Gophers as geomorphic agents in the Colorado Front Range subalpine zone

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Abstract

Gophers are significant geomorphic agents in many landscapes. We document activity of the Northern Pocket Gopher (*Thomomys talpoides*) in two small subalpine meadows (1050-1800 m²) of the Front Range, Colorado, USA. We tracked locations and volumes of mounds and subnivean infilled tunnels over one year and probed the thickness of the biomantle within one meadow. We infer that only 5-7 gophers occupied each meadow, implying a gopher density of 28-67 ha⁻¹. Fractional areal coverage of the meadows by diggings suggests that within 49-95 years gophers would fully resurface the meadows. Annual volumes of excavated soil correspond to the equivalent of ~1 mm of material spread evenly over the meadows. Probed meadow resistance depths reveal a pattern we interpret to be stone lines at roughly 15 cm depths; implied vertical turnover times are therefore roughly 150 years. These spatial and temporal patterns imply that gophers should be able to churn the biomantle on approximately century timescales

and should fully resurface the meadow areas in similar timescales. These field data also contribute to an investigation of lateral sediment transport; given the local slope of the landscape, gopher-driven sediment transport within our two study sites suggests a landscape diffusivity of $0.008 \text{ m}^2\text{y}^{-1}$. At no time do gophers occupy the forest. As evidenced by subnivean infilled tunnels, winter activity is restricted to the upslope (and hence upwind) meadow edges, which correspond to high snow cover and warm ($> \sim 0^\circ\text{C}$) shallow subsurface soil temperatures. Subsequent activity expands downhill into the meadows and shows a distinct pulse of mound activity in late summer through early fall prior to snowfall. Local forest fire history has led to much more extensive meadows in the past, suggesting that the geomorphic influence of gophers in the landscape is much more widespread than the present distribution of meadows and may cover the entire subalpine region of the Front Range on millennial timescales.

Keywords: biogeomorphology; gopher; hillslope; landscape evolution

1. Introduction

Biological agents and their effects are ubiquitous within landscapes and can be observed on daily timescales. Deer-generated game trails, beaver-constructed dams, and ant-generated mounds are several examples of the geomorphic impacts of animals that one can stumble across on many landscapes. However, despite early interdisciplinary acknowledgement that biology plays a role in landscape evolution (Darwin, 1881; Gilbert, 1909), geomorphologists and biologists have largely worked independently. Even today, geomorphology largely ignores the role of the biosphere or acknowledges it only in a broad, large-scale sense (Butler, 1995). This may be because of fundamental differences between the two sciences when approaching problems.

When presented with a question, instead of focusing on how animals and landscape evolution are interwoven, Yoo et al. (2005) stated that an ecologist may concentrate on population dynamics while a geomorphologist may concentrate on the energy that molds and drives the landscape. Here we honor what is observed to be the primary geomorphic player within the subalpine landscape of the Colorado Front Range, the Northern Pocket Gopher (*Thomomys talpoides*) and provide a framework for understanding what drives the spatial and temporal patterns of landscape change.

The Northern Pocket Gopher, *Thomomys talpoides*, is a medium-sized rodent: mean male total length = 206.8 mm, mean female total length = 203.0 mm (Miller, 1964); in Utah, mean adult male mass = 104.4 g, mean adult female mass = 91.4 g (Anderson, 1978). While slight on an individual scale, they are often abundant and have a large geographic range that spans a large fraction of western North America (Verts and Carraway, 1999). More broadly, pocket gophers comprise multiple species within six genera widely distributed across North and Central America.

Fig. 1. (A) The general pattern of gopher activity in a boulder-strewn, sloping meadow-forest landscape. Gophers inhabit the meadows but not the forests. Gopher mounds develop in a patchy fashion within the meadows, presumably each patch belonging to a solitary gopher. These patches generally occupy the less rocky portions of this glacial till mantled surface. (B) Subsurface cross section (C–C') of gopher-driven sediment transport. Material is transported from the ground-parallel feeding tunnel up through a lateral tunnel where it is deposited on the surface as a mound. Material is then exposed to diffusive transport processes that move material downslope. Gopher transport of sediment is described by Gabet (2000) as consisting of two discrete horizontal distances: that from the centroid of the tunnel to the burrow exit/entrance (a'), and that from the burrow exit/entrance to the centroid of the mound (b'); their surface-parallel counterparts are a and b .

70

71 All pocket gophers are fossorial rodents that build an intricate system of tunnels and mounds
72 (Fig. 1). The subsurface gopher tunnel system can be separated into two parts: (i) shallow
73 feeding tunnels constructed parallel to the ground surface that are utilized for harvesting roots,
74 and (ii) a deeper set of tunnels and chambers that are utilized for nesting and food storage (e.g.,
75 Miller, 1957; Reichman and Seabloom, 2002). The feeding tunnels connect to the ground
76 surface through short tunnels, referred to as laterals (Fig. 1). Laterals are utilized to rid the
77 tunnel system of excavated material (Vleck, 1981). The first of the three primary gopher-
78 generated geomorphic features are found at the exit of these tunnels: surface mounds (Figs. 2 and
79 3A).

