

Biotic origin for Mima mounds supported by numerical modeling



Emmanuel J. Gabet ^{a,*}, J. Taylor Perron ^b, Donald L. Johnson ^{c,1}

^a Department of Geology, San Jose State University, San Jose, CA 95192, USA

^b Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA 02139, USA

^c Department of Geography and GIS, University of Illinois, Urbana, IL 61801, USA

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ABSTRACT

Mima mounds are ~1-m-high hillocks found on every continent except Antarctica. Despite often numbering in the millions within a single field, their origin has been a mystery, with proposed explanations ranging from glacial processes to seismic shaking. One hypothesis proposes that mounds in North America are built by burrowing mammals to provide refuge from seasonally saturated soils. We test this hypothesis with a numerical model, parameterized with measurements of soil transport by gophers from a California mound field, that couples animal behavior with geomorphic processes. The model successfully simulates the development of the mounds as well as key details such as the creation of vernal pools, small intermound basins that provide habitat for endemic species. Furthermore, we demonstrate that the spatial structure of the modeled mound fields is similar to actual mound fields and provides an example of self-organized topographic features. We conclude that, scaled by body mass, Mima mounds are the largest structures built by nonhuman mammals and may provide a rare example of an evolutionary coupling between landforms and the organisms that create them.

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1. Introduction

Mima mounds (Fig. 1A, B) are hillocks found on all continents except Antarctica (Horwath Burnham and Johnson, 2012a). In North America, they are most common and conspicuous in the grasslands and shrublands of the western half of the continent, from the Mississippi River to the Pacific Rim, and from southern Canada into Mexico. They range from sea level to above tree line in widely disparate climates, plant communities, geologic substrates, landforms, slope aspects, and soils (Arkley, 1948; Cox and Allen, 1987; Horwath Burnham and Johnson, 2012c). The type site for these features is the Mima Mound Prairie in Washington State (lat, long: 46.88917, –123.05111).

Typically circular or elliptical in planform, Mima mounds have heights from 0.1 to 2 m, diameters from 2 to 50+ m (Horwath Burnham and Johnson, 2012a), and densities from several to ~50 mounds/ha (Reed and Amundson, 2012). They can number in the millions in large Mima mound fields, as they once did in many California tracts and still do in some areas of the Central Valley (CA). In level or gently sloping areas, low saddles of soil connect adjacent mounds to form basins that fill with water seasonally to create vernal pools (Nikiforoff, 1941), ephemeral habitat for endemic and endangered plants and animals (Helm and Vollmar, 2002). Despite their wide geographic distribution, ecological importance, and visually arresting topography, the genesis of the mounds has long been a matter of debate (Washburn, 1988).

Commander Charles Wilkes of the U.S. Navy provided the first published account of Mima mounds in 1848. During the course of a naval expedition around the Pacific Rim, Commander Wilkes made a special detour to a mound field in Puget Sound (WA) to investigate these enigmatic features. Impressed by the size of the mounds and their numbers, he concluded that they had been built by human labor (Wilkes, 1848). In 1860, members of a railroad survey hypothesized that they were formed subaerially by giant roots or underwater by whirlpools (Cooper, 1860). Since then at least 30 different explanations have been put forward, including chemical dissolution, glacial activity, artesian pressure, eolian erosion, gas venting, and earthquakes (Campbell, 1906; Nikiforoff, 1941; Scheffer, 1947; Washburn, 1988; Berg, 1990). It has also been proposed that the mounds are created by pocket gophers, burrowing members of the endemic North American family Geomyidae (Campbell, 1906; Dalquest and Scheffer, 1942; Scheffer, 1947; Arkley and Brown, 1954; Cox and Allen, 1987). According to this theory, known as the Fossorial Rodent hypothesis, gophers construct Mima mounds as a response to seasonally saturated soils; in the winter, the mounds sit above perched water tables and afford the gophers relatively dry conditions. This hypothesis was advanced on the basis of observations that (i) the mounds exist in areas with shallow soils overlying an impermeable hardpan layer, and (ii) the mounds are typically populated by gophers. It is also notable that the surface area of an average mound, ~40 m² (Reed and Amundson, 2012), is similar to the home range of gophers, ~35 m², solitary animals known to be aggressively territorial (Reichman et al., 1982).

The occupation of mounds by gophers does not, by itself, prove that gophers built the mounds – they could be living in them opportunistically. An important step in demonstrating that gophers can at least maintain the mounds was the discovery, through the displacement of

* Corresponding author. Tel.: +1 408 924 5035; fax: +1 408 924 5055.

E-mail address: manny.gabet@sjsu.edu (E.J. Gabet).

¹ Deceased.

