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Original article

Linking ecosystem engineers to soil processes: a framework using the Jenny State Factor Equation

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Abstract

Understanding biotic influences on soil processes is a major research frontier made challenging by organismal diversity, variation in distribution, and variety of interactions. Nevertheless, two fundamental influences can be recognized: assimilation/dissimilation (uptake, metabolism, wastes, death) and physical ecosystem engineering (non-assimilatory/dissimilatory, organismally-induced, structurally-mediated changes in energy and materials in the abiotic environment). Because many organisms can engineer soils, predicting their effects is particularly challenging. Here we use Hans Jenny's State Factor Equation as a flexible, integrative tool for understanding these effects. We distinguish organismal influences via engineering from those of assimilation/dissimilation, explicitly placing engineers into the equation as independent state factors. We then ask: What abiotic state factors does an engineer affect? What relationships among state factors does it change? How does this affect soil processes? Using examples from our work, we illustrate use of this conceptual framework for a physical process—soil erosion; a chemical process—desalination; and a biogeochemical process—denitrification. We show that the framework can be used to: Identify conditions for small or large engineering effects on soil processes; assess engineer impacts on multiple soil processes; compare effects of different engineers on a given soil process; and integrate effects of multiple engineers on a single soil process.

Keywords: Conceptual framework; Ecosystem engineering; Climate; Relief; Parent materials; Organisms; Assimilation/dissimilation; Time; Soil physical, chemical, and biogeochemical processes; Soil erosion; Soil desalination; Denitrification; Burrowing crab; *Chasmagnathus granulatus*; Desert porcupine, *Hystrix indica*; Desert isopod, *Hemilepistus reaumuri*; Biotic crusts; Shrub, ant, geophyte mounds

1. Linking ecosystem engineering and soil processes: challenge and approach

1.1. The challenge

Understanding biotic influence on soil processes is a major research frontier [81,88,96] made challenging by organismal diversity, variation in distribution, and variety of interactions. Nevertheless, we can recognize two fundamentally important pathways of organismal influence. First is via assimilation and dissimilation; i.e. energy and material uptake, metabolism, waste production, and death—responsible for much of the "bio" in biogeochemical processes (Fig. 1). Here, influence arises via energy and material transfers from soil to organism, to organism, and back to soil. Effects on soil processes can be understood by applying principles of energy conservation, mass balance, stoichio-

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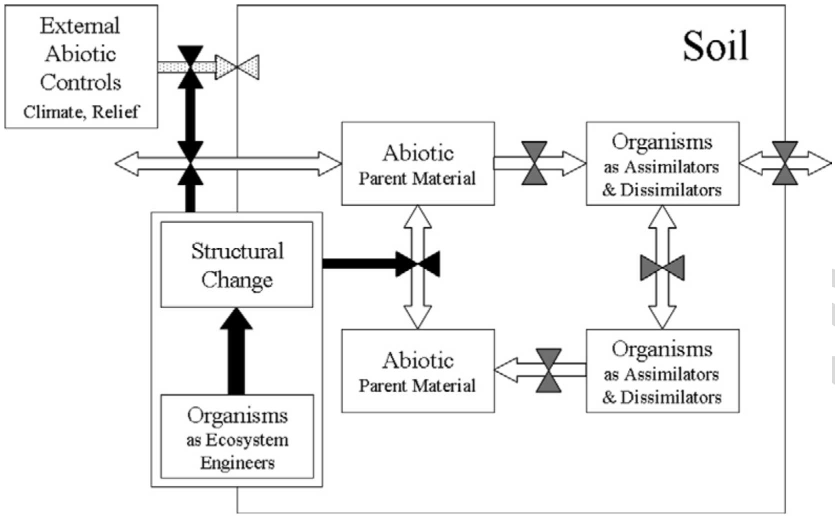


Fig. 1. Conceptual representation distinguishing two fundamental pathways of organismal influence on soil processes: assimilation/dissimilation and physical ecosystem engineering. The location of state factors (climate, relief, parent material, organisms as ecosystem engineers, and organisms as assimilators/dissimilators) are shown in compartments. Energy and material flows (white arrows) in and out of the soil system: From abiotic to abiotic compartments (physical and chemical soil processes); from abiotic to organismal compartments (assimilation); from organismal to organismal compartments (assimilation and dissimilation); and from organismal to abiotic compartments (dissimilation). These flows are under external abiotic control (dotted bow tie symbol). Physical ecosystem engineering involves organismally-mediated changes in physical structure above, on or in the soil (black arrow). These structural changes result in control over soil physical and chemical process, control over abiotic inputs and outputs from soil, and modulation of external abiotic controls (black bow tie symbols). As a result, physical ecosystem engineers influence assimilatory- and dissimilatory-related flows (gray bow tie symbols), including biogeochemical processes.

metry, predator/prey relationships, direct resource competition, food webs, and so forth [45]. Second is via physical ecosystem engineering—organismally-induced, structurally-mediated changes in the amount, distribution and composition of energy and materials in the abiotic environment that arise independent or irrespective of changes due to assimilation or dissimilation [44,45]. Engineering influence can be understood by examining how organismal structures or structures made by organisms from abiotic or biotically-derived materials change the abiotic environment. These abiotic changes result in control or modulation of physical and chemical soil processes and abiotic resources and non-resource environmental factors that then affect assimilatory/dissimilatory components (Fig. 1).

Soils and sediments are probably the most highly physically engineered of all environments [45]. Many organisms change physical structure within, on and above the soil. These structural changes directly affect many soil physical and chemical processes (Table 1) and have numerous consequences for biogeochemical processes via altered abiotic resources and abiotic non-resource environmental factors (Table 2). The variety of ways organisms can physically engineer soil, the diversity of taxa modifying structure, and the numerous soil processes involved make predicting physical ecosystem engineering effects on soil processes particularly challenging. To meet this challenge we need an approach linking ecosystem engineering to soil processes that can integrate the extensive knowledge of soil physicists, chemists, geomorphologists, plant, animal and microbial ecologists and ecosystem scientists.

