Oikos 119: 1862–1869, 2010
doi: 10.1111/j.1600-0706.2010.18782.x

Subject Editor: Jonathan W. Moore. Accepted 30 August 2010

A framework for understanding physical ecosystem engineering by organisms

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While well-recognized as an important kind of ecological interaction, physical ecosystem engineering by organisms is diverse with varied consequences, presenting challenges for developing and using general understanding. There is also still some uncertainty as to what it is, and some skepticism that the diversity of engineering and its effects is amenable to conceptual integration and general understanding. What then, are the key cause/effect relationships and what underlies them? Here we develop, enrich and extend our extant understanding of physical ecosystem engineering into an integrated framework that exposes the essential cause/effect relationships, their underpinnings, and the interconnections that need to be understood to explain or predict engineering effects. The framework has four cause/effect relationships linking four components: 1. An engineer causes structural change; 2. Structural change causes abiotic change; 3. Structural and abiotic change cause biotic change; 4. Structural, abiotic and biotic change can feedback to the engineer. The first two relationships describe an ecosystem engineering process and abiotic dynamics, while the second two describe biotic consequence for other species and the engineer. The four relationships can be parameterized and linked using time-indexed equations that describe engineered system dynamics. After describing the relationships we discuss the utility of the framework; how it might be enriched; and briefly how it can be used to identify intersections of ecosystem engineering with fields outside ecology.

Ecosystem engineering by organisms (Jones et al. 1994, 1997a) is now well-recognized as an important general kind of ecological interaction of basic and applied relevance (Crooks 2002, Rosemond and Anderson 2003, Boogert et al. 2006, Byers et al. 2006, Wright and Jones 2006, Cuddington et al. 2007). Yet ecosystem engineering is diverse with varied consequences, presenting challenges for developing general understanding from case studies that can then be applied to other studies. There is also still some uncertainty as to what engineering is and is not; some skepticism that the diversity of engineering and its effects is amenable to conceptual integration and general understanding; and continued debate over the value of the mechanistic approach that underlies the concept (Reichman and Seabloom 2002a, 2002b, Wilby 2002, Wright and Jones 2006, Cuddington 2007, Wilson 2007, Jones and Gutiérrez 2007).

Here we develop, enrich and extend our extant understanding of physical ecosystem engineering into an integrated framework that exposes the essential cause/effect relationships, their underpinnings, and the interconnections that need to be understood to explain or predict engineering effects, and that can help make sense of, and generalize from, case studies (Jones et al. 1994, Berkenbusch and Rowden 2003, Wright and Jones 2006). Our objectives are to amplify and clarify what physical engineering is, and show that the diversity of cause and effects is amenable to general understanding. We thereby hope to facilitate theory development and modeling, hypothesis formulation, comparison and generalization, empirical study and methodological development in this rapidly growing field of research. We also hope that by formally exposing the relationships and their underpinnings, the framework will help other fields such as geomorphology, environmental engineering, and evolutionary biology, identify their points of intersections with ecosystem engineering.

Framework: engineering cause and effect relationships

Four general cause and effect relationships link four components (Fig. 1): 1. An engineer causes structural change; 2. Structural change causes abiotic change; 3. Structural and abiotic change cause biotic change; 4. Structural, abiotic, and biotic change can feedback to the engineer. The first two relationships

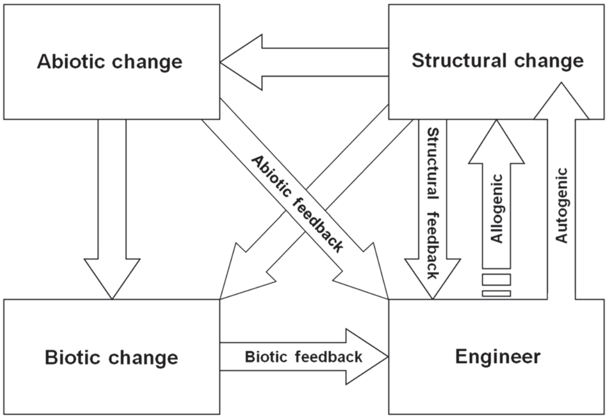

Figure 1. Physical ecosystem engineering by organisms. The cause/effect relationships representing an engineered system. The solid arrow for autogenic engineering represents the physical manifestation of organismal structure inserted into the abiotic milieu. The striped arrow for allogenic engineering represents the action of the engineer on other living or non-living structure.

describe an ecosystem engineering process and abiotic dynamics, while the second two describe biotic consequence for other species and the engineer (Jones and Gutiérrez 2007). All four relationships may need to be interconnected to understand engineered system dynamics. Most of the sections below contain an overview followed by more detailed explanations.