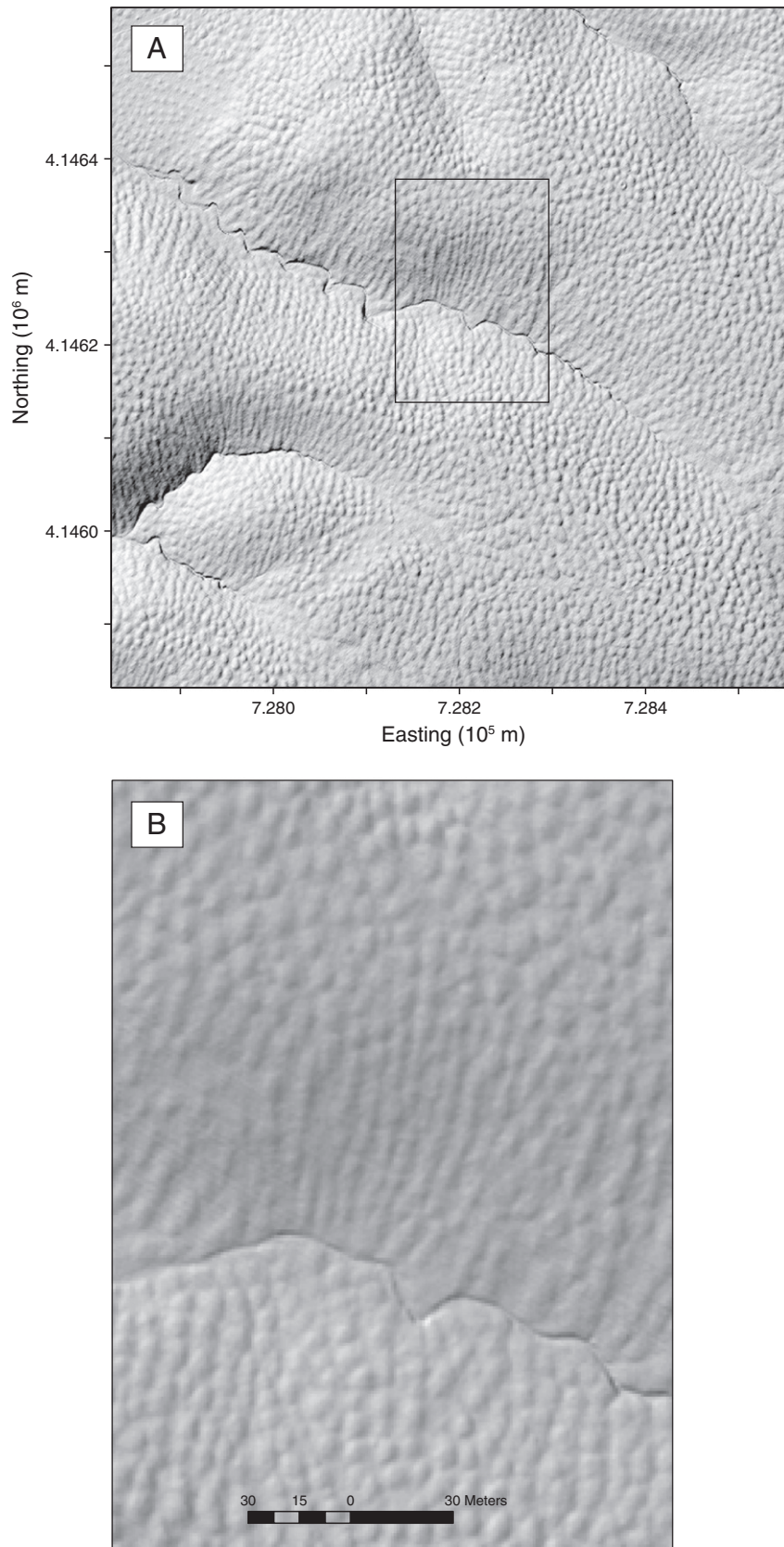


Fig. 1. (A) Mima mounds near Merced (CA). Hillshade image created from LiDAR data. (B) Magnified view of area delimited by box in (A). Note linear features on sloping terrain formed by the alignment and coalescing of multiple mounds.

metal tracers, that they push soil uphill in Mima mound fields (Cox and Allen, 1987). This behavior is surprising because studies in environments without mounds have documented a net downslope movement of material by gophers (Black and Montgomery, 1991; Gabet, 2000). Another revelation from the tracer measurements is that gophers direct the soil toward the mound centers, even at distances of 5–7 m from the mound edges (Cox and Allen, 1987); gophers in Mima mound fields, therefore, seem to be aware of local topographic highs and orient their burrowing accordingly. Whereas the tracer experiments suggest that gophers can maintain Mima mounds, it leaves unanswered the question of whether they build them. A biotic origin for these features could provide evidence that biological processes can impart a topographic signature of life on the Earth's surface (Dietrich and Perron, 2006).

Because the mounds appear to form slowly, over timescales of decades to centuries, numerical simulations provide an avenue for testing the Fossorial Rodent hypothesis. We developed a rule-based model that incorporates the effects of gopher behavior on sediment transport to determine whether local soil transport by burrowing animals can explain the emergent characteristics of Mima mound fields, such as their transient development and spatial arrangements. To ensure consistency, the model is parameterized based on data primarily from California, where Mima mounds have been studied the most, and from sites inhabited by the Botta pocket gopher (*Thomomys bottae*).

2. Methods

2.1. Modeled burrowing activity

A key parameter in the model is the rate of burrowing activity. Estimates of soil volumes displaced by gophers annually range from 0.53 to 1.73 m³ (Cox and Allen, 1987). Given the spread in these measurements, we use the intermediate value of 0.9 m³ (Richens, 1966). Dividing this volume by an estimate of a gopher's home range, 35 m² (Reichman et al., 1982), yields a 0.026-m-thick layer of soil displaced every year. Further, with an average burrow diameter of 0.06 m (Gabet, 2000), the cross-sectional area of a typical tunnel is 2.8 × 10⁻³ m² and, therefore, 321 m of tunnel must be dug annually to generate the volume of soil displaced. The planform area affected by gophers each year can be determined as the product of annual burrowing length by one gopher, burrow diameter, and animal density. Thus, with a typical animal density of 119 gophers/ha (Seabloom and Reichman, 2001), 23% of the landscape is burrowed yearly. A potentially important variable that is unaccounted for in these calculations is the texture of the soil: the energetic cost of burrowing varies greatly depending on soil density and cohesion (Vleck, 1979). Nevertheless, any uncertainties in our estimates affect the rate at which the mounds are built but not their spatial distribution or their size.

2.2. Model space and rules

The model space is divided into a grid of 10-cm × 10-cm cells, and the calculations at each cell are based on an 8-cell neighborhood. When the model is initiated, the model space consists of a 0.24-m-thick mantle of mobile soil overlying an immobile layer; the latter simulates the hardpan that acts as an impenetrable barrier to downward burrowing and subsurface flow. The soil surface is roughened by Gaussian noise (1σ = 0.01 m) to create a flat surface with randomly distributed minor topographic relief (Fig. 2A). The initial thickness of mobile soil was determined by assuming a conical shape for the Mima mounds surveyed by Nikiforoff (1941) in the Central Valley and estimating the average soil thickness contained within them (the soil in the intermound areas consisted of a claypan and was considered to be immobile; Vleck, 1979).

