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The role of pocket gophers as subterranean ecosystem engineers

O.J. Reichman and Eric W. Seabloom

Pocket gophers (Geomysidae) and their ecological cognates worldwide have profound impacts on ecosystems, from consuming vegetation to altering the soil physically. The rodents excavate vast burrow systems and deposit tailings in abandoned tunnels and on the ground surface. Energetic costs of excavations are extremely high, placing a premium on optimizing the location of burrows. The resulting disturbance patterns alter physical and biotic processes fundamentally. Recent studies reveal that the extensive excavations and their associated impacts generate a dynamic mosaic of nutrients and soil conditions that promotes diversity and maintains disturbance-dependent components of plant communities. Furthermore, these disturbances significantly accelerate erosion and downslope soil movement on shallow slopes and inhibit them on steep slopes.

Ecosystem engineers are those organisms that modify, maintain and create

habitats [1]. The discussions about ecosystem engineering have become complex and, perhaps, trivialized by characterizing any influence on the environment as a form of engineering. Because all plants and animals affect the physical environment in some way, from their simple presence (autogenic; e.g. tree branches as habitats) to altering

a substrate (allogenic; e.g. footprints on the surface of the soil), little is gained by classifying all organism–environment interactions as engineering.

Clearly, however, there are organisms that alter the physical environment significantly in nonincidental ways that strongly affect other organisms. Some – such as beavers, which construct dams to flood areas, providing protection and resources for themselves and generating a complex, diverse habitat for other organisms – truly engineer their environment [2]. If the concept of ecosystem engineers is to be useful, then biologically mediated change to the physical environment should be distinctive from processes that are strictly abiotic (e.g. soil movement resulting from rainsplash) and large relative to the purely physical processes operating in the system. Here, we show that subterranean mammals meet both of these criteria.

We focus on the ways in which subterranean herbivorous mammals (concentrating primarily on North American pocket gophers *Thomomys bottae*)

Box 1. Effects of pocket gophers on plant community dynamics

One of the major influences of subterranean rodents is mediated through their effects on the life history of plants. The initial formation of mounds smothers live plants and litter and slows the rate of succession [a,b]. The mounds serve as gaps in the vegetation, in some cases enhancing germination in otherwise crowded plant communities. Mortality of seedlings tends to be very high on mounds, because of exposure to herbivores and dry soil conditions, but those individuals that survive are larger and produce more seeds than do their neighbors embedded in the surrounding plant community matrix [c].

Although plant biomass is significantly decreased directly over burrows and mounds, plants adjacent to the disturbances benefit from the reduced competition for resources (light, water and nutrients) and grow large. A study in the tallgrass prairie of Kansas indicated that plant biomass ($\text{g} \cdot 100 \text{ cm}^{-2}$) over burrows and mounds was significantly reduced but that biomass extending 10 cm from the disturbances exhibited enhanced biomass (Fig. 1; white bars represent samples on or near burrows, green bars are from mounds; mean \pm SE) [d]. In turn, this inhibits plant biomass farther away from the disturbance, generating a competition-induced wave of biomass that extends the swath of influence of a burrow or mound up to 0.4 m on each side of the disturbance (Fig. 1).

In the absence of pocket gophers *Thomomys bottae*, high soil fertility leads to increased plant biomass, which, in turn, reduces light availability at the surface. Pocket gophers can uncouple this relationship by reducing biomass through herbivory and mound deposition. This increases resource heterogeneity and generates greater plant species diversity [a,e]. Thus, it is probable that gophers are important for maintaining or restoring the disturbance-dependent elements of native plant communities [f].

