990–1991 by B. Hockett and provides ~18 000 specimens (Hockett, 1993). HC was excavated in 1993 by D. Madsen and D. K. Grayson and provides ~184 000 specimens (Grayson, 2000b).

As explained below, the similar taphonomic and geomorphologic histories of these two sites minimizes the potential for variation due to differences in the accumulation and preservation of skeletal remains (Terry, 2010a, b). In addition, paleoclimate reconstructions near TLC and HC show surprisingly asynchronous local climate histories (Benson *et al.*, 2002; Reinemann *et al.*, 2009; Fig. 1). These two factors permit an extraordinarily well-controlled assessment of biotic responses to climate change across two sites in a natural system (Fig. 1).

Working with predator-derived skeletal remains

Predation is a common mechanism by which small-mammal skeletal remains enter the fossil record (Mellet, 1974; Andrews, 1990). Owls and other raptors regurgitate pellets that consist of matted hair packed with the undigestible hard parts of their small-mammal prey (the bones, teeth, and claws). Caves and rock shelters are common roost sites in arid environments and can be actively used by raptor populations for millennia (e.g. Hadly, 1996; Grayson, 2000a). This results in significant accumulations of small-mammal skeletal debris in depositional settings that are highly conducive to preservation (Andrews, 1990).

Small-mammal fossil assemblages typically represent a composite signal amassed by multiple predator species (Hadly, 1999). Individual strata are also time-averaged over centuries to millennia (Terry, 2008a, b). These two factors have important implications for the capture of ecological information by skeletal remains. First, input from multiple sources buffers the death assemblage against being overly influenced by variation in predator identity or selectivity (Hadly, 1999; Terry, 2010a). Although undoubtedly present, such variation is likely minimal at TLC and HC, as analysis of skeletal breakage patterns through time have shown large owls to be the dominant source of skeletal material over the duration of their depositional histories (Terry, 2007, 2010b). Second, temporal averaging dampens short-term (seasonal to decadal-scale) prey population dynamics, allowing longer-term (centennial to millennial) trends to emerge (Terry, 2008a). Death assemblages provide useful ecological information even at shorter time-scales, however. Indeed, by comparing the composition and structure of recent and subfossil pellet-derived small-mammal remains to modern and historical trapping surveys, Terry (2010a, b) showed that the skeletal remains of TLC and HC provide exceptionally high-quality, high-resolution abundance data on the local small-mammal community. These factors confer confidence that the temporal shifts we observe in the composition and structure of the small-mammal communities at TLC and HC represent true biotic responses to changes in the environment.

Radiocarbon chronology

Radiocarbon dating of the HC material indicates that this record extends back at least 8285 ± 40 ^{14}C years BP (Madsen, 2000). Radiocarbon dating of the TLC material indicates a maximum age of $11\,263 \pm 83$ ^{14}C years BP (Terry, 2010a). Radiocarbon age estimates were converted into calendar years before present (AD 1950) using OxCal 4.1 (Bronk Ramsey, 1995, 2001) with the IntCal04 calibration curve for the Northern Hemisphere (Reimer *et al.*, 2004). OxCal takes into account both the uncertainty associated with the experimental measurement of radiocarbon in samples as well as uncertainty associated with the radiocarbon calibration curve (expressed as a function of time) to return a Bayesian posterior probability distribution of calibrated dates for each sample. We selected the best-supported calibrated age based on these distributions for our chronologies for each site.

To create a robust temporal framework for our analyses, we constructed age models for both caves based on relationships between stratum depth and calibrated radiocarbon age. Our models were built using a cubic spline function following Fritsch & Carlson (1980) that preserves monotonicity (increasing or decreasing slopes) between intervals. We then inferred ages for any undated strata using this model (Table 1).

Abundance dynamics

Fossil specimens included in this analysis consist of cranio-mandibular elements from 1/4" and 1/8" mesh sizes identified to species when possible by comparison with reference material obtained from trapping surveys conducted at each site (Terry, 2008b) supplemented with additional material (including size data) from the collections of the Burke Museum, the Field Museum of Natural History, and the Utah Museum of Natural History. Fossil material from HC was identified by D. K. Grayson (Grayson, 2000b; Terry, 2008b). Historical material from HC and historical and fossil material from TLC was identified by R. C. Terry (Terry, 2010a,b). Four of the 24 taxa included in this study (*Microtus* spp., *Mustela* spp., *Peromyscus* spp., and *Urocyon* spp.) could not be identified to the species level due to the difficulty of distinguishing between the skeletal remains of congeners. The use of genus level identifications in such situations is standard practice (see Blois *et al.*, 2010; Grayson, 2000b), and we discuss the implications of this for our analyses below. Data represent estimates of the number of identified specimens (NISP) per species per stratum (following Grayson, 1984). Abundance data were sample size standardized to the smallest stratum for each cave before analysis using rarefaction (iterative subsampling without replacement; 10 000 iterations; TLC: $n = 60$; HC: $n = 154$; Table 2).

Climate data

Independent local paleoclimate data near TLC were obtained from $\delta^{18}\text{O}$ sediment profiles from Pyramid Lake located ~ 16 km south of TLC and extending back to ~ 7600 calibrated years BP (Benson *et al.*, 2002). The paleoclimate record used for analysis of the HC faunal record extends back to ~ 6700 calibrated years BP and was obtained from chironomid reconstructions in a sediment core from Stella Lake in Great Basin National Park (Reinemann *et al.*, 2009), located ~ 240 km south of HC. At each site, we fit these data with spline smoothing functions and lowess smoothing curves in order to extract paleoclimate estimates that were temporally aligned to the faunal data. Both fitting regimes provided similar results, so we only present analyses with the spline-fit paleoclimate data.

Because the temporal resolution of the paleoclimate data was finer than that of the faunal data [strata are likely time-averaged over centuries (Terry, 2008b)], we analytically time-averaged the paleoclimate data symmetrically around each estimated stratum age over a range of values (0, 100, 250, and 500 years of time averaging). All analyses were repeated at each of the time-averaging values, with results robust to time

averaging. Unless otherwise specified, we present results using mean values with 95% confidence intervals on the standard error of the mean for all time-averaging values.

Geographic affinity categorization

To assign species a geographic affinity, we obtained GIS range data from the NatureServe Database for each of the 24 species present at one or both of the fossil localities (<http://www.natureserve.org>). We also compiled unique locality information from the Mammal Networked Information System (MaNIS; <http://manisnet.org>) for each of the same 24 species. We projected these points in ArcGIS (ESRI 1999–2006; Beyer, 2004) using a North American Equidistant Conic projection and compared the NatureServe ranges with the geographic coverage of MaNIS data to identify potential sampling bias. All data were restricted geographically to west of the Rocky Mountains since we were interested in the potential for north-south migration in western North America as opposed to east-west migration across this topographic barrier. We also discarded all data points with locality georeferencing error greater than 10 km.

