COMMENTARY

Energy flow and the “grassification” of desert shrublands

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In our directionally and continuously changing world, history still matters, and it does so in increasingly novel and important ways. Human adaptation to global change will rely heavily on robust baselines of historic environmental variability and detailed understanding of how both past and modern ecosystems have responded to both individual and multiple stressors. The question of global change has motivated an upsurge in paleoecological studies that span the late Quaternary and the modern era, and has inspired a growing consideration of time as a fundamental axis in ecology (1). A major challenge in developing pertinent ecological baselines remains how to fuse, into continuous time series, observations and experiments from living systems with paleoecological reconstructions from the same sites (2, 3). Tracing and disentangling complex responses to environmental stress from paleological to present-day communities is especially daunting; for example, how climate change; accelerated land use; and biological invasions are influencing the flows of water, nutrients, and energy. The paper by Terry and Rowe in PNAS (4) is a shining example of how modern ecology and paleoecology can be spliced together to decipher how ecological processes unfold over time scales inaccessible to direct observation or experimentation, and how they can be disrupted by human impacts.

The study reports on a multidimensional analysis of bone remains from a cave in North America’s Great Basin to evaluate how energy flow, and not just species distributions and abundances, could be changing fundamentally in the modern era. Terry and Rowe (4) focus on small mammal bones in well-stratified deposits accumulated below an owl’s roost inside Homestead Cave, a wave-constructed cavern near the regressing shoreline of Pleistocene Lake Bonneville and just west of its Holocene remnant, the modern Great Salt Lake, in north-central Utah. Homestead Cave deposits span the past 13,000 y; were excavated meticulously; and have been studied extensively for plant, small mammal, bird, artiodactyl, fish, ostracode, and gastropod remains, producing an impressive array of publications (5, 6).

For their part, Terry and Rowe (4) took advantage of nearly 200,000 small mammal bones recovered from excavations at Homestead Cave to quantify how allocation of energy among functional groups fluctuated and compensated through time, and the degree to which current energy use dynamics align with the past. Insights from this study were particularly hard won. Repeated live trapping near the cave and careful monitoring of currently accumulating bones below the roost have shown that buried bone assemblages piled up over a restricted window of time and closely mirror the function and structure of corresponding living communities at the time of deposition (7, 8).

Terry and Rowe’s methods for measuring energy flow through time (4) are relatively straightforward, and mimic ways in which ecologists currently consider the roles of small mammals in desert food webs, in which the relatively small granivores tend to drive and maintain plant diversity (9, 10). They estimated abundance, standardized to sample size, from the number of identified specimens per species per stratum in the cave sediments, and assimilated body mass information for each species from look-up tables. Energy flow in kilojoules per day was calculated using metabolic and scaling parameters. Species were binned into four functional (body mass) groups corresponding to natural breaks in the distribution of body sizes for the small mammals present in the Homestead record, and also on their general dietary (carnivore, herbivore, granivore, and insectivore) and habitat (xeric or mesic and open or closed vegetation) preference. The relationship between environmental change and energy flow was evaluated through comparisons with the oxygen isotope record in a Greenland ice core and with the pollen record in a lake sediment core from the nearby Great Salt Lake.

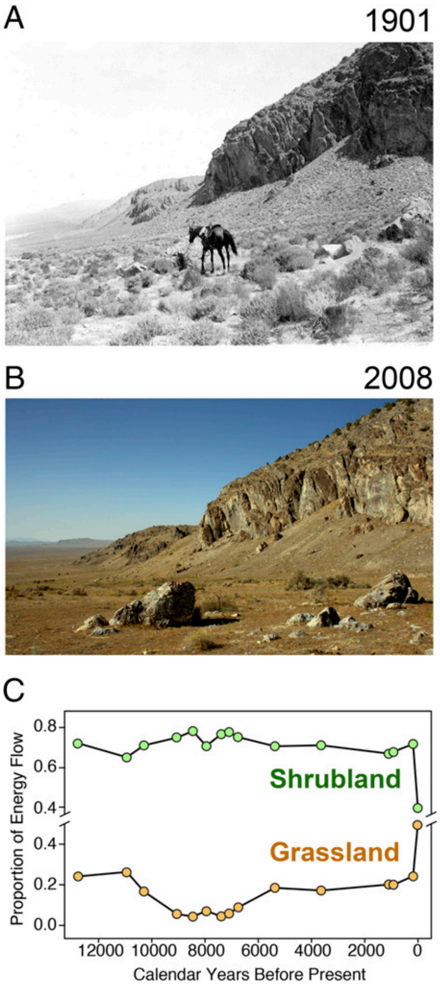

Fig. 1. Repeat photographs of the site where cheatgrass has replaced shrubland at the base of the Cedar Mountains, west of Salt Lake City and only 50 km southeast of Homestead Cave. (*A*) Photograph taken by G. K. Gilbert in 1901. Courtesy of the US Geological Survey, Denver Library Photographic Collection. (*B*) Photograph taken in 2008. Image courtesy of Garry Rogers (Agua Fria Open Space Alliance, Inc.). (*C*) Data from ref. 4.