1.2. The approach

Here we present such an approach using Hans Jenny's well-known State Factor Equation [42]. The equation has five factors that can be used to explain and predict spatial patterns of soil properties [3,31,35,43,55] (for equation explanation see Textbox 1):

$$\text{Soil Process} = f(\text{Climate, Relief, Parent Material, Organisms, Time}) \qquad \text{Eqn. 1}$$

Climate (C) includes macro- and micro-climatic variables (e.g. precipitation, temperature, light, wind); relief (R) includes macro- and micro-topography (e.g. landscape position, elevation, aspect, slope, local relief); parent material (P) includes mineral type, particle size, organically-derived materials and various physical and chemical properties (e.g. permeability, erodibility, infiltration capacity); organisms (O) encompasses all biota—microbes, plants and animals; and time (T) represents dynamic system change.

Table 1
Examples of effects of physical ecosystem engineering by organisms above, on and within soils on abiotic environmental conditions, soil variables and processes

Engineering activity	Abiotic environmental change	Soil variables/processes affected	Examples	References
(A) *Above soil surface*				
Canopy growth	Creation of shade via light interception	Decreased soil thermal amplitude. Increased soil moisture via decreased evaporation	Plants (ubiquitous)	[8,66,80]
	Decreased wind velocity via interception	Increased moisture and nutrient availability via enhanced atmospheric deposition	Trees and Shrubs	[66,74,89,90]
		Increased sedimentation	Plants (ubiquitous)	[68,74]
	Reduced kinetic energy of raindrops via interception	Restricted soil particle splash and decreased potential soil movement	Plants (ubiquitous)	[12,17]
(B) *On soil surface*				
Litter production	Reduced light and water vapor diffusion via interception/insulation	Decreased soil thermal amplitude. Increased soil moisture via decreased evaporation	Plants (ubiquitous)	[29]
	Reduced raindrop impact via interception/ cushioning	Restricted soil particle splash and decreased potential soil movement	Plants (ubiquitous)	[30]
Secretion of extra-cellular polymers	Decreased water infiltration via decreased pore space	Decreased soil moisture and enhanced surface runoff	Microbial soil crusts	[26]
	Binding of soil particles into aggregates	Increased resistance to wind and water erosion	Microbial soil crusts	[52,92]
Trampling	Increase/decrease soil compaction	Increased/decreased soil permeability and increased shear strength	Cattle, sheep, humans, other large mammals	[53,54,63,85]
Herd movement across slopes (large scale trampling)	Decreased slope stability via loading	Increased down slope transport of soil aggregates via slope failure	Large mammals	[38,40]
(C) Within soils				
Root growth	Increased soil porosity and aggregate stability	Increased soil aeration and infiltration	Plants (ubiquitous)	[22]
Hydraulic lift	Redistribution of water from depth to soil surface	Increased moisture at soil surface	Herbs, grasses, shrubs, trees	[14]
Burrowing	Creation of pores or conduits in soil matrix	Increased soil aeration and infiltration	Small mammals, arthropods, earthworms, crustaceans	[23,24,48,77]
	Increased surface area for gas exchange between soils and atmosphere	Increased sediment oxidation via O_2 diffusion through burrow walls	Earthworms	[64]
Pit digging	Alteration of surface topography	Increased soil moisture via water accumulation and retention. Increased deposition of soil and organic matter via trapping of particles transported by wind or runoff	Large and small mammals	[1,83]
Soil displacement during burrowing or digging	Exposure of material to wind action, splash or flushing via deposition on surface	Increased erosion	Mammals, birds, reptiles, arthropods, earthworms	[39,40,50,65,67, 94]
Litter transport into burrows	Translocation of litter from soil surface to burrows	Change in amount and distribution of organic matter and nutrients	Anecic earthworms, land crabs, termites	[47,59,97]
Removal of surface soil and deposition at depth either by ingestion and subsequent defecation as casts or by direct attachment to body surface	Translocation of surface applied lime ($CaCO_3$) to deeper soil layers	Decrease in soil acidity	Anecic earthworms	[5,15]
Particle sorting, relocation and cementation during feeding or nest construction	Changes in sediment grain-size distribution, aggregation and pore space	Increased or decreased soil stability, aeration and water infiltration	Earthworms, ants, termites	[19,20,49,51]

Table 2
Examples of biogeochemical consequences of physical ecosystem engineering by organisms

Change in soil variables/processes	Biogeochemical consequences	Examples	References
Increased soil moisture via shading	Increased microbial respiration and litter decomposition	Trees	[98]
Decreased soil temperature via shading	Decreased soil respiration	Tallgrass prairie	[87]
Loosening of soil and increased exposure to air via soil excavation and deposition on the surface	Increased rates of nitrogen mineralization and nitrification	Pocket gophers	[79]
Burial of litter-derived organic carbon within mineral soil	Increased microbial biomass and respiration rates in mineral soil	Earthworms	[34]
Storage of litter in subsurface galleries	High nitrogen mineralization in galleries and potential for nitrogen leaching to surrounding soil	Termites	[97]

Textbox 1
Equation annotations

Equations show a soil physical, chemical or biogeochemical process (e.g. soil erosion, desalination or denitrification rate) as a function of up to six general state factors, each separated by commas. Each state factor is indicated by text (Eqns. 1 and 2; e.g. Climate) or by a capital letter abbreviation (Eqns. 3–22; e.g. C, R), where C = Climate; R = Relief; P = Parent Material; E = Engineers; A = Assimilators/Dissimilators; T = Time). Eqns. 3–22 contain one or more variables in square parenthesis separated by commas that follow the state factor abbreviation in the equation (e.g. C [rain, wind, tide]). These variables specify the general state factor for a particular example. Other important variables that are the result of interactions among state factors (i.e. runoff, absorption, soil export, export) are shown as text below an equation.