We categorized the geographic affinity for each species at each cave as follows: First, using the northern and southern extremes of each species' range in western North America, we calculated the proportion of the geographic range lying south of each cave (Table 3). Species with >60% of their range to the south of a given cave were designated as having a southern affinity. Species with <30% of their range to the south of a given cave were designated as having a northern affinity. Species with range proportions between these two cutoff points were designated as having no affinity (i.e., the cave occurs near the middle of the species' geographic range).

Functional group categorization

While the geographic range integrates ecological and evolutionary information for a given species over both space and time, we used dietary functional groups to take a finer-scale approach to categorizing species that focuses specifically on autecology. To categorize species, we used a combination of the functional group assignments presented in Badgley & Fox (2000) and Reed *et al.* (2006) that were built from exhaustive literature reviews (Table 3).

Analysis

At the community scale, we used cross-correlations to explore the relationship between the geographic composition of the community and Holocene climatic change in terms of both species presence/absence through time as well as dominance of the community by individuals from species with a given geographic affinity (i.e., northern, southern, or no affinity). More specifically, we tested the prediction that during climatic warming, local communities witnessed an increase in species and individuals with a southern geographic affinity. We then assessed all species-level relationships between Holocene

Table 1 Temporal frameworks used for analyses of Two Ledges Chamber (TLC) and Homestead Cave (HC)

Stratum	Type	Calibrated modal age BP (age range)	Mean $\delta^{18}\text{O}$	SD $\delta^{18}\text{O}$	Original name	Source
<i>TLC</i>						
1	Known	Modern	30.61	0.25	TLC bulk	Terry (2008a, b)
2	Dated	288 (0–467)	30.47	0.10	D4, Spit 1	Hockett (1993)
3	Dated	317 (12–385)	30.40	0.10	D4, Spits 3 and 4	Hockett (1993)
4	Inferred	884	30.20	0.13	D4, Spits 5 and 6	Hockett (1993)
5	Dated	1709 (1513–1998)	30.36	0.05	D4, Spits 7 and 8	Hockett (1993)
6	Inferred	2251	30.32	0.10	D4, Spit 9	Hockett (1993)
7	Inferred	2597	30.03	0.15	D4, Spit 10	Hockett (1993)
8	Inferred	2955	No data		D4, Spit 11	Hockett (1993)
9	Dated	3553 (3340–3864)	29.29	0.19	D4, Spits 12 and 13	Hockett (1993)
10	Inferred	4960	29.02	0.10	D4, Spits 15 and 16	Hockett (1993)
11	Dated	6090 (5755–7156)	28.75	0.09	D4, Spits 17 and 18	Hockett (1993)
12	Dated	7556 (6493–9422)	28.21	0.27	D4, Spits 19 and 20	Hockett (1993)
Stratum	Type	Calibrated modal age BP (age range)	Mean MJAT ($^{\circ}\text{C}$)	SD MJAT ($^{\circ}\text{C}$)	Original name	Source
<i>HC</i>						
1	Known	Modern	10.80	0.12	HC bulk	Terry (2008a, b)
2	Inferred	150	10.97	0.06	Stratum 18	Grayson (2000b)
3	Dated	930 (798–1053)	10.47	0.20	Stratum 17	Grayson (2000b)
4	Dated	1095 (985–1264)	9.77	0.29	Stratum 16	Grayson (2000b)
5	Dated	3640 (3481–3829)	9.75	0.04	Stratum 12	Grayson (2000b)
6	Dated	5377 (4881–5589)	10.69	0.08	Stratum 11	Grayson (2000b)
7	Dated	6752 (6020–7307)	10.05	0.16	Stratum 9	Grayson (2000b)

Chronologies are based on calibrated radiocarbon dates (IntCal 04 Calibration Curve). Calibrated age range represents 95.4% probability; calibrations carried out in OxCal 4.0. Paleoclimate estimates for each stratum represent spline estimated values averaged over 0, 100, 250, and 500 years of time averaging.

Table 2 Summary of number of identified specimens (NISP) data for Two Ledges Chamber (TLC) and Homestead Cave (HC) with sample standardized abundances (NISP_s ± 95% CI) in parentheses