Engineer causes structural change

An engineer species autogenically and/or allogenically (Jones et al. 1994) causes structure formation in the abiotic environment, creating a new structural state relative to a baseline, unmodified state. The degree of structure formation via construction and maintenance is a function of per capita engineering activity (hereafter activity) and engineer density (Jones et al. 1994; Table 1, Eq. 2). For example, coral reefs grow; a pair of beaver builds a dam. Unless maintained, engineered structures, like all physical structures, undergo structural decay toward a baseline structural state. Their persistence in the absence of maintenance is a function of the intrinsic durability of the structural materials and the intensity of structurally destructive forces (Jones et al. 1997a; Table 1, Eq.3). Engineer death (for autogenic) and structure abandonment (for allogenic) therefore leave decaying structural legacies (Hastings et al. 2007). Structural change over time is thus the sum of structure formation by the engineer minus structural loss via decay (Table 1, Eq. 1). For convenience, we sometimes treat structure formation, decay and change as synonymous with structure. Structure is the defining physical intermediary between the engineer and all other cause/effect relationships, and the physical properties of structures are central to understanding these relationships.

Autogenic and allogenic origin

Autogenic structures are physical manifestations of living organisms inserted into the abiotic environment (e.g. tree, oyster reef, microbial biofilm). Allogenic structures are formed by the engineer in the abiotic environment from non-living or living materials (e.g. burrow, dam, leaf tie). Many mobile animals are obvious allogenic engineers (e.g. beaver). Many sessile organisms are obvious autogenic engineers (e.g. trees). However, engineers can be mobile and autogenic (e.g. shells of living crabs create epibiont habitat), sessile and allogenic (e.g. plant root growth creates soil macropores), and simultaneously auto- and allogenic (e.g. many plants, microbial soil surface crusts).

Table 1. Parameters and time($_t$)-indexed equations (magnitudes, rates, frequencies) for engineered system dynamics. As illustrated throughout the text, the general notations make no assumptions about the shapes of relationships; include the potential for first or higher order interaction terms; allow one or more independent variables to have zero values if not relevant (e.g. $B = 0$ and $S = 0$ in Eq. 7 when there is only an abiotic feedback to engineer density); allow for substituation across equations (e.g. P and ρ for K, when an engineer generates kinetic energy); and can be specified for particular study systems (e.g. inclusion of parameters describing the shape of the relationship, system-specific covariates and additional variables).

S: Structural state (physical properties)
F: Structure formation by engineer (construction and maintenance)
D: Structural decay
P: Per capita engineering activity
ρ: Engineer density
R: Intrinsic durability of structural materials
I: Intensity of structurally destructive forces
A: Abiotic state (relevant abiotic variables)
K: Kinetic energy (other than K generated by P, ρ)
M: Abiotic materials (fluids, solids)
B: Biotic state as biotic response variables of interest

Structural change
$S_{t+1} = S_t + F_t - D_t$ …………………………………… Eq. 1
Where:
$F_t = f(P_t, \rho_t)$ …………………………………………… Eq. 2
$D_t = f(R_t, I_t)$ …………………………………………… Eq. 3
S_0 = Baseline unmodified structural state

Abiotic change
$A_{t+1} = f(A_t, S_t, K_t, M_t)$ ………………………………… Eq. 4
A_0 = Baseline unmodified abiotic state

Biotic change
$B_{t+1} = f(B_t, S_t, A_t)$ …………………………………… Eq. 5
B_0 = Baseline unmodified biotic state

Engineering feedbacks
$P_{t+1} = f(P_t, S_t, A_t, B_t)$ ……………………………… Eq. 6
$\rho_{t+1} = f(\rho_t, S_t, A_t, B_t)$ ……………………………… Eq. 7

