Energy flow and functional compensation in Great Basin small mammals under natural and anthropogenic environmental change

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Edited by Stephen T. Jackson, US Geological Survey, Tucson, AZ, and accepted by the Editorial Board June 16, 2015 (received for review December 18, 2014)

Research on the ecological impacts of environmental change has primarily focused at the species level, leaving the responses of ecosystem-level properties like energy flow poorly understood. This is especially so over millennial timescales inaccessible to direct observation. Here we examine how energy flow within a Great Basin small mammal community responded to climate-driven environmental change during the past 12,800 y, and use this baseline to evaluate responses observed during the past century. Our analyses reveal marked stability in energy flow during rapid climatic warming at the terminal Pleistocene despite dramatic turnover in the distribution of mammalian body sizes and habitat-associated functional groups. Functional group turnover was strongly correlated with climate-driven changes in regional vegetation, with climate and vegetation change preceding energetic shifts in the small mammal community. In contrast, the past century has witnessed a substantial reduction in energy flow caused by an increase in energetic dominance of small-bodied species with an affinity for closed grass habitats. This suggests that modern changes in land cover caused by anthropogenic activities—particularly the spread of nonnative annual grasslands—has led to a breakdown in the compensatory dynamics of energy flow. Human activities are thus modifying the small mammal community in ways that differ from climate-driven expectations, resulting in an energetically novel ecosystem. Our study illustrates the need to integrate across ecological and temporal scales to provide robust insights for long-term conservation and management.

Significance

Small mammals play a critical role in the maintenance of desert ecosystems. Using Quaternary fossils from the Great Basin, we show that energy flow through a small mammal community during today’s heightened climate warming differs from that experienced during natural rapid warming in the past. This discrepancy highlights a modern breakdown in energetic compensation among functional groups, and stresses the importance of novel anthropogenic impacts, such as the replacement of shrublands by invasive annual grasses introduced to North American deserts more than a century ago. Use of the fossil record to untangle the effects of climate and anthropogenic habitat change on ecosystem function today is thus critical for understanding how ecosystems will respond to future environmental change.

Author contributions: R.C.T. and R.J.R. designed research; R.C.T. performed research; R.C.T. analyzed data; and R.C.T. and R.J.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. S.T.J. is a guest editor invited by the Editorial Board.

See Commentary on page 9504.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1424315112/-/DCSupplemental.
closed grass habitats. Modern land cover change caused by anthropogenic activities and the associated expansion of nonnative annual grasslands is thus changing how energy flows through this community in ways that deviate from its climate-driven dynamics of the past.

Results
The Great Basin has experienced a dynamic Quaternary history set against a unique physiography. At the height of the last glacial maximum (ca. 20,000 y BP), vast pluvial lakes covered much of the Basin’s low-elevation valleys, whereas montane regions were connected by forest and sagebrush-steppe vegetation (8). Analysis of packrat middens and pollen cores from the Bonneville Basin have shown that rapid warming at the end of the Pleistocene (punctuated by the Younger Dryas) drove a regional shift in vegetation. Pluvial lakes contracted, conifers and sagebrush-steppe habitats retreated upslope, and xeric adapted plant communities dominated by shadscale (*Atriplex* spp.) and greasewood (*Sarcobatus* spp.) expanded in the now warm and dry low-elevation valleys. Small mammals, known to play critical roles in Great Basin ecosystems through their maintenance of plant communities and as a prey base for an array of predators, tracked this environmental change closely (11–13).

Homestead Cave sits west of the modern Great Salt Lake and was formed by wave incision from Pleistocene Lake Bonneville (14). With the lake’s rapid retreat ca. 13,500–12,000 y BP (8, 15), the cave became an owl roost site (14, 16). Owls regurgitate pellets that include the undigested bones of their small-mammal prey. Roost sites that remain active for millennia, like Homestead Cave, thus accumulate a layered buildup of skeletal remains through time. Such deposits represent unparalleled ecological archives that reflect the living community from which skeletal remains were drawn with high fidelity (17).