80

81 **Fig. 2.** Photograph illustrating one of two study sites where gopher mounds have been surveyed
82 throughout the snow-off season. Flags mark surveyed gopher mounds, each survey being
83 flagged by a different color of flag. Patchy thin snow in the meadow signifies the onset of
84 winter.

85

86 The second is an infilled tunnel (Knight, 2009) (Fig. 3B) or earth cylinder (Warren, 1937).
87 These features are produced when a meadow is blanketed in snow, at which time gophers will
88 emerge from the soil to forage for plant material and, in doing so, create snow tunnels. Later,
89 they will further utilize these surface-level tunnels to rid the subsurface of their tillage (e.g.,
90 Grinnell, 1923). As a result, they generate dense soil cylinders that are revealed when the snow
91 retreats in early spring. The third geomorphic feature is a stone line (Fig. 3C).

92

93

94 **Fig. 3.** Three primary geomorphic features generated by gophers. (A) A surface mound. Surface
95 area and average height of mounds are measured to acquire mound volume; geospatial position
96 was also documented. (B) Several infilled tunnels emerging from beneath melting snow cover.
97 Infilled tunnel volumes are calculated by assuming a cylindrical geometry and collecting length
98 and height measurements; we assumed a constant diameter in the horizontal dimension for all
99 infilled tunnels. Geospatial position was also documented. (C) A gopher tunnel with a stone on
100 the floor of the tunnel (beneath pencil).

101

102 Stone lines are concentrations of stones at some depth beneath the ground surface and reflect a
103 threshold grain size, generally around 2.5 cm (Verts and Carraway, 1999), below which gophers
104 can excavate and above which gophers will dig around. As gopher tunneling continues, larger
105 grains will drop to a uniform depth that effectively records the maximum depth to which the
106 gophers are excavating. This depth, and the stones that accumulate at this depth, are referred to
107 as stone lines (Johnson, 1989). At the same time, the finer material will become more
108 concentrated above the stone line to produce what is called the biomantle, which includes the
109 surface mounds (Johnson, 1989).

110 For the pocket gopher, benefits of being fossorial (hidden from predators' vision, protection from
111 extreme weather events, and access to plant roots; Vleck, 1979) must outweigh the fact that
112 gophers utilize 360-3400 times the amount of energy tunneling than would be required to move
113 the same distance on the surface (Vleck, 1979). Furthermore, the pocket gopher is close to
114 indifferent to the drudgery of working against gravity. Seabloom et al. (2000) suggested that the
115 energetic costs associated with shearing and pushing soil horizontally through a tunnel system
116 are three orders of magnitude higher than the cost associated with lifting soil against gravity.
117 Gophers prefer to construct lateral tunnels on the downslope side of the connecting feeding
118 tunnel and at an angle that does not exceed the angle of repose (Seabloom et al., 2000); the angle
119 is a function of soil cohesion and is low enough to prevent lateral tunnels from collapsing inward
120 (Vleck, 1981).

121 The large energetic cost of excavation also suggests a premium for behaviors that maximize the
122 benefits of excavations, especially with regard to food acquisition and neighboring gophers
123 (Reichman et al., 1982). Substantial research has focused on how gophers strategize their tunnel
124 and burrow geometries. Pocket gophers minimize the cost of burrowing by choosing very

specific segment lengths between the lateral tunnels (Vleck, 1981) while constructing, in some cases, intricate tunnel systems over 100 m long (e.g., Criddle, 1930; Smallwood and Morrison, 1999). Importantly, the spacing between individual burrow systems remains fairly constant regardless of vegetation type (Reichman et al., 1982). Gophers are less mobile once they have found a hotspot for food resources. Reichman et al. (1982) suggest that burrow length and the quantity of off-shooting tunnel branches are inversely proportional to the availability of food.

The geomorphic effect of the pocket gopher has also been investigated. Ellison (1946) discusses the pocket gopher's role as an erosional agent within the Wasatch Plateau; while not the primary cause of erosion in this landscape, it is still deemed a noteworthy erosional agent. Thorn (1978) identified the pocket gopher as the dominant geomorphic agent in the alpine tundra of the Front Range near our field site. Black and Montgomery (1991) studied gopher activity in a grassland basin in northern California by documenting all gopher-generated surface mounds and concluded that the burrowing of mammals is the primary process driving sediment transport in their field area. Gabet et al. (2003) illustrated that at low gradients gopher bioturbation generates a greater sediment flux than purely physical processes. Butler and Butler (2009) demonstrated that gopher-generated mounds and infilled tunnels are less compacted than the surrounding undisturbed soils and argued that these low density mounds and infilled tunnels may promote seedling establishment within the alpine treeline. Gopher-driven microtopographic variation on fertilized plots versus unfertilized plots was monitored by Inouye et al. (1997). Smallwood and Morrison (1999) reported a variety of excavation statistics (including mean mound volume, tunnel length, and burrow volume) for several pocket gopher species. Gabet (2000) documented gopher-generated sediment transport near Santa Barbara, California, and explored its dependence on slope angle. Cox and Allen (1987) discussed gopher-driven sediment transport as a process

responsible for mima mounds; this has now been supported by numerical modeling (Gabet et al., 2014). Finally, Zaitlin and Hayashi (2012) and references therein discussed how the pocket gopher has the potential to drive geomorphic change on sloping landscapes. In this contribution, we add to this list by documenting the temporal and spatial trends in gopher-driven surface processes, the intensity of gopher activity, and associated geomorphic impacts within the subalpine zone of the Colorado Front Range.