Assigning an organism to one, the other, or both categories is less important than what structural origins can reveal about constraints on construction and maintenance and the onset of structural legacies. Autogenically engineered structures will form if the organism can grow in that environment. Construction and maintenance are intrinsic given resources for growth and repair. The onset of structural legacy is the death of the engineer. In contrast, allogenic engineering requires that the environment be structurally modifiable (e.g. soil not too compact for digging) and that additional extrinsic materials, if required, are available to the engineer (e.g. trees for making beaver dams). Maintenance, if it occurs, will be determined by activity, density, and, where needed, the availability of additional construction materials. The onset of structural legacy is cessation of construction and maintenance.

Structure formation and baseline

The requirement that an organism cause structure formation distinguishes abiotic effects of physical ecosystem engineering from abiotic forces such as climatic and geologic processes causing the same abiotic change and biotic response (cf. Reichman and Seabloom 2002a, Wilson 2007; e.g. wind and elephants both create tree tip up mounds, Pickett et al. 2000). Equally important, the requirement distinguishes engineering from the inevitable abiotic changes caused by organisms via the universal trophic processes of energy and material uptake and release.

Structural change caused by an engineer can involve addition (e.g. tree branches to beaver dam), removal (e.g. earth from burrow, coral collapse), reconfiguration (e.g. leaf tying by caterpillars, plant re-growth of new architectural form), redistribution (e.g. forest floor litter to nesting burrow), and combinations thereof. The resulting structural state may be maintained (e.g. beaver dam repair, tree re-growth) or further changed (e.g. burrow extension, coral growth). Structure formation causes a departure from a baseline structural state – an otherwise equivalent place without that structural change (e.g. savannah grassland area without tree vs with tree; open leaves vs leaves tied by caterpillars; soil without vs with burrows). Dynamic reference states can be used for progressive structure formation (e.g. burrow system extension, coral reef growth rates).

Engineer activity and density

Engineering activities encompasses all things an organism does that cause structure formation within an abiotic milieu. This encompasses: plant growth; animal trail formation via movement; beaver dam building and repair for predator avoidance, shelter, and food access and storage; and a great many human environmental modification activities (Jones et al. 1994) from agriculture to river channelization, although we will not address human engineering here. Non-teleological postulates about the reasons for activities (i.e. intent is not implied; Power 1997, Jones et al. 1997b) may suggest: 1. Whether activities are likely facultative or obligate; 2. When and where activities may occur; 3. What types of structure formation might result; 4. Whether or not the engineer will maintain the new structural state; and 5. The likelihood of positive or negative feedbacks from the engineering to the engineer.

While structure formation can be the simple product of activity and density, it can be a more complex function; i.e. there can be interaction terms in Table 1, Eq. 2 (Note this can be the case for all equations in Table 1). Such interactions can occur if, for example, activity is size or stage-dependent (e.g. saplings vs trees; juvenile vs adult animals), engineering is cooperative (e.g. social fossorial mammals), or causes interference (e.g. fog interception by windward trees creates fog water shadows for leeward trees, del Val et al. 2006).

Structural decay, legacies and persistence

Engineered structures are subject to variable abiotic (e.g. wind erosion) and biotic (e.g. decomposition of wood structures) forces that cause continuous structural deterioration at rates affected by material durability (e.g. wood vs rock), although this can be offset by endogenous (autogenic) or exogenous (allogenic) maintenance. Structural legacies resulting from autogenic engineer death or allogenic engineer abandonment are, by definition, not maintained, although allogenic legacies may be subsequently re-engineered (e.g. beaver re-building abandoned dams; abandoned burrow re-occupation). Legacy persistence is determined by structural decay rates (Table 1, Eq. 3), and decay may or may not involve other structural forms along the way (e.g. beaver dam to abandoned dam to wetland to forested riparian zone, Wright et al. 2004). Persistence is highly variable (Hastings et al. 2007), ranging from the very ephemeral, as in the bubble nets made by humpback whales for fishing (Sharpe 1984), to very long-lived or near zero rates of return, i.e. hysteresis (e.g. 4000 year-old termite mounds, Moore and Picker 1991; contemporary effects of Holocene fossil clam beds, Gutiérrez and Iribarne 1999).

