

1 A process-based model linking pocket gopher (*Thomomys*
2 *bottae*) activity to sediment transport and soil thickness

3 **Kyungsoo Yoo***

4 **Ronald Amundson**

5 *Division of Ecosystem Sciences, University of California, Berkeley, California 94720, USA*

6 **Arjun M. Heimsath**

7 *Department of Earth Sciences, Dartmouth College, Hanover, New Hampshire 08755, USA*

8 **William E. Dietrich**

9 *Department of Earth and Planetary Science, University of California, Berkeley, California*

10 *94720, USA*

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12 *Corresponding author e-mail: kyoo@nature.berkeley.edu.

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14 ¹GSA Data Repository item 2005xxx, photographs, equation derivation, biological power
15 quantification and anisotropic power expenditure, and application of soil thickness dependence
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18 80301, USA.

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20 **ABSTRACT**

21 While earth-dwelling organisms assist in shaping earth surfaces and are simultaneously
22 affected by the environment they inhabit, a conceptual framework is not yet available to describe

23 the feedback. We introduce a model that connects soil burrowing animal's population density to
24 sediment transport via energy. The model, combined with available data from California
25 hillslopes where soil erosion is driven by pocket gophers (*Thomomys bottae*), suggests that a
26 gopher annually expends ~9 KJ of energy or ~1% of reported burrowing energy expenditure in
27 generating sediment transport. The model is used to evaluate the case that gophers prefer to
28 populate thicker soils. The results suggest that this behavior may drastically dampen the spatial
29 and temporal variations of soil thickness and gopher populations, implying that burrowing
30 organisms may create landscapes distinct from those affected by abiotic processes.

31 Keywords: **sediment transport; bioturbation; pocket gopher; soil thickness; hillslope.**

32 INTRODUCTION

33 More than a century after Darwin estimated the landscape denudation rates caused by
34 earthworms (Darwin, 1881), a formidable barrier still exists in mechanically describing the
35 interplay between biological and earth surface processes. Ecologists focus on organisms'
36 populations, but geomorphologists focus on the energy involved in carving landscapes. We
37 develop a model that links the energy behind geomorphic processes to the populations of
38 burrowing organisms. By applying the model to hillslopes where pocket gophers (*Thomomys*
39 *bottae*) drive sediment transport and the soil production rate from bedrock is known (Dietrich et
40 al., 1995; Gabet, 2000; Heimsath et al., 1997), we suggest that gopher population dynamics may
41 significantly modulate the spatial and temporal dynamics of hillslope soil thickness and hillslope
42 morphology.

43 GOPHER ENERGY INPUT TO SOIL TRANSPORT

44 Sediment transport, when generated by organisms, is ultimately powered by the
45 photosynthesized energy. To incorporate the biological energy, we modified a sediment transport

46 model (Roering et al., 1999; Andrews and Bucknam, 1987) in which sediment flux ($\tilde{q}_s = L^2T^{-1}$)
 47 is the product of the volume of moving soil ($V = L^3$) per area ($A = L^2$) and sediment velocity ($u =$
 48 LT^{-1}). The sediment velocity is determined by a physical law, $P = Fu$, where P is power ($=$
 49 ML^2T^{-3} , where M is mass), and F is a resistance ($=MLT^{-2}$). Where a single species dominates
 50 sediment transport, the power input per area (P/A) is the product of organism's population
 51 density ($N = L^{-2}$) and its individual power input (P_i).

$$52 \quad \tilde{q}_s = \frac{V}{A}u = \frac{P/A}{F/V} = \frac{NP_i}{F/V}. \quad (1)$$

53 Following Roering et al. (1999), downslope sediment flux (\tilde{q}_d) is resisted by friction but
 54 aided by gravity ($F/V = \mu\rho_s g \cos\theta - \rho_s g \sin\theta$, where μ = the effective friction coefficient, $\rho_s =$
 55 soil bulk density (ML^{-3}), g = the gravitational acceleration constant [LT^{-2}], and θ = slope angle).
 56 The upslope sediment flux (\tilde{q}_u) is resisted by friction and gravity ($F/V = \mu\rho_s g \cos\theta + \rho_s g \sin\theta$).
 57 If a fraction ψ of the power is directed downslope, the gross fluxes are:

$$58 \quad \tilde{q}_d = \frac{V}{A}u_d = \left(\frac{\psi P_i}{\rho_s g \mu} \right) \frac{N}{1 - (-\nabla z / \mu)}, \quad (2)$$

59 and

$$60 \quad \tilde{q}_u = \frac{V}{A}u_u = \left(\frac{(1 - \psi)P_i}{\rho_s g \mu} \right) \frac{N}{1 + (-\nabla z / \mu)}. \quad (3)$$

61 where z = elevation of the ground surface [L].