Taxon	1	2	3	4	5	6	7	8	9	10	11	12
TLC												
<i>Ammospermophilus leucurus</i>	-	1 (1 ± 0)	1 (1 ± 0)	-	2 (1.3 ± 0.7)	2 (1.4 ± 0.6)	1 (1 ± 0)	-	-	2 (1.5 ± 0.5)	2 (1.5 ± 0.5)	5 (2.8 ± 2.1)
<i>Chaetodipus formosus</i>	276 (25.7 ± 7.3)	13 (6.1 ± 2.9)	49 (8.7 ± 5.2)	13 (12.4 ± 0.6)	24 (12.1 ± 3.9)	25 (15.6 ± 4.4)	16 (11.8 ± 3.1)	7 (6.5 ± 0.5)	14 (10.6 ± 2.4)	16 (10.1 ± 2.9)	5 (9.5 ± 3.4)	17
<i>Dipodomys deserti</i>	8 (1.4 ± 1.6)	2 (1.3 ± 0.7)	-	-	-	-	-	-	-	1 (1 ± 0)	-	-
<i>Dipodomys merriami</i>	73 (6.8 ± 5.2)	10 (4.7 ± 3.3)	8 (1.8 ± 2.2)	7 (6.7 ± 0.3)	6 (3.1 ± 1.9)	1 (1 ± 0)	4 (3.0 ± 1.0)	3 (2.8 ± 0.2)	5 (3.8 ± 1.2)	7 (4.4 ± 2.6)	4 (3.4 ± 2.6)	6
<i>Dipodomys microps</i>	26 (2.6 ± 3.4)	8 (3.8 ± 2.2)	12 (2.4 ± 2.6)	2 (1.9 ± 0.09)	7 (3.5 ± 2.5)	4 (2.5 ± 1.5)	2 (1.6 ± 0.4)	5 (4.7 ± 0.3)	8 (6.1 ± 1.9)	4 (2.6 ± 1.4)	6 (4.5 ± 2.5)	8
<i>Dipodomys ordii</i>	41 (3.9 ± 4.1)	2 (1.3 ± 0.7)	1 (1 ± 0)	-	3 (1.7 ± 1.3)	-	1 (1 ± 0)	1 (1 ± 0)	3 (2.3 ± 0.7)	1 (1 ± 0)	-	1 (1 ± 0)
<i>Lemmiscus curtatus</i>	-	13 (6.1 ± 2.9)	36 (6.4 ± 4.6)	1 (1 ± 0)	2 (1.3 ± 0.7)	4 (2.5 ± 1.5)	5 (3.7 ± 1.3)	3 (2.8 ± 0.2)	2 (1.6 ± 0.4)	4 (2.6 ± 1.4)	-	-
<i>Microdipodops megacephalus</i>	-	3 (1.7 ± 1.3)	19 (3.5 ± 3.5)	5 (4.8 ± 0.2)	6 (3.1 ± 1.9)	6 (3.8 ± 2.2)	4 (3.0 ± 1.0)	2 (1.9 ± 0.1)	-	3 (2.0 ± 1.0)	2 (1.8 ± 1.2)	3
<i>Microtus</i> spp.	13 (1.7 ± 2.3)	2 (1.3 ± 0.7)	7 (1.7 ± 2.3)	-	2 (1.3 ± 0.7)	1 (1 ± 0)	2 (1.6 ± 0.4)	1 (1 ± 0)	2 (1.6 ± 0.4)	7 (4.4 ± 2.6)	4 (5.6 ± 2.4)	10
<i>Mustela</i> spp.	-	-	-	-	1 (1 ± 0)	-	-	-	-	-	-	-
<i>Neotoma cinerea</i>	14 (1.7 ± 2.3)	2 (1.3 ± 0.7)	8 (1.8 ± 2.2)	3 (2.9 ± 0.1)	1 (1 ± 0)	1 (1 ± 0)	3 (2.3 ± 0.7)	1 (1 ± 0)	2 (1.6 ± 0.4)	-	4 (1.4 ± 0.6)	2
<i>Neotoma lepida</i>	18 (2.0 ± 1.9)	44 (20.8 ± 5.2)	53 (9.4 ± 5.5)	7 (6.7 ± 0.3)	10 (5.0 ± 2.9)	14 (8.8 ± 3.2)	12 (8.9 ± 2.1)	11 (10.3 ± 0.7)	8 (6.1 ± 1.9)	13 (8.2 ± 2.8)	7 (6.2 ± 2.8)	11
<i>Onychomys torridus</i>	6 (1.2 ± 1.7)	-	10 (2.1 ± 1.9)	7 (6.7 ± 0.3)	1 (1 ± 0)	2 (1.5 ± 0.5)	3 (2.3 ± 0.7)	1 (1 ± 0)	5 (3.8 ± 1.2)	3 (2.0 ± 1.0)	2 (1.4 ± 0.6)	2
<i>Perognathus longimembris</i>	13 (1.7 ± 2.3)	-	29 (5.2 ± 3.8)	4 (3.8 ± 0.2)	12 (6.0 ± 3.0)	19 (11.9 ± 3.1)	10 (7.4 ± 2.6)	17 (15.9 ± 1.1)	5 (3.8 ± 1.2)	8 (5.1 ± 1.9)	2 (2.3 ± 1.7)	4
<i>Peromyscus</i> spp.	106 (9.9 ± 5.1)	10 (4.7 ± 3.3)	39 (7.0 ± 5.0)	10 (9.5 ± 0.5)	23 (11.6 ± 4.4)	8 (5.0 ± 2.0)	13 (9.6 ± 2.4)	6 (5.6 ± 0.4)	14 (10.6 ± 2.4)	8 (5.1 ± 1.9)	7 (7.9 ± 3.2)	14

<i>Reithrodontomys megalotis</i>	47 (4.4 ± 3.6)	34 (6.1 ± 3.9)	3 (2.9 ± 0.1)	6 (3.1 ± 1.9)	2 (1.6 ± 0.4)	2 (1.9 ± 0.1)	3 (2.3 ± 0.7)	9 (5.7 ± 2.3)	1 (2.3 ± 1.7)	4 (2.3 ± 1.7)
<i>Thomomys bottae</i>	3 (1.1 ± 0.9)	12 (2.8 ± 3.2)	1 (1 ± 0)	9 (4.5 ± 2.4)	2 (1.6 ± 0.4)	3 (2.8 ± 0.2)	4 (3.1 ± 1.0)	3 (2.0 ± 1.0)	1 (2.3 ± 1.7)	2 (2.3 ± 1.7)
<i>Thomomys talpoides</i>	-	7 (1.7 ± 2.3)	-	-	-	-	-	1 (1 ± 0)	1 (1.4 ± 0.6)	2 (1.4 ± 0.6)
<i>Thomomys townsendii</i>	-	-	-	1 (1 ± 0)	-	-	2 (1.6 ± 0.4)	1 (1 ± 0)	1 (1.4 ± 0.6)	2 (1.4 ± 0.6)
<i>Urocyon spp.</i>	-	8 (2.9 ± 2.1)	4 (1.8 ± 2.2)	4 (2.1 ± 1.9)	1 (1 ± 0)	1 (1 ± 0)	2 (1.6 ± 0.4)	4 (2.6 ± 1.4)	11 (6.7 ± 3.3)	12 (6.7 ± 3.3)

NISP data generated through iterative subsampling without replacement to the smallest stratum (stratum 11, $n = 60$, 10 000 iterations).

Taxon	Stratum						
	1	2	3	4	5	6	7
<i>HC</i>							
<i>Ammospermophilus leucurus</i>	-	-	47 (3.0 ± 2.9)	32 (5.1 ± 3.9)	119 (6.1 ± 4.9)	53 (5.5 ± 4.5)	91 (5.3 ± 4.7)
<i>Chaetodipus formosus</i>	33 (16.3 ± 5.7)	-	14 (1.5 ± 1.5)	2 (1.1 ± 0.9)	6 (1.1 ± 0.9)	-	-
<i>Dipodomys microps</i>	51 (25.3 ± 6.7)	46	693 (42.6 ± 10.4)	271 (43.4 ± 9.6)	1092 (55.7 ± 11.3)	448 (46.6 ± 10.3)	968 (56.1 ± 11.9)
<i>Dipodomys ordii</i>	22 (10.9 ± 4.1)	1	22 (1.8 ± 2.2)	11 (2.1 ± 2.9)	32 (2.0 ± 2.0)	10 (1.6 ± 1.4)	22 (1.8 ± 2.2)
<i>Lemmys curtatus</i>	-	-	9 (1.3 ± 1.7)	2 (1.1 ± 0.9)	-	1 (1 ± 0)	1 (1 ± 0)
<i>Microtus spp.</i>	-	-	1 (1 ± 0)	1 (1 ± 0)	1 (1 ± 0)	1 (1 ± 0)	-
<i>Mustela frenata</i>	-	-	-	-	4 (1.1 ± 0.9)	1 (1 ± 0)	4 (1.1 ± 0.9)
<i>Neotoma cinerea</i>	-	-	6 (1.2 ± 0.8)	193 (30.9 ± 9.1)	-	-	870 (50.4 ± 11.5)
<i>Neotoma lepida</i>	-	41	753 (46.3 ± 10.7)	65 (10.4 ± 5.6)	866 (44.0 ± 11.0)	557 (57.7 ± 11.3)	188 (11.0 ± 6.1)
<i>Onychomys leucogaster</i>	4 (2.1 ± 1.9)	-	15 (1.5 ± 1.5)	5 (1.4 ± 1.6)	5 (1.1 ± 0.9)	2 (1.1 ± 0.9)	7 (1.2 ± 0.8)
<i>Perognathus longimembris</i>	-	2	36 (2.5 ± 2.5)	18 (3.0 ± 3.0)	12 (1.3 ± 1.7)	3 (1.1 ± 0.9)	22 (1.7 ± 2.3)
<i>Perognathus parvus</i>	-	-	6	2	-	-	-

Continued

Table 2. (Contd.)