Physical properties of structures

Structures are diverse in dimension and composition (e.g. aragonite, wood, soil, tied leaves) with physical properties directly relevant to their effects (e.g. size of beaver dam relative to water impounded; mollusk shell roughness and epibiont living space). Functionally, structural change can be most usefully considered as altered physical properties. The particular properties invoked will depend on the response variables of interest. For example, aquatic plant effects on hydrodynamics invoke mechanical impedance, while an animal burrow as a predator refuge invokes dimensions. Reflectance, albedo, thermal capacity, friability, and compaction illustrate other physical properties. Equating structure to physical properties facilitates hypotheses formulation about abiotic change, biotic change and engineer feedbacks and opens the door to comparison among superficially disparate engineers (Byers 2007).

Structure as intermediary

There are four ways to construe the relationships between structural change and other framework components (Fig. 1). First, the physical properties of non-living structures can be a focus, as is sometimes the case in biogeomorphology (e.g. soil mound topography created by engineers). Although this kind of structural change is, by definition, a form of abiotic change, it can be understood from processes of structure formation and decay (i.e. Table 1, Eq. 1, 2, 3). Formation dynamics will be affected if engineer feedbacks occur (Table 1, Eq. 2, 6, 7), requiring some understanding of such feedbacks. Beyond that, the rest of the framework may not be required. Second, structural change can cause abiotic change; this is addressed below. Third, the physical properties of living and non-living structures can have direct biotic effects (e.g. living space); we address these under Structural and abiotic change cause biotic change. Fourth, structural change can directly feedback to the engineer (e.g. conspecific living space), which we address under Engineer feedbacks.

Structural change causes abiotic change

Abiotic change is a new abiotic state relative to a structurally unmodified abiotic state. As with structural change, dynamic reference states can be used for progressive abiotic change. Abiotic change is the result of structure interacting with kinetic energy and materials within an abiotic milieu (Table 1, Eq. 4). For example, coral reefs attenuate wave action, and beaver dams create ponds and increase sedimentation. Such effects involve work (sensu W in physics) being done on structure by kinetic energy (e.g. storm attenuation), or vice versa (e.g. erosion), often accompanied by changes in the distribution of material fluids and solids (e.g. impoundment and sedimentation).

The magnitudes of such effects often depend on abiotic conditions; i.e. they have abiotic context-dependency. Abiotic decay toward a baseline unmodified abiotic state is a function of the decay of structure. The diversity of structurally-mediated abiotic changes can be constrained to those abiotic variables an investigator knows or postulates to be relevant to either abiotic change per se (e.g. heat balance, hydrology, erosion, sedimentation) or a biotic consequence of interest.

Abiotic change per se may be considered an appropriate end-point of the framework for investigators focusing only on such variables (e.g. hydrologists, sedimentologists, environmental engineers) with one important caveat. Dynamic understanding of engineer-induced abiotic change will require an understanding of engineer feedbacks, if they occur.

Structure, kinetic energy, fluids and solids

Engineered abiotic changes are the result of interactions between structure, kinetic energy, fluids and solids. Work is done on structure by kinetic energy or vice versa, and redistribution of fluids and solids is often the result of this work. Collectively these relationships explain why, for example, microbial crusts generate runoff, beaver dams create ponds, trees act as wind breaks, and animal burrowing increases erosion.

Physical structures inserted into kinetic energy flows (radiant energy as light, heat; sound; energized fluids) cause reflection, conversion to potential energy, and dissipation to other forms of energy that can then do less work (e.g. heat). Thus trees deflect and attenuate wind creating mechanical movement and sound. Coral reefs and salt marshes attenuate storm surges. Litter reduces rain splash impact and soil mounds absorb heat. The structural properties relevant to predicting abiotic change for energy-based abiotic variables (e.g. temperature, wind, waves) are those responsible for energy reflection, conversion and dissipation (e.g. absorbance, mechanical resistance, etc.).

When engineers alter physical structure they can make materials more or less prone to removal by kinetically energized fluids (wind, rain, fluvial, runoff). For example, bioturbation introduces fine sediments into water flows, while plant 'weathering' and animal digging form erodible materials. Conversely, litter burial by earthworms, soil compaction by hoofed mammals and root stabilization all reduce erodibility. Here, structural properties relevant to interactions with energized fluids – such as friability, particle size, and compaction – predict abiotic change (e.g. material export, landslip).