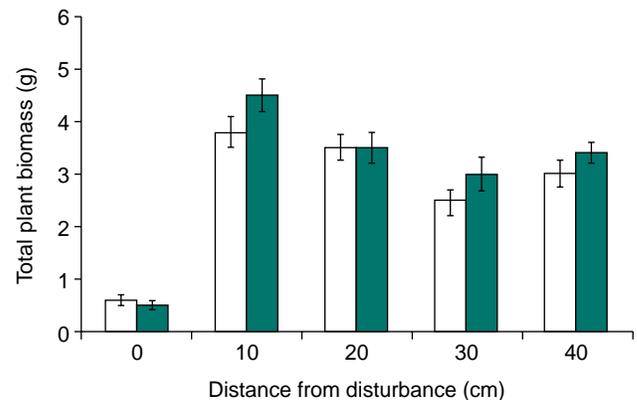


Fig. 1

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function as keystone ecoengineers [3], generating distinct patterns of soil heterogeneity and altering or accelerating processes inherent in physical systems. Specifically, we consider the role of subterranean herbivorous mammals in affecting the soil in ways that differ from strictly abiotic processes.

Ecological characteristics of subterranean herbivorous mammals

Subterranean herbivorous mammals affect the physical environment profoundly, in some estimates changing it as much as all abiotic influences combined [4,5]. However, these animals are virtually unseen in the dense, opaque soil, and their effects are poorly known and underappreciated. As with most herbivores, the direct consumption of vegetation by subterranean herbivores can be measured, but the indirect effects, mediated through alteration of the physical environment, are less easily detectable.

Most mammals that burrow into or through the ground do so to shelter in dens [6]. However, there are insectivorous and herbivorous mammals that spend virtually their entire lives below ground. Subterranean insectivorous mammals, such as moles (Talpidae), forage through the ground by simply

nudging the soil aside. Herbivorous mammals, including all North American pocket gophers (Geomyidae) and their ecological cognates in Africa (Bathyergidae), Europe (Spalacidae) and South America (Ctenomyidae), burrow through the ground and displace large quantities of soil (other rodent families also have some subterranean members [7]).

Subterranean herbivorous mammals feed primarily on plant roots [8], the loss of which affects plants more significantly than does the loss of leaves. For example, Reichman [9] found that losing 25% of roots had a larger effect on goatsbeard *Tragopogon dubius* than did losing 75% of the leaves. Grasses, with diffuse root systems, tend to be less affected by root herbivory than are forbs, which tend to have a taproot (Box 1).

To find plants, pocket gophers excavate horizontal tunnels, usually at the depth of greatest root density (a depth of 6–20 cm). Soil from the tunnels is deposited in older tunnel segments or on the surface as mounds. Some species excavate dens that are up to 1.5 m deep. The rodents range in size from 40 g to 1.2 kg, with population densities up to scores per hectare [10]. Uniformity of the subterranean habitat has led to a convergence in

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Box 2. Balancing foraging efficiency and territoriality: complex spatio-temporal patterns of pocket gopher mound formation

The average distance between branches within a burrow system of an individual is significantly less than the average distance between branches of adjacent burrow systems. Furthermore, the spacing between adjacent burrows is highly uniform, producing a buffer zone between burrows [a]. This pattern occurs over areas that differ significantly in productivity, suggesting that the buffer zones are related to social interactions, rather than to food resources.

Results from a spatially explicit plant competition model [b] illustrate the effect of between-burrow buffer size on the spatial distribution of plants (Fig. 1). The upper panel of Fig. 1 shows that the distributions of annual (white) and perennial (green) plants reflect the pattern of the underlying disturbances generated by the gopher burrows (the colors in the lower panels of Fig. 1 represent the burrows of different individuals). When the buffer is half the normal width (0.6 m; Fig. 1a) the distributions of these plant types are uniform and well mixed. As the buffer size increases to normal buffer width (1.2 m; Fig. 1b) the plant types become more spatially segregated, and this pattern is even more pronounced when buffers are twice the normal width (2.4 m; Fig. 1c). The net result of the buffers is to increase diversity by generating refugia for various plant types.

The disturbance generated by excavations tends to increase the dominance of annuals, the favored food of pocket gophers *Thomomys bottae* [c]. This positive feedback system generates conflicting circumstances for pocket gophers. Empirical [d] and modeling [b] results indicate that, in the long term, increased disturbance by gophers yields higher forb densities, which increases foraging efficiencies and, ultimately, gopher densities.