In rule 1, at each annual time step, 23% of the cells ('gopher cells') are randomly chosen to be burrowed by gophers (from Section 2.1). The nearest high spot, weighted by distance, to each gopher cell within a 5-m radius is identified as the 'target cell.' Given that gophers are

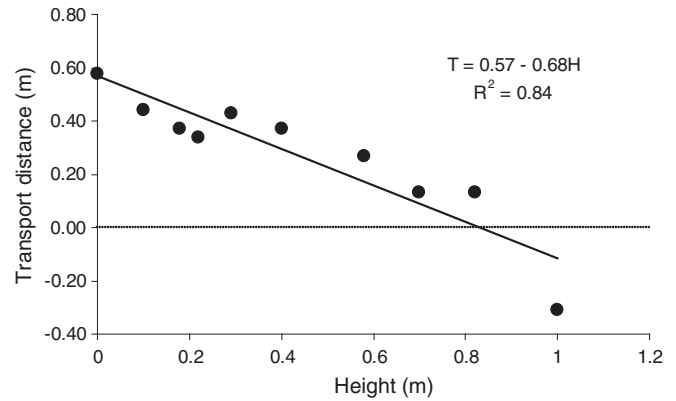


Fig. 2. Transport distance toward the mound center decreases with height above the intermound areas. At heights >0.84 m, transport distance is negative, signifying that it is in a direction away from the mound center. Data are based on the displacement of tracers over the course of one year (Cox and Allen, 1987). Measurements were made at the Miramar mound site near San Diego, CA (lat, long: 32.846944, -117.137392).

more likely to be aware of high spots nearer to them, elevations (H ; m) are weighted with

$$H^* = He^{-kD} \quad (1)$$

where H^* is the weighted elevation, k is a spatial decay constant (m^{-1}), and D is horizontal distance (m). Note that elevations are relative to the impermeable layer, which is taken to be the base level (i.e., $H = 0$). The value for k cannot be determined a priori; because simulations indicated that it is positively correlated with mound diameter, its value (0.018) was chosen such that modeled mounds grow to the same average diameter, 7.3 ± 1.9 m, as the mounds near Merced, CA (Reed and Amundson, 2012). Note that although rule 1 describes a tendency for pushing soil toward the high spots, in accord with Cox and Allen's (1987) tracer data, it could also be interpreted as a tendency to move material away from the wetter topographic lows.

Rule 2 determines the transport distance as a function of elevation above the immobile layer. Previously published data from a study using tracers (Cox and Allen, 1987) revealed an inverse relationship between elevation (H ; m) and transport distance (T ; m) in the direction of the local high spot: $T = 0.57 - 0.68H$ (Fig. 2). With the transport distance calculated, a 0.026-m-thick layer of soil (from Section 2.2) is moved in the direction of the target cell identified by rule 1. Observations indicate that at slopes steeper than 10–12°, gophers push all of the burrow tailings downhill, perhaps to avoid having soil fall back into their tunnels (Gabet, 2000). This limit is supported by the downslope elongation of mounds where the regional hillslopes exceed this same range of slope angles (Reed and Amundson, 2012). Therefore, in rule 2, the model does not allow any uphill transport of soil by gophers on slopes steeper than 11°. Finally, in accord with the tracer data (Fig. 2), when the height of the gopher cell is >0.84 m, the transport distance is negative (i.e., away from the local topographic high). In this case, a downslope direction is randomly selected.

With rule 3, any slope steeper than the angle of repose (32°) immediately collapses to a stable angle (30°). Rule 4 simulates the downslope flux of material by soil creep processes with

$$q_s = \frac{KS}{\mu^2 - S^2} \quad (2)$$

where q_s is the volumetric flux per unit width (m²/y), K is diffusivity (m²/y), μ is a critical gradient (m/m), and S is hillslope gradient (m/m) (Roering et al., 1999). Values for K (0.008 m²/y) and μ (1.25) were estimated from a study in a gopher-free region with a climate similar to the Central Valley of California (Avouac et al., 1993). Eq. (2) is applied to the

entire model space at each time step; the gradient of each cell is based on the elevation difference with its steepest downslope neighbor in an 8-cell neighborhood. Note that, at the low slopes common on Mima mounds, the sediment flux by soil creep is <10% of the flux by gophers, and thus uncertainties in the parameterization of this process should have minimal effects.

Finally, it is important to recognize that the model is run at an annual time-step whereas the burrowing activity of gophers varies seasonally. Because digging activity is much higher in moist soils (Miller, 1948; Cox and Allen, 1987; Romanach et al., 2005), transport toward topographic highs during the wet season is likely to account for a large fraction of the annual bioturbation flux. In addition, the data from the tracer experiments used to determine transport distances were collected over the course of a year and, thus, account for wet and dry season transport. Thus, the model rules summarized above are intended to describe the net transport over an annual cycle.

2.3. Topographic surveys of developing mounds

The rate of mound building in the simulations was tested against a topographic survey of mounds emerging from a previously leveled and plowed agricultural field. Farming activity on the KCL Ranch (on the Carrizo Plain, California) ended in the early 1980s and, since then, the land has not been subjected to anthropogenic impacts (Horwath Burnham and Johnson, 2012b). Over the past 30 years, mounds have begun to reform and, although still low, are identifiable by tall tufts of grass sprouting from them. In January 2012, all the mounds ($n = 20$) within a 2.5-ha area were surveyed with a tape, stadia rod, and self-leveling level. Fresh gopher-burrow spoils were widespread throughout the mounds and a gopher was seen digging in one of the mounds as it was being surveyed. Burrows of the Giant Kangaroo Rat (*Dipodomys ingens*) were also noted in the area. Because these animals forage on the soil surface (Shaw, 1934), we assumed that their burrowing activity was low relative to that of the gophers, which subsist primarily on belowground plant parts and, thus, must dig continuously (Reichman and Seabloom, 2002).