Taxon	Stratum						
	1	2	3	4	5	6	7
<i>Peromyscus</i> spp.	131 (64.9 ± 9.1)	17	(1.2 ± 0.8) 205 (12.6 ± 6.4)	(1.1 ± 0.9) 61 (9.8 ± 6.2)	187 (9.5 ± 6.5)	49 (5.1 ± 4.9)	147 (8.5 ± 5.5)
<i>Reithrodontomys megalotis</i>	41 (20.3 ± 5.7)	1	96 (5.9 ± 5.1)	33 (5.3 ± 4.7)	25 (1.7 ± 2.3)	3 (1.1 ± 0.9)	16 (1.5 ± 1.5)
<i>Spilogale putorius</i>	—	—	—	1 (1 ± 0)	1 (1 ± 0)	1 (1 ± 0)	1 (1 ± 0)
<i>Thomomys bottae</i>	3 (1.7 ± 1.3)	4	72 (4.5 ± 4.5)	49 (7.8 ± 5.1)	41 (2.4 ± 2.6)	20 (2.4 ± 2.6)	61 (3.7 ± 3.5)
<i>Urocyon</i> spp.	26 (12.9 ± 5.1)	42	528 (32.6 ± 9.4)	215 (34.5 ± 9.5)	639 (32.4 ± 9.6)	333 (34.6 ± 9.4)	258 (15.0 ± 7.1)

NISP data generated through iterative subsampling without replacement to the smallest stratum (stratum 2, $n = 154$, 10 000 iterations).

abundance dynamics and paleoclimate at each cave. This analysis focused on a subset of 19 species that were present in at least four time intervals (Table 3). We summarized these results independently with respect to both geographic affinity and dietary functional groups of species, testing the prediction of *in situ* increases in the abundances of species with environmental tolerances and autecologies conducive to warming conditions. No autocorrelation was evident in any of the time-series. We assessed significance between pairs of time-series using permutation tests (1000 iterations). Finally, to investigate how the species-level results related to community-scale patterns, we integrated the categorical variables of geographic affinity and functional group using regression-tree analyses of each small-mammal community. Regression trees are increasingly being used in the analysis of complex ecological datasets to find major subdivisions within data as well as extract the most relevant predictor variables (e.g. Davidson *et al.*, 2007). This approach uses recursive partitioning of a response variable where the between-group sum of squares is maximized at each split (Therneau & Atkinson, 1997). Our use of regression trees permitted graphical representation of the relative importance of geographic affinity and functional group in explaining the direction and strength of each species' abundance-climate correlation. Unless otherwise noted, all analyses were conducted in the R statistical framework version 2.9.2 (R Core Development Team, 2009; <http://www.r-project.org>). Regression-tree analysis was carried out using the *rpart* package (version 3.1-45; Therneau & Atkinson, 2009).

Results

Community level

As the climate warmed and dried over the last ~ 7500 years at TLC, both the proportional richness of small-mammal species with a southern affinity and the overall dominance of the community by individuals from species with a southern affinity increased (richness: $r = 0.54$, $P = 0.032$; dominance: $r = 0.72$, $P = 0.013$; 100 years of time averaging; Fig. 2a). At HC, a similar signal emerges, with peaks in the proportional richness of southern species and dominance of the community by southern individuals aligning with periods of relative warmth in this region of the Great Basin over the last ~ 7000 years. The correlations between climate and the two measures of southern community composition (species presence and dominance) are substantially weaker at HC and are not significant (richness: $r = 0.45$, $P = 0.144$; dominance: $r = 0.23$, $P = 0.307$; 100 years of time averaging; Fig. 2b). This is not surprising given that there are fewer strata within the last ~ 7000 years at HC, thus statistical power is reduced. Furthermore, the youngest time interval (last century) shows evidence of substantial anthropogenic alteration of the landscape (Terry, 2010b). If we exclude this stratum, the correlations at HC remain insignificant (due to low

Table 3 Geographic and functional assignments and mean Holocene abundance-climate correlations for small-mammal species at Two Ledges Chamber (TLC) and Homestead Cave (HC)

Taxon	Functional group	TLC		HC	
		Geographic affinity	Mean $r \pm 95\%$ CI	Geographic affinity	Mean $r \pm 95\%$ CI
<i>Ammospermophilus leucurus</i>	Omnivore	Southern	-0.87 ± 0.02	Southern	-0.38 ± 0.16
<i>Chaetodipus formosus</i>	Granivore	Southern	0.44 ± 0.08	Southern	0.75 ± 0.14
<i>Dipodomys deserti</i>	Granivore	Southern	–	na	na
<i>Dipodomys merriami</i>	Granivore	Southern	0.06 ± 0.02	na	na
<i>Dipodomys microps</i>	Herbivore	Southern	-0.58 ± 0.02	Southern	-0.15 ± 0.11
<i>Dipodomys ordii</i>	Granivore	Southern	0.36 ± 0.07	Southern	0.30 ± 0.14
<i>Lemmys curtatus</i>	Herbivore	None	0.38 ± 0.06	None	–
<i>Microdipodops megacephalus</i>	Granivore	Southern	0.56 ± 0.02	na	na
<i>Microtus</i> spp.	Herbivore	Northern	-0.89 ± 0.03	Northern	–
<i>Mustela</i> spp.	Carnivore	None	–	na	na
<i>Mustela frenata</i>	Carnivore	na	na	Southern	–
<i>Neotoma cinerea</i>	Herbivore	Northern	-0.33 ± 0.07	Northern	–
<i>Neotoma lepida</i>	Herbivore	Southern	0.20 ± 0.06	Southern	0.54 ± 0.14
<i>Onychomys leucogaster</i>	Insectivore	na	na	Southern	0.49 ± 0.11
<i>Onychomys torridus</i>	Insectivore	Southern	0.06 ± 0.06	na	na
<i>Perognathus longimembris</i>	Granivore	Southern	0.39 ± 0.08	Southern	-0.19 ± 0.09
<i>Perognathus parvus</i>	Granivore	na	na	None	–
<i>Peromyscus</i> spp.	Omnivore	None	0.11 ± 0.03	None	0.44 ± 0.11
<i>Reithrodontomys megalotis</i>	Granivore	Southern	0.23 ± 0.04	Southern	0.29 ± 0.12
<i>Spilogale gracilis</i>	Carnivore	na	na	Southern	–
<i>Thomomys bottae</i>	Herbivore	Southern	0.18 ± 0.05	Southern	-0.40 ± 0.09
<i>Thomomys talpoides</i>	Herbivore	None	0.60 ± 0.06	na	na
<i>Thomomys townsendii</i>	Herbivore	Northern	-0.28 ± 0.08	na	na
<i>Urocyon</i> spp.	Omnivore	None	-0.69 ± 0.04	None	0.05 ± 0.07

Correlations are averaged over the following time-averaging windows: 0, 100, 250, and 500 years.