Rather than writing component state factor interactions as a large number of additional equations, we use an abbreviated visual indicator for any interactions among state factors that are discussed in the text. These visual indicators are lines with one or more arrowheads distinguished by letter and line types (e.g. a, solid; b dotted lines). The arrow head(s) indicate the direction of effect of one or more state factors on other state factors, or on other important variables. When more than one visual indicator is present, they should be read in alphabetical sequence in order to understand the interactions. Some of the interactions shown in previous equations are omitted from subsequent equations for visual clarity (runoff in Eqns. 12 and 15).

While Jenny's original goal was to create solvable equations, the more general utility of the equation is its flexibility in organizing influences on soil processes into categories that expose functional connections and help identify important parameters [3,35]. While general, the equation is made operational for a given process by invoking specific aspects of state factors. The selected variables and their associated state factor are determined by question posed, scale under consideration, precedent, logical consistency, and convenience [35]. The equation has been used to address processes as diverse as carbon dynamics (e.g. [69]) and trace gas fluxes (e.g. [55]), and as a conceptual tool for integrating ecological research (e.g. [35]).

Our approach is conceptual not mathematical, illustrative not comprehensive. We do not derive specific mathematical formulations and we primarily use examples from our work. In essence, the framework takes the Engineers (E) out of the Organisms term of Eq. (1), leaving behind Organisms as Assimilators/Dissimilators (A), placing the engineers in the equation as an independent state factor:

$$\text{Soil Process} = f(\text{C, R, P, Engineers, Assimilators/Dissimilators, T}) \qquad \text{Eqn. 2}$$

The E state factor interacts with the C, R, P and A factors, and all factor interactions can change over T. We then ask: What abiotic state factors does an engineer affect? What relationships among state factors does it change? How does this affect soil processes? We show that the framework can help reveal the requirements for an engineer to affect soil processes, and can be used to: Identify conditions under which an engineer should have a small or large effect on a soil process; assess the impact of an engineer on multiple soil processes; compare and contrast effects of different engineers on a given soil process; and integrate effects of multiple engineers on a given soil process. We illustrate the framework with four examples of engineer effects on the physical process of soil erosion; one example of a soil chemical process—desalination; and an outline coupling engineering to a biogeochemical process—denitrification.

2. Ecosystem engineering, state factors and soil processes

2.1. Physical Process—Erosion

We start with a state factor equation for physical erosion rates with no biotic influence. This and other engineer-free models are considered nulls:

$$\text{Erosion Rate} = f\,(C[\text{rain, wind, tide}],\ R[\text{slope}],\ P[\text{erodibility}]) \qquad \text{Eqn. 3}$$

Climate could be rain, wind or tide—the erosion force; relief such as slope modifies strength of the erosion force; and parent material includes properties describing erodibility. For reasons that will become apparent, we can modify Eqn. 3 to represent physical erosion and sediment export from a *Spartina densiflora* marsh into an adjacent estuary in coastal Argentina:

$$\text{Sediment Erosion Rate} = f\,(C[\text{tide}],\ R[\text{slope}],\ P[\text{erodibility}]) \qquad \text{Eqn. 4}$$

Climate is now only the tidal regime. Time can be added by recognizing that as erosion proceeds, slope can change, and sediment erodibility can change as more readily erodible components are lost (Eqn. 5). Hence both R[slope] and P[erodibility] are functions of prior erosion (Eqn. 5a).

There can be other interaction terms. For example, slope affects the erosive force of tides (Eqn. 5b). Since this interaction is implicit in the model, we may or may not need to expose it to understand relationships. The utility of exposing such terms depends on whether or not they are best thought of as operating independently or interactively. For example, if another form of relief had a different relationship with tide than slope, such as depressions that reduced sediment export, explicit consideration of such terms would be of value. In general, whether or not we include terms, or treat interactions implicitly or explicitly, should be judged on their value in exposing relationships and contingencies that account for spatial or temporal variation in processes. Adding complexity for completeness should be balanced against omission for parsimony. Fig. 2.

2.1.1. Tidal erosion and crab ecosystem engineering

We can use Eqn. 5 to explore erosion effects of the burrowing crab, *Chasmagnathus granulatus* found in marshes of Southwestern Atlantic estuaries (Southern Brazil to Northern Argentinean Patagonia [10]; Fig. 2a). Crabs are very abundant, ca. 70 m^{-2} [9,36]. They make extensive burrows that trap sediment, leaving excavated sediment piles next to burrows that get exported by tides [11]; (Fig. 2b, c). Crabs are more active in summer than winter [21]. During summer they excavate an estimated 547 g sediment m^{-2} day^{-1}, with burrows trapping 172 g sediment m^{-2} day^{-1}, a net excavation of 375 g sediment m^{-2} day^{-1} [36]. We can add the engineer (E) *C. granulatus* to the physical erosion model of Eqn. 5:

$$\text{Sediment Erosion Rate} = f\,(C[\text{tide}],\ R[\text{slope}],\ P[\text{erodibility}],\ E[\textit{C. Granulatus}],\ T[\text{erosion}] \qquad \text{Eqn. 6}$$

By appropriate sampling of burrow and excavation pile sizes that reflect variation in crab size [36], we can estimate average *per capita* engineering impact, so the engineer state factor term becomes crab density (Eqn. 7), with density increasing parent material erodibility via formation of surface sediment piles that can be exported by tides (Eqn. 7a). We can add another relief term, topography of the crab-excavated sediment pile and burrow; and because crabs are seasonally active, we can add a time factor, engineering season.