While physical kinetic energy is central to the above kinds of abiotic effects, some engineers can also generate the kinetic energy contributing to abiotic change (Gutiérrez and Jones 2006). For example, many species of sediment invertebrates pump water in and out of their constructed burrows via body movement (e.g. polychaetes, callianassid shrimp).

Structure/kinetic energy interactions change fluid distribution and materials dissolved or suspended in them. Materials are redistributed when kinetic energy is redirected, and deposited when kinetic energy is converted to potential energy or dissipated. Thus, beaver dams and hoof prints create impoundments. Plant canopies intercept water and nutrients in wind-driven fog. Animal-made pits trap wind-driven seeds and organic matter. Burrows redistribute soil water. In this situation, the requirement that kinetic energy first interact with structure in order to alter fluid and material distribution invokes different physical properties. In the above examples these would include storage volume, turbulent roughness, microtopography and permeability, respectively.

When only structure and extrinsic kinetic energy are involved in abiotic change (e.g. thermal effects of structure), then $M = 0$ in Table 1, Eq. 4; when fluids and solids are also involved, as in many cases above, then $M \neq 0$; and when the engineer provides the kinetic energy (e.g. hoof prints, burrow irrigation), then K is substituted by P and ρ.

Abiotic context-dependency

Shrub mounds increase annual plant species richness via runoff water capture in the Negev desert, but the effect magnitude is influenced by annual precipitation amount (Wright et al. 2006). Coastal erosion by burrowing marine isopods is affected by wave intensity (Talley and Crooks 2007). Trees act as wind breaks only when there is wind. Not all parent materials are equally amenable to compaction or bio-erosion, and so on. Predicting structural influence on the abiotic environment when it involves interactions among structure, kinetic energy, fluids and solids generally requires consideration of the way the abiotic milieu can affect such interactions.

Abiotic decay and structure

Structures decay toward a baseline structural state. Since structural change determines abiotic change, return to a baseline structural state via decay equates to reversion to a baseline abiotic state. Abiotic variables can therefore be considered as decaying toward some baseline abiotic state as a direct function of the decay of structure.

Structural and abiotic change cause biotic change

Biotic change (here we exclude effects on the engineer, addressing this under Engineer feedbacks) is a new biotic state relative to a structurally and abiotically unmodified biotic state (Table 1, Eq. 5). There are two non-exclusive pathways (Fig. 1): 1. Structural change can directly affect biota (i.e. structural effects per se); and 2. Structurally-mediated abiotic change can affect biota (i.e. Structural change causes abiotic change; see above). In the first pathway, the physical properties of living and non-living structures are sufficient to account for some biotic effects. For example, the fractal dimensions of bark surfaces may approximate living space for organisms. Animal resting locations (e.g. nests, roosts, perches) and altered physical living space (Jones et al. 1997a; e.g. mollusk shells, tree holes) can fit this situation, as can structure-based enemy-free space used by other species (Rozas and Minello 1998). Changes in the physical attributes of structures due to the engineer (e.g. altered size, shape, dimension, etc.) may adequately describe such effects (i.e. in Table 1, Eq. 5, $S \neq 0, A = 0$). In the second and perhaps most common pathway (i.e. in Table 1, Eq. 5, $S = 0, A \neq 0$), the abiotic variables of potential relevance encompass consumable energy and materials (e.g. nutrients, water), constraining or enabling abiotic conditions (e.g. temperature, salinity, redox), and abiotic cues used by organisms (e.g. sound attenuation, temperature).

As a null hypothesis, biotic change can be viewed solely as a function of the altered structural or abiotic states (i.e. structural or abiotic determinism), depending on the pathway considered. Given some predicted or observed difference between engineered and unmodified structural or abiotic states, the direction and magnitude of a new biotic state can be predicted by combining such differences with an underlying structural or abiotic dose/biotic response relationship that describes the degree to which species are limited, constrained or otherwise influenced by the physical properties of structure or abiotic variables across a range of values of those variables (Fig. 2). Since species vary in their sensitivity to structural properties and abiotic variables, biotic effects will depend on the degree of limitation or constraint species experience relative to the degree of structural or abiotic change. Weak and strong, positive and negative effects, as well as no effects are therefore to be expected (Jones et al. 1997a, Jones and Gutiérrez 2007). Since many engineers change multiple structural and abiotic variables (e.g. beaver, Naiman et al. 1988) there can be convergent or divergent biotic effects, requiring an integrative or multivariate construal of the relationships in Fig. 2.