Sample-size standardized total energy flow through the small mammal community (23 species weighing < 500 g; Table S1) remained remarkably constant at Homestead Cave from the end of the Pleistocene (ca. 12,800 y BP) through the Holocene to the Modern (A.D. 1905; Fig. 1A). Despite overall stability in energy flow, functional turnover occurred at ca. 11,000 y BP among body size groups: energy flowing through species in the largest and smallest size classes decreased but was compensated for by an increase in energy flowing through species in the middle size classes (Fig. 1B). Turnover across the end Pleistocene to early Holocene transition is also apparent when species are categorized functionally by their habitat and dietary associations. That is, a loss in energy flowing through mesic habitat specialists was offset by a compensatory increase in the energy flowing through xeric habitat specialists (Fig. 1C). In contrast, herbivores remained the dominant functional contributor to energy flow across this environmental transition (Fig. 1D). This stability occurred despite shifts in the species and individual body size distributions of herbivores toward smaller sizes (Fig. S1A), and despite a 40% replacement of the species within the herbivore guild. It was caused by an abundance/body size tradeoff, as the shift toward smaller herbivore species (e.g., *Dipodomys microps* and *Neotoma lepida*) was compensated for by an increase in the abundance of herbivores (Fig. S1B).

Cross-correlation analysis with global ($\delta^{18}O$ record) (18) and regional (Great Salt Lake pollen core) (15) environmental proxies indicate that changes in energy flow through the small mammal community were tightly associated with the rapid climate-driven environmental change of the terminal Pleistocene (all $r > 0.89, P < 0.001$; Fig. 2A–C and Tables S2 and S3). Energy flow through xeric-adapted specialists and intermediate body sizes increased as the climate warmed and dried and xeric habitats became increasingly available. However, the response of the small mammal community was not instantaneous, lagging behind changes in regional vegetation and global climate on the order of 185–230 and 350–600 y, respectively (Tables S2 and S3). At the local scale, energy flowing through mesic-adapted small mammals was tightly correlated with the proportion of fish found in the Homestead Cave record [a proxy for the proximity of Lake Bonneville (19); $r = 0.83, P = 0.002$; Fig. 2D and E].

In contrast to the stability of energy flow and functional group turnover of the terminal Pleistocene, energy flow within the past century declined markedly (Fig. 1A). This decline was associated with a shift in species and in individual body size distributions
to toward smaller sizes, with little to no compensation from other size classes (late Holocene individual mean, 83.8 g; Modern individual mean, 46.3 g; Figs. 1B and 3A and B and Fig. S2 A and B). Furthermore, the largest size class disappeared from the record entirely by this time. Although the energy flowing through the smallest size class showed a small increase in the past century, it has not compensated for the loss of energy flowing through the intermediate size classes that were dominant for most of the Holocene. Simultaneously, there has been a decrease without compensation in the energy flowing through herbivores and xeric habitat specialists, also differing from the dynamics seen at the terminal Pleistocene (Fig. 1 C and D). As with body size, although there has been a small increase in the energy flowing through granivores, it is insufficient to offset the losses seen among herbivores (Fig. 1D).

It is worth noting that the proportional amount of energy allocated to the smallest size class and the granivores today is much higher than it has ever been since the late Pleistocene. Recategorizing species at Homestead Cave based on their tendency to thrive in closed grass vs. open shrub-dominated habitats brings this distinction into focus: the past century has witnessed an energetic dominance as temperatures increased in the early Holocene. It also suggests mechanisms for the recent breakdown of this compensation.

In general, metabolic theory predicts that smaller body sizes (greater surface area-to-volume ratios) are advantageous under higher temperatures because of an increased capacity for heat dissipation (22, 23). The decline in energy flowing through the largest size class at the terminal Pleistocene at Homestead Cave conforms to this expectation. Theory and experiments also suggest that the smallest of species may be at a disadvantage under warming as a result of size-dependence in the width of their thermal neutral zone (TNZ) and their rates of evaporative water loss. This, too, is consistent with the observation at Homestead Cave that the intermediate size classes, not the smallest, rose to energetic dominance as temperatures increased in the early Holocene. Although mammals of all sizes tend to have similar upper critical temperatures at which their metabolism increases to dissipate heat to the environment, the lower critical temperature at

**Discussion**

Climate-Driven Environmental Change and Energetic Response in Small Mammals. The literature on the temporal dynamics of energy flow and functional compensation is limited to modern-day ecological studies spanning at most several decades (3, 4, 6, 20), with only one historical snapshot comparison extending back to a century (5). This is despite the urgent need to understand natural variability and establish baselines against which to evaluate ecosystem function in today’s rapidly changing world (21). The wealth of ecological information recorded in Quaternary paleontological archives allows us to track energy flow through small mammal communities over much deeper time scales, enabling the decoupling of biotic responses to environmental change driven by natural climatic forcing from those driven by a century of novel anthropogenic impacts.