62 Gabet (2000) reported that as slope becomes steeper, gophers move excavated soil to the
 63 downslope to prevent back filling. We limit this paper, however, to isotropic power expenditure
 64 ($\psi = 0.5$) to focus on the effect of population density on sediment transport. The anisotropic
 65 power expenditure is discussed in the supplementary information.¹ For the isotropic case, net
 66 sediment flux is:

$$\tilde{q}_s = \tilde{q}_d - \tilde{q}_u = \left(\frac{NP_i}{\rho_s g \mu^2} \right) \left(\frac{(-\nabla z)}{1 - |\nabla z / \mu|^2} \right). \quad (4)$$

68 On low gradient slopes, this model approximates linear transport model:

69 $\tilde{q}_s = K(-\nabla z)$, where K = diffusivity (Culling, 1963). Given that 72% of the sediment in a
 70 coastal California grassland was produced by gophers (Gabet and Dunne, 2003), for
 71 simplification our model assumes that all soil transport is caused by gophers. Because the
 72 collapse of gopher burrows also contributes to sediment transport, the energy input in our
 73 model is a maximum value.

74 We first calculated an individual gopher's power input (P_i) using data from grass-
 75 covered hillslopes at Sedgwick Ranch in southern California and Tennessee Valley in
 76 central California, where the relationships between sediment transport and the slope
 77 gradient have been determined (Gabet, 2000; Fernandes and Dietrich, 1997) (Table 1).
 78 Equation 4 was compared to these relationships to determine the power input per area (= NP_i)
 79 that most closely fit the relationship (for more information, see supplementary
 80 information [see footnote one]). The NP_i was divided by the gopher density for the P_i
 81 value. The density was calculated by dividing the mound production rate per area at
 82 Sedgwick Ranch ($1.13 \text{ m}^{-2} \text{ yr}^{-1}$) (Gabet, 2000) by the annual mound production per
 83 gopher (~ 80 per gopher), which we obtained by dividing the burrowing length per gopher
 84 (120 m yr^{-1} in Bandoli, 1981) by the burrow length per mound (1.47 m in Seabloom et
 85 al., 2000).

86 The calculated power input (NP_i) was $\sim 120 \text{ J m}^{-2} \text{ yr}^{-1}$ at Sedgwick Ranch (for more
 87 information, see supplementary information [see footnote one]), and the estimated gopher
 88 density is $\sim 140 \text{ ha}^{-1}$ (mean western North America value = $53 \pm 49 \text{ ha}^{-1}$; Smallwood and

89 Morrison, 1999). Consequently, the P_i is $\sim 9 \text{ KJ yr}^{-1}$. Likewise, the sediment transport at
 90 Tennessee Valley consumes $\sim 80 \text{ J m}^{-2} \text{ yr}^{-1}$. Assuming the P_i identical to that of Sedgwick
 91 Ranch, the gopher density is $\sim 90 \text{ ha}^{-1}$ for Tennessee Valley.

92 The P_i value is 1% of the gopher's energy expenditure on burrowing. $\sim 3\text{--}6 \text{ KJ}$ of energy
 93 is used to burrow 1 m in fine sand to loamy soils (Vleck, 1979; Seabloom et al., 2000). For a
 94 gopher who burrows 120 m annually (Bandoli, 1981), the annual burrowing energy is 400-700
 95 KJ. Most energy is thus involved in shearing, mixing, and elevating soils rather than in
 96 generating net downslope transport. The gross sediment flux (the sum of \tilde{q}_d and \tilde{q}_u in equations
 97 2 and 3), with the estimated power input of Tennessee Valley, ranged from $\sim 50 \text{ cm}^2 \text{ yr}^{-1}$ (at a
 98 slope gradient of 0) to $140 \text{ cm}^2 \text{ yr}^{-1}$ (at a slope gradient of 1). These rates will turnover the soil
 99 material in the upper 50 cm of a 1 m^2 area in only 100-40 yr, which is consistent with
 100 observations of rapid artifact burial in California (Johnson, 1990). In terms of ecosystem energy,
 101 the net sediment transport uses an extremely small fraction ($\sim 0.001\%$) of the net primary
 102 productivity ($\sim 3.3 \text{ MJ m}^{-2} \text{ yr}^{-1}$: Callaway et al., 1991) in California grasslands.