2. Study area

Our study area (Fig. 4) consists of two meadows in the subalpine of the Colorado Front Range within the Boulder Creek Critical Zone Observatory (Anderson et al., 2012, 2013). This region was glaciated during the Pleistocene (Madole et al., 1998); glacial till mantles both study sites. Two meadow sites referred to as the ‘upper site’ (area = 1800 m², elevation = 3010 m) and ‘lower site’ (area = 1050 m², elevation = 2975 m) were established in the summer of 2013. Meadows were selected based primarily upon (i) notable gopher activity, (ii) a sloping surface, (iii) sharp forest-meadow boundaries, and (iv) being representative of the general geomorphic setting (e.g., mantled with glacial till). The two sites are surrounded by forest composed primarily of lodgepole pine and aspen, with lesser numbers of limber pine, Engelmann spruce, and Douglas fir. Ungulates, including elk, mule deer, and moose (Armstrong et al., 2011), roam, graze, and sleep in both study sites.

Fig. 4. Zoomed-in (A) and zoomed-out (B) views of LiDAR-derived digital elevation model (DEM) provide the topographic context of the upper site (green dot) and the lower site (orange dot) in the Front Range just west of Boulder, Colorado. Both sites were glaciated during the Pleistocene as can be recognized by observing the glacially sculpted landscapes of nearby Green Lakes and 4th of July Valleys (B). Both sites are located immediately outboard of moraines generated during the Last Glacial Maximum in an older moraine complex. Glacial till is prevalent mantling both sites, as shown within the lower site (C) and upper site (D).

3. Methods

Surface mounds were monitored on an approximately weekly basis once snow had largely melted off the sites. Fresh mounds were identified by (i) being composed primarily of fines with a lack of cobbles and gravels in the freshly excavated, visible mound surface coating; (ii) low density of the mound material; and (iii) a lack of vegetation. The GPS coordinates of mound locations were documented using a handheld Trimble GeoXT GNSS device equipped with Terra Sync version 2.3. Reported maximum accuracy for these data are 0.3 to 1 m in open-canopy conditions (average 0.3-0.5 m accuracy) and 0.5 to >1.0 m in closed canopy conditions (average >1.0 m accuracy) (Chamberlain, 2002; Trimble, 2005). Raw position data were differentially corrected in Pathfinder Office version 5.40 (Trimble Navigation Limited, Sunnyvale, CA, USA) against data collected and archived by UNAVCO (39°59'43.994'' N, 105°15'44.2794'' W, elevation 1667 m). The corrected coordinates were exported as shapefiles in Universal Transverse Mercator 84 (UTM 84). By surveying on an approximately weekly basis, misidentification of 'old' (generated prior to the 2014 digging cycle) versus 'new' mounds was minimized as the metrics utilized to identify a mound as 'new' become less prominent over time. Furthermore, the high frequency of our observations allowed us to document when an individual mound was enlarged; we tabulated such an expansion as an independent 'mound-building event'; for the remainder of this paper we refer to each 'mound-building event' as simply a 'mound'. We documented mound volumes by measuring the surface area of the base and the average height of each mound. Mounds were marked with a pin flag, carefully placed to avoid invasion of the connecting tunnel (Fig. 2). In cases where a mound expanded in volume between visits, full mound volume was documented and the new mound material was calculated by subtraction of the prior volume.

198 Infilled tunnels were documented directly after snow retreated from the forest-meadow edges in
199 the spring of 2014. The infilled tunnel locations were documented using the same Trimble
200 system. Infilled tunnel volumes were calculated by assuming a cylindrical geometry and
201 collecting length and height measurements. The length of the infilled tunnel was measured by
202 mirroring the infilled tunnel surface with a rope and then measuring the length of the rope. To
203 calculate the cross-sectional area, we assumed a 7-cm width for all infilled tunnels in the
204 horizontal dimension, measured the height of the infilled tunnel, and then averaged the two to
205 acquire an average radius. If infilled tunnel sections overlapped vertically, the overlapping
206 sections were considered to be a part of one and the same infilled tunnel.

207 All trees within the meadows and at the forest margins at the plot borders were identified to
208 species, mapped using the same Trimble system, and measured. Size was quantified by height
209 for trees under 2 m tall or diameter at breast height (DBH) if over 2 m tall.