This model can be simplified. If we consider the excavated pile and burrow as a unit, with a net contribution to erodibility as the difference between excava-

$$\text{Sediment Erosion Rate} = f\,(C[\text{tide}],\ R[\text{slope}],\ P[\text{erodibility}],\ T[\text{erosion}] \qquad \text{Eqn. 5}$$

$$\text{Sediment Erosion Rate} = f\,(C[\text{tide}],\ R[\text{slope, topography}],\ P[\text{erodibility}],\ E[\text{density}],\ T[\text{erosion, season}]) \qquad \text{Eqn. 7}$$

Fig. 2. a. Adult male burrowing crab, *C. granulatus* (ca. 3 cm carapace width). b. Crab, burrows and *S. densiflora*. c. *S. densiflora* and mudflat at Mar Chiquita coastal lagoon, Argentina, showing extensive crab burrows and excavations. (Photos: a. O.O. Iribarne; b. J.L. Gutiérrez; c. C.G. Jones).

tion and sediment trapping, we can drop the relief topography term. If the parent material does not vary in intrinsic erodibility—all sediments are soft enough for crabs to dig to the same degree (generally true; J.L. Gutiérrez, personal observation)—we can drop the parent material erodibility term. If we use a seasonally weighted annual average for crab activity, and ignore long-term effects of prior erosion on slope and sediment erodibility, we can drop the time term. We have then simplified Eqn. 7 to:

$$\text{Sediment Erosion Rate} = f\,(C[\text{tide}],\ R[\text{slope}],\ E[\text{density}]) \qquad \text{Eqn. 8}$$

The example shows how to expand and contract the equation, adding or removing complexity as needed, while noting assumptions made when dropping terms. It also shows how to incorporate general engineering factors such as *per capita* activity, density and seasonality of engineering activities.

2.1.2. Soil erosion and porcupine ecosystem engineering

A second example from the southern Negev Desert Highlands, Israel, has a more complex null physical erosion model. This region receives only 100 mm annual rainfall in winter and spring [95]. Numerous small watersheds with rocky slopes and colluvial mid-

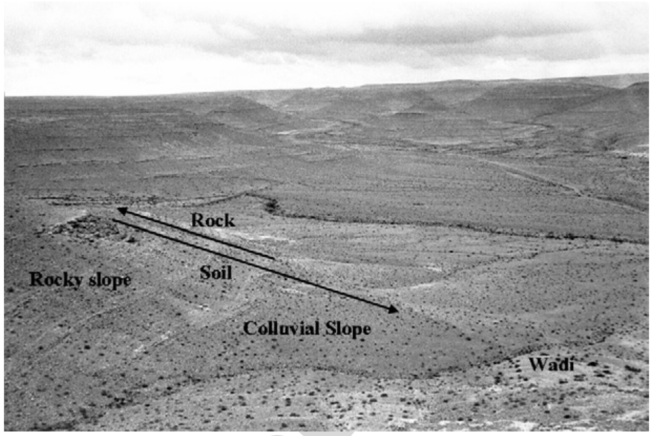


Fig. 3. The Negev Desert Highlands, Israel, showing part of a small watershed with a rocky and colluvial slope, and a Wadi. There is a progressive down slope decrease in rock and increase in soil indicated by arrows. (Photo: C.G. Jones).

slopes run down to Wadis, or dry riverbeds. From the top of the slope to the Wadi there is progressively less rock and more soil [95]; (Fig. 3). Small amounts of rain on lower slopes causes little soil erosion, while the same amount falling on impervious rock at the top generates down slope runoff with high erosive force, moving soil from lower down the slope towards the Wadi to a degree depending on the amount of rain per rain event [95]. Our initial null State Factor Equation, similar to the salt marsh erosion model (see Eqn. 4), has rain as climate, slope as relief, and two parent materials with different properties—impervious rock and erodible soil (abbreviated as "rock" and "soil", respectively):

$$\text{Soil Erosion Rate} = f\,(C[\text{rain}],\ R[\text{slope}],\ P[\text{rock, soil}]) \qquad \text{Eqn. 9}$$

C[rain], R[slope] and P[rock] collectively generate runoff from the top of the watershed (Eqn. 10a) that removes erodible soil to lower down the slope as local soil export (Eqn. 10b). Over time, soil erosion changes the rock to soil ratio of the two parent materials (Eqn. 10c), exposing more rock (Eqn. 10d) that increases runoff (Eqn. 10a), which increases soil erosion (Eqn. 10b) —an important positive feedback [73,77] (Fig. 4).

Now consider an ecosystem engineer, the desert porcupine, *Hystrix indica* (Fig. 4a) that digs when foraging for geophyte bulbs, making pits and mounds [76]; (Fig. 4b). Porcupines dig only where they find geophytes, which grow on slopes and valleys. Local density of porcupine digs reflects geophyte density, but porcupine density is independent of geophyte density since they feed on many other foods [7]. We can add this engineer into the null model (see Eqn. 9), for simplicity ignoring the time component (Eqn. 11). Here,

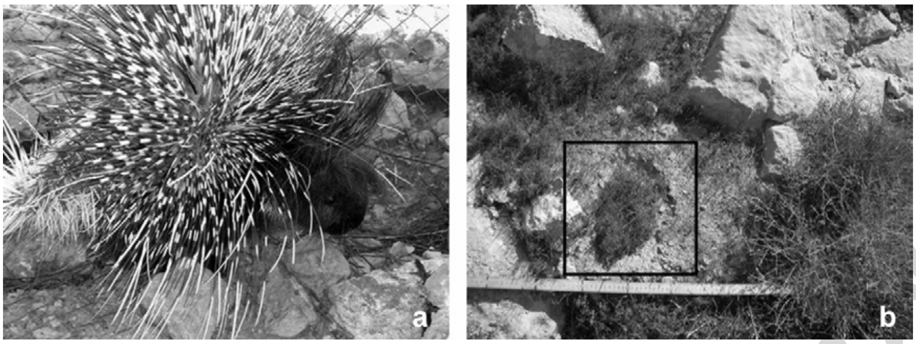


Fig. 4. a. Desert porcupine, *H. indica*. b. Vertical view of a porcupine pit and mound (black rectangle is 30 × 30 cm). Annual plants grow in the pits and on the mounds using locally stored runoff water ([7,37]). (Photos: a. http://wwwlb.aub.edu.lb/~webeco/porcupine5.htm; b. M. Shachak).