103 **MODEL: SOIL THICKNESS AND GOPHER POPULATIONS**

104 Now we couple gopher density and soil thickness. Soil thickness is a balance between
 105 soil production from bedrock and soil erosion (Dietrich et al., 1995). The erosion rate is the
 106 difference between sediment inputs and outputs (for derivation, see supplemental information
 107 [see footnote one]):

$$108 \quad E = \nabla \cdot \tilde{q}_s \approx \left(\frac{NP_i}{\rho_s g \mu^2} \right) \left(\frac{-\nabla^2 z}{1 - |\nabla z / \mu|^2} \right). \quad (5)$$

109 The soil erosion rate is a function of both slope curvature and the density of soil perturbing
 110 organisms.

111 Compensating for the erosion, soil is produced from bedrock, the rate of which decreases
 112 exponentially with increasing soil thickness (Heimsath et al., 1997):

$$113 \quad P = \frac{\rho_r}{\rho_s} \phi_o e^{-H/\alpha}, \quad (6)$$

114 where H = vertical soil thickness, ρ_r = bedrock bulk density, ϕ_o = soil production rate of bare
 115 rock [LT^{-1}], and α = e-folding depth of the soil production rate.

116 Thus soil thickness is:

$$117 \quad \frac{\partial H}{\partial t} = \underbrace{\frac{\rho_r}{\rho_s} \phi_o e^{-H/\alpha}}_{\text{soil production rate}} - \underbrace{\frac{NP_i}{\rho_s g \mu^2} \frac{-\nabla^2 z}{1 - |\nabla z/\mu|^2}}_{\text{soil erosion rate}}. \quad (7)$$

118 In modeling gopher density, we factored in the observation that gophers preferably
 119 populate thicker soils with greater plant productivity, soil moisture, and room for burrowing and
 120 nesting (Howard and Childs, 1959; Nevo, 1979; Black and Montgomery, 1991). An equation is
 121 constructed such that the gopher density is minimum (N_o) at zero soil thickness, increases with
 122 soil thickening, reaches a maximum density (N_m) at a certain soil thickness, and then does not
 123 respond to further soil thickening. We found a similar relationship in the density-dependent
 124 population model (Begon et al., 1996 p. 247), and modified it to describe gopher population
 125 density versus soil thickness:

$$126 \quad N = \frac{N_m}{1 + (N_m/N_o - 1)e^{-rH}}. \quad (8)$$

127 where r is a constant [L^{-1}] that adjusts the shape of the relationship between the density and soil
 128 thickness.

129 These models have two major assumptions. First, it is approximated that the soil
 130 production rate is indirectly linked to gopher densities due to their effect on soil thickness. We
 131 do not explicitly model how gophers disrupt saprolite (Heimsath et al., 1997) due to inadequate

132 data on this process. Second, hillslope morphology is assumed to be constant because steady
133 state soil thickness develops much faster ($\sim 10^3$ yr) (Dietrich et al., 1995) than steady state
134 hillslope morphology ($\sim 10^5$ – 10^6 yr) (Roering, et al., 2001; Fernandes and Dietrich, 1997). Since
135 these time scales depend on hillslope scale (Fernandes and Dietrich, 1997), this assumption may
136 not be valid in all circumstances.

137 Below we simulate how gophers' preference for thicker soils may spatially and
138 temporarily affect gopher densities and soil thicknesses by solving equations 7 and 8. In
139 calculating the spatial distribution of soil thickness, soil thickness was assumed to be at steady
140 state. The models are parameterized using the data from Tennessee Valley (Table 1).