210 The presence or absence of stone lines was documented by pounding 1.27-cm-diameter rebar
211 into the ground until substantial resistance was encountered. This was performed at the upper
212 site along multiple transects spanning the meadow region. Sampled lines were spaced 4 m apart,
213 each transect was between 60 and 70 m long and was sampled at 2-m increments. Three
214 measurements were surveyed at each location, avoiding surface glacial till. Meadow regions
215 were denoted as areas in which tree density was significantly lower than in the continuous forest.
216 We probed a total of 185 locations (555 total surveyed points) within the meadow. We surveyed
217 depth to resistance within the forest region as well, but the resistance encountered while
218 surveying within the forest could result from either stones or roots and thus the interpretation of
219 the resistance depths is ambiguous. We therefore omit further discussion of forest probe data.
220 On the other hand, as very few trees occur in the meadows and we find no roots in the one small

pit we were allowed to dig in the meadow, we are confident that resistance in the meadow is very largely from stones alone. To judge whether gophers are likely to have created the distribution of depths we found, we also ran a simulation model 100 times to determine depths to resistance in a randomized glacial till subsurface. In each model run we placed ~190 (model run dependent) nonoverlapping clasts of a variety of sizes within a subsurface cross section that is 10 m wide and 1.2 m deep. Cell width and height are 1 cm. The radius for a clast is calculated by evaluating the absolute value of the following: 5 cm plus 10 cm multiplied by a pseudorandom value drawn from the standard normal distribution. For each of the 100 simulations, at each cm along the width of the cross section, the depth to the shallowest clast in the subsurface is evaluated and recorded. If no clast exists at a given location, then the maximum depth of the cross section (120 cm) is recorded. A probability distribution function (pdf) of the minimum depth to clasts is generated at the end of each model run by dividing by the total number of probed locations (1000).

We monitored subsurface temperatures with Thermochron iButtons between 11 July 2014 and 10 June 2015. The thermistors were inserted along a single transect at five locations spanning the meadow-forest pair, roughly 20 m into the meadow, 5 m into the meadow, the forest-meadow boundary, 5 m into the forest, and 20 m into the forest. At each location, one thermistor was deployed at 2 cm depth and one at 10 cm depth; surface duff was excluded from the soil depth measurements.

We monitored snow depth during the 2014-2015 winter at the forest-meadow edge at the upper site with time-lapse photography. Each day, multiple still photos captured a view that includes a vertical PVC pipe erected from the ground (supported by a deeply inserted rebar rod) and painted at 10-cm intervals; snow depth was estimated based upon where the snow intersected the painted

markings on the PVC pipe. A snow depth time series was generated from one photograph from each winter day taken at either 10 or 11 a.m.

4. Results

4.1. Excavation data

We documented a total of 515 mounds and 66 infilled tunnels at the upper site, which has an area of 1800 m². Average mound height was 5 cm, average mound surface area was 597 cm², and average mound volume was 4006 cm³. The average cross-sectional area of tunnel-fills was 27 cm² with average length of 122 cm. Average tunnel-fill volume was 3849 cm³.

We surveyed a total of 131 mounds and 35 infilled tunnels at the lower site (area = 1050 m²). Average mound height was 6 cm, average mound surface area was 722 cm², and average mound volume was 5842 cm³. Average cross-sectional area of tunnel-fills was 25 cm², and the average length was 63 cm. Average tunnel-fill volume was 1614 cm³.

In total, material volumes of 2.32 m³ and 0.82 m³ (Fig. 5) were brought to the surface in the form of mounds and infilled tunnels at the upper and lower sites, respectively. Dividing by the area of each meadow, this equates to an average of 1.3 and 0.8 mm of material being brought to the surface over the upper and lower sites, respectively, within one annual digging cycle. Whereas gopher activity was not uniform in either meadow, the calculation provides a general metric to estimate the long-term geomorphic effect of gophers within the landscape.

Combined surface areas of mounds and infilled tunnels in the upper and lower sites are 36 m² and 11 m², respectively. This is equivalent to 2% and 1% of the total area of the upper and lower sites, respectively, and implies that the upper and lower sites will be resurfaced in time scales of 49 and 95 years, respectively.

The temporal pattern of mound formation at each site (Fig. 5) reveals three distinct patterns of gopher activity: (i) tunnel-fills are constructed during the winter season and are

Fig. 5. Time series of surficial geomorphic work accomplished by gophers at each site (top panel = upper site; bottom panel = lower site). Three distinct patterns of gopher activity appear: (i) infilled tunnels (red) are constructed during the winter and are revealed when the snow retreats in the spring/early summer, (ii) gopher mound generation was minor in mid-summer, until (iii)

mound activity explodes at both sites in early-mid-August and then trails off in early-mid-October before winter sets in in early November.

revealed when the snow retreats in the spring, (ii) gopher mound generation was rare during early to mid-summer, until (iii) mound activity accelerated at both sites in early-mid-August and then trails off in early-mid-October. Infilled tunnels are found only at the forest meadow edge. Mounds emerge only in the meadow and in a ‘patchy’ fashion. We saw no gopher activity within the forest (Fig. 6).

Fig. 6. Spatial relationship between mounds (blue/purple circles), infilled tunnels (red circles), and trees (green dots) at the upper (top panel) and lower (bottom panel) sites. Landscape slopes downhill to the right in both cases. Dominant wind is also west-to-east, so that the upslope edge of the meadow is also the upwind edge. Infilled tunnel and mound circle sizes are scaled by volume. Dates in the key denote the date when specific mounds were surveyed. To the extent that infilled tunnels are proxies for gopher location in the winter, gophers appear to spend the winter months primarily along the upslope, upwind forest-meadow edge. If mounds are proxies

for gopher location during all other months, gophers spend these months primarily within the meadow region. We hypothesize that this is driven by the spatial pattern of snow depth, which in turn dictates the subsurface temperatures (see Fig. 8).