Modern ecological studies interpret energy flow as a direct reflection of total resource availability because their data typically are standardized by sampling effort (2, 3, 5). In contrast, paleontological data from modern, subfossil, and fossil specimens are standardized by sample size. Estimates of energy flow at Homestead Cave therefore cannot be interpreted as a direct reflection of absolute resource availability. This limits direct comparison with modern ecological studies, but nonetheless provides insight into the compensatory dynamics of community functional structure and the contribution of individual and species body size distributions to sample-standardized energy flow. The consideration of metabolic theory, a century-scale resurvey of small mammals in a Great Basin mountain range (5), and decadal-scale studies of granivorous rodents at the Portal long-term ecological research site in Arizona (20) offers hypotheses for the mechanisms controlling the functional compensation and energetic stability exhibited by Homestead Cave’s small mammals across the terminal Pleistocene environmental transition. It also suggests mechanisms for the recent breakdown of this compensation.

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**Fig. 2.** The temporal alignment of energetic turnover by habitat group with environmental proxies from global to local scales. (A) δ18O global climate proxy from the North Greenland Ice Core Project (18). (B) Regional pollen core record from Great Salt Lake (14, 15) expressed as the percentage of xeric pollen species. Energy flow through xeric (C) and mesic (D) habitat specialist small mammals. (E) Temporal dynamics of fish remains found in the Homestead Cave record (19) reflect the proximity of Lake Bonneville’s shoreline. Turquoise line represents the proportion of fish in the Homestead Cave record; gray line represents the absolute count of fish specimens (i.e., NISP), ranging from 0 to 5000.

**Fig. 3.** Body size distributions expressed as probability densities reveal a shift through time toward smaller species (A, reflecting community composition) and individuals (B, reflecting composition and abundance). Each line represents an individual stratum, color-coded by time.
which thermoregulatory heat production increases to compensate for heat loss occurs at higher ambient temperatures as body size decreases (24). This results in smaller species having narrower TNZs than larger species (23, 24). Furthermore, small species must also increase metabolism at a faster rate than larger species when ambient temperatures extend beyond their TNZ, and lose water proportionally faster above their upper critical temperature (23, 25). Thus, small species are more susceptible to evaporative water loss than their larger counterparts. The fact that the rate of decline in energy flowing through the smallest body sizes across the terminal Pleistocene boundary is slower than the rate of decline for the largest body sizes ($F = 36.6, P < 0.001$) adds support to the idea that such distinct mechanisms may be driving the energetic responses of end-member body-size classes.

Alternatively, because of their narrower TNZ, smaller-bodied species may also be more susceptible to climate variability. Temperature seasonality near Homestead Cave has been inferred to be highest at the terminal Pleistocene, declining monotonically thereafter throughout the Holocene (26). The dramatic changes in small mammal energy flow ca. 11,000 y BP thus appear unlikely to have been driven by this seasonality trend given that peak seasonality occurred before the energetic restructuring of the mammal community, and that energy flow stabilized for the rest of the Holocene despite a continued decline in seasonality.

In addition to metabolic constraints, competition may have played a role in driving the restructuring of energy flow through Homestead Cave’s small mammals at the terminal Pleistocene. The increase in energy flowing through xeric specialists across this transition is consistent with the documented expansion of xeric habitats through time (8), and includes the xeric-adapted kangaroo rats (Dipodomys spp.), which are intermediate in size. Decades of experiments in the deserts of the Southwest have shown that kangaroo rats are competitively dominant over smaller species, resulting in a strong partitioning of resources by body size (27, 28). Thus, it is possible that a chance association between habitat affiliation and body size may have substantially altered the community’s framework of biotic interactions in a way that suppressed smaller-bodied species.

Our use of multiple paleoenvironmental proxy records spanning global to local scales suggests that lags of several hundred years occurred between the global climate system ($\delta^{18}O$), the regional habitats (pollen), and the energetic restructuring of the local small mammal community (Tables S2 and S3). Climate variability superimposed on the warming trend at the terminal Pleistocene may have moderated the long-term demographic responses of xeric-adapted plant and small mammal species, thereby slowing the rate at which these communities shifted in response (29). Alternatively, the apparent lags could reflect a temporal offset between global and regional climates, or an artifact of differing chronology reconstructions and temporal resolutions of the records. However, the chronology of Homestead Cave is among the best-resolved in North America and is not suggestive of a systematic bias that could account for this lag (30). Furthermore, the lag between the decline of fish remains at Homestead Cave and the small mammal energy flow (Fig. 2 D and E) reinforces the hypothesis that the apparent lags between small mammals, regional habitats, and the global climate are not artifactual.