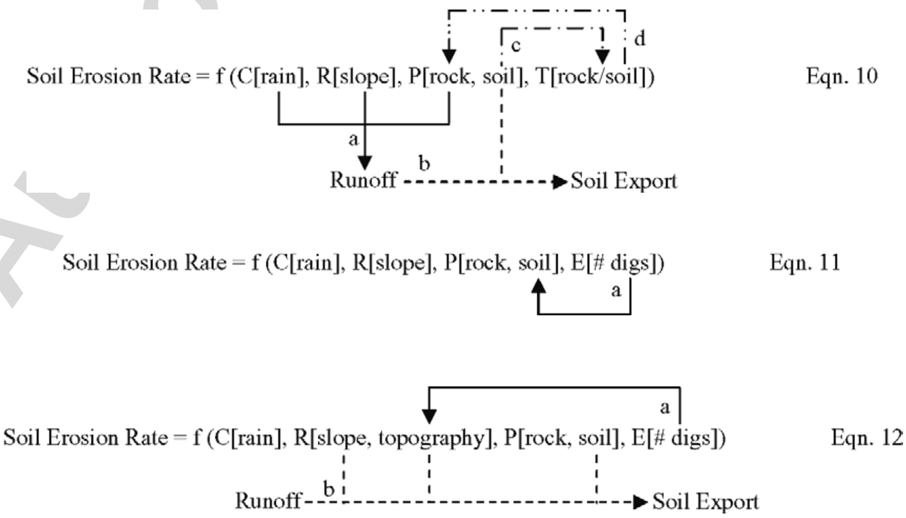
the number of porcupine digs is the most appropriate engineer term. In contrast to the crab example, *per capita* impact is highly variable because it depends on other foods as well as geophytes, and local density is highly variable because porcupines are highly mobile, foraging over large areas [2]. Like crabs, digging affects the erodibility of the soil parent material (Eqn. 11a) creating erodible soil that can be removed by runoff. Porcupine digs are similar in size, shape and form wherever they occur, producing more or less the same amount of potentially erodible soil [76].

Porcupine digging also creates relief as local topography (Eqn. 12a). Like crab digging, the pits trap eroded material, while the mounds erode faster than the surrounding surfaces [95]. In contrast to the crab example where we subsumed local topography (see Eqn. 8), here we need to consider this engineer-created relief. Digs have a non-uniform influence on soil erosion depending on slope location [95]. Runoff —a function of C[rain], R[slope] and P[rock] (not shown in Eqn. 12, see Eqn. 10a)—interacts differently with the local topography of pits and mounds depending on slope position (Eqn. 12b). Pits at the top of slopes fill faster and mounds erode more quickly than those at the bottom, so upslope digs contribute more to soil erosion than those in valleys [37].

While this example reveals some basic similarities between crabs and porcupines—relief as slope, engineer effects on parent material erodibility, and engineer creation of local topography—there are important differences in null models (Negev runoff complexity), engineer metrics (*per capita* vs. *per* dig effects), and engineer/other state factor interactions (runoff, slope and porcupine-generated topography).

2.1.3. Soil erosion and ecosystem engineering by crusts and other organisms

For the third example we stay in the Negev, moving to an area with 200 mm annual rainfall on gently undulating slopes with no exposed rock (Fig. 5a). Here, ecosystem engineering is carried out by a microbial community of cyanobacteria, fungi, bacteria and algae that



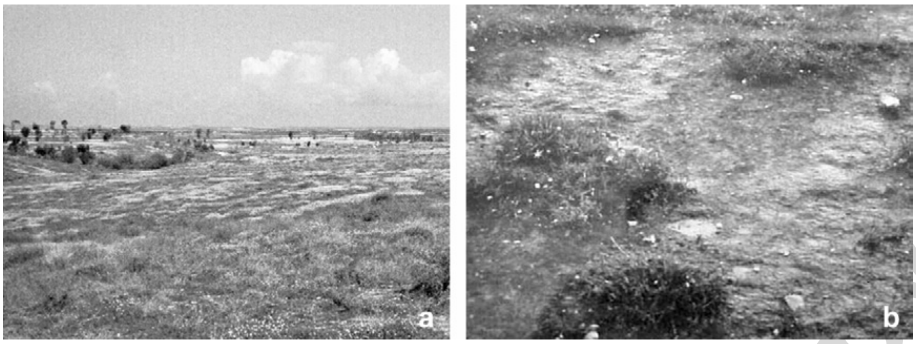


Fig. 5. a. Spring in Sayaret Shaked in the northern Negev Desert, Israel, showing the gently undulating terrain with annual plants and shrubs. b. Patches of crusted soil in between patches of vegetation. Runoff is generated from these crusted surfaces during rain, as shown in the highly reflective vegetation-free areas. (Photos: a. C.G. Jones; b. M. Shachak).

produce a mucopolysaccharide secretion that binds the soil surface forming an erosion-resistant, water impervious crust, much like a plastic sheet [26,46]. During rain events this crust generates runoff (Fig. 5b).