2.4. Analysis of mound spatial arrangement

A high resolution digital elevation model (DEM) for the Merced Mima field (Reed and Amundson, 2006) provides another opportunity to test the simulations. Because the model was calibrated to yield mounds with average diameters similar to those at the Merced site, simulated mound diameter is not a useful criterion with which to test the model. Instead, we compared the spatial arrangement of the modeled mounds with the arrangement of real mounds in 35 1-ha subregions within a 2-km \times 2-km region of the laser altimetry survey of the Merced mound field (Fig. 3A). Most subregions are ridgetops, which have gentler background slopes and curvatures than valley sideslopes or valley bottoms and typically have more uniform mound characteristics. We developed an automated procedure that identifies mound centers, draws a Voronoi polygon around each center point, and computes statistics describing the distribution of polygon shapes (Fig. 3B). For the Merced subregions, we calculated the Laplacian of elevation, $\nabla^2 z$, which provides a map of concave-up and concave-down areas (Fig. 3B) that is insensitive to trends in the background topography associated with larger scale ridges and valleys. The Laplacian was measured from the coefficients of a least-squares quadratic surface fit to the elevations within a small radius (4 m in the case of the Merced mounds). Mound centers were then identified as local minima in the Laplacian. Mound centers identified with these procedures are qualitatively insensitive to moderate variations in the smoothing and fitting parameters and coincide with visually identified mound centers. In the numerical model output (24 simulations on 80-m \times 80-m grids), mound centers were identified as local maxima in elevation after the elevation grid was smoothed with a Gaussian filter with a standard deviation of

1.25 m to remove pixel-scale roughness (Fig. 3C). Local maxima were required to be at least 2.5 m apart to avoid counting compound mounds with two peaks as two separate mounds; in these cases, the tallest peak was selected. In addition, the outermost 5 m of the model domain were excluded from the analysis to avoid edge effects. For each mound field, defined by the boundaries of the model domain or the topography in an area of interest, we constructed Voronoi polygons around the mound center points (Fig. 3B, C). Only bounded polygons, which have all sides defined by neighboring points, were retained. For comparison with the natural and modeled mounds, we analyzed 1000 sets of 114 points (the same as the number of model mounds in Fig. 3C) with random x and y coordinates using the same procedure applied to the mound centers (Fig. 3D).

We characterized the spatial arrangement of mounds by measuring two properties. The first, the variability of mound spacing, is determined by calculating the square root of the area of each polygon, L (a quantity proportional to the average distance of a mound from its neighbors), and taking the mean, L_{av} , and the standard deviation, σ_L . The quantity σ_L/L_{av} (i.e., the coefficient of variation) is a dimensionless measure of the variability of mound spacing that is independent of mound size. The second property, the packing geometry, has square and hexagonal packing as endmembers. To quantify the packing geometry, the total length of the four longest sides of each Voronoi polygon was divided by the polygon perimeter, yielding a ratio that is 2/3 for a perfect hexagon and 1 for a four-sided polygon. This ratio was then transformed into a measure of polygon 'squareness', ranging from 0 for a perfect hexagon to 1 for a four-sided polygon, by multiplying it by 3 and subtracting 2. The packing index is the mean of this quantity for all polygons in a mound field.

3. Results

3.1. Simulated mound growth and morphology

In the early stages of a simulation, soil is transported toward the randomly distributed topographic highs (Fig. 4A, B; Video 1). As some high points grow faster than others, they increase their source area for soil and grow even taller, thereby strengthening the positive feedback between mound height and center-directed sediment transport. Because the gophers are likely responding to soil moisture, the topography is essentially a proxy for wetness and, as the high points get higher and the lows lower, the moisture contrast becomes stronger through time. The radius of attraction of each high spot continues to grow until it abuts the source areas of neighboring high spots, at which time the general platform shapes and positions of the mounds become established (Fig. 4B, C). In the model, this general spatial organization emerges within the first few decades, a result supported by our observations of the 30-year-old mounds on the Carrizo Plain. The mounds then grow vertically until (i) all the available soil is contained within the mounds, (ii) the mounds have reached their maximum height, and (iii) the sides of the mounds have slopes of 11° . At this point, usually by 500 years, the mound field has reached topographic steady state (Fig. 5).

The simulated landscapes exhibit key details seen in real mound fields. The model recreates the variety of shapes seen in the field, including circular, elliptical, and compound mounds, and it reproduces the low saddles of soil connecting contiguous mounds, thereby creating isolated depressions that mimic vernal pools (Fig. 5). In addition, the model correctly reproduces the rate of mound building: after 30 years of model time, simulated mound heights average 0.25 ± 0.02 m ($n = 117$), statistically similar (t -test, $p > 0.999$) to the Carrizo Plain mounds, 0.24 ± 0.07 m ($n = 20$). Admittedly, given the uncertainties in the volumetric transport rate, the potential differences in soil texture between the Carrizo Plain and Central Valley sites that could affect burrowing rate (Vleck, 1979), and the unknown impact of digging by kangaroo rats at the Carrizo site, the similarity of the simulated and observed mound-building rates may be fortuitous. Finally, the simulated