141 **SPATIAL DISTRIBUTION OF SOIL THICKNESS AND GOPHER POPULATIONS**

142 The spatial simulations were made for points on hillslopes with constant curvatures and
143 slope gradients (20%) for two scenarios (Fig. 1A): (1) the gopher density (90 ha^{-1}) is constant,
144 and (2) the density increases with soil thickness (the maximum density is twice the density in
145 scenario 1). Scenario 1 is mathematically identical to Roering et al.'s (1999) model where power
146 input was spatially constant, while in scenario 2 gopher density is spatially heterogeneous. We
147 parameterized equation 8 with the following values: $r = 0.1 \text{ cm}^{-1}$, $N_o = 1 \text{ ha}^{-1}$, and $N_m = 180 \text{ ha}^{-1}$,
148 so that the animal density (Fig. 1A) starts to increase rapidly at 30 cm soil thickness, and reaches
149 steady-state at 60 cm, mimicking observations by Howard and Childs (1959).

150 The resulting soil thickness varies from 10 cm to 160 cm in scenario 1 (Fig. 1B). For
151 scenario 2, the soil thicknesses varied less from 40 cm to 120 cm because of the negative
152 feedbacks: while thin soils on convex slopes experience increased soil production rates, they
153 support a smaller gopher population, which reduces soil erosion rates. The gopher density ranged
154 from 40 to 180 ha^{-1} in scenario 2. An opposite relationship occurs on less convex slopes, where

155 decreasing convexity leads to soil thickening and greater gopher populations, elevating soil
156 erosion rates, which prevents soil thickening.

157 This exercise implies that the soil thickness distribution may differ for the landscapes
158 experiencing biotic versus abiotic sediment transport. We compared Tennessee Valley and Black
159 Diamond in central California (Figs. 1C and 1D). At Black Diamond little bioturbation exists due
160 to soil shrinking and swelling in the clay-rich Vertisol, and abiotic soil creep dominates the
161 sediment transport. We used the published diffusivities and soil production rates (Table 1) at
162 these two sites to calculate the steady-state soil thickness distributions and compared them to the
163 measured data.

164 The model with constant diffusivity explains 49% of the data at Black Diamond. At
165 Tennessee Valley, soil thicknesses are less curvature-dependent than the model prediction with
166 constant diffusivity. Our model (equation 7) generates a line that best fits the measured data ($r^2 =$
167 0.28) at Tennessee Valley when the gopher density rapidly increases as soil thicknesses exceed
168 30 cm (inset of Fig. 1D), a pattern corresponding to field observations (Howard and Childs,
169 1959). In summary, some of the differences between the thickness versus curvature relationships
170 from Tennessee Valley and Black Diamond are explainable by soil thickness–dependent gopher
171 populations.

172 Two aspects of the comparison deserve further discussion. First, the data scatter is larger
173 at Tennessee Valley than at Black Diamond, suggesting that gopher-driven soil transport is
174 stochastic. Second, the best-fit model at Tennessee Valley does not predict the bare rocks that
175 appear on highly convex areas and required a non-zero gopher density for a soil of zero
176 thickness. Gophers are unlikely to burrow in soils thinner than their burrow sizes (~5 cm). Thus
177 other agents may replace the gopher's role. We observed sparse vegetation on thin soils, which

178 suggests that soil disturbance such as rain splash and animal steps may erode the bare soils
179 efficiently enough to expose the underlying rock.

180 **TEMPORAL DYNAMICS OF SOIL THICKNESS AND GOPHER POPULATIONS**

181 Climate induced gopher population dynamics may affect soil thickness. We solved the
182 transient soil thickness model (equation 7) with gopher density (equation 8) as a crude means of
183 considering the geomorphic responses to the shift from Pleistocene forest to Holocene grassland
184 in California (Rypins et al., 1989), which may have favored gophers. We evaluate two scenarios
185 (Fig. 2A): (1) a doubling of the constant animal density, and (2) a doubling of the maximum
186 density (N_m in equation 8) for thickness dependent gopher populations as a consequence of a
187 climate change. Scenario 1 can be associated with abiotic soil creep. A 20% slope gradient with
188 negative curvatures of 0.01 m^{-1} and 0.03 m^{-1} were used. After a model run for 10^4 yr with steady
189 state soil thickness and gopher densities, the gopher densities were altered. The finite difference
190 form of equation 7 was used with the parameters from Tennessee Valley (Table 1).