### Have Human Activities Yielded an Energetically Novel Ecosystem?

Many of today’s ecosystems have departed from their historical trajectories (31). Such novel ecosystems pose a challenge for conservation and management. The decrease in total energy flow, the increase in energy flowing through small quadrupedal grass-affiliated species, and the lack of functional compensation over the past ca. 100 y at Homestead Cave stand in stark contrast to the dynamics seen in this community’s Quaternary past. These changes are evident despite an apparent stability in the species list, showing that ecological novelty can arise at multiple ecological levels. The coincidence of this Modern shift in energy flow with changes in land cover parallels experimental, observational, and historical resource work in implicating an anthropogenic fingerprint that extends beyond the effects of recent climate change.

Evidence that the legacies of anthropogenic land cover change have shifted energy flow over the past century in the Great Basin can be seen in the modern and historical small mammal communities of the Ruby Mountains in Nevada (5). Like Homestead Cave, this system experienced declines in energy flow through herbivores and xeric specialists over an ca. 80-y interval, despite substantial warming. These shifts occurred across the entire elevational gradient, implicating a primary role for climate change (5). However, declines were greatest at low elevations most comparable with the desert community of Homestead Cave. The fact that these low elevations also experienced the highest levels of anthropogenic impact (10) suggests a strong secondary contribution of human habitat alteration (5).

Given the wave of invasive plant species that has swept across the Great Basin in the past century, it is possible that today’s habitats provide lower-quality resources than did habitats of the past (32, 33). Thus, climate-driven habitat restructuring at the terminal Pleistocene may have preserved overall ecosystem productivity, while anthropogenically driven habitat conversion today has decoupled productivity from climate. Foremost among these invasions has been the introduction and spread of cheatgrass (Bromus tectorum) in the late 1800s. Invasion of this drought-tolerant exotic annual has resulted in myriad direct and indirect effects, most notably an increase in the frequency, severity, and size of wildfires (9). Furthermore, as an annual, cheatgrass can outcompete native perennials, reducing plant diversity and homogenizing vegetation cover (10). The collective effects of this invasion in the Great Basin are transforming native shrublands into annual grasslands dominated by exotic species (9).

Small mammal communities are directly impacted by this invasion as a result of the resulting alteration of habitat structure from one that is open to one that is closed (32, 33). Although grasses were certainly present and often abundant in the Holocene shrublands of the northern Bonneville Basin, they were perennial native bunch grasses that maintained an open habitat structure (7, 9). Open habitats have long been known to favor larger heteromyid species such as kangaroo rats (Dipodomys spp.) because of their bipedal locomotion and other adaptations for predator avoidance (34). Other studies have shown that closed habitats shift the competitive advantage to smaller quadrupedal species. For example, work at Portal indicates that a precipitation-driven closing of habitats caused a shift in the body size distribution of granivorous small mammals from a mean individual size of 73.4 to 33.7 g over a 24-y time period (3). Reider et al. (35) have shown that, although cheatgrass significantly reduces sprint speed for all species, this is disproportionately so for larger saltatory species. Furthermore, Lightfoot et al. (36)
have recently shown that species affiliated with natural annual grasslands in the Chihuahuan desert exhibit greater reproductive potential, and thus faster population responses to changes in resources, than shrub-affiliated species. Thus, although cheatgrass appears to negatively impact most if not all small mammal species (32, 33), small, grass-affiliated quadrupedal species might be expected to prosper compared with their larger and/or shrub-affiliated counterparts.

The recent dynamics of other species at Homestead Cave are consistent with a propagation of indirect effects driven by biotic interactions within the small mammal community, rather than the direct effects of land cover change. For example, Chaetodipus formosus (a small quadrupedal granivore) shows a recent increase in its contribution to energy flow. This increase is unlikely the direct result of altered plant communities by virtue of C. formosus’ primary association with rocky substrates. Manipulative experiments at Portal have shown Chaetodipus spp. to increase in abundance in the absence of kangaroo rats (27, 37). Other species exhibiting increases at Homestead Cave (e.g., R. megalotis and P. maniculatus) have also been shown to increase when kangaroo rats are experimentally removed (37). Thus, in addition to recent changes in land cover favoring small grass-affiliated quadrupeds, the increase in energy flowing through these species may also be caused in part by competitive release via a reduction in energy used by bipedal kangaroo rats.