Our null physical erosion model (Eqn. 13) has rain as climate, slope as relief, and soil erodibility as a parent material property. We then add our crust engineering community. Here, *per capita* effects and density are not really appropriate, but crust area is a good index [46]. Crust reduces soil erodibility (Eqn. 13a), and this reduction is relatively uniform wherever crust occurs [95]. In contrast to crabs and porcupines that both increase soil erodibility, crust converts potentially erodible soil into non-erodible soil, reducing erosion.

Crust simultaneously reduces parent material permeability (Eqn. 14a). As a consequence, C[rain], R[slope], and crust-altered P[permeability] interact to generate runoff (Eqn. 14b). This interaction is directly analogous to the C[rain], R[slope] and P[rock] interaction in the previous Negev null model (see Eqn. 10a) and illustrates how engineers can create parent material functional analogs to impervious rock.

Soil erosion is higher from soil surfaces without crusts compared to crusted soil [25,26]. Crusted slopes generate an erosive force—runoff—whose intensity increases down slope [95]. All things being equal, lower slopes should have greater erosion rates compared to upper slopes. However, interspersed among crusted areas are other engineer-created parent material topographic/permeability modifications—mounds of un-crusted, permeable soil made by shrubs, ants and geophytes [27,74,91]; (Fig. 6a–c; Eqn. 15a). While space precludes a detailed analysis here, functionally, these structures all absorb runoff water generated by adjacent crusted areas (see Eqn. 14b), allowing it to infiltrate deep into the soil, dissipating the erosive force [78] (Eqn. 15b).

Erosive force dissipation can only occur here because slopes are gentle. In steeper areas the higher erosive force of runoff removes structures at a faster

Soil Erosion Rate = f (C[rain], R[slope], P[erodibility], E[crust area]) Eqn. 13

a

a

Soil Erosion Rate = f (C[rain], R[slope], P[permeability, erodibility], E[crust area]) Eqn. 14

b

Runoff

a

Soil Erosion Rate = f (C[rain], R[slope], P[permeability, erodibility, topography], E[crust area , # mound builders]) Eqn. 15

Runoff - - b - - - - - - - - - - ▶ Adsorption

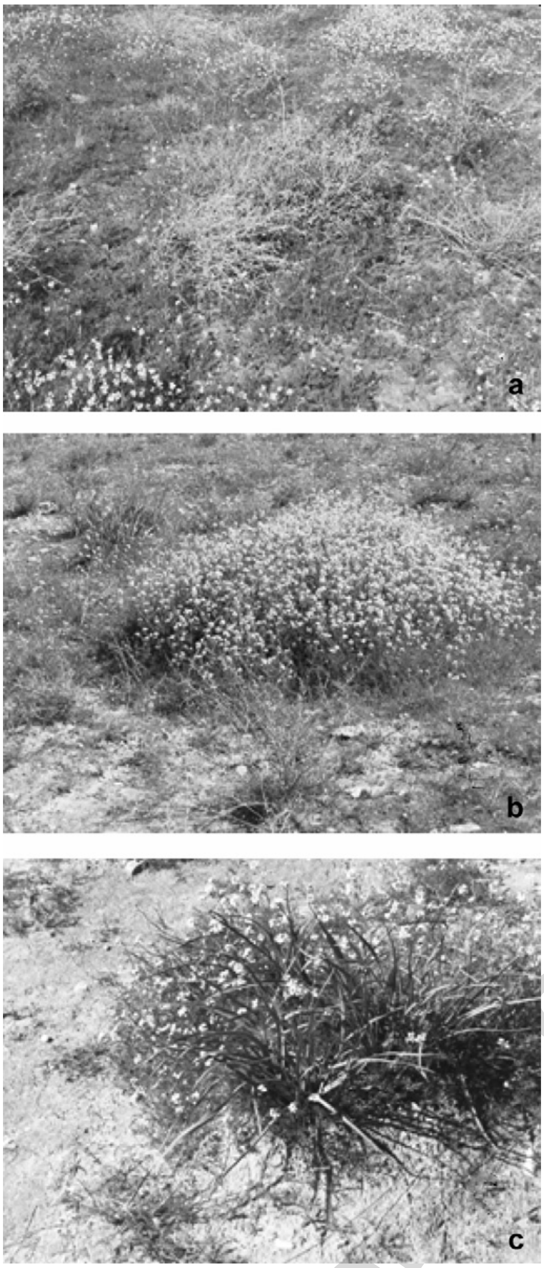


Fig. 6. Vertical views of un-crusted permeable soil mounds (ca. 20 cm–1.5 m dia., 5–40 cm height) made by a. Shrubs (*Noea mucronata*); b. Ants (*Messor arenarius*); c. Geophytes (*Asphodelus ramosus*). These structures occur in between the crusted soil patches (Fig. 5). (Photos: C. G. Jones).

rate than they are built. This complex set of interactions between engineers and other state factors means that erosion from areas with crust and mounds is lower than areas with crust and no mounds.

This example illustrates how we can use the State Factor Equation to integrate the influence of multiple, functionally different and similar engineers within one system on the same soil process.

2.1.4. Soil erosion and isopod ecosystem engineering

Our last erosion example is the desert isopod, *Hemilepistus reaumuri* (Fig. 7a), which also occurs in the rocky Negev watersheds that get 100 mm annual rainfall (Fig. 3). Here, loessial soil depth varies from 0.5 m up slope to 2.0 m down slope. The deeper soils include upslope soil eroded via runoff from more rocky portions of slopes, and have higher infiltration rates [95]. Isopods are more abundant in the mid-slope (6.8–8.0 individuals m^2) than lower slope (2.0–3.2 individuals m^2) [75].