191 For both scenarios, soil thickness decreased as gopher densities increased (Figs. 2B and
192 2C). The thickness reduction, however, was greatest for the scenario 1: with a negative curvature
193 of 0.01 m^{-1} , soils thinned from 57 cm to 26 cm (Fig. 2B). On more convex slopes (0.03 m^{-1}), a
194 doubled animal density removed the soil cover within 1 k.y. (Fig. 2B). In contrast, for scenario 2,
195 the soil thickness reductions were minor, and new steady-state thicknesses developed faster for
196 the negative curvature of 0.01 m^{-1} (Fig. 2C). This small change in soil thickness is due to a
197 negative feedback between soil erosion and gopher density mediated by soil thickness. Despite
198 the doubling of maximum densities induced by favorable climate change, the actual densities,
199 limited by soil thickness, may increase only slightly in a few thousand years (Fig. 2D).

200 Finally, a biological feedback with soil thickness has potential impacts on hillslope morphology.
201 A soil thickness–dependent gopher density buffers the soil thickness from abrupt changes.
202 Because soil production rate depends on soil thickness (Heimsath et al., 1997), the ecological
203 characteristics of gophers may ultimately cause more spatially homogenous landscape lowering
204 rates, and thus preservation of hillslope morphologies over time periods longer than that
205 predicted by linear sediment transport models.

206 **CONCLUSIONS**

207 Only a small fraction of an ecosystem’s photosynthetic energy is used for soil transport,
208 but this energy profoundly affects the characteristics of the land surface. The feedbacks between
209 burrowing animals and hillslope soils likely have a measurable impact on soil thickness
210 distribution, its response to environmental changes, and the shape of the landscape. Many
211 biological soil perturbations have been described, and this study offers opportunities to
212 parameterize them in a quantitative, process-oriented geomorphic framework, with the ultimate
213 goal of understanding the interaction between life and landscapes.

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273 *Biogeochemical Cycles*, v. 19, GB3003, doi: 10.1029/2004GB002271.
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274 Figure 1. Spatial simulation of soil thickness and gopher population density. A: Two scenarios of
275 gopher population density versus soil thickness. B: Simulated steady-state soil thicknesses and
276 gopher densities versus hillslope curvature for each scenario. C–D: Measured and modeled soil
277 thickness versus curvature relationships at abiotic Black Diamond and biotic Tennessee Valley.
278 Data (circles) are from Yoo et al. (2005). Solid lines are calculated with spatially constant
279 diffusivities (Table 1). Inset in D describes the soil thickness–dependent gopher density (N in
280 equation 7) that allows the model to generate the dashed linear fit.

281
282 Figure 2. Temporal simulation of soil thickness and gopher population density. A: Two scenarios
283 of gopher population density change. B: Modeled soil thicknesses over time in scenario 1. C:
284 Modeled soil thicknesses over time in scenario 2. D: Modeled gopher population densities over
285 time for scenario 2. B–D: The solid lines represent the simulation results with a negative
286 curvature of 0.01 m^{-1} and a slope gradient of 0.2, and the dotted lines represent the results with a
287 negative curvature of 0.03 m^{-1} and a slope gradient of 0.2.

288

288 Table 1. PARAMETERS USED IN THE SOIL EROSION MODEL (EQ. 5) AND SOIL PRODUCTION
 289 FUNCTION (EQ. 6) FOR THE STUDIED FIELD AREAS
 290

Parameter	Quantity (Location)	Reference
Diffusivity (K in $\tilde{q}_s = K(-\nabla z)$)	50 cm ² yr ⁻¹ (Tennessee Valley)	Heimsath et al., 1997
	74 cm ² yr ⁻¹ * (Sedgwick Ranch)	Gabet, 2000
	360 cm ² yr ⁻¹ (Black Diamond)	calculated from McKean et al., 1993
Soil production rate from exposed rock (ϕ_0 in Eq. 6)	77 m Myr ⁻¹ (Tennessee Valley)	Heimsath et al., 1997
	1255 m Myr ⁻¹ (Black Diamond)	calculated from McKean et al., 1993
e-folding depth of soil production rate (α in Eq. 6)	43 cm (Tennessee Valley)	Heimsath et al., 1997
	27 cm (Black Diamond)	calculated from McKean et al., 1993
Bulk density of soil sediment (ρ_s)	1.25 g cm ⁻³	This study
Ratio of soil and bedrock bulk densities (ρ_s/ρ_t)	2	Heimsath et al., 1997
Effective coefficient of friction (μ in Eq. 2-5)	1.27 [†]	Roering et al., 1999