Conclusions
Paleoecology provides a much-needed framework for evaluating natural variability and past responses to environmental change. Importantly, data from the fossil record can be compiled across all levels of ecological organization, enabling a comprehensive understanding of biotic response. As such, fossils are increasingly recognized for their unique role in conservation, especially in evaluating the health of modern systems, forecasting changes in biodiversity, and disentangling the relative roles of natural and anthropogenic drivers in structuring modern systems (38).

The small mammal community at Homestead Cave shows compensatory dynamics among functional groups that stabilized energy flow over millenial timescales, even during the rapid climate-driven habitat restructuring of the terminal Pleistocene. The dynamics of energy flow seen over the past century stand in contrast to this climate-driven habitat restructuring, and are instead consistent with an anthropogenically driven change to vegetation structure that favors species that thrive in closed, grass-dominated habitats. The Modern Great Basin ecosystem thereby deviates substantially from Quaternary baseline conditions and from climate-based expectations. How widespread this alteration of energy flow is across other ecosystems is unknown. However, grass invasions are not unique to the Great Basin, having occurred in all of North America’s deserts in the past century (39, 40). The establishment of novel plant communities, altered fire regimes, and thus altered ecosystem function is therefore likely to be common across these arid and semiarid environments. These observations underscore the need to incorporate projections of anthropogenic habitat conversion, in addition to climate, into predictions of biotic change.

Conservation paleobiology aims to inform the establishment of baseline targets by tapping into natural archives that record the ecological range of conditions before the onset of today’s intense anthropogenic impacts (1). However, such efforts alone may fail to recognize that anthropogenic impacts in the recent historical past have strongly shaped Modern ecosystems, pushing them beyond their natural ranges and thus limiting the utility of paleontological insights to future conservation. Conversely, neontological efforts to establish baselines within the historical past may fail to recognize the already degraded state of their conservation targets and the limited range of environmental conditions these shorter timescales encompass (21). Only by merging historical and deeper-time perspectives can we evaluate the dynamics of the past and the present to recognize the ways in which rapid climate change and anthropogenic stressors interact to shape today’s ecosystems. This integration of temporal scales will be essential for anticipating and effectively managing the novel ecosystems that are bound to shape in the coming decades.

Methods
Study System. The Homestead Cave record consists of 18 strata, with ca. 184,000 identified skeletal specimens (11, 14). Specimens are primarily derived from owl pellets, representing regurgitated prey remains that accumulated beneath a long-term roost site (11). Deposition has been relatively continuous, with the geochronological framework spanning the past ca. 12,800 constrained by 101 accelerator MS (AMS) 14C dates (14, 30). Modern samples (1,186 identified specimens representing ca. 100 y of deposition) were collected from the surface of the cave from 2004 to 2006 (41) and dated by AMS 14C. Dates were converted to calendar years standardized to the year A.D. 1950 by using OxCal 4.1 (42) and the IntCal 09 calibration curve (43).

Specimens were identified by using measurements and morphological comparisons to reference material (11, 41). We limited the analysis to species < 500 g to minimize potential bias on the part of the owls. Larger prey, such as lagoophilous and typically not consumed whole (44), and thus have a reduced probability of entering the fossil record. We also restricted our analysis to craniodental elements because not all postcranial bone types were identified for all species. Only two of the 23 taxa (Microtus spp. and Peromyscus spp.) could not be identified to species as a result of great similarity in the skeletal elements of congenerics. Thus, Microtus spp. contains two possible species of equivalent body size and functional categorization, and Peromyscus spp. contains as many as three possible species of equivalent body size. Although Peromyscus spp. could differ in their habitat affinities, specimens are likely dominated by P. maniculatus [the most widespread generalist found in North America and the only Peromyscus species caught near Homestead Cave in recent trapping surveys (41)] and thus were categorized as such.

Accounting for Taphonomy. Paleoecological reconstructions require an assessment of the sources, magnitudes, and directions of bias. By using characteristic damage patterns as a taphonomic fingerprint, Terry (16) identified that assemblages of small mammals at Homestead Cave were produced by large-bodied nocturnal owls throughout its depositional history. “Live/dead” comparisons have also shown that the ecological information recorded in the cave’s deposits is highly representative of the living system from which specimens are drawn in regard to richness, evenness, and the proportional abundance structure of the community (41). High ecological fidelity confirms the utility of such fossil data for establishing ecological baselines and assessing community dynamics through time.