4.2. Probing depths

At the upper site, the depth to significant probe resistance in the meadow (Fig. 7A) reveals a median resistance depth of 15 cm and a distribution that shows a distinct peak at 9-18 cm depth. This contrasts with our modeled probability of encountering a clast, which declines monotonically with depth in all simulations (Fig. 7B). The modeled and observed distributions differ significantly, implying that some process has altered the subsurface since the glacial till was deposited. We suggest that the primary process is the digging of gophers and that they have generated stone lines akin to that documented by Johnson (1989).

Fig. 7. (A) Upper site meadow stone line survey data (red) juxtaposed with the mean of the modeled stone line simulation (black) also shown in (B). The depth to significant probe resistance within the meadow reveals a median resistance depth of 15 cm. The distribution displays a distinct maximum between the depths 9-18 cm. This contrasts with the model, in which the peak occurs in the top-most bin, 2.5-7.5 cm. (B) All 100 model realizations of the depth to resistance in randomized subsurfaces. One of the realizations of the randomized glacial till subsurface is shown in the inset. All modeled distributions display a maximum in the top-most bin and show no maximum at depth.

4.3. Subsurface temperatures and snow depth

At the forest-meadow boundary, snow was first present on 27 October 2014 and last appeared 23 May 2015. A maximum snow depth of 1.23 m was recorded on 26 February 2015. The mean snow depth between first and last snow was 0.55 m. Subsurface thermistors were deployed at 2- and 10-cm depths; when recovered, some were found at greater depths, up to 3 cm deeper than their deployment depths. They recorded temperatures between 11 July 2014 and 10 June 2015; temperatures were not recorded at the beginning of the winter season. As we did not measure temperatures or snow depth in winter 2013-2014, during which the infilled tunnels we documented in spring 2014 were dug, we take temperatures and snow depth recorded during the 2014-2015 winter season (Fig. 8) as a proxy for the 2013-2014 winter season. Subsurface temperatures demonstrate a disparity between meadow regions and the forest-meadow boundary; winter temperatures within the meadow were significantly colder than at the forest-meadow boundary (Fig. 8).

Fig. 8. Temperature time series collected at 2-cm (red time series) and 10-cm (green time series) depths at three locations: 20 m into the meadow, 5 m into the meadow, and the forest-meadow boundary. Snow depth measured at the forest-meadow boundary is displayed in black on the right panel. At 20 m into the meadow (left panel) the temperature is mostly below freezing (blue line = 0°C) and oscillates significantly during the winter, presumably reflecting minimal snow cover. At 5 m into the meadow from the upslope, upwind meadow edge (middle panel), mid-winter temperature is more steady and warmer at ~0°C; whereas at the meadow edge (right panel), the temperature is yet warmer at ~1°C during the period of deep snow cover. Data was not collected in late 2014.

5. Discussion

Within the subalpine zone of the Colorado Front Range, gophers inhabit meadows but not forests. To explore the long-term geomorphic effect of gophers on the meadow-forest system of the subalpine zone of the Front Range, we utilize this observation along with three primary conclusions from our fieldwork: (i) gopher activities result in the equivalent of ~1 mm of

excavated material being deposited across the surface of a meadow each year, (ii) discrete gopher digging patterns can be identified in time and in space at both sites, and (iii) stone lines exist within the meadow region that suggest long-term effects of gopher digging. Here, we explore how gophers have influenced the landscape in the vertical and lateral dimensions.

5.1. Spatial and temporal digging patterns

Despite the ability of the northern pocket gopher to live in a greater set of soil types and range of topography than any other pocket gopher species in Colorado (Miller, 1964), clearly the gophers do not penetrate the forests. Infilled tunnels, which are excavated strictly when snow completely/partially blankets a meadow during the winter, are found primarily at the forest-meadow edge. Mounds, which are generated primarily in August through October, exist strictly within the meadow region and in a ‘patchy’ pattern. Gophers are relatively solitary (e.g., Miller, 1948) and antisocial animals (e.g., Miller, 1957); therefore it is likely that each aggregation of mounds was generated by one gopher. This implies that ~5-7 gophers inhabited each meadow (Fig. 6), and suggests that gopher densities are 28-39 and 48-67 ha⁻¹ in the upper and lower sites, respectively. These numbers overlap with those acquired in Vaughan’s (1969) study within subalpine Colorado parks, where densities of 6.2-12.4 and 14.8-34.6 ha⁻¹ were observed in early summer and late summer, respectively.

By utilizing the infilled tunnels and mounds as proxies for gopher subsurface location, the data suggests gophers spend the winter months at the forest-meadow edge and then migrate into the meadows (as well as continue to dig near the forest-meadow edges) where they reside until the ensuing winter. We hypothesize that the winter trends are driven primarily by the spatial pattern of snow depth. Snow serves as an insulator and thus governs the thermal state of the near-surface soil. In a study in the alpine landscape on nearby Niwot Ridge, Thorn (1978) found that gopher

density was much higher where snow was thicker (lee side and saddle of the ridge) than on the windswept west-facing hillslope. He later reported (Thorn, 1982) that the spatial variability of gopher activity and associated disturbance is dependent upon winter snowpack. During the winter within the more complex ecosystem of the forested subalpine environment, we observe that the temperature at depth is more steady and warmer at the forest-meadow edge, where snow is deep, and is colder and oscillates significantly toward the center of the meadow, where snow is thin (Fig. 8). Snow is deeper at the forest-meadow edge because of protection from the wind, in contrast with the windswept, thinly snow-mantled meadow center (Figure 9).