–, species that are present in the faunal record but occur in < 4 strata, thus no abundance-climate correlations were obtained for these species; na, species not present at a given site. Only the subset of 19 species for which abundance-climate correlations were obtained are included in the species-level analyses.

power) but the dominance correlation increases substantially and follows the same trend as observed at TLC (richness: $r = 0.39$, $P = 0.233$; dominance: $r = 0.45$, $P = 0.167$; 100 years of time averaging).

Species level

No consistent relationship was observed between climate and each species' abundance dynamics with respect to their geographic affinity (Fig. 3; Table 3). For example, at both TLC and HC, species categorized as having southern geographic affinities showed a large range of abundance-climate correlations. However, species responses were not idiosyncratic across sites, with 70% of the species shared between TLC and HC showing similar responses to independent changes in local climate conditions at both caves (Fig. 4).

When species are categorized by dietary functional groups, a clearer segregation of species emerges at TLC (Fig. 5a). At this site, granivores show a significant

positive correlation with climate warming ($r = 0.34$, $P = 0.005$), while omnivores show a strongly negative but nonsignificant trend ($r = -0.48$, $P = 0.252$). At HC the responses of dietary functional groups to climate are less clear (Fig. 5b).

Regression trees for TLC and HC reveal remarkable congruence of the variables involved in the hierarchical partitioning of each communities species-specific abundance-climate correlations (Fig. 6). These recovered six terminal branches (species associations) at TLC and four terminal branches at HC. At both caves, the primary node separated granivorous species from all other dietary functional groups. Granivores at both caves show a strong positive mean correlation between their abundance dynamics and climate warming (TLC: mean $r = 0.34$; HC: mean $r = 0.29$). The secondary node concerned geographic affinity, separating species with no distinct geographic affinity (i.e. caves are located near the middle of the north-south extent of a species' geographic range) from species with a southern or

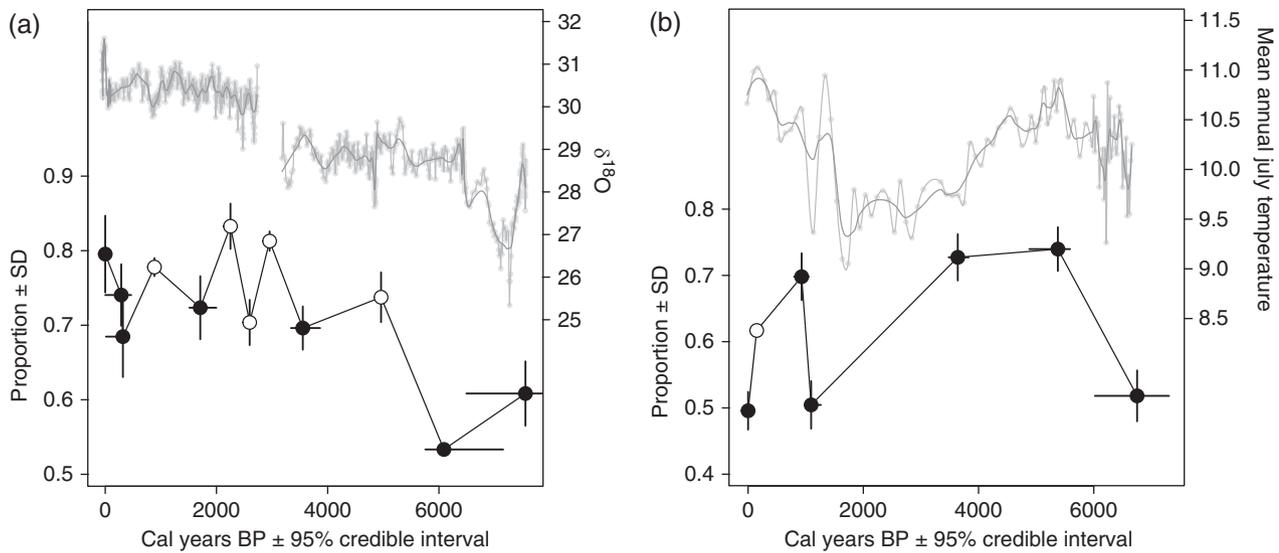


Fig. 2 The dominance of local small-mammal communities by individuals from species with a southern geographic affinity has positively tracked climate warming during the Holocene. (a) Two Ledges Chamber. Upper gray lines display a $\delta^{18}\text{O}$ paleoclimate reconstruction from sediment cores taken in Pyramid Lake by Benson *et al.* (2002). The raw data (points) have been fit with both spline and loess smoothing functions (light and dark lines, respectively). Higher values indicate a shift to warmer and drier conditions through the Holocene. (b) Homestead Cave. Upper gray lines display a chironomid-based paleoclimate reconstruction from Great Basin National Park by Reinemann *et al.* (2009). Data points and smoothing lines follow the same protocol as at Two Ledges Chamber. At both caves, the lower black set of data points represent the proportion of individuals in each community that are from species with a southern geographic affinity. Filled circles represent strata with known ages from radiocarbon dating. Open circles represent undated strata for which ages have been inferred using a spline-fit age model. Results shown at a time-averaging window of 100 years.

northern affinity. At TLC, the node containing species with no geographic affinity is further subdivided according to functional group, separating omnivorous from herbivorous species. These herbivores with no strong geographic affinity, show a mean positive response to climate warming at TLC ($r = 0.49$), and are not present at HC. The species within the omnivorous group, while present at both caves, show highly variable within- and between-group correlations with climate warming. Within species that have a clear southern or northern geographic affinity, the next node at both caves again concerns a functional group variable, separating out the omnivorous Antelope Ground Squirrel (*Ammospermophilus leucurus*) that has a southern geographic affinity but nevertheless shows a negative correlation between its abundance and climate warming. Finally, herbivores with a northern geographic affinity are separated from herbivores with a southern geographic affinity at TLC and show a strong negative mean correlation between their abundance dynamics and climate warming (mean $r = -0.50$).