Two isopod parents and offspring collectively dig to a depth of up to 1 m where soil moisture is about 10% [75]. If they fail to reach moist soil, the family perishes [73,77]. During digging the family moves large amounts of soil from the burrow to the surface by eating the soil, defecating and carrying the brick-like fecal pellets to the surface around the burrow entrance (Fig. 7b). The pellets remain until periodic major overland runoff events from the rocky part of the watershed wash this soil into the lower slope or into the Wadi [95].

The null physical erosion equation, to which we then add this engineer, is similar to the porcupine example (see Eqn. 9). The engineer variable is isopod density reflecting *per family* impact of digging down to sufficiently moist soil for survival (Eqn. 16). Similar to the crab and porcupine examples, isopod impacts on soil erosion are via alteration of soil parent material erodibility (Eqn. 16a)—redistribution of deep soil to the surface in erodible form (soil fecal pellets), followed by export (Eqn. 16c) via major runoff events (Eqn. 16b).

An interesting feature is the potential for a positive feedback between engineer and soil erosion at the slope scale over time [73,75]. In the mid-slope there is sufficient exposed rock to locally generate runoff, and soil is deep enough to store runoff generated locally and higher up the slope [95]. In contrast, in the lower slope, while there is accumulated soil that could store water, there is insufficient rock to locally generate runoff, and most of the upslope runoff has already infil-

a

Soil Erosion Rate = f (C[rain], R[slope], P[rock, erodible soil], E[density]) Eqn. 16

b

$$\text{Runoff} \xrightarrow{c} \text{Soil Export}$$

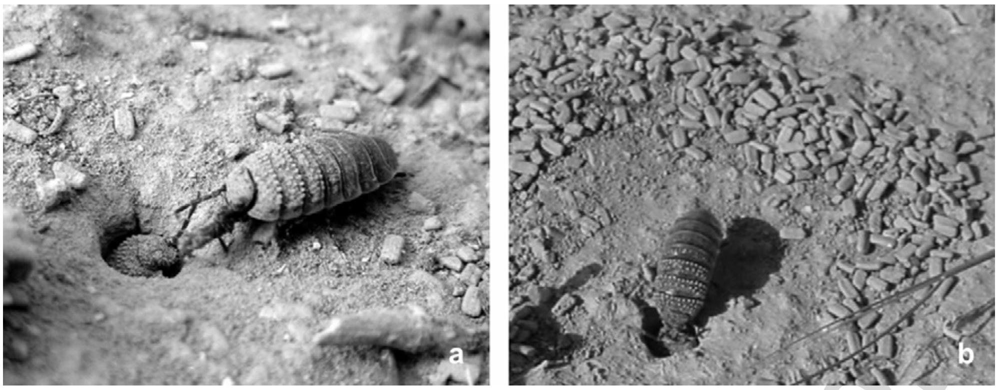


Fig. 7. a. Pair of adult desert isopods, *H. reaumuri* (ca. 1 cm length), removing a soil fecal pellet from a burrow. b. Previously removed pellets (1–2 mm length) can be seen distributed in a circle around the burrow entrance. (Photos: M. Segoli).

trated into mid slope soils. Thus, soil moisture in the lower slope is relatively low. Isopods survive in areas where there is enough water stored in soil during the dry season [4,13,62]. Isopod density is therefore higher in the mid-slope; hence local erosion due to isopods is also higher here [75]. Over the long term, isopod-induced soil erosion (Eqn. 17g, a) should increase the rock to soil ratio (Eqn. 17b), leading to: more exposed rock (Eqn. 17c); greater amounts of locally produced runoff during rain (Eqn. 17d); more water infiltrating the soil and greater stored soil moisture (Eqn. 17e); more suitable isopod habitat and higher isopod density (Eqn. 17f); higher erosion (Eqn. 17g); and so on.

Consequently, isopods may improve their environment by increasing watershed erodibility [73], illustrating some complexities of feedbacks to engineers from their engineering [44,45,93]. Although engineer effects on physical soil processes are similar to some abiotic forces, feedbacks can result in a very different dynamic behavior.

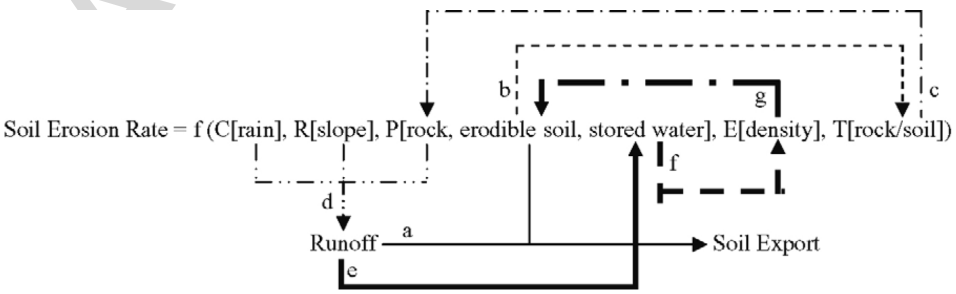
2.2. Chemical process—desalination by desert isopods

Isopods also illustrate engineering integration with State Factors for a chemical soil process—desalination. Like most arid regions, soils in the Negev slowly accumulate a deep salt layer as percolating water moves minerals down and evaporates [95]. Here our abiotic precondition null (Eqn. 18) has rain and evaporation as climate; relief as slope (largely less steep, less rocky areas); parent material as initial salt content and distribution (abbreviated as salt), and infiltration capacity. Time enters simply as a slow process:

Soil Salination Rate = f (C[rain, evaporation], R[slope], P[salt, infiltration capacity], T) Eqn. 18

As isopods dig down they reach the salt pan, bringing saline soil to the surface in fecal pellets ([77]; see Fig. 7b). During periodic overland runoff events this saline soil is washed down slope. With major events, material can be carried into the Wadi and out of the watershed [95]. The isopod desalination effect therefore accompanies their erosion effect. For simplicity we assume salination has occurred, and drop time, slope and infiltration capacity from Eqn. 18. We add the engineer to what is now a simple desalination rate model using the same engineer density variable as in soil erosion (see Eqn. 16). The engineering is best thought of as redistribution of salts from depth to surface in the parent material term (Eqn. 19a).