Conversely, mounds are highly patchy in distribution, as a result of area-restricted searching by gophers [e]. When gophers enter a rich patch of food, they tend to make more branches in their burrows and decrease the turning radius of burrow segments, focusing their activity in the resource patch [f].

Because the buffers are not used for foraging by gophers, they counter the positive relationship between disturbance and the gopher's favored food types. This decreases foraging efficiency and limits gopher densities. As noted, these buffers are apparently maintained for social purposes, although the exact advantages are unknown.

This territorial behavior constrains the ability of gophers to benefit from the positive feedback between foraging intensity

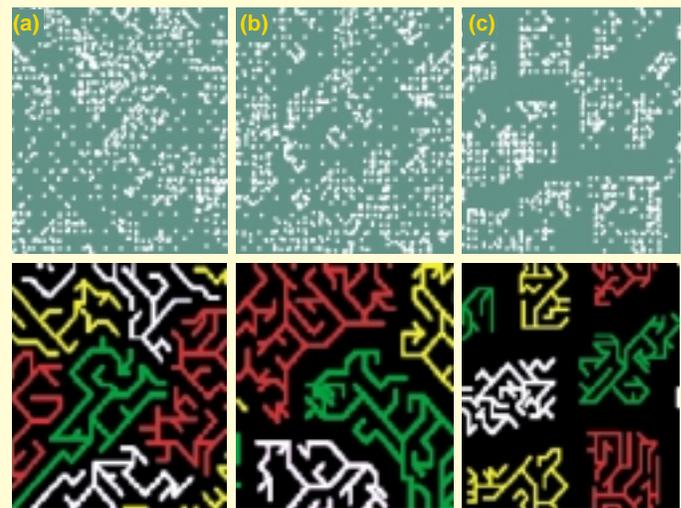


Fig. 1

and efficiency. Using simulation models, Seabloom and Reichman [b] found that territorial behavior in pocket gophers could decrease foraging efficiency by 10% by lowering the availability of preferred annual plants (Fig. 1).

The interaction of foraging and territorial behavior leads to complex spatio-temporal patterns of pocket gopher disturbances, such that mounds are highly aggregated at spatial scales that are less than the size of a gopher territory and at short time periods of the order of a few weeks. However, at larger spatial scales, mounds are regular in their distribution, as a result of the presence of undisturbed buffers between adjacent territories [e].

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morphological, physiological and behavioral traits that have evolved for life underground (e.g. powerful muscles for digging, tolerance of low O₂ and high CO₂ levels, and great sensitivity to soil vibrations [3, 7, 11]).

The subterranean lifestyle is extraordinarily expensive – it costs from 360 to 3400 times as much energy to dig 1 m as it does to walk 1 m on the surface [12]. Anderson and MacMahon [13] found that the Idaho pocket gopher *Thomomys talpoides* consumes 30% of the subterranean net primary productivity in an alpine meadow. The energy flow through some subterranean herbivore communities could approach that of much larger aboveground herbivores [8]. The energetic overhead for maintaining a subterranean existence puts a premium on making

the correct choice about where to dig (Box 2).

Smallwood and Morrison [14] summarized burrow characteristics, excavation rates and soil volumes from many studies, involving six species of pocket gophers. The amount of soil moved by these pocket gophers is immense, ranging from 3.4 to 57.4 m³ ha⁻¹ yr⁻¹ (with a mean across all species of 17.8 m³ ha⁻¹ yr⁻¹) [14]. Burrows can underlay 7.5% of the ground [15]. Mounds made by individuals of a single species can cover 5–8% of an area, and as much as 30–50% of an area over the course of a year [8, 16]. In South Africa, where three species of mole rats *Bathyergus suillus*, *Cryptomys hottentotus* and *Georchus capensis* are sympatric but segregated by depth, mounds can cover 25% of the ground surface at any one time [17]. To put

these values in perspective, studies have shown that soil movement by pocket gophers is one of the major sources of sediment transport in natural systems [4]. Recent studies allow us to couple the magnitude of excavations by subterranean herbivorous mammals with their influence on specific processes, setting the context for the nature and scope of the impact of these animals on ecosystems.