Estimating Energy Flow. We generated abundance estimates (N) using the number of identified specimens (NISP) per species per stratum, sample-size standardized to the smallest stratum using iterative subsampling without replacement (10,000 iterations, 41). Energy-flow estimates were calculated separately for each species as \( E_i = a N_i M_i b \) (Fig. 5), where \( a \) and \( b \) are allometric parameters and \( M_i \) is a species’ average mass [Macroecological Database of Mammalian Body Mass (MOM), version 4.1 (45)]. We used the theoretically predicted scaling exponent of \( b = 3/4 \) (46) and \( a = 5.69 \) for rodents based on the field metabolic rates from Nagy et al. (47) reft with a scaling exponent of 3/4 (3). Estimates of energy flow are expressed as a rate (kilojoules per day) and account for the fact that individuals of small body size use more energy per unit mass than do large individuals.

Our analyses did not directly account for potential intraspecific shifts in body mass through time. Considerable heterogeneity in the direction and magnitude of individual size responses of vertebrates to climate warming is evident, especially among rodents (23). We therefore assumed that any such shifts were of minor importance relative to turnover in species composition and abundance structure. An exception is the genus Neotoma, which exhibits a tight body mass-temperature relationship (22). We thus repeated our analysis scaling Neotoma cinerea and N. lepida body size by time period (22), but found no qualitative change in the energy flow patterns (Figs. 53 and 54).

Data Analysis. We evaluated species and individual body size distributions through time by using kernel density plots (Gaussian kernel with nd=0

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Each proxy was temporally aligned with the Homestead Cave record by spline smoothing functions (R-function: spline, method=mono.H.FC) before analytically time-averaging it to a symmetric moving window (ranging from 0 to 500 y) around the age estimate for each stratum. We then cross-correlated each pair of time series to determine the strength of the relationship between proxies and the energy flow of small-mammal habitat and body size groups, assessing significance by using permutation tests. The magnitude of temporal lags was determined by shifting the δ¹⁸O and pollen core records by 1-y increments relative to the Homestead Cave record, each time refitting the core records with a time-averaged spline and retesting the cross-correlation. Lag analysis was not performed for the fish proxy data because the number of time points in the fish record is equal to the number of time points in the small mammal record. The magnitude of the assumed time-averaging window did not qualitatively impact our results or change determinations of significance (Tables S2 and S3).

ACKNOWLEDGMENTS. We thank D. K. Grayson and D. B. Madsen for access to the Homestead Cave database; Hill Air Force Base and the Utah Test and Training Range for access to Homestead Cave; and M. Novak, J. H. Miller, E. A. Rickart, two anonymous reviewers, and the manuscript editor for comments that strengthened the quality and clarity of this manuscript. Collection of modern specimens and AMS ¹⁴C analysis was funded by National Geographic Society Grant CRE 8173-07 (to S. Kidwell and R.C.T.) and the Departments of Integrative Biology at Oregon State University (R.C.T.) and Coalition Resources and the Environment at the University of New Hampshire (R.J.R.).

Fig. S1. (A) The mean species (black) and individual (gray) body sizes of herbivores decreased from the late Pleistocene to the Modern. The early Holocene decrease in body sizes was compensated for by an increase in mean herbivore abundance (B). The low contribution of herbivores to energy flow in the Modern (Fig. 1D) resulted from the combination of small body sizes and low abundances. Box plots represent the median and upper and lower quartiles, with box plot width proportional to sample size. Whiskers include the most extreme values within 1.5 times the interquartile range.
**Fig. S2.** Mean species and individual body size for the Homestead Cave small mammal community from the late Pleistocene to the Modern. (A) Mean species body size peaks in the middle Holocene, followed by a marked decrease into the Modern. In contrast, mean individual body size (B) remains relatively constant through the Holocene, but exhibits a dramatic decrease in the Modern. Box plots represent the median and upper and lower quartiles, with box plot width proportional to sample size. Whiskers include the most extreme values within 1.5 times the interquartile range.