Discussion

The ability to predict how a local community and its constituent species are likely to respond to future

climatic change is a primary goal for conservation. Small mammals play many critical roles in the maintenance of ecosystems, influencing plant communities through seed and fungal spore dispersal (Brown & Heske, 1990; Johnson, 1996), and serving as a prey base for larger predators (Craighead & Craighead, 1956). Small mammals are well known to respond to environmental change (Hadly, 1996; Grayson, 2000a, 2006; Moritz *et al.*, 2008; Rowe *et al.*, 2010), but there are many context-dependent factors that influence a species' risk of extinction (Davidson *et al.*, 2007). Drawing upon the wealth of information preserved in the recent fossil record enables us to evaluate how small-mammal communities and species abundances have responded to past episodes of climatic change, thus better anticipate how today's species and communities are likely to change under a future of continued climatic warming. Our analyses suggest that geographic affinity and functional group information on species (meso-scale variables readily obtainable from the published literature and public databases) can do much to predict single-taxon abundance dynamics, which when aggregated provide insight into how Great Basin small-mammal communities will respond to climatic warming in the future.

Our expectation was that as climate warmed and dried over the past ~ 7500 years in the Great Basin,

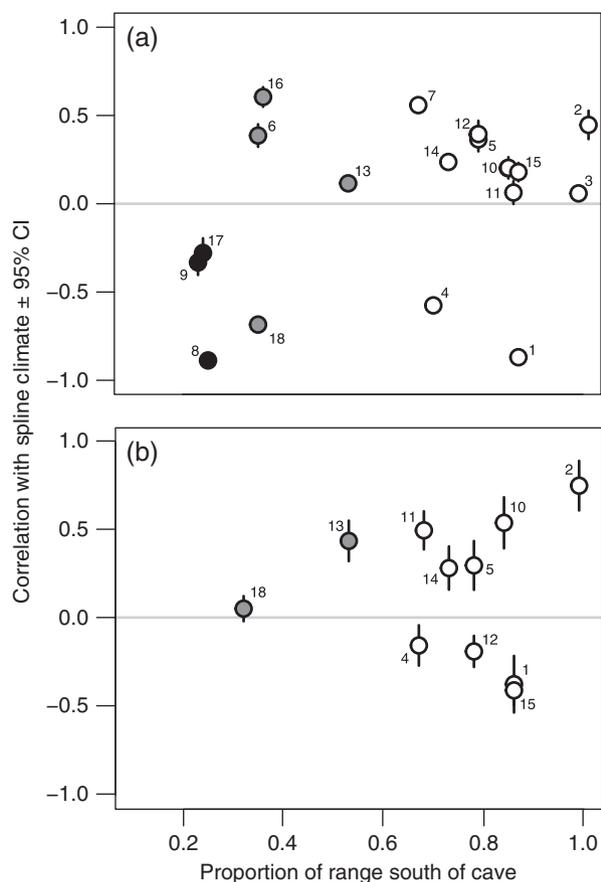


Fig. 3 Correlations between species' abundance dynamics and climate with respect to geographic affinity at (a) Two Ledges Chamber (TLC) and (b) Homestead Cave (HC). Points represent the correlation of each species' abundance dynamics with climate averaged across all windows of time averaging (see main text). Open circles represent southern species; black circles represent northern species; grey circles represent species for which the caves are located in the middle of their geographic ranges. Numbers denote species identities as follows: 1, *Ammospermophilus leucurus*; 2, *Chaetodipus formosus*; 3, *Dipodomys merriami*; 4, *Dipodomys microps*; 5, *Dipodomys ordii*; 6, *Lemmiscus curtatus*; 7, *Microdipodops megacephalus*; 8, *Microtus* spp.; 9, *Neotoma cinerea*; 10, *Neotoma lepida*; 11, *Onychomys torridus* (TLC) and *O. leucogaster* (HC); 12, *Perognathus longimembris*; 13, *Peromyscus* spp.; 14, *Reithrodontomys megalotis*; 15, *Thomomys bottae*; 16, *Thomomys talpoides*; 17, *Thomomys townsendii*; 18, *Urocitellus* spp.

small-mammal communities would show a proportional increase in both the presence and dominance of species with a southern geographic affinity, as temperate species shifted poleward and species with environmental tolerances conducive to warming conditions increased in abundance. Consistent with these community-scale predictions, we see both a higher proportion of southern species and an increased dominance of southern individuals during periods of increased tem-

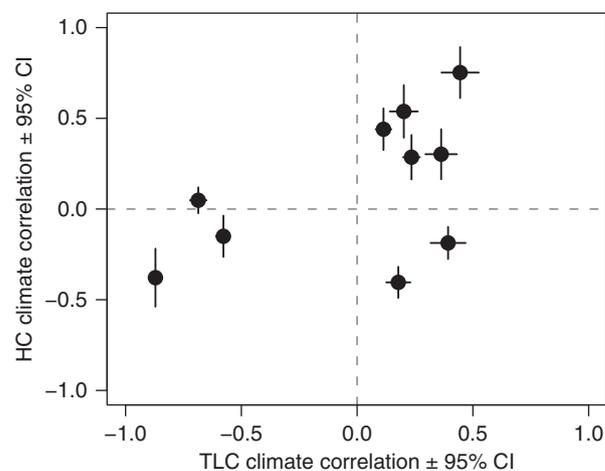


Fig. 4 Correlation cross-plot for shared species at Two Ledges Chamber (TLC) and Homestead Cave (HC). Points represent the correlation of each species' abundance dynamics with climate, averaged across all windows of time averaging (see main text).

perature and aridity at both TLC and HC, despite asynchronous local climate histories. At both sites, stronger correlations were seen between climate and community dominance indicating that the primary response of these communities occurred *in situ* via increases in the population sizes of resident species (Fig. 2). This supports the recent finding by Blois *et al.* (2010) that the abundance structure of a community is likely to shift before changes in species composition become manifest. Recovering a weaker pattern at HC is not surprising given the shorter species list, fewer time intervals available for analysis, and greater distance between this site and the available paleoclimate record. Despite these factors, emergence of this general pattern at two independent sites strengthens the prediction that we can expect point localities to show a trend of increasing dominance by southern-sourced individuals with warming in the future.

The conservative inclusion of genus-level identifications did not affect our results with respect to geographic affinity, as the most likely constituent species identities would not have altered our categorization. *Urocitellus* spp. specimens are likely *U. mollis* (see Grayson, 2000b), having no northern or southern affinity with respect to TLC and HC. *Microtus* spp. specimens are either *M. montanus* or *M. longicaudus*, both of which have a northern geographic affinity. *Peromyscus* spp. specimens likely represent *P. maniculatus* (see Terry, 2010b), a species with no northern or southern affinity. Alternative categorization of *Peromyscus* spp. specimens into *P. boylei*, *P. crinitis*, or *P. truei* would only strengthen our observed results as all have southern geographic affinities. Finally, the *Mustella* spp. specimens at TLC