Many kinds of biotic responses (aut-ecological, population, community, ecosystem; Hastings et al. 2007) can be addressed via structural and/or abiotic determinism. Responses include effects on organismal growth and reproduction; species abundances and distributions; species interactions (e.g. competitive dominance); and ecosystem processes such as primary productivity and biogeochemical process rates. There is a very extensive literature on biotic responses to and coupling with both structure and the abiotic environment (e.g. fractal dimensions, nutrient cycling) that can inform expectations for dose/response relationships.

Engineer feedbacks

Engineer feedbacks occur when activity or density are a function of the engineered structural, abiotic, or biotic states (Table 1, Eq. 6, 7; Jones et al. 1994, 1997a, Gurney and Lawton 1996, van Breemen and Finzi 1998, Gutiérrez et al. 2003, Jouquet et al. 2006, Barot et al. 2007, Cuddington et al. 2009). For example, beaver ponds reduce beaver movement costs and predation risk (Rosell and Parker 1996, Allers and Culik 1997). The three, non-exclusive feedback pathways – structural, abiotic and biotic (Fig. 1) – can affect activity and/or density, and feedbacks can be positive and/or negative on the same or different time scales. Consideration of the potential for feedbacks can inform why engineers may engineer, when and where they might do so, and when structural maintenance or abandonment might be expected. Since engineer feedbacks will change the engineering, knowing whether or not feedbacks occur is integral to understanding the dynamics of engineer-induced change irrespective of whether an investigator is focusing on structural change (e.g. mound topography), abiotic change (e.g. sedimentation), biotic change (e.g. species richness), or engineer population dynamics.

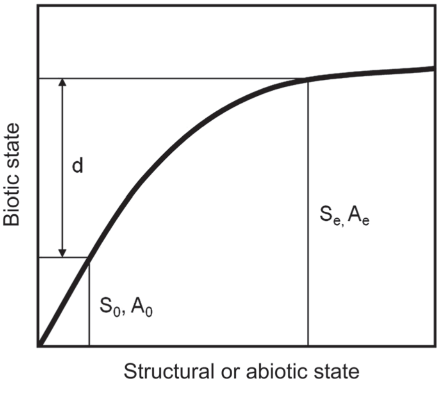

Figure 2. Structural and abiotic determinism. The predicted difference (d) in the biotic state is a function of an underlying relationship between the values of a structural property or an abiotic dose and a biotic response (hypothetical bold curve), and the degree to which the engineered structural state (S_e) or abiotic state (A_e) differs from the baseline unmodified structural state (S_0) or abiotic state (A_0). The same relationship applies to engineer feedbacks from the structure or abiotic environment (i.e. biotic state = engineer).

Feedback pathways

Structural feedbacks occur when engineer-induced changes in the physical properties of structure affect the engineer (i.e. Table 1, Eq. 6, 7 when $S \neq 0, A = 0, B = 0$). Conspecific living space and structures made for mate attraction (e.g. bower bird constructs) conform to this kind of feedback. As with biotic responses to structural change, this kind of feedback can be viewed as structural determinism; i.e. a function of an underlying relationship between the values of structural properties and engineer responses, and the degree of difference between engineered and unmodified structural states (Fig. 2). Abiotic feedbacks occur when the engineer is affected solely by the abiotic changes it causes (i.e. increase or decrease its abiotic resources or conditions; i.e. Table 1, Eq. 6, 7 when $A \neq 0$, $S = 0$, $B = 0$). As with biotic responses to abiotic change, this kind of feedback can be viewed as abiotic determinism; i.e. a function of an underlying abiotic dose/engineer response relationship, and the degree of difference between engineered and unmodified abiotic states (Fig. 2). Biotic feedbacks occur when the engineering affects abiotic conditions for other species that then affect the engineer via other kinds of ecological interactions (e.g. animal engineers influencing their food supply by engineering; engineered refugia affecting predation; plant engineers affecting abiotic conditions of their microbial mutualists; Table 1, Eq. 6, 7 when when $B \neq 0, S = 0, A = 0$). This third feedback pathway has greater potential for context-dependency and dynamic complexity because it first depends on the responses of other biota to the engineered abiotic state, and then depends on the relationship between the engineer and the altered biotic state. All three kinds of feedbacks can occur together (Table 1, Eq. 6, 7 when S, A and $B \neq 0$).