Effects on soil biogeochemistry

Because of the high food demand engendered by their energetically expensive lifestyle, pocket gophers reduce plant biomass significantly through direct herbivory (Box 1). There are indications, however, that the net long-term effect of pocket gophers is to increase plant biomass [18], probably because of the effect of the rodents on soil nutrients. These influences are the result of both the construction and refilling of extensive subterranean tunnels and the deposition of soil mounds on the surface (Fig. 1).

Mounds can have higher or lower nutrient content, moisture, water-holding capacity or concentration of organic matter than do intermound areas, depending on the depth from which the soil was excavated and the extent of subsequent weathering [19,20]. For example, soils tend to be most fertile near the surface, and, having been formed from deeper strata, mounds might represent patches of low soil fertility compared with the adjacent surface [21,22]. The organic content of mounds could be further reduced by the extraction of edible plant parts before the soil is deposited on the surface [19]. However, in highly organic soils, nutrient-rich layers could be brought to the less fertile soil surface [23]. Differential movement of soil by erosion might also lower cation exchange capacity, pH buffering and pH [19].

Similar to tillage, excavation loosens soil aggregates, creating more surface area for nitrification and mineralization [19,20]. This pattern is further complicated by the nature and amount of vegetation that decomposes under a mound after it is formed. Because the base of a mound is a moist microclimate, burial of vegetation by gopher mounds increases decomposition rates of litter, producing local nutrient 'hot spots' [19,24].

Effects on soil structure and movement

Direct effects

Some of the important influences of soil displacement are directly related to the movement and placement of soil. For example, as much as 59% of the soil from new excavations may be backfilled into old burrows, rather than deposited as mounds on the surface [25]. The soil backfilled into old burrows is 15% less compact than is the surrounding, mature soil matrix [8], even though the rodents pack it tightly into the vacant tunnels. Mounds exhibit an even lower bulk density, 10–40% lower than the underlying consolidated soil [20,26,27].

Mounds affect the microtopography of soil surfaces significantly. Areas with high mound densities

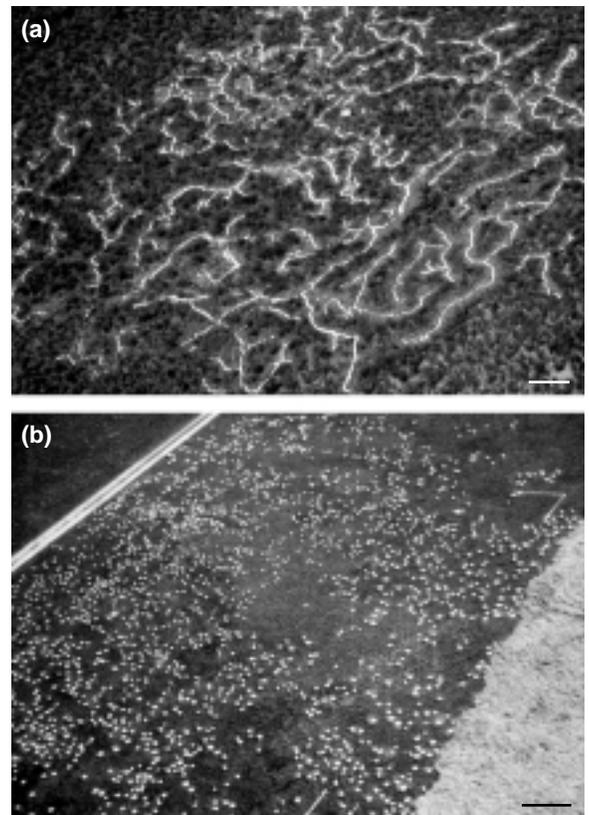


Fig. 1. Aerial photographs of gopher burrows (a) and mounds (b). Note the relatively uniform spacing of the burrows [15] and the patchy distribution of mounds. Scale bars = 5 m.

exhibited greater microtopographical variation and a greater mean height than did adjacent areas with lower mound densities [28]. Other studies [4] have described a 'mammalated microtopography' resulting from mound degradation and uneven surfaces generated by collapsing burrows.