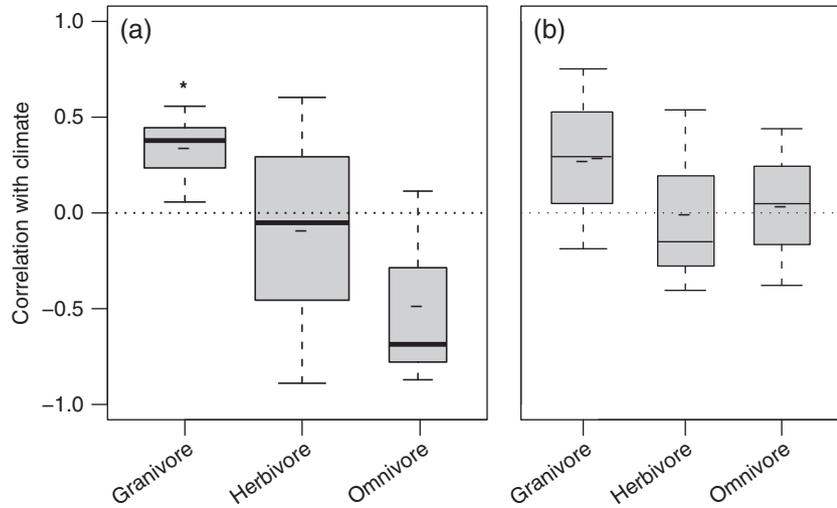


Fig. 5 Correlation of abundance dynamics with local climate for dietary functional groups at (a) Two Ledges Chamber (TLC) and (b) Homestead Cave (HC). Boxplot width scaled by sample size ($n = 3-8$). *Mean correlation significantly different from 0 at $\alpha = 0.05$.

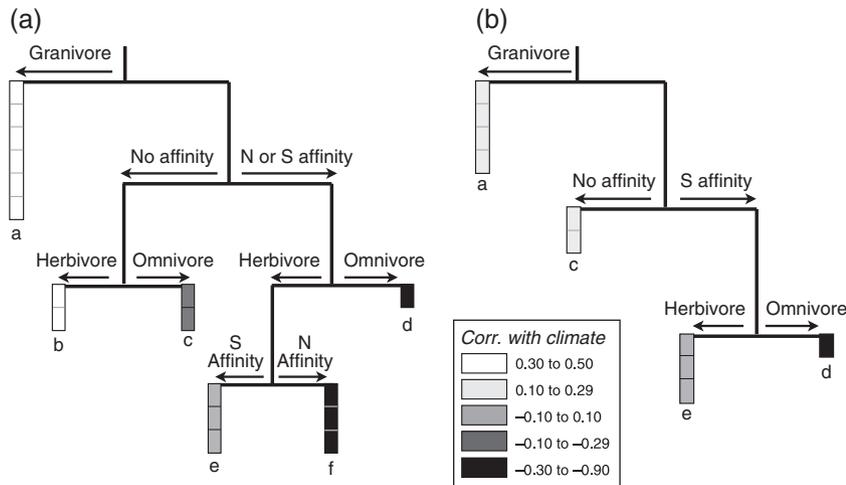


Fig. 6 Regression tree analysis reveals the same hierarchical importance of predictor variables at Two Ledges Chamber (TLC) (a) and Homestead Cave (HC) (b). Tree branch lengths are scaled by the number of species in each association (from $n = 1$ to 6) and colored by mean abundance-climate correlation strength. Species associations are also remarkably consistent between caves and are denoted by lower case letters. (a) TLC $r = 0.34$, HC $r = 0.29$; *Chaetodipus formosus*, *Dipodomys merriami* (present at TLC only), *D. ordii*, *Microdipodops megacephalus* (present at TLC only), *Perognathus longimembris*, *Reithrodontomys megalotis*. (b) Present at TLC only, $r = 0.49$; *Lemmys curtatus*, *Thomomys talpoides*. (c) TLC $r = -0.27$, HC $r = 0.24$; *Peromyscus* spp., *Uroditellus* spp. (d) TLC $r = -0.87$, HC $r = -0.37$; *Ammospermophilus leucurus*. (e) TLC $r = -0.066$, HC $r = -0.0058$; *Dipodomys microps*, *Neotoma lepida*, *Thomomys bottae*. (f) Present at TLC only, $r = -0.50$; *Microtus* spp., *Neotoma cinerea*, *Thomomys townsendii*. Total variance explained: TLC $r^2 = 0.80$; HC $r^2 = 0.44$.

are rare (occur in <4 strata), thus do not influence community-level results and were not included in the species-level analyses.

Understanding the generality of this community-level pattern requires comparison across multiple systems and taxonomic groups. Unfortunately the current literature provides few comparative standards, as the use of fossil community data with the approach we present is novel. We can gain some insights from a

recent study by Myers *et al.* (2009), where 30 years of climatic warming in the northern Great Lakes region has resulted in a small-mammal community increasingly dominated by species and individuals with a southern geographic distribution. These decadal-scale changes are consistent with expectations under climate warming (Parmesan, 2006) and mirror our centennial-scale results. However, anthropogenic land-use within the last century can confound patterns of community-

change as evidenced by a recent study of small-mammal communities in the mountains of Utah. Despite a century of climatic warming in this system, Rowe (2007) documented counterintuitive increases in the abundances of mesic species (many of which have more northern geographic distributions), associated with a release from grazing pressure.

Fossil data permit us to step back before the anthropogenic land-use impacts of the last century. Thus our predictions more closely represent climate-only scenarios. Counter to the climate-driven patterns detected by Myers *et al.* (2009), we found that abundance dynamics at the species level were not well explained by geographic affinity at either site (Fig. 3). The community-level increase in the proportional dominance of southern species with warming that we detect at TLC and HC thus results from a complex interplay between increasing abundances of some taxa and decreasing abundances of others. Species having southern affinities at TLC exhibited correlations in species-level abundance dynamics and climate that ranged from strongly positive (abundance increases as climate warms) to strongly negative (abundance decreases as climate warms). Furthermore, some of the species most strongly correlated with climate (e.g. *A. leucurus*) responded in the opposite manner as predicted by their geographic affinity at both sites (e.g. southern geographic affinity but inverse response to climate warming).

This loss of predictability at the species level could be caused by the canceling out of individual species responses to climate. Yet we see the same scale-dependent loss of predictability at the two independent sites, suggesting that aspects of species autecology not captured by geographic affinity are also controlling their response. We find further support for this hypothesis when we compare the abundance-climate correlations of species shared between the two independent sites (Figs 4 and 6). While the strength of the correlations between abundance and climate vary, shared species generally show concordant responses to climate at TLC and HC in both sign and magnitude. Thus despite the idiosyncratic signal of species responses to climate within a site, across-site responses to climate are remarkably consistent within a species. This result is surprising given that these two sites represent independent local communities with independent sets of interacting species that differ in their identities and abundances. Furthermore, it suggests that the intrinsic life history of a species may exert a more powerful control on response to climate than local interactions.