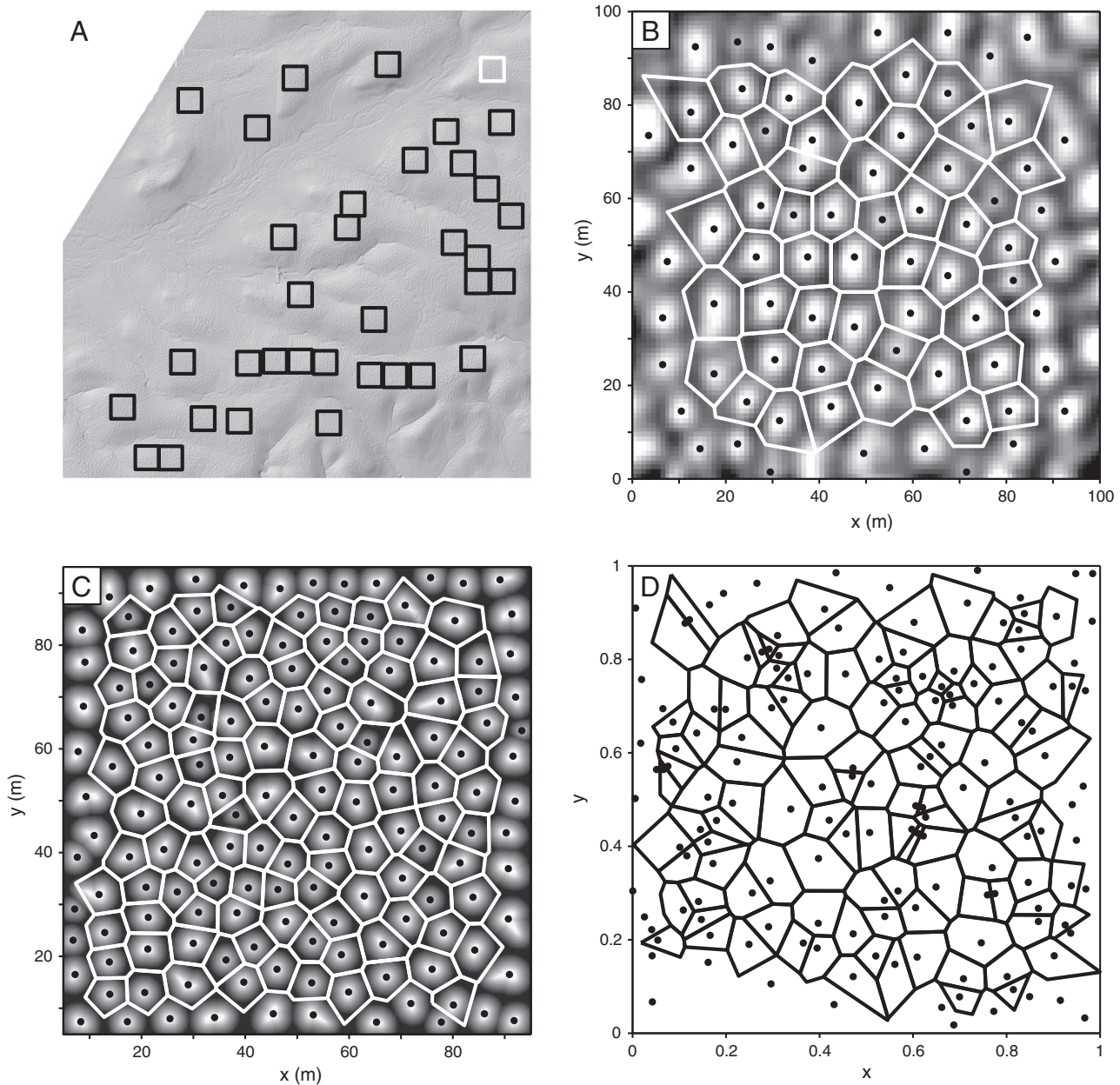


Fig. 3. Spatial analysis of Mima mounds. (A) Shaded relief map of Mima mound field near Merced, CA, based on airborne laser altimetry (lat, long: 37.408626, -120.439815). 100×100 m squares outline the 35 subregions analyzed in this study. (B) Voronoi polygons for subregion in (A) outlined by white box. Gray-scale is proportional to the Laplacian of elevation, $\nabla^2 z$ (dark areas are concave-down, light areas are concave-up). (C) Voronoi polygons for model simulation at steady-state. Gray-scale is proportional to elevation (light areas are high, dark areas are low). (D) Voronoi polygons for an array of points with random coordinates. Points in (B) and (C) mark mound centers identified from local extrema in the Laplacian (B) or elevation (C). Note that partial mounds with no local extrema within the grid are excluded in (B), and only bounded Voronoi polygons (polygons with all sides defined by neighboring points) are included in (B–D).

mounds reach an equilibrium height of 0.84 m, similar to the range found for real mounds. Note, however, that this height is a consequence of the deterministic model rule, derived from the tracer measurements, that moves soil away from mound centers when elevations exceed 0.84 m. In reality, this value may vary according to local and seasonal conditions.

3.2. Spatial arrangement of real and simulated mound fields

A plot of the packing index vs. σ_L/L_{av} defines a phase space for the spatial arrangement of Mima mounds (Fig. 6). The location (0,0) corresponds to perfect hexagonal packing, and the location (0,1) corresponds to perfect square packing. The Merced Mima mounds are nearly uniformly spaced ($\sigma_L/L_{av} \approx 0.1$) and exhibit a packing geometry that is

slightly more square than hexagonal. For the modeled mound fields, we measured their spatial properties at two elapsed times: 85 years, when the modeled mounds have the same average height as the Merced mounds, 0.44 m (Reed and Amundson, 2012), and 500 years, after the mounds have reached steady-state. After 85 years, the modeled mounds have a spatial arrangement that is statistically very similar to the Merced site (Fig. 6). After 500 years, the simulated mounds have a slightly more uniform spacing and hexagonal packing, although the 95% confidence region of the modeled mounds overlaps with that of the Merced mounds. Given that the Merced mounds are thought to be much older than a century (Campbell, 1906), their slightly more square packing could reflect the tendency of mounds to become somewhat aligned on sloping surfaces (Reed and Amundson, 2012) (the land surface underlying the Merced field is gently sloping, even in the relatively