These incremental effects are impossible to observe in progress and are difficult to measure. A more obvious influence on the landscape are mima mounds, persistent circular hummocks up to 2 m in height and 50 m in diameter. The generation of mima mounds has been ascribed to several sources [29], the most parsimonious explanation being the activity of fossorial mammals. In North America, South America and Africa, mima mounds co-occur with subterranean rodents, especially in areas of shallow soil [30,31]. Initial excavations away from the center of a territory produce a net movement of soil back towards the center. Soil depth gradually increases, usually followed by the growth of preferred plant types, eventually leading to the mounds being separated by shallow soil in the interstices, a pattern of spatial heterogeneity that persists for many years.

Altered and accelerated physical processes

The lower bulk density of mounds promotes erosion by wind and water, from the flushing of loose soil to rainsplash [4,19,20]. As the finer soil particles get blown or washed away, a more consolidated matrix,

Box 3. Relationship between hillslope and soil movement by pocket gophers

The standard model for the movement of soil downslope is linear with the rate of soil erosion directly related to hillslope (i.e. gravity). Pocket gophers *Thomomys bottae* influence this relationship in both components of their excavation activities: the movement of excavated soil below ground; and the deposition of mounds on the surface.

Seabloom *et al.* [a] have shown that the underground component is independent of hillslope angle and exhibits a pattern that emerges directly from the energetics of tunnel construction. Calculations show that the aspects of tunnel construction that are independent of hillslope (e.g. shearing and pushing soil horizontally through the tunnels) are three orders of magnitude more costly than are the functions of moving soil in relation to hillslope (i.e. gravity), making the latter cost trivial compared with that of the major components of excavating soil.

With regard to mound deposition, Gabet [b] points out that, although the linear model of downslope soil movement can be easily derived from first physical principles, it has been subjected to few empirical tests. By incorporating the aboveground effects of soil displacement by pocket gophers, he discovered that soil movement scaled in a nonlinear fashion with hillslope angle. Specifically, rather than a continuous increase in soil flux with hillslope angle (dashed line in Fig. 1), there is an initial rapid increase in soil flux at lower angles, followed by a range of slopes near the midpoint of the relationship, at which soil flux is invariant to changes in slope. This is followed by another rapid increase in flux rate, with the entire relationship illustrated by a solid line in Fig. 1 and described by a third-order polynomial regression with $r^2 = 0.97$ (vertical bars = standard errors).

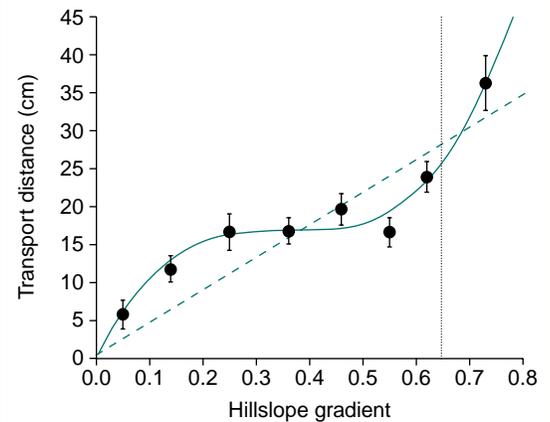


Fig. 1

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The initial rapid increase occurs when pocket gophers discharge soil preferentially on the downhill slope side of their tunnel opening to prevent soil falling back into the burrow from the uphill slope [a]. At the midranges of hillslope angle, terraces form on the downhill slope as soil accumulates. This terracing pattern persists until the hillslope exceeds the angle of repose (vertical line in Fig. 1), at which point the terraces collapse, generating another rapid increase in downhill soil flux.