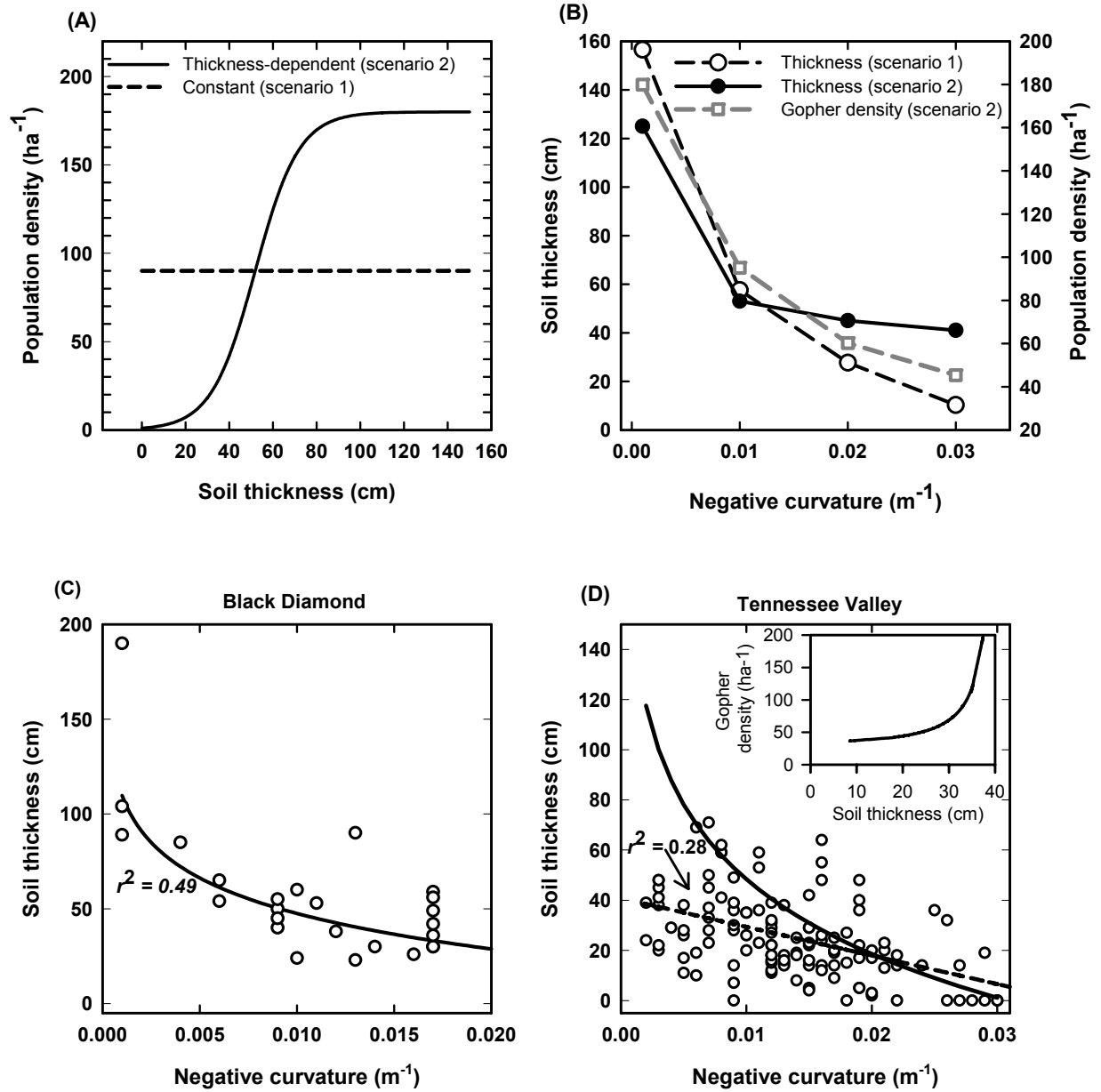
*Gabet (2000) reported this value as a linear approximation of the ratio between gopher mounds driven sediment transport vs. slope gradient.