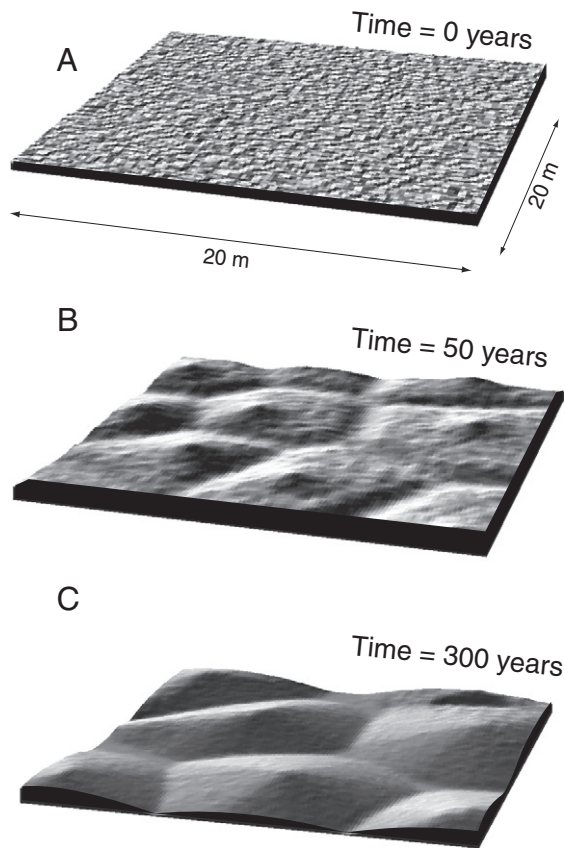


Fig. 4. Simulated development of Mima mounds from a rough, low-relief initial surface (A). (B) After 50 years, mound heights range from 0.4 to 0.5 m. (C) After 300 years, mound heights range from 0.6 to 0.8 m. 10× vertical exaggeration.

flat areas that we analyzed). Alternatively, the lower average height of the Merced mounds relative to those studied by Nikiforoff (1941) suggests that the Merced site has thinner soils; and so it is possible that the mound geometry there became fixed earlier in their evolution. Nevertheless, the spatial arrangements of the modeled mounds and the

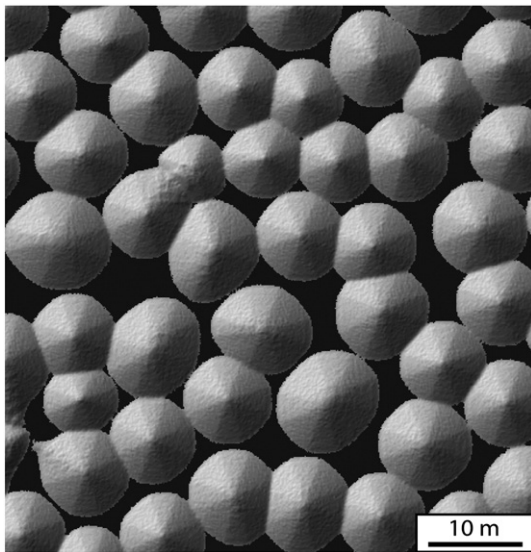


Fig. 5. Modeled steady-state mounds display the variety of shapes seen in natural mound fields, including circular, elliptical, and compound mounds. Low-lying areas colored black to simulate vernal pools. The mounds are slightly faceted because the model moves sediment in eight discrete directions.

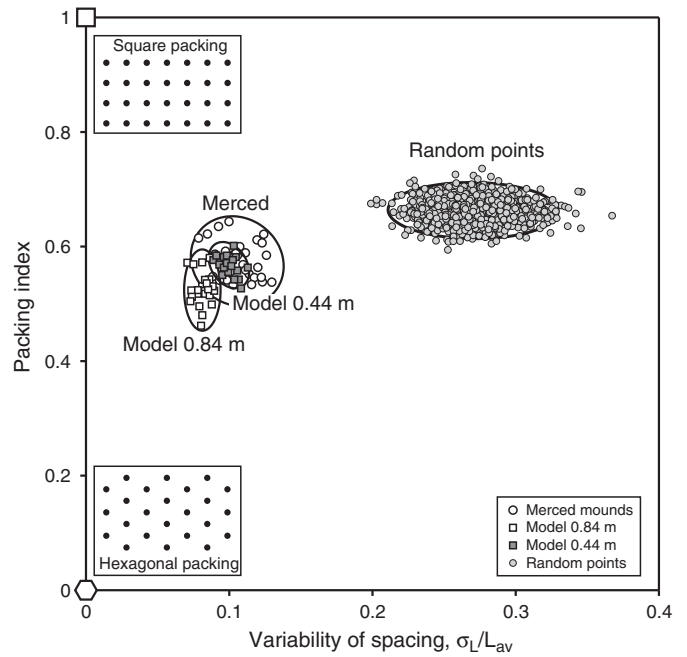


Fig. 6. Phase plot characterizing the packing geometry of Mima mounds. Horizontal axis measures the coefficient of variation of L , a proxy for mound spacing, and vertical axis measures the continuum from hexagonal packing to square packing, as illustrated by the inset arrays of dots. Each data point is the mean for a measured or modeled mound field; ellipses are 95% confidence regions. The ‘0.44 m’ and ‘0.84 m’ mounds correspond to 85 and 500 years of model time, respectively. The ‘random points’ correspond to fields of points created by selecting x and y coordinates from a random uniform distribution.

Merced mounds are much more similar to one another than either is to randomly arranged points (Fig. 6), demonstrating that both the observed and modeled mounds have a far more organized pattern than would be expected by chance and providing evidence that the model has captured the processes essential to the formation of these features.