Feedback parameters, signs and time scales

Feedbacks will occur if any of the following 3 conditions hold: 1. Activity is sensitive to the engineered structural, abiotic or biotic states; 2. Activity is affected by density and density is altered by demographic feedbacks arising from engineer-induced structural, abiotic or biotic change (i.e. engineering-induced changes in birth, death, immigration or emigration; Wright et al. 2004); 3. Density is altered by such demographic feedbacks. The requirement that demographic changes be a function of the engineered structural, abiotic or biotic states to qualify as an engineering feedback distinguishes such effects from 'pure' density-dependent demographic influences. Activity change can be expressed as altered structure formation (i.e. construction or maintenance; as growth/architectural form for autogenic engineering).

Feedbacks can be positive or negative, and may co-occur on the same or different time scales. For example, beaver lodges provide shelter (positive abiotic) and impoundments reduce predator access (positive biotic). However, the dam can sometimes cause extensive riparian zone flooding, reducing food supplies (delayed negative biotic).

Integration: engineered system dynamics

The temporal dynamics of an engineered system can be described by parameters and time-indexed equations linking the four cause/effect relationships (Table 1). Models interconnecting some of these relationships (primarily engineer on abiotic and abiotic on engineer) show complex system dynamics with multiple equilibrium states depending on parameter values (Gurney and Lawton 1996, Wright et al. 2004, Cuddington and Hastings 2007, Cuddington et al. 2009). Temporal lags that introduce greater dynamic complexity will likely be common (Cuddington and Hastings 2004, Jones et al. 2006) because structure formation and decay, biotic responses to structural and abiotic change, and engineer responses to structural, abiotic and biotic change are rarely instantaneous.

It is clear that other factors extrinsic to the framework (i.e. independent of and unaffected by the engineering) will nevertheless result in altered system dynamics relative to an engineered system that is entirely self-organized. These include: 1. Extrinsic influences on engineer activity and density (e.g. other resources, other abiotic conditions, natural enemies); 2. Effects of biota on abiotic nutrient pools via assimilation/dissimilation; and 3. Other biotic interactions that influence the response of the biota to structural or abiotic change. Such factors may need to be integrated or factored out for full dynamic understanding. It is worth noting that exogenously driven structural change (e.g. hurricanes obliterating local tree microclimatic effects) is encompassed in the framework under decay (Table 1, Eq. 3).

Finally, since engineered systems are driven by ecological factors, the dynamics will differ from systems driven solely by physical forces, even if the latter result in the same general kind of structural and abiotic changes and biotic responses (cf. Reichman and Seabloom 2002a, Wilson 2007).

Discussion and conclusion

We think the framework encompasses the key relationships, underpinnings and interconnections found in a great many cases of physical ecosystem engineering, although the degree to which it is sufficient to encompass all cases remains to be seen. Even if sufficient, the framework can undoubtedly benefit from enrichment. Three general questions with specific examples help illustrate this point. 1. Although the equations in Table 1 can be specified for a given system, do certain kinds of engineers or environments lead to sub-categories of equations, or does the inherent variety of engineering preclude this? For example, does the form of Eq. 4 (Table 1) fundamentally differ if the source of kinetic energy interacting with structure to bring about abiotic change is extrinsic or engineer-generated? 2. Are there missing relationships relevant to certain classes of cases? For example, if there is abiotic context-dependency, can this be dealt with simply by including A_0 into Eq. 4 (Table 1), or does it require a different relationship? 3. Are some relationships sometimes redundant? For example, to what degree can abiotic change be subsumed when structure is construed as living space?