[†]This value is from a forested Oregon coastal range, which may differ from the values in California grasslands. The power input varies with the range of μ values (e.g., 1 to 2) by a factor of ~4, which is still small considering that sediment transport consumes only 1 % of a gopher's burrowing power input. Additionally, this affects our model simulation only slightly because all simulations were conducted for a gentle slope where the gradient (0.2) is much less than the μ values.

291

292

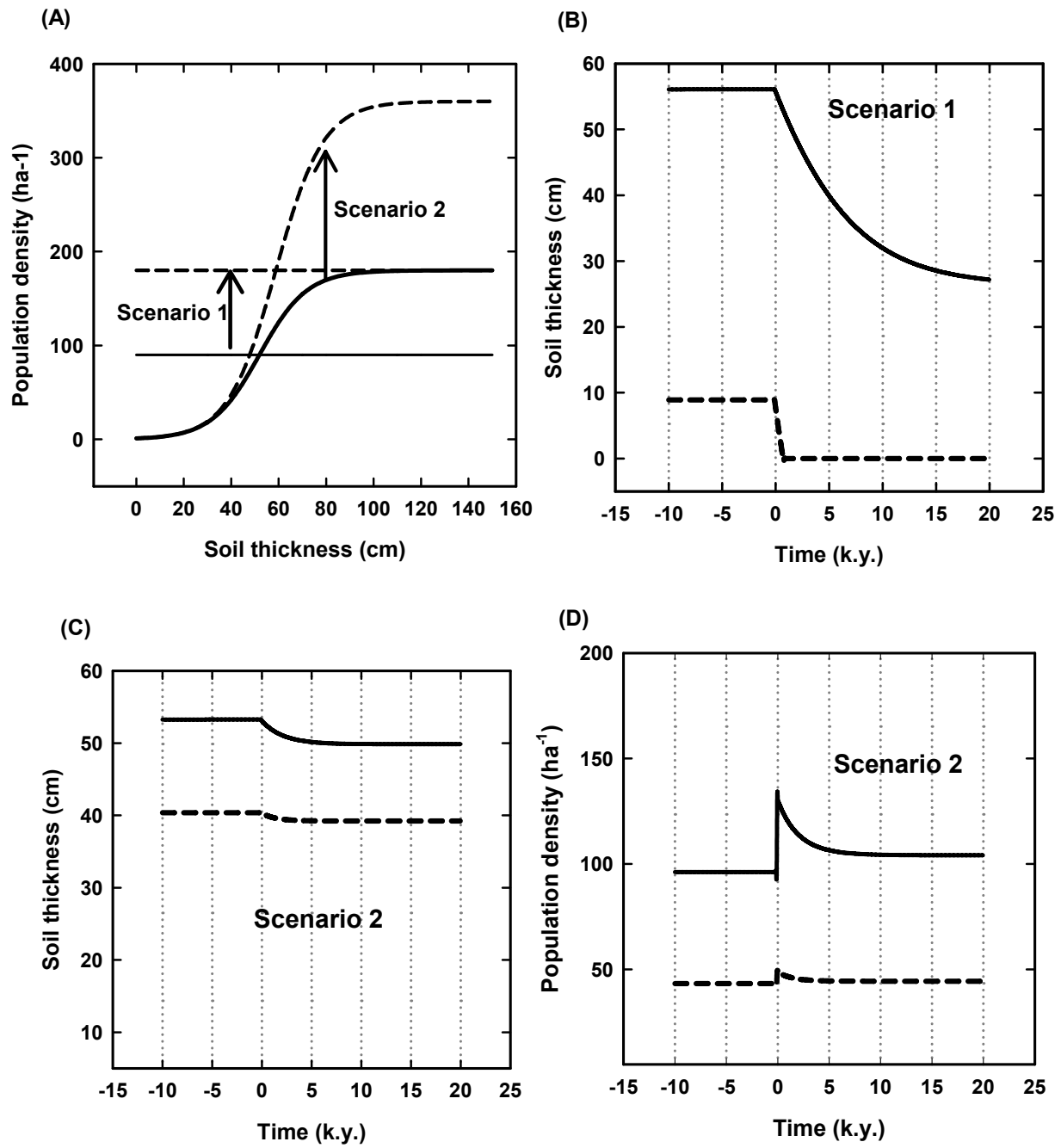
292 Fig. 1 Yoo et al.



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294 Fig. 2 Yoo et al.



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