4. Discussion

4.1. Self-organization of Mima mound fields

Our results demonstrate that large, uniformly spaced mounds can be formed by the local, small-scale burrowing behavior of gophers. In addition, the formation of Mima mounds highlights the role that competition for resources plays in the emergence of uniformly spaced features with spatial extents greater than the length scales of the processes that create them. Because the time scale of mound construction (10^2 years) is much greater than a gopher’s lifespan (10^0 years), the existence of a mound is essentially independent of the actions of any individual gopher; in a sense, then, it is the mounds that compete with each other for available soil. Indeed, field observations indicate that the distance between mounds increases with mound size, suggesting that a limited supply of soil controls their growth (Cox, 1990). Similarly, competition for runoff leads to the regular spacing of valleys and ridges as large watersheds grow at the expense of smaller ones (Perron et al., 2009). In both of these cases, positive feedbacks amplify small, randomly distributed, initial advantages to create coherent large-scale patterns, a common feature of self-organized systems (Resnick, 2000). In addition, just as stream piracy can incorporate one watershed into another (e.g., Garcia, 2006), the simulations suggest that large mounds occasionally capture and subsume smaller ones. Although two mounds may initially be isolated from each other, a bridge of soil develops between the pair and acts as a conduit for passing material from the smaller to the larger feature (Fig. 7A, B). From model observations, capture occurs when a mound becomes sufficiently tall that it begins to ‘attract’

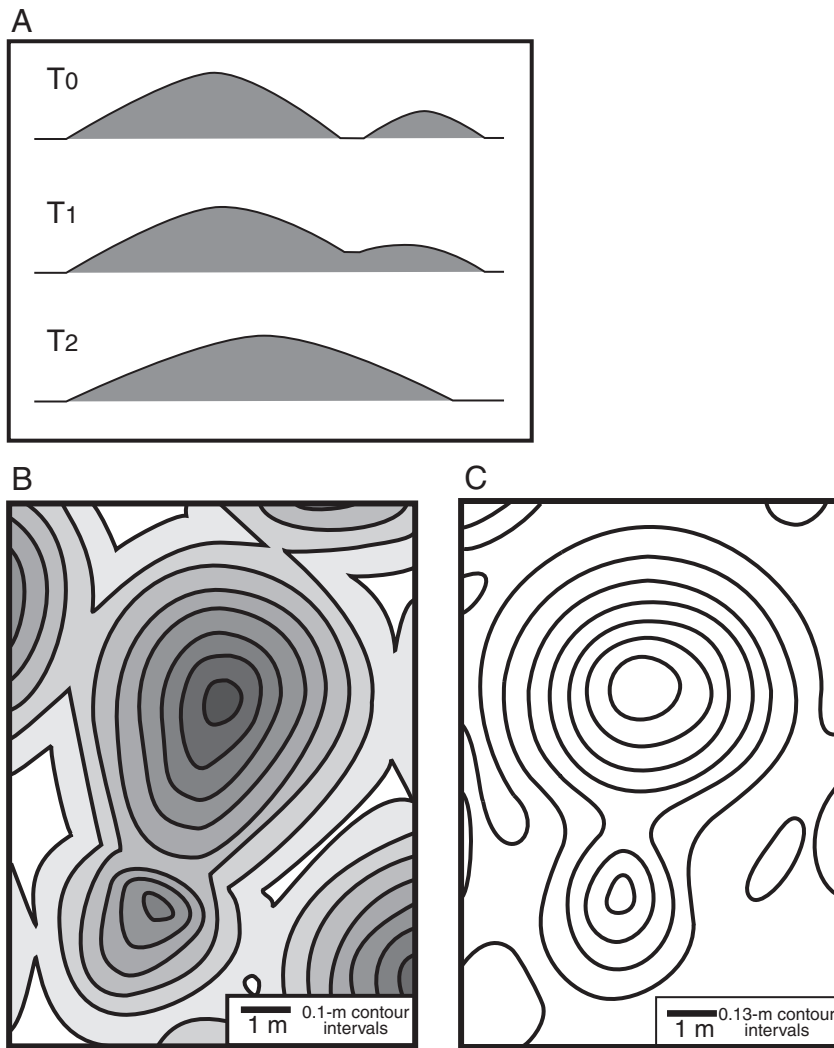


Fig. 7. (A) Profile view of mound capture from model simulation: T_0 – initial stage, T_1 – capture, and T_2 – complete assimilation. (B) Planform view of mound capture (stage T_1) during model simulation. Darker shading represents higher elevations. (C) A topographic survey of mounds, digitized from Nikiforoff (1941), appears to show a large mound in the process of cannibalizing a smaller one. Note similarities between (B) and (C).

soil from the base of a smaller adjacent mound. Erosion of the smaller mound's base steepens its slope, accelerating soil creep that draws soil away from its center. Soil eroded from the smaller mound is transported toward the center of the larger mound until the former has been completely absorbed. These observations from the model are supported by detailed topographic surveys in California's Central Valley, which appear to show mounds in the process of being consumed (Fig. 7C). Presumably when a mound is abandoned, a gopher in an adjacent mound may extend its range into the uninhabited one and direct the soil toward its own; this process is likely bolstered by these animals' highly territorial behavior (Reichman et al., 1982). Mound cannibalization is similar, in a general way, to the capture of smaller shoreline capes by larger ones (Thieler and Ashton, 2011). These three examples (Mima mounds, watersheds, and capes) suggest that the gradual evolution of self-organized topographic features may be punctuated by rare but dramatic changes.