This finding resonates with other paleontological investigations focused on large-mammal communities in North America. Graham *et al.* (1996) and Lyons (2003) showed that species' geographic ranges shifted in

different directions and at different rates in response to environmental fluctuations at the end of the Pleistocene. This resulted in communities with no modern analogues. The individualistic responses of species implies that mammal communities are unpredictably emergent and stresses the importance of autecology in explaining how species respond to environmental change.

Clearly the meso-scale variable of geographic affinity by itself does not fully explain individual species' responses to climate warming. But to what degree does geographic affinity interact with species' biology to drive the community-level patterns we observe? Analysis of dietary functional group at the species level reveals higher within-site consistency in explaining species' responses to climate at TLC (Fig. 5). Granivores show a strong mean positive correlation with climate ($r = 0.34 \pm 0.14$), while omnivores show a nonsignificant negative correlation ($r = -0.48 \pm 0.59$; Fig. 5). At HC this pattern is less clear due to a shorter species list and fewer time intervals under analysis. As with geographic affinity, genus-level functional group categorization of *Microtus* spp., *Mustela* spp., *Peromyscus* spp., and *Urocyon* spp. has no effect on the results or interpretations due to the functional similarity of the potential congeneric species within each group.

Recursively partitioning the correlation between each species' abundance dynamics and climate revealed the same hierarchical causal structure and species groupings at both sites (Fig. 6). Recovery of this structure at sites with independent Holocene climate histories that share some, but not all, of their species is remarkable, indicating that the interactions between dietary functional group, geographic affinity, and climatic change are relatively consistent regardless of local-scale interspecific interactions within each separate community.

The emergence of granivorous life history as the most important consideration for species responses to climatic change in this desert system suggests that the indirect feedback between small mammals and climate-mediated plant dynamics can be more important than direct physiological responses to warming for many of these animals. This supports the finding by Hadly (1996) in a temperate forest system (Yellowstone National Park) that life history plays an important role in determining abundance changes for species that show strong habitat associations. Granivores are particularly diverse in the deserts of western North America (Kelt *et al.*, 1996), exerting a keystone influence on the structure and dynamics of desert plant communities through seed predation and dispersal (Brown & Heske, 1990; Heske *et al.*, 1994). Seeds can persist in desert soils for long periods of time, avoiding desiccation while waiting for conditions conducive for germination

(Chambers & MacMahon, 1994). Thus seeds represent an abundant source of food and water for granivores that are consistently available during periods of increased aridity (Brown *et al.*, 1979; Brown & Harney, 1993), potentially allowing their populations to thrive while other small-mammal species decline.

Forecast for the future

Our results provide insight into the dynamics of small-mammal communities from times before the onset of intense anthropogenic modification of both the climate and the landscape. They thereby highlight the unique contributions the fossil record can make towards understanding the baseline conditions and dynamics of natural systems. Climatic change in the Great Basin is underway (Beever *et al.*, 2010). Recent 50-year climate projections for the Great Basin suggest that mean annual temperatures will warm by $\sim 2^\circ\text{C}$ while mean annual precipitation will decrease by 100 mm (Leung *et al.*, 2004). Our results show that while we can expect to see some southern species moving northward, the bulk of future community responses to climatic warming will manifest as an increase in the dominance of species with a southern affinity that are already present. However, not all southern species will show this response because it is mediated by species autecology – specifically, a granivorous life history. Based on fossil evidence and species biology, we would expect granivorous species to thrive under a future of warmer and drier conditions in the Great Basin, independent of their geographic affinity. At the same time, we also expect species with a northern geographic affinity or an herbivorous diet to decline or show minimal response to climatic warming.

Despite the utility of the fossil record for making predictions, as we look to the future it is imperative that we also consider the multitude of novel anthropogenic impacts that have shaped the Great Basin landscape over the last century. Of particular relevance is the introduction and spread of the exotic annual cheatgrass (*B. tectorum*). First observed in the late 1800s, this invasive species is now recognized as a major threat to the stability of desert ecosystems, converting sagebrush communities to annual rangelands and covering $\sim 40\,000\,000$ ha of the intermontane west (Knapp, 1996; Novak & Mack, 2001; Rimer & Evans, 2006; Bradley, 2009).

Recent work has shown that this invasion negatively impacts Great Basin granivores: populations show dramatic declines in both species richness and overall abundance following cheatgrass invasion (Gitzen *et al.*, 2001; Ostoja, 2008; Larrucea & Brussard, 2008). Furthermore, manipulative experiments have shown

that granivores prefer seeds from native annual and perennial grasses over cheatgrass seeds (Ostojka, 2008). Kelrick *et al.* (1986) suggest a plausible mechanism for this result: cheatgrass is covered in nonnutritive tissues with persistent awns, resulting in increased handling time and decreased foraging efficiency. It has also been suggested that the decline in granivorous rodents following cheatgrass invasion may be due to a loss in structural complexity of the vegetation (thus loss of microhabitats) coupled with increased difficulty navigating the thick herbaceous cover of annual grasses (many granivores use bipedal saltatory locomotion) (Gano & Rickard, 1982; Gitzen *et al.*, 2001).

While cheatgrass thrives in the wake of landscape disturbances (e.g. fires), the spread of cheatgrass is primarily controlled by precipitation (Bradley, 2009). Given climate projections of increased aridity in the Great Basin over the coming century, the geographic extent of cheatgrass will continue to expand, with estimates suggesting an increase in invulnerable area by 45% by 2100 (Jones & Monaco, 2009). This poses a major threat to small-mammal biodiversity in the Great Basin. Based on insights from the fossil record, under a climate-only scenario, we would expect granivorous species to thrive over the coming century. But the habitat degradation caused by cheatgrass invasion preferentially impacts granivores, indicating that the group predicted to thrive in the coming century is actually threatened as well.

In summary, while general predictions based on geographic affinities are powerful and relevant at the community scale in this system, knowledge of species' life history allows us to refine and better inform species-specific conservation practice in light of our warming future. The Holocene perspective offered by the fossil record provides a unique and highly valuable context for modern studies conducted at annual to centennial temporal scales. It is within such a historical comparative framework that we can highlight groups of specific conservation concern and begin to address the degree to which the chronic and pervasive combinations of anthropogenic climate change and habitat degradation differ from anything experienced by biotic systems in the recent past.

Acknowledgements

We thank D. K. Grayson and B. Hockett for access to specimens and data from Homestead Cave and Two Ledges Chamber, respectively. We also thank L. Benson for paleoclimate data from Pyramid Lake and S. A. Reinemann for paleoclimate data from Stella Lake. M. Novak, R. Rowe, P. Harnik, A. Rominger and the Hadly lab greatly strengthened this project through many helpful discussions and comments on drafts. We also thank three anonymous reviewers for their insightful comments and

suggestions. Finally, we thank M. Novak and S. Wang for statistical advice. This research was supported by a NOAA Climate and Global Change Postdoctoral Fellowship to R. C. T., administered by the University Corporation for Atmospheric Research.

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