Fig. 9. Photograph of the upper site, looking upslope from near the bottom of the study plot. One can observe minimal to zero snow cover in the center of the meadow whereas the snow appears thickest at the most upslope zone along the forest-meadow boundary.

Additional drivers of gopher digging patterns could potentially be linked to the onset of breeding season (Miller and Bond, 1960; Cox and Hunt, 1992), the availability of herbaceous food (Cox

and Hunt, 1992), and soil moisture (e.g., Miller, 1948; Verts and Carraway, 1999, and references therein). These links remain to be explored. While gopher tunnel system spacing is roughly uniform at study sites in northern Arizona (Reichman et al., 1982) and likely others inhabited by pocket gophers, such as shortgrass prairies (Grant et al., 1980), alfalfa fields (Miller, 1957), and grassland basins (Black and Montgomery, 1991), this is most likely not the case within our study area in any particular year. Assuming that mounds are a proxy for subsurface tunnel location, clearly the tunnel spacing at our study sites is not uniform on an annual basis (Fig. 6). This may be related to the high concentration and random locations of large boulders in the glacial till in which this landscape is developed. This undoubtedly governs gopher tunneling strategies and vegetation dynamics within the meadows.

5.2. Intensity of gopher excavations

Here we begin to discuss the details of the lateral and vertical sediment transport driven by gopher excavation activity. In this study, average mound volumes were 4006 and 5842 cm³ for the upper and lower sites, respectively. We note that disparity in reported mound volumes between this study and others (Smallwood and Morrison, 1999, and references therein, report an average mound volume of 0.0158 m³ for *T. talpoides*) could result from a variety of reasons. One of these, in our case, is that volume measurements are dependent on the interval between surveys and the definition of ‘mound’. Expansion of individual mounds was captured by our approximately weekly surveying. In our terminology, each expansion is considered to be a new ‘mound’ because it is a unique and independent ‘mound-building event’; if mounds were surveyed less frequently, only the final mound product would be noted and would therefore be larger. Mound volumes can also vary depending on the measurement technique and on weather: wet and windy conditions are more prone to transport sediment from the original mound

position. Thus, instead of comparing average mound volume, we compare the total amount of material that surfaces during the year when investigating the broader geomorphic impact of gophers on the landscape. Therefore it is the 2.32 and 0.82 m³ of material that was excavated to the surface in the form of mounds and infilled tunnels at the upper and lower sites, respectively, on which we focus.

The intensity of gopher excavation at our sites is ~2.32 m³/1800 m² and 0.82 m³/1050 m² at the upper and lower sites, respectively, or roughly 12.9 and 7.8 m³ha⁻¹y⁻¹ for the upper and lower sites, respectively. This falls within but at the low end of the excavation rates reported for some other settings (1.43-832.95 m³ha⁻¹y⁻¹) (Smallwood and Morrison, 1999, and references therein). These numbers are more informative than average mound volumes when assessing gopher impact on landscape evolution because they are rates rather than volumes. In the next section, we utilize these values along with stone lines to evaluate the geomorphic signal of gophers.

5.3. Stone lines generated by gopher activity

We had anticipated that the probing data would reveal stone lines in the meadows, as indeed we found. We acknowledge that the method we used cannot distinguish between rocks, roots, or other impenetrable objects. However, in the primarily open meadows (Figs. 4C and 4D), we assume the depth to resistance is generated by cobbles in the subsurface. Test pits were not dug to explore the details of the subsurface -- excavation is not permitted within the study areas because this is an archaeologically sensitive area. To explore what one might expect in a glacial till with randomly distributed cobbles at depth, we model the depth to resistance distribution in a randomly assembled glacial till. We suggest that the model results (Fig. 7) implies that the original random distribution of clasts with depth has been significantly altered and further suggest that this reflects the digging of gophers. Furthermore, the observed depth of maximum

resistance accords with the known preference of gophers to dig in the rooting zone of plants, their food source. If gophers generate the stone lines and gophers are not to be found in present forests, we argue that robust probing resistance data within the forest region, which is able to distinguish between stones and roots, would be very useful in assessing the longevity of forests.