We can then combine this desalination rate equation (see Eqn. 19) with the isopod erosion rate equation (see Eqn. 16) to produce a combined soil erosion and desalination rate equation (Eqn. 20), where engineer-created



Eqn. 17

erodible soil containing salt (Eqn. 20a) is exported (Eqn. 20c) via runoff (Eqn. 20b). This example illustrates how the approach can be used to couple two different soil processes affected by the same engineer.

2.3. Biogeochemical process—denitrification and engineering

Our last example is a work in progress trying to develop models predicting engineer effects on biogeochemical processes. We illustrate the approach and some predictions for a part of one process—denitrification—in particular, the influence of oxygen inhibition when carbon and nitrate are not limiting [84]. The null equation includes climate as water and oxygen, with water reducing oxygen content [71] (Eqn. 21a). Parent materials are soil properties affecting air and water movement, of which soil texture and drainage class are particularly important as denitrification regulators [33]. Because the process is biogeochemical, not physical or chemical, we need to include organisms as assimilators/dissimilators; these are the denitrifiers. For simplicity, we ignore relief and time. We reasonably assume, based on numerous studies, that denitrification rates will tend to be high in anoxic soil (e.g. wet and poorly drained soils) and low in oxic soils (e.g. mesic to dry, well-drained) [84].

Engineers can be added in a variety of ways. They can affect parent material structure, altering air and water movement via aggregate, macro- and micro-pore formation/destruction (Eqn. 22a). Numerous studies have shown that biologically derived soil aggregates act as anaerobic denitrification microsites [41,57,70, 72]. Such "hotspots" also form around pieces of freshly decaying organic matter [16,56,58,60] and inside earthworm casts [28,61,82]. They can affect climate as oxygen, increasing it via root injection (e.g. [6]) or decreasing it via respiratory removal (Eqn. 22b ; e.g. [32]). They can affect climate as water, decreasing it via evapotranspiration (e.g. [33]) or increasing it via other microclimate effects, such as forming a wet blanket like *Sphagnum* (Eqn. 22c [86]).

The model predicts when engineers will have large or negligible effects on denitrification rates. In general, engineers should decrease denitrification in anoxic soils when they remove water, add oxygen and increase drainage via formation of aggregates, macro- and micropores (e.g. formation of aerobic, raised muskrat lodges in wetlands [18]). However, such engineering should have little or no effect on denitrification in oxic, well-drained soils. In contrast, engineers should increase denitrification in oxic soils when they add water, remove oxygen, decrease drainage (via destruction of large aggregates, macro- and micro-pores) or add anaerobic microsites (small aggregates and other "hotspots", see above). Again, such engineering should have negligible effects on denitrification in poorly drained, anoxic soils.Whether or not such a simple model makes good qualitative predictions remains to be seen. Nevertheless, this brief, simplified example illustrates the potential for the state factor approach to provide insights into ecosystem engineering effects on biogeochemical processes.

a

Soil Desalination Rate = f (P[salt], E[density]) Eqn. 19

a

Soil Erosion & Desalination Rate = f (C[rain], R[slope], P[rock, erodible soil, salt], E[density]) Eqn. 20

b

Runoff —c→ Export

Soil Denitrification Rate = f (C[water, 0_2], P[fluid movement properties], A[denitrifiers]) Eqn. 21

a

Soil Denitrification Rate = f (C[water, 0_2], P[fluid movement properties], E[species], A[denitrifiers]) Eqn. 22

a

b

c

3. Conclusion

Given existing rich understanding of controls on physical, chemical and biogeochemical processes, and an understanding of how an ecosystem engineer affects the abiotic environment, linking ecosystem engineering with soil processes ought to be straightforward. So what is achieved by formalizing such common knowledge into engineering state factor equations?

The framework may not be necessary for straightforward cases. Nevertheless, we think the approach gives structure to common understanding, helping us organize possibilities for even straightforward cases by forcing explicitness about the way the ecosystem engineer and other state factors interact. Some examples we explored, and no doubt many others, are actually quite complex, and here the framework may be particularly useful in helping: identify conditions where an engineer should have a small or large effect on a soil process; assessing impacts of an engineer on multiple soil processes; comparing and contrasting effects of different engineers on the same soil process; and integrating the effects of multiple engineers on the same soil process.

We also suggest that the approach can assist the design of empirical case studies by: indicating appropriate gradients of state factors to investigate; highlighting likely important engineer interactions with state factors; indicating where and when it may be appropriate to remove an engineer or conduct experimental engineering work in the absence of the engineer. The framework can assist design by revealing required contingencies for an engineer effect and identifying conditions where effects should be small or large.

While case studies are important, ecologists seek general principles. We clearly cannot study every engineer, every soil process and every ecosystem. We realize that some of the examples we used may not specifically apply in other soil systems, nevertheless, while the exact structure of Engineer State Factor Equation models will vary from case to case, the general approach stays the same across cases. Thus an analysis of many cases could expose generalities in model structure that allow for comparison across systems and engineers, helping reveal what is general and what is idiosyncratic.

We are certainly not going to argue that this illustrative and somewhat preliminary framework is a panacea for linking ecosystem engineering effects of species with soil processes; nonetheless we hope it will prove useful.

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