Terry and Rowe (4) found evidence of compensation associated with species turnovers during the Pleistocene/Holocene transition. Decreased energy flowing through species in the largest and smallest size classes, as well as the most mesic classes, was compensated for by increased energy flow in the middle-sized and most xeric classes. Energy

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flow then remained surprisingly constant through the Holocene (Fig. 1*C*). By comparison, the most dramatic change occurred in the past century, when energy flow declined markedly with a shift toward small body size species, particularly granivores associated with closed grass habitats, without compensation from the other body size, diet, or habitat classes. Terry and Rowe (4) attribute declines in both species diversity and energy flow to the alien cheatgrass (*Bromus tectorum* L.) invasions that swept over the Great Basin and the Intermountain West during the past century (Fig. 1 *A* and *B*). Small mammal bone assemblages from uninvaded sites elsewhere in the region do not exhibit similar shifts in community composition and structure (7, 8, 11).

Cheatgrass is an annual grass introduced multiple times during the late 19th century from Eurasia into the United States via ship ballast, contaminated crop seed, and packing materials. Encouraged by disturbance associated with railroads, mining, cereal grain agriculture, and livestock grazing, cheatgrass quickly spread throughout the Intermountain West, becoming prevalent in the Great Salt Lake area by ~1910 (12). Cheatgrass germinates in the fall, overwinters as a seedling, and completes its short life cycle in the spring. After unusually wet winters/springs and during the ensuing dry summers, the dead plants fuel expansive and more frequently recurring wildfires, promoting a grass-fire cycle in which cheatgrass recovers quickly at the expense of less resilient native shrubs and grasses. Between 1990 and 2008, more than one-fifth of the Great Basin had burned at least once, with cheatgrass fueling most of these wildfires, many of which spread into adjacent woodlands and forests (13). Other nonnative grass invasions are similarly "grassifying" the Mojave, Sonoran, and Chihuahuan Deserts to the south (14).

Contemporary studies of numerous invaded sites across the Great Basin also show marked declines in small mammal richness and community abundance, with an increasing percentage of cheatgrass cover (even after the shrub cover was lost) and time since invasion (15). These changes likely result from both direct (decrease in food or habitat availability or restricted mobility) and indirect (decreased shrub cover and increased fire frequency) effects. Shifts in these small mammal communities can have cascading effects through both higher and lower trophic levels, causing disruptions in ecosystem structure and function.

The paper by Terry and Rowe in PNAS is a shining example of how modern ecology and paleoecology can be spliced together.

"Grassification" is not only having an impact on fire and erosional regimes (16) but is also altering the energy and water balance over vast areas of western North America. Annual grasses such as cheatgrass, for example, senesce earlier and have shallower roots, reducing annual evapotranspiration and leaving excess water for fire-tolerant plants with deeper roots, many of which are also nonnative (17). These disruptions are unprecedented in the Holocene, and are likely to worsen as cheatgrass and other invasive and flammable grasses continue to gain a foothold in western North America. The impacts are not just ecological but also increasingly socioeconomic. This commentary was written in early July, as cheatgrass was drying out and regional fire alerts were being issued following a dry winter but a wet May across the western United States. The higher fire risks associated with grassification are compromising regional economies and lifestyles, with losses of life and property, increased fire suppression costs, reduced property values and tourist revenues, and interruptions in transportation and other essential services.

Understandably, paleoecologists have focused substantial skill and energy on investigating past ecological responses to climate change as a blueprint for the future. Broad-scale grassification of desert shrublands may be compounded by global warming (18, 19), but it has been in progress for more than a century in western North America and surely would have happened despite the buildup of greenhouse gases. The paper by Terry and Rowe (4) not only underscores the profound impacts that accelerated land use and invasions are having worldwide but also the increasing role that paleoecologists can play in appraising them (20).

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