The framework structure appears wellsuited for single engineering species; the focus of the majority of studies in the literature. However, we think the framework can often have utility for understanding multiple engineers, commensurate with reality in most ecosystems. When one species of engineer has dominant control over structure and the abiotic environment, the framework can be first applied to that species. Effects of other engineers can be addressed by considering how the dominant engineer sets the structural or abiotic stage for other engineers (i.e. S_0 or A_0, Table 1), either concurrently or sequentially. Two or more engineers that are independent (i.e. change different structural or abiotic variables and do not affect each other) can be treated as such by applying the framework to each species. More or less co-dominant but interdependent engineers (i.e. alter the same structural or abiotic variables in concert or opposition and/or can affect each other) require the parsing of effects among them and consideration of inter-engineer feedbacks; a modified, engineer-interactive framework could be used for a limited number of engineers. With further modification, the framework might be applicable to complex engineering communities or networks (i.e. multiple co-acting engineers with a variety of structural, abiotic and biotic effects and feedbacks), although this is clearly a challenge for the future beyond the scope of this paper. For example, density and per capita engineering activity would have to be replaced by community properties (e.g. biomass/composition, per unit biomass or area activity, respectively); while structure formation, abiotic and biotic change, and feedbacks become reflections of community properties.

In its current form the framework provides a formal structure serving a number of purposes. They include: 1. Providing criteria for ascertaining whether observed biotic changes or feedback effects are due to engineering as opposed to other kinds of interactions that could have the same net effects (e.g. trophic relations); 2. Providing criteria for predicting whether engineering effects will be strong or weak, and what context-dependencies will also influence their magnitude; 3. Identifying which of the cause-effect relationships and underlying variables are most relevant to answering different kinds of investigator questions about structural change, or abiotic change, or biotic change, or engineer dynamics, or some combination of these; 4. Indicating how relationships can be interconnected into a temporally dynamic context; 5. Guiding the translation of general relationships into case studies and the abstraction of generalizations from case studies; 6. Posing new questions (e.g. can relationships between engineer structure formation and decay (Table 1, Eq. 1, 2, 3) be used to predict patterns and consequences of structural and abiotic heterogeneity? Which of the 3 engineer feedback pathways are the most important?); and 7. Aiding methodology (e.g. if engineer feedbacks are common and central to engineer dynamics, what are the best ways to experimentally decouple the engineering from the feedbacks?). These purposes illustrate a more general ambition for the framework of aiding theory development via generalization, comparison, modeling and case study design, with the ultimate goal of engendering better predictions of which species will have significant engineering effects and what those effects will be.

Finally, we think the framework serves two additional general purposes. First, ecosystem engineering research is increasingly being cited outside of ecology in fields where there is a legitimate intersection. These include geomorphology, environmental engineering, conservation and restoration, soil science and agriculture, evolutionary biology (extended phenotype/organism, niche construction; Turner 2000, Odling-Smee et al. 2003), as well as other areas. We hope the framework can help investigators in these fields and in ecology identify the how best to interconnect their interests. For example, when engineer feedbacks occur they must be understood to gain dynamic biogeomorphological understanding. The key features of feedbacks are the points of intersection with evolutionary considerations of fitness. Second, for those unfamiliar with the concept, or with some uncertainties, the framework provides a contemporary, systematic synthesis that clarifies what physical ecosystem engineering is, exposes the commonalities underlying its diversity, and shows how the mechanistic approach underlying the concept can be used to understand this diversity.

Acknowledgements – This paper resulted from a Working Group ('Habitat modification in conservation problems: modeling invasive ecosystem engineers') at the National Center for Ecological Analysis and Synthesis – a Center funded by NSF (Grant no. DEB-94–21535), the Univ. of California at Santa Barbara, and the State of California. Ohio Univ. and the Univ. of California Davis provided additional support. We thank David L. Strayer for help with Table 1, and Working Group members Kim Cuddington, Alan Hastings and William G. Wilson for their insights. CGJ thanks the Cary Inst. of Ecosystem Studies, the state and region of the Île de France (Chaire Internationale de Recherche Blaise Pascal, via the Fondation de l'École Normale Supérieure), le Ministère de l'Alimentation de l'Agriculture et de la Pêche, and AgroParisTech for financial support. Contribution to the program of the Cary Inst. of Ecosystem Studies.

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