

Process-based model linking pocket gopher (*Thomomys bottae*) activity to sediment transport and soil thickness

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ABSTRACT

Burrowing organisms assist in shaping earth surfaces and are simultaneously affected by the environment they inhabit; however, a conceptual framework is not yet available to describe this feedback. We introduce a model that connects the population density of soil-burrowing animals to sediment transport via energy. The model, combined with available data from California hillslopes where soil erosion is driven by pocket gophers (*Thomomys bottae*), suggests that a gopher annually expends ~9 kJ of energy, or ~1% of reported burrowing energy expenditure, in generating sediment transport. The model is used to evaluate the case that gophers prefer to populate thicker soils. The results suggest that this behavior may drastically dampen the spatial and temporal variations of soil thickness and gopher populations, implying that burrowing organisms may create landscapes distinct from those affected by abiotic processes.

Keywords: sediment transport, bioturbation, pocket gopher, soil thickness, hillslope.

INTRODUCTION

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

GOPHER ENERGY INPUT TO SOIL TRANSPORT

Sediment transport, when generated by organisms, is ultimately powered by the photosynthesized energy. To incorporate the biological energy, we modified a sediment transport model (Roering et al., 1999; Andrews and Bucknam, 1987) in which sediment flux ($\tilde{q}_s = L^2T^{-1}$) is the product of the volume of moving soil ($V = L^3$) per area ($A = L^2$) and sediment velocity ($u = LT^{-1}$). The sediment velocity is determined by a physical law, $P = Fu$, where P is power ($= ML^2T^{-3}$, where M is mass),

and F is a resistance (MLT^{-2}). Where a single species dominates sediment transport, the power input per area (P/A) is the product of an organism's population density ($N = L^{-2}$) and its individual power input (P_i).

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

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

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

and

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

where z is the elevation of the ground surface [L].

Gabet (2000) reported that as a slope becomes steeper, gophers move excavated soil to the downslope to prevent backfilling. We limit this paper, however, to isotropic power expenditure ($\psi = 0.5$) to focus on the effect of population density on sediment transport. The an-

isotropic power expenditure is discussed in the GSA Data Repository.¹ For the isotropic case, net sediment flux is:

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

On low-gradient slopes, this model approximates the linear transport model: $\tilde{q}_s = K(-\Delta_z)$, where K = diffusivity (Culling, 1963). Given that 72% of the sediment in a coastal California grassland was produced by gophers (Gabet and Dunne, 2003), for simplification our model assumes that all soil transport is caused by gophers. Because the collapse of gopher burrows also contributes to sediment transport, the energy input in our model is a maximum value.

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

The calculated power input (NP_i) was ~120

¹GSA Data Repository item 2005179, photographs, equation derivation, biological power quantification and anisotropic power expenditure, and application of soil thickness dependence on biological activity, is available online at www.geosociety.org/pubs/ft2005.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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TABLE 1. PARAMETERS USED IN THE SOIL EROSION MODEL AND SOIL PRODUCTION FUNCTION FOR THE STUDIED FIELD AREAS

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_o in equation 6)	77 m Myr ⁻¹ (Tennessee Valley)	Heimsath et al., 1997
	1255 m Myr ⁻¹ (Black Diamond)	calculated from McKean et al., 1993
	43 cm (Tennessee Valley)	Heimsath et al., 1997
e-folding depth of soil production rate (α in equation 6)	27 cm (Black Diamond)	calculated from McKean et al., 1993
	1.25 g cm ⁻³	This study
Bulk density of soil sediment (ρ_s)	2	Heimsath et al., 1997
Ratio of soil and bedrock bulk densities (ρ_s/ρ_r)	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.

J m⁻² yr⁻¹ at Sedgwick Ranch (for further information, see the Data Repository), and the estimated gopher density is ~140 ha⁻¹ (mean western North America value = 53 ± 49 ha⁻¹; Smallwood and Morrison, 1999). Consequently, the P_i is ~9 kJ yr⁻¹. Likewise, the sediment transport at Tennessee Valley consumes ~80 J m⁻² yr⁻¹. Assuming the P_i is identical to that of Sedgwick Ranch, the gopher density is ~90 ha⁻¹ for Tennessee Valley.