**Fig. S3.** Temporal dynamics of energy flow through the small mammal community of Homestead Cave from the late Pleistocene to the Modern (mean and 95% CI, sample-size standardized to \( n = 341 \) individuals per time point). (A) Total energy flow over the Holocene. (B) Energy flow through four body size classes. Neotoma body sizes were varied as much as 25% over time following Smith and Betancourt (22) in light of the tight relationship between temperature and body size documented in this genus. Specifically, *Neotoma cinerea* body sizes were specified as 400 g in the late Pleistocene, 350 g in the early Holocene, 300 g in the middle Holocene, and 325 g in the late Holocene. *Neotoma lepida* body sizes were specified as 200 g in the late Pleistocene, 175 g in the early Holocene, 150 g in the middle Holocene, and 162.5 g in the late Holocene. Open circles represent zero energy flow.
Fig. S4. Temporal dynamics of energy flow across functional groups (mean and 95% CI, sample-size standardized to \( n = 341 \) individuals per time point). (A) Energy flow through three habitat groups. (B) Energy flow through three dietary functional groups. Body size scaling for Neotoma followed the procedure described in Fig. S3. Open circles represent zero energy flow.

Table S1. Body mass, metabolic rate, and functional group assignments for small mammal species (< 500 g) at Homestead Cave

<table>
<thead>
<tr>
<th>Species</th>
<th>Mass, g</th>
<th>Metabolic rate, kJ/d</th>
<th>Dietary group</th>
<th>Habitat group</th>
<th>Shrub or grass affinity</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Ammospermophilus leucurus</em></td>
<td>103.674</td>
<td>184.87</td>
<td>Omnivore</td>
<td>Xeric</td>
<td>Shrub</td>
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<td><em>Brachylagus idahoensis</em></td>
<td>142.337</td>
<td>234.48</td>
<td>Herbivore</td>
<td>Xeric</td>
<td>—</td>
</tr>
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<td><em>Chaetodipus formosus</em></td>
<td>19.45</td>
<td>52.7</td>
<td>Granivore</td>
<td>Xeric</td>
<td>—</td>
</tr>
<tr>
<td><em>Dipodomys microps</em></td>
<td>54.6</td>
<td>114.29</td>
<td>Herbivore</td>
<td>Xeric</td>
<td>Shrub</td>
</tr>
<tr>
<td><em>Dipodomys ordii</em></td>
<td>60.4</td>
<td>123.28</td>
<td>Granivore</td>
<td>Xeric</td>
<td>Grass</td>
</tr>
<tr>
<td><em>Lemmiscus curatus</em></td>
<td>28.275</td>
<td>69.77</td>
<td>Herbivore</td>
<td>Xeric</td>
<td>Shrub</td>
</tr>
<tr>
<td><em>Microdipops megacephalus</em></td>
<td>10.45</td>
<td>33.07</td>
<td>Granivore</td>
<td>Xeric</td>
<td>Shrub</td>
</tr>
<tr>
<td><em>Microtus spp.</em></td>
<td>41.5165</td>
<td>93.06</td>
<td>Herbivore</td>
<td>Mesic</td>
<td>Grass</td>
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<tr>
<td><em>Mus musculus</em></td>
<td>15</td>
<td>43.37</td>
<td>Omnivore</td>
<td>Generalist</td>
<td>Grass</td>
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<tr>
<td><em>Mustela erminea</em></td>
<td>70</td>
<td>137.7</td>
<td>Carnivore</td>
<td>Mesic</td>
<td>—</td>
</tr>
<tr>
<td><em>Mustela frenata</em></td>
<td>147.001</td>
<td>240.22</td>
<td>Carnivore</td>
<td>Generalist</td>
<td>—</td>
</tr>
<tr>
<td><em>N. cinerea</em></td>
<td>299.151</td>
<td>409.29</td>
<td>Herbivore</td>
<td>Mesic</td>
<td>Shrub</td>
</tr>
<tr>
<td><em>N. lepida</em></td>
<td>163.75</td>
<td>260.46</td>
<td>Herbivore</td>
<td>Xeric</td>
<td>Shrub</td>
</tr>
<tr>
<td><em>Orychomys leucogaster</em></td>
<td>27.925</td>
<td>69.12</td>
<td>Insectivore</td>
<td>Xeric</td>
<td>Grass</td>
</tr>
<tr>
<td><em>Perognathus longimembris</em></td>
<td>7.6</td>
<td>26.04</td>
<td>Granivore</td>
<td>Xeric</td>
<td>Shrub</td>
</tr>
<tr>
<td><em>Perognathus parvus</em></td>
<td>21.775</td>
<td>57.36</td>
<td>Granivore</td>
<td>Xeric</td>
<td>Shrub</td>
</tr>
<tr>
<td><em>Peromyscus spp.</em></td>
<td>21.283</td>
<td>56.38</td>
<td>Omnivore</td>
<td>Generalist</td>
<td>Grass</td>
</tr>
<tr>
<td><em>Reithrodontomys megalotis</em></td>
<td>9.375</td>
<td>30.49</td>
<td>Granivore</td>
<td>Generalist</td>
<td>Grass</td>
</tr>
<tr>
<td><em>Spilogale gracilis</em></td>
<td>340.997</td>
<td>451.52</td>
<td>Carnivore</td>
<td>Generalist</td>
<td>—</td>
</tr>
<tr>
<td><em>Tamias minimus</em></td>
<td>43.6</td>
<td>96.54</td>
<td>Omnivore</td>
<td>Generalist</td>
<td>—</td>
</tr>
<tr>
<td><em>Thomomys bottae</em></td>
<td>114.749</td>
<td>199.49</td>
<td>Herbivore</td>
<td>Generalist</td>
<td>—</td>
</tr>
<tr>
<td><em>Thomomys talpoides</em></td>
<td>130.083</td>
<td>219.17</td>
<td>Herbivore</td>
<td>Generalist</td>
<td>—</td>
</tr>
<tr>
<td><em>Urocitellus mollis</em></td>
<td>165.4</td>
<td>262.43</td>
<td>Omnivore</td>
<td>Generalist</td>
<td>Grass</td>
</tr>
</tbody>
</table>
Table S2. Cross-correlations and temporal lags (in years)
between regional and global paleoenvironmental proxies
and energy flowing through xeric small mammals