5.4. Stone lines as evidence for vertical sediment transport

Gophers appear to be efficient bioturbators. Here we assess the timescales for turnover of the meadow biomantle. Miller (1957) stated that 80% of the Sacramento Valley pocket gopher tunnel system is found in the upper 31 cm of the soil, with 40% existing between 15 and 21 cm. Reichman and Seabloom (2002) stated that pocket gophers primarily dig between 6 and 20 cm depth. Our data on depth to significant resistance (= stones) peaks at ~15 cm within the meadows. This echoes the data of this prior research, suggesting that we may interpret the resistance measurements (Fig. 7) as a stone line generated by gopher digging habits (Johnson, 1989). From the total material excavated to the surface and area of each meadow, we calculate an aerial average of 1.3 and 0.8 mm of excavated material spread over the upper and lower sites, respectively [= $(2.32 \text{ m}^3/1800 \text{ m}^2)$ and $(0.82 \text{ m}^3/1050 \text{ m}^2)$]. Utilizing these values and the stone line depth of 15 cm, we infer that the top 15 cm of the study meadows will completely turn over approximately once every couple centuries [= $[150 \text{ mm}/(1.3 \text{ mm/y})]$ to $[150 \text{ mm}/(0.8 \text{ mm/y})]$ years]. Apparently, the mixing of the near subsurface of a meadow is therefore expected to be accomplished relatively quickly by gopher activity. These timescales are roughly comparable to the decadal-century timescales required for areal resurfacing of the meadows: 49.4 and 95.4 years for the upper and lower sites, respectively.

5.5. Surface mounds and lateral sediment transport

Gabet (2000) noted that material mobilized by gophers can be broken into two horizontal distances and argued that volumetric sediment transport rate, q_s [L^3/LT], resulting from gopher excavation may be evaluated using

$$q_s = MPR * V * (a' + b') \quad 1$$

where MPR is the mound production rate [number of mounds $L^{-2} T^{-1}$], V is average mound volume [L^3/mound], and the distances a' and b' are related to distances a and b measured parallel to the hillslope:

$$\begin{aligned} a' &= a \cos(\alpha) \cos(S) \\ b' &= b \cos(S) \end{aligned} \quad 2$$

where a is the hillslope parallel distance between the centroid of the tunnel and tunnel opening, b is the hillslope parallel distance between the tunnel opening and mound centroid (Fig. 1B), S is the slope of the hill, and α is the angle between the tunnel and the line of steepest descent (the fall line). The subsurface transport distance, a , was not surveyed in this study but is calculated by back-calculating the tunnel distance required to produce the observed mound/infilled tunnel volume (we assume a tunnel radius of 3 cm). We incorporate infilled tunnel data into all appropriate calculations, given that they represent a significant amount of material excavated and relocated to the surface; they are considered and quantitatively examined here in the same fashion as mounds. We assume that α is 0 and thus assume that all tunnels are constructed directly downslope; this yields a maximum downslope transport estimate. We also assume that for all mounds/infilled tunnels the surface component of motion $b = 0.05$ m. Table 1 displays the values that we use.

Table 1 Values utilized to perform Gabet (2000) sediment transport calculations

Parameter	Upper site value	Lower site value	Note
MPR	0.32 mounds * m ⁻² *y ⁻¹	0.16 mounds * m ⁻² *y ⁻¹	Includes infilled tunnels and mounds
V	0.004 m ³	0.005 m ³	Includes infilled tunnels and mounds
a	1.41 m	1.75 m	Back-calculated utilizing V and assumed tunnel radius = 3 cm
b	0.05 m	0.05 m	Estimated
α	0	0	Assumption that tunnels are constructed downslope and parallel to line of steepest decent
S tangent(slope)	0.23	0.17	Acquired from LiDAR
a'	1.37 m	1.73 m	Equation 2
b'	0.05 m	0.05 m	Equation 2

465

466 We utilize Eq. (1) and values in Table 1 to calculate volumetric transport rates of 0.002 and
 467 0.001 m³m⁻¹y⁻¹ for the upper and lower sites, respectively. This can be transformed to a
 468 sediment mass discharge rate [M/L/T] utilizing Eq. (3):

469
$$Q = \rho_r q_s \quad 3$$

470 where ρ_r is the density of regolith and is assumed to be 1500 kg/m³. Equation (3) yields mass
 471 discharge rates of 2.75 and 2.08 kg¹m⁻¹y⁻¹ for the upper and lower sites, respectively. If we
 472 assume a common hillslope geomorphic transport law of the form $Q = -kS$, where S is the
 473 tangent of the slope, we may estimate the hillslope transport efficiency, k , and landscape
 474 diffusivity, κ , as

$$k = \frac{Q}{S} \quad 4$$

$$K = \frac{k}{\rho_r} \quad 5$$

475 The resulting transport efficiencies, k , are 11.7 and 12.2 kg¹m⁻¹y⁻¹ for the upper and lower sites,
 476 respectively; and the diffusivity, κ , is 0.008 m²y⁻¹ for both the upper and lower sites.

Full accounting of the geomorphic roles of gophers in the evolution of a given landscape requires field documentation of surface and subsurface transport distances. At our sites, displacements of surficial material (Fig. 1B) can be attributed to diffusive processes (e.g., Anderson and Anderson, 2010) such as frost heave, rainsplash, and biological agents, including ungulates (Fig. 10). Ungulates leave large, deeply embedded footprints on the surface that presumably collapse tunnels and disturb mounds in the vertical and downslope directions (Fig. 10). Furthermore, frequent matted patches of grasses are observed suggesting that ungulates frequently rest or sleep within the meadows. When the mounds initially erupt, their densities are lower than that of undisturbed ground (Butler and Butler, 2009). Thus, the evolution of mounds should include any motion during the redensification of the material. We observe that mounds evolve to become flatter as they age, and we hypothesize that this occurs from rainsplash and other processes that promote settling. We hypothesize that rainsplash that occurs during the early life of a mound, when they are relatively bald of vegetation and therefore lack cohesion associated with roots, also promotes preferential downslope motion of the fine grains (Gabet and Dunne, 2003, 2004; Furbish et al., 2007,2009). This should result in a flattening or deflation of the mound and should coarsen its surface.