4.2. Potential refinements to the model

The goal of this project was to simulate the formation of mounds by gopher activity using a minimum number of rules to drive the model. The similarity in the spatial organizations of the simulated and natural mounds (Fig. 6) suggests that we have captured the essence of mound creation; however, several refinements to the model could be made in

future versions. First, the model was run on a tilted surface to explore whether our rule set was sufficient to create the long, slope-parallel linear mounds observed on steep terrain (Fig. 1B) and, although the simulated mounds did elongate in the downslope direction and align themselves somewhat parallel to the slope, they did not coalesce into the ridge-like features seen in real mound fields (Fig. 8). This mismatch suggests that, on sloping surfaces, the flow of water may have an important effect on the ultimate disposition of the soil, either by eroding it or by altering the digging behavior of the gophers. Second, although there is field evidence for mound capture (Fig. 7C), the number of these events in the simulations seemed higher than would be expected in nature. In the early stage of each simulation, there was a wide distribution of mound diameters and, over time, the smaller ones were consumed by their larger neighbors. In the real world, a gopher needs a minimum home range for foraging, thereby setting a lower limit on the size of mounds. Incorporating gophers' foraging and territorial behavior, therefore, might simulate the initial development of mound fields more accurately and reduce the high number of mound captures. Finally, the simulated mounds had sharper apices than those in Merced, a geometric difference attributable to the model's low volume of available soil (based on Central Valley data) and the reversal of transport direction at the 0.84-m threshold (based on the tracer data from San Diego, CA). A larger volume of soil or a lower threshold would have produced mounds with broader tops but, because of the limited

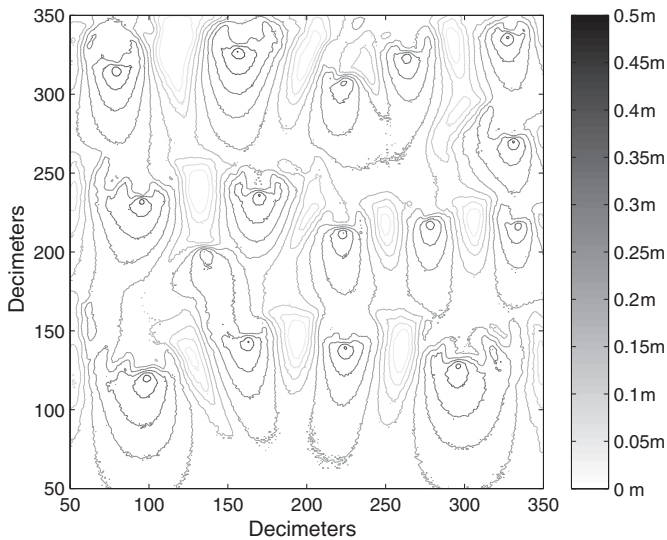


Fig. 8. Modeled mounds on 20° slope; the bottom of the figure is the hillslope's lower boundary. Although the mounds are somewhat aligned down the slope, they did not coalesce into the linear ridges seen in the field.

data available for parameterization, we were required to combine observations from different locations.

4.3. Are *Mima* mounds a topographic signature of life?

To our knowledge, beaver dams are the only structures built by nonhuman mammals comparable in size to *Mima* mounds. The volume of a typical beaver dam is 23 m³ (Gurnell, 1998) and a beaver weighs ~20 kg (McNab, 1963); *Mima* mounds have average volumes of 13.8 m³ (Reed and Amundson, 2012) and pocket gophers weigh ~0.15 kg (Reichman et al., 1982). With these values, the average structure-size-to-body-mass ratio for *Mima* mounds is ~100 m³/kg, whereas the ratio for beaver dams is only ~1 m³/kg, 2 orders of magnitude smaller. Therefore, scaled by body mass, *Mima* mounds are the largest known structures built by nonhuman mammals. In addition, because a single field can be dotted by millions of mounds, the formation of these features represents a significant degree of ecosystem engineering (Reichman and Seabloom, 2002).

But does this large-scale landscape modification by gophers constitute a topographic signature unique to life (Dietrich and Perron, 2006)? We propose that it does not. At the scale of a mound field, the gophers' burrowing behavior is similar to small-scale abiotic mechanisms that form larger scale features such as ice wedge polygons, mud cracks, stone circles (Kessler and Werner, 2003), and other regular space-filling patterns that result from nearly isotropic landscape processes (Hallet, 1990). Furthermore, the development of smooth, convex landforms is common to many abiotic geomorphic processes (Culling, 1965). Indeed, if the shapes of *Mima* mounds were uniquely biological, it is unlikely that so many different explanations would have been proposed for their origin for nearly 200 years.

Even if the biological origins of the *Mima* mounds cannot be divined solely from their topographic expression, their construction has interesting evolutionary implications. The strong association of the mounds with poorly draining soils suggests that mound creation is not an incidental consequence of foraging behavior but is, instead, an adaptive response to local conditions. The net uphill transport of soil in these environments contrasts with the typical gopher behavior of pushing soil downhill (Black and Montgomery, 1991; Gabet, 2000) and, although small relative to the cost of shearing soil from tunnel walls, there is an energetic cost to pushing soil against gravity (Vleck, 1979). It therefore appears that the downhill transport of soil by gophers is a default behavior that is overridden when saturated soils provide a cue to push

soil uphill; indeed, downhill transport is observed at the top of the tallest mounds where the soil is elevated above the water table and presumably drier (Cox and Allen, 1987). This conclusion raises two questions. First, can all gophers switch their digging direction in response to soil moisture cues, or is this an adaptation specific to populations inhabiting regions with seasonally saturated soils? Second, are the mounds found on other continents formed by other burrowing animals that have evolved this same adaptive behavior? If so, *Mima* mounds may be a rare example of an evolutionary coupling between landforms and the organisms that inhabit and shape them.

5. Conclusions

The origin of *Mima* mounds, small hillocks that can number in the millions in single fields, has been a matter of debate for centuries. To explore the Fossorial Rodent hypothesis, one of the theories advanced to explain the formation of these features, we developed a numerical landscape evolution model that incorporates observations of sediment transport by pocket gophers. In the simulations, mounds emerge spontaneously and develop the same self-organized patterns as natural mound fields. We conclude that *Mima* mounds are the largest structures built by nonhuman mammals.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.geomorph.2013.09.018>.

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