<table>
<thead>
<tr>
<th>Time averaging</th>
<th>δ¹⁸O Lag</th>
<th>Correlation</th>
<th>P value</th>
<th>Percentage of xeric pollen</th>
<th>Lag</th>
<th>Correlation</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>363</td>
<td>0.925</td>
<td>&lt;0.001</td>
<td>227</td>
<td>0.902</td>
<td>0.002</td>
<td></td>
</tr>
<tr>
<td>200</td>
<td>369</td>
<td>0.916</td>
<td>&lt;0.001</td>
<td>224</td>
<td>0.901</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>300</td>
<td>591</td>
<td>0.908</td>
<td>&lt;0.001</td>
<td>215</td>
<td>0.901</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>400</td>
<td>511</td>
<td>0.912</td>
<td>&lt;0.001</td>
<td>200</td>
<td>0.900</td>
<td>0.001</td>
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</tr>
<tr>
<td>500</td>
<td>497</td>
<td>0.914</td>
<td>&lt;0.001</td>
<td>184</td>
<td>0.900</td>
<td>&lt;0.001</td>
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</tr>
</tbody>
</table>

Sensitivity of the lag magnitude was assessed over a range of analytical
time-averaging windows of the paleoenvironmental proxy. Cross-correlation
significance was established via permutation tests.

Table S3. Cross-correlations and temporal lags (in years)
between regional and global paleoenvironmental proxies
and energy flowing through small mammals of intermediate
body size

<table>
<thead>
<tr>
<th>Time averaging</th>
<th>δ¹⁸O Lag</th>
<th>Correlation</th>
<th>P value</th>
<th>Percentage of xeric pollen</th>
<th>Lag</th>
<th>Correlation</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>100</td>
<td>355</td>
<td>0.916</td>
<td>&lt;0.001</td>
<td>227</td>
<td>0.907</td>
<td>0.001</td>
<td></td>
</tr>
<tr>
<td>200</td>
<td>362</td>
<td>0.906</td>
<td>&lt;0.001</td>
<td>226</td>
<td>0.906</td>
<td>&lt;0.001</td>
<td></td>
</tr>
<tr>
<td>300</td>
<td>393</td>
<td>0.896</td>
<td>0.001</td>
<td>221</td>
<td>0.905</td>
<td>0.001</td>
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</tr>
<tr>
<td>400</td>
<td>490</td>
<td>0.898</td>
<td>&lt;0.001</td>
<td>213</td>
<td>0.904</td>
<td>&lt;0.001</td>
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</tr>
<tr>
<td>500</td>
<td>557</td>
<td>0.901</td>
<td>&lt;0.001</td>
<td>198</td>
<td>0.904</td>
<td>&lt;0.001</td>
<td></td>
</tr>
</tbody>
</table>

Sensitivity of the lag magnitude was assessed over a range of analytical
time-averaging windows of the paleoenvironmental proxy. Cross-correlation
significance established via permutation tests.