The P_i value is 1% of the gopher's energy expenditure for burrowing. Approximately 3–6 kJ of energy are used to burrow 1 m in fine sand to loamy soils (Vleck, 1979; Seabloom et al., 2000). For a gopher that burrows 120 m annually (Bandoli, 1981), the annual burrowing energy is 400–700 kJ. Most energy is thus used for shearing, mixing, and elevating soils rather than for generating net downslope transport. The gross sediment flux (the sum of \tilde{q}_d and \tilde{q}_u in equations 2 and 3), with the estimated power input of Tennessee Valley, ranged from ~50 cm² yr⁻¹ (at a slope gradient of 0) to 140 cm² yr⁻¹ (at a slope gradient of 1). These rates will result in soil turnover in the upper 50 cm of a 1 m² area in only 40–100 yr, which is consistent with observations of rapid artifact burial in California (Johnson, 1990). In terms of ecosystem energy, the net sediment transport uses an extremely small fraction (~0.001%) of the net primary productivity (~3.3 MJ m⁻² yr⁻¹; Callaway et al., 1991) in California grasslands.

MODEL: SOIL THICKNESS AND GOPHER POPULATIONS

We coupled gopher density and soil thickness. Soil thickness is a balance between soil production from bedrock and soil erosion (Dietrich et al., 1995). The erosion rate is the

difference between sediment inputs and outputs (for derivation, see the Data Repository [footnote 1]):

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

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

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

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

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

Thus soil thickness is:

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

In modeling gopher density, we factored in the observation that gophers preferably populate thicker soils with greater plant productivity, soil moisture, and room for burrowing and nesting (Howard and Childs, 1959; Nevo, 1979; Black and Montgomery, 1991). An

equation was constructed such that the gopher density is minimum (N_o) at zero soil thickness, increases with soil thickening, reaches a maximum density (N_m) at a certain soil thickness, and then does not respond to further soil thickening. We found a similar relationship in the density-dependent population model (Begon et al., 1996, p. 247), and modified it to describe gopher population density versus soil thickness:

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

where r is a constant [L⁻¹] that adjusts the shape of the relationship between the density and soil thickness.

These models have two major assumptions. First, they approximate that the soil production rate is indirectly linked to gopher densities due to their effect on soil thickness. We do not explicitly model how gophers disrupt saprolite (Heimsath et al., 1997) due to inadequate data on this process. Second, hillslope morphology is assumed to be constant because steady-state soil thickness develops much faster (~10³ yr) (Dietrich et al., 1995) than steady-state hillslope morphology (~10⁵–10⁶ yr) (Roering et al., 2001; Fernandes and Dietrich, 1997). Because these time scales depend on hillslope scale (Fernandes and Dietrich, 1997), this assumption may not be valid in all circumstances.