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composed of larger particles and stones, is entrenched.

Soil excavation by pocket gophers has two components: the displacement of soil along underground tunnels; and the deposition and subsequent movement of soil above ground. In light of excavations by gophers, recent reconsideration of models for downslope soil movement has altered the standard model that assumes that soil flux is described by a linear relationship between hillslope gradient (i.e. gravity) and movement rate. This basic model has been applied successfully across a wide range of scales, from single hillslopes [32] to entire mountain ranges [33].

Seabloom *et al.* [27] have shown that the underground component of soil movement is invariant to hillslopes (Box 3), suggesting hillslope angle is not a factor in underground soil movement by pocket gophers. Gabet [34], testing the linear model using the movement of soil generated during tunnel construction by pocket gophers on oak savanna hillslopes in southern California, found clear evidence of a nonlinear relationship between aboveground soil movement and hillslope angle (Box 3). He further

noted that the resulting nonlinear pattern of soil flux yielded a greater net movement of soil downhill than did the more traditional linear model of soil flux on slopes steeper than the angle of repose of soil. Thus, the dynamics of tunnel excavation and mound deposition result in a pattern of erosion that deviates strongly from that expected as a result of forces driven solely by physical processes.

As with the burrows of other animals [35], gopher burrows have a major influence on water movement by concentrating runoff into fast-flowing conduits [5]. Under certain conditions, gopher burrows can become underground pipes, tunneling water from the surface down hillslopes. It has been suggested that this piping can generate significant erosion, eventually leading to the collapse of the burrow roof and the initiation of a surface gully [36]. On a smaller scale, the entrances to gopher burrows, even when refilled, can form 'terrecettes', small benches with ecologically significant microsite characteristics [5].

Net effects

The net effects of burrow excavation, backfilling, mound production and the subsequent movement of soil by physical forces generate vertical soil mixing and horizontal heterogeneity. Although these might appear to oppose one another, they occur in orthogonal axes, generating a complex matrix of impacts by gophers. Mixing tends to take place vertically, with soil from a depth of 5 cm to 1.5 m being brought to the surface. Concurrently, burrows can collapse, moving surface soil to a lower depth.

There is much spatial heterogeneity produced in the horizontal plane, yielding a mosaic of soil conditions. These range from the barren sere of a new mound to the nutritional 'hot spot' produced after the vegetation under an aging mound begins to decompose. With hundreds of mounds produced per hectare, the surface is dotted with microsites that vary in nutrient content, moisture, density and particle size. The pattern becomes more complicated as plants germinate on the mounds or re-sprout from under them, further modifying local conditions. This is a dynamic process, with new burrows being excavated, old ones being refilled and mounds being produced almost constantly over a given area. These activities occur in spatially and temporally explicit ways that also influence the system (Box 2).

Prospects

If the concept of an 'ecosystem engineer' is to be meaningful, it is important to establish the ways in which biological activities yield net effects that are different from those of purely physical processes. Recent results reveal that the excavation activities of gophers and their ecological kin affect many features of plant communities and the soil. Large alterations occur as the rodents dislodge soil, changing nitrification and mineralization rates, bulk density and moisture regimes. Soil is actively displaced some distance from its source, which accelerates ongoing physical processes, such as mixing and erosion. These activities generate a dynamic mosaic of soil patches that vary spatially in explicit patterns and are a unique outcome of the social and foraging behavior of these animals (Box 2).

Evidence suggests that the magnitude of these effects is large, in some cases constituting a major factor in soil dynamics [4,5]. The excavation and displacement of soil are important factors in the movement of soil downslope, in soil mixing and in maintaining the patchiness of soils. In turn, these influences interact with weather patterns and local vegetation in complex ways. The outcome of all the effects that gophers have on ecosystems is difficult to predict accurately, but it is clear that subterranean herbivorous mammals are a major physical force in the ecosystems in which they occur [3].

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