Butler and Butler (2009) have hypothesized that tree seedling establishment may be promoted by the presence of mounds with their reduced soil density. We have witnessed the rapid colonization/recovery of grasses and forbs on the mounds. Recovery of plant cover should increase the cohesion associated with each species' root structure and provide a canopy that serves as an umbrella to damp the direct effects of rain and wind. As the duration of exposure to these vegetation elements will limit the degree to which mound material may be moved

downslope, we encourage a future study linking vegetation dynamics to gopher-driven sediment transport.

Fig. 10. Ungulates are subaerial biogeomorphic agents. (A) A hoof print embedded in a gopher mound is a common sight. (B) A time-lapse image captures a deer grazing at dusk at the upper site; note pin flags in the distance denoting mound locations.

5.6. Landscape-scale lateral transport processes

We hypothesize that the forest-meadow subalpine landscape of the Front Range is more broadly impacted by gopher-generated geomorphic work in the long term. This scenario requires that the meadow-forest boundaries be relatively mobile and in particular that areas now dominated with forests were once meadows. We propose that this can occur in three ways: (i) long-term climate-driven changes in forest versus meadow cover, including the increase in tree cover after glaciation; (ii) invasion of gophers into areas cleared of tree cover by natural forest fires; and (iii) anthropogenic-driven declines in tree cover due to cutting and to deliberate and accidental fires.

First, estimates of forest expansion to higher elevations over the last 10.6 ka within the Medicine Bow Mountains in nearby Wyoming (e.g., Minckley et al., 2012) suggested that in the past many areas that are mostly forested now (including the surroundings of our study sites) were solely or predominantly meadows. Because northern pocket gophers are abundant in alpine and subalpine habitats, this would have allowed far larger extent of their effects in the past. The forest-meadow systems within the subalpine of the Front Range will have moved about sufficiently since moraines were formed ~18 ka that the landscape has been repeatedly subjected to the efficient alterations of the surface by hot-spots of gopher activity in the meadows.

Second, forest fires wipe the landscape clean of tree cover, allowing gophers to reestablish in these now unforested areas. A patchy meadow-forest complex will likely evolve as the landscapes recover. This may involve self-organization of the forest-meadow complex in part by competition between tree encroachment and gopher herbivory. Sibold et al. (2006) documented that a roughly 30,000-ha region of subalpine forest within the nearby Rocky Mountain National Park has experienced 22 stand-replacing fires between 1654 and 2002; fires occur within this landscape on approximately decadal timescales. It is therefore plausible that our study sites have experienced a similar fire history, given the fire history of the montane and subalpine zones of the Front Range (Veblen and Lorenz, 1991), and thus that forest fires have repeatedly reset the position of the forest-meadow boundaries at our sites. Charred tree stumps and surface wood in nearby meadows suggest that fire has indeed recently affected the landscape. This would imply that the meadow-forest system has repeatedly reestablished itself, likely in different places over time, effectively randomizing the effects of gophers on the landscape. This suggests a possible mechanism by which the geomorphic impacts of gophers have migrated through the entire landscape.

Finally, within the montane and subalpine zones of the Front Range, forests have significantly reorganized over the last 150 years in response to anthropogenic activities that include logging, mining, town construction, and railroad construction (Veblen and Lorenz, 1991). The decades to century-scale forest migration back into cleared lands in the aftermath of these disturbances suggests that gophers have had the opportunity to impact much of the Front Range landscape.

While feedbacks between gophers and the forest edge through herbivory of seedlings is not required for the gophers to have had a significant impact on the landscape, we have initiated a numerical modeling effort to explore the nature of the meadow-forest pattern evolution that depends upon the relationship between tree age, tree density, and gopher density. By exploring the possibility that gophers mediate the evolution of the forest-meadow boundary, we will probe the full richness of this ‘forest-meadow-gopher’ system.

6. Conclusions

Within the subalpine zone of the Colorado Front Range, meadows dot the forested landscape. Within this till-mantled landscape, the Northern Pocket Gopher clearly is the dominant geomorphic worker within the meadows and is not a player in the forests. At the meadow scale on an annual timescale, spatial and temporal patterns of gopher-generated surface mounds and infilled tunnels reveal that the transport of sediment by gophers is neither steady nor uniform. The seasonal pattern likely reflects subsurface temperatures that are, in turn, governed by patterns of snow depth. Field documentation during 2014 suggests that gophers play a significant role in vertically churning the ~15-cm-thick biomantle of the meadow on approximately century timescales. We capture the efficiency of lateral gopher sediment transport with a landscape diffusivity, κ , of $0.008 \text{ m}^2\text{y}^{-1}$. Forest-meadow boundaries are not stationary; meadow-forest complexes repeatedly self-organize in the aftermath of fires and other

natural and anthropogenic disturbances. Over millennial timescales, the migration of meadows will inevitably spread the influence of gophers in vertically churning the biomantle and in transporting sediment downslope in this landscape.

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