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

SPATIAL DISTRIBUTION OF SOIL THICKNESS AND GOPHER POPULATIONS

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

The resulting soil thickness varies from 10

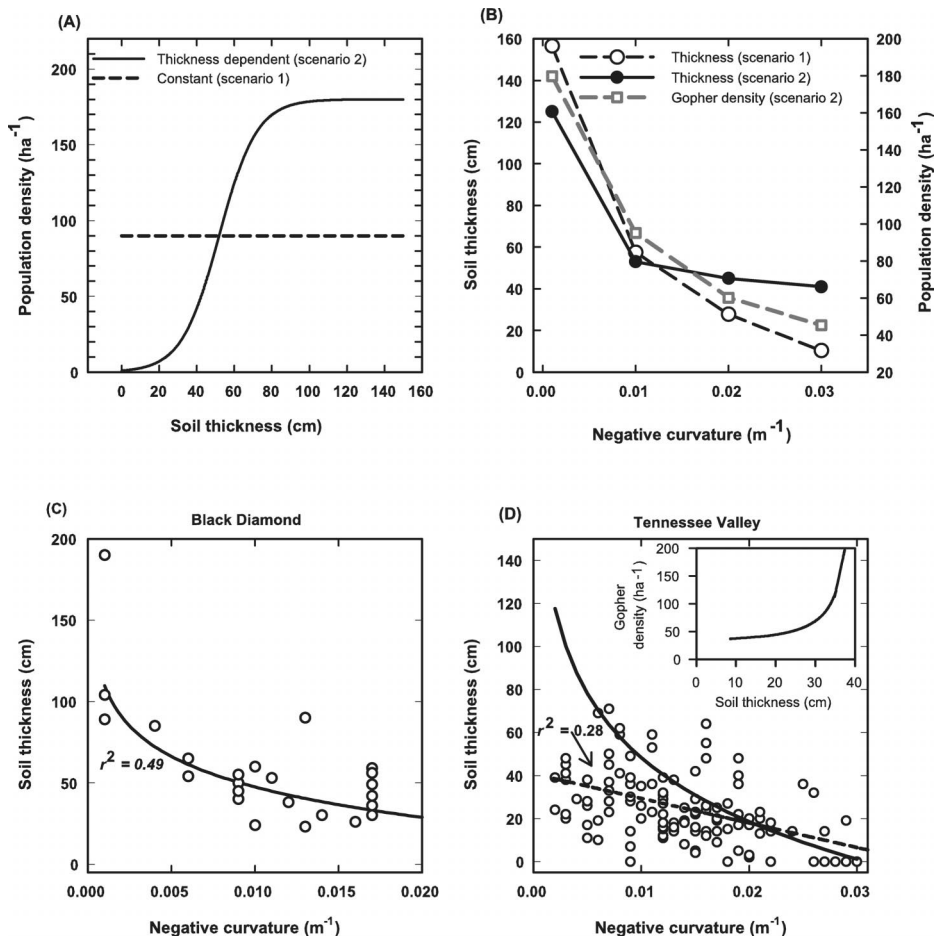


Figure 1. Spatial simulation of soil thickness and gopher population density. A: Two scenarios of gopher population density vs. soil thickness. B: Simulated steady-state soil thicknesses and gopher densities vs. hillslope curvature for each scenario. C–D: Measured and modeled soil thickness vs. curvature relationships at abiotic Black Diamond and biotic Tennessee Valley. Data (circles) are from Yoo et al. (2005). Solid lines are calculated with spatially constant diffusivities (Table 1). Inset in D describes soil thickness–dependent gopher density (N in equation 7) that allows model to generate dashed linear fit.

cm to 160 cm in scenario 1 (Fig. 1B). For scenario 2, the soil thicknesses varied less from 40 cm to 120 cm because of the negative feedbacks: while thin soils on convex slopes undergo increased soil production rates, they support a smaller gopher population, which reduces soil erosion rates. The gopher density ranged from 40 to 180 ha^{-1} in scenario 2. An opposite relationship occurs on less convex slopes, where decreasing convexity leads to soil thickening and greater gopher populations, elevating soil erosion rates, which prevents soil thickening.

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

the steady-state soil thickness distributions and compared them to the measured data.

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

Two aspects of the comparison deserve further discussion. First, the data scatter is larger at Tennessee Valley than at Black Diamond, suggesting that gopher-driven soil transport is stochastic. Second, the best-fit model at Tennessee Valley does not predict the bare rocks that appear on highly convex areas and re-

quired a non-zero gopher density for a soil of zero thickness. Gophers are unlikely to burrow in soils thinner than their burrow sizes (~ 5 cm). Thus other agents may replace the gopher's role. We observed sparse vegetation on thin soils, which suggests that soil disturbance such as rain splash and animal steps may erode the bare soils efficiently enough to expose the underlying rock.

TEMPORAL DYNAMICS OF SOIL THICKNESS AND GOPHER POPULATIONS

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

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

A biological feedback with soil thickness has potential impacts on hillslope morphology. A soil thickness–dependent gopher density buffers the soil thickness from abrupt changes. Because soil production rate depends on soil thickness (Heimsath et al., 1997), the ecological characteristics of gophers may ultimately cause more spatially homogeneous landscape lowering rates, and thus preservation of hillslope morphologies over time periods longer

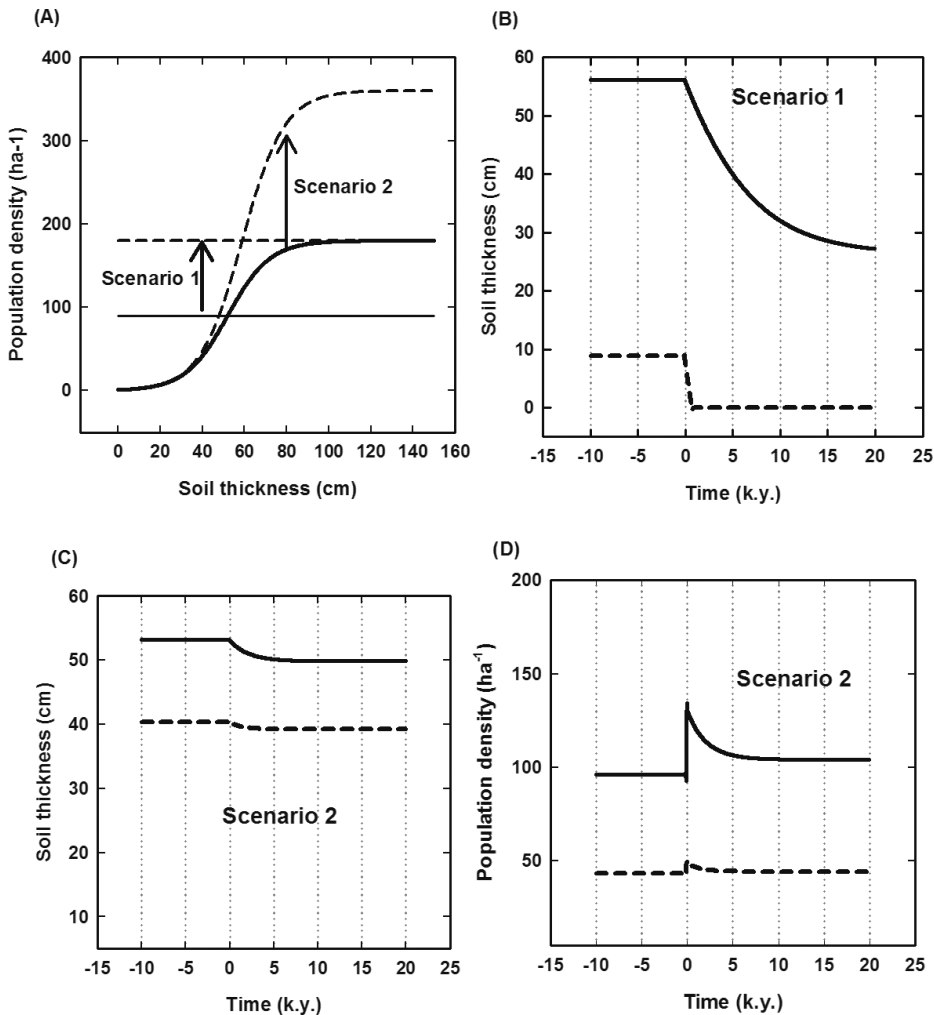


Figure 2. Temporal simulation of soil thickness and gopher population density. **A:** Two scenarios of gopher population density change. **B:** Modeled soil thicknesses over time in scenario 1. **C:** Modeled soil thicknesses over time in scenario 2. **D:** Modeled gopher population densities over time for scenario 2. **B–D:** Solid lines represent simulation results with negative curvature of 0.01 m^{-1} and slope gradient of 0.2, and dotted lines represent results with negative curvature of 0.03 m^{-1} and slope gradient of 0.2.

than that predicted by linear sediment transport models.

CONCLUSIONS

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

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