

# *Ecosystem engineering*

## *Key concepts*

- Allogenic and autogenic ecosystem engineering
- Cycle of habitat condition
- Ecosystem engineering is a cause of low site occupancy
- Habitat-occupancy lags
- Engineering induced Allee effects

## *A new question*

We have already seen that natural populations do not necessarily simply grow to carrying capacity and persist at that level, but rather exhibit a rich variety of dynamical phenomena. In addition to our earlier questions about the existence and cause of population cycles we will now add a second question: Why are some habitat patches vacant? The topic of this chapter, *ecosystem engineering*, is a theory that aims to answer both questions.

## *Ecosystem engineers*

An ecosystem engineer is a species whose individuals physically or chemically modify their environments in ways that feed back to effect the fitness of other individuals in the population. *Allogenic* ecosystem engineering refers to modification of external environmental features. For instance, *bioturbation* by the burrowing of oligochaete earthworms results in greater soil porosity, oxygenation, and respiration. *Auto-genic* ecosystem engineering occurs when individuals of the species themselves become the environment for other organisms. For instance, trees, coral heads, and marine kelp all constitute important structural features of the ecosystems they inhabit. Some organisms perform both allogenic and autogenic actions. For instance, freshwater and marine



Figure 1: North American beaver (*Castor canadensis*).

mussels both filter particles from the overlying water, increasing clarity, and create surface roughness and interstitial habitat between individuals. Ecosystem engineering is universal within the major branches of the tree of life (Table 1) and a major driver of evolution.<sup>1</sup> The consequences of ecosystem engineering for population and community ecology are only just beginning to be explored, however.

<sup>1</sup> F.J. Odling-Smee, K.N. Laland, and M.W. Feldman. *Niche construction: the neglected process in evolution*. Princeton University Press, 2003

Kingdom	Engineering process
Eubacteria & Archaeobacteria	Decomposition Metabolic byproduction (ammonia, oxygen) Nitrogen fixation Allelopathy
Protists	Physical/chemical weathering Soil creation Photosynthesis Oxygen production
Fungi	Decomposition Physical/chemical weathering Soil creation Moisture retention Mineral extraction Creation of environmental structure
Plants	Photosynthesis Physical/chemical weathering Alteration of hydrology Soil stabilization Microclimate modulation Nutrient retention/cycling Allelopathy Scattering and absorption of light Wind obstruction
Animals	Construction of nests, burrows, cases, caches, dens Protection of nursery environments Nutrient retention/cycling Soil compaction Decomposition of coarse organic matter

Table 1: Universality of ecosystem engineering in the tree of life.

The beaver (*Castor canadensis*) is an important ecosystem engineer of forested areas of North America. Beaver dams alter both aquatic and terrestrial habitats. For instance, beaver dams reduce discharge in streams creating still water pond habitats contain pelagic zones.

Density of aquatic invertebrates behind beaver dams by be two to five times that of nearby streams. Beavers significantly affect the carbon cycle in a landscape and may be a source of atmospheric methane. Flooding of the riparian zone creates wetland habitat for a wide range of specialist species. Finally, beavers are “central place foragers” cutting ametric ton of wood per year. Clear cutting of riprarian forests for building material opens light gaps and reduces canopy cover.<sup>2</sup> All of these are examples of the effects of ecosystem engineering.

### *Effects of ecosystem engineering on population dynamics*

What effect do ecosystem engineering have on population dynamics? So far in this class we have considered only *direct feedbacks* of population size on population dynamics. But, the effects of ecosystem engineering outlive the individuals that performed the modification. Therefore, to account for these *indirect feedbacks* we must now consider another variable, let’s call it  $h$ , to measure the quality of the habitat. Then the population size  $n$  affects  $h$  through ecosystem engineering and  $h$  feeds back to affect  $n$  through the environment’s usual effects on growth and reproduction.

How do we incorporate this idea into a model for the population dynamics. First, recall that in the logistic model for density-dependent population growth,  $dn/dt = rn(1 - n/k)$ , the parameter  $k$  also sets the equilibrium population size (assuming also that  $r > 0$ ), which we called the carrying capacity. We may think of carrying capacity as in index of habitat quality (the higher the habitat quality the more individuals the ecosystem can support), suggesting that we replace  $k$  in the logistic equation with our  $h$ . Unlike  $k$ , however, we will allow  $h$  to change as a result of ecosystem engineering activities. How does habitat change? Following Gurney & Lawton<sup>3</sup>, we consider habitat change of three kinds:

- Habitat may be improved up by ecosystem engineering (+)
- Habitat may be degraded through use (-)
- Degraded habitat may recover to an unimproved state (+)

This list suggests that we will also need quantities  $u$  and  $d$  to track unimproved and degraded habitat respectively. Then, the state of the environment moves according to a cycle (Figure 2). Assuming a total quantity of habitat  $\phi$  made up only of usable habitat ( $h$ ), degraded habitat ( $d$ ), and unimproved habitat ( $u$ ), we have the identity

$$\phi = h + d + u. \quad (1)$$

<sup>2</sup> Robert J. Naiman, Carol A. Johnston, and James C. Kelley. Alteration of north american streams by beaver. *BioScience*, 38(11):753–762, 1988

<sup>3</sup> W. S. C. Gurney and J. H. Lawton. The population dynamics of ecosystem engineers. *Oikos*, 76(2):273–283, 1996

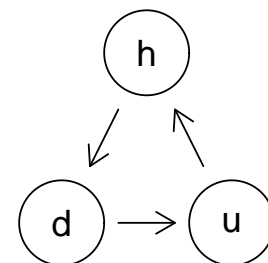


Figure 2: Cycle of habitat condition when acted on by an ecosystem engineer.

According to the theory of Gurney & Lawton,  $u$  converts to  $h$  in proportion to the amount of unimproved habitat and number of ecosystem engineers acting on it at rate  $\alpha$ . Additionally, individuals in a population of ecosystem engineers cooperatively improve  $u$  to  $h$  with a per capita mutual benefit  $\beta$ . Finally, degradation through use occurs at rate  $\delta$ . Together, these assumption imply that the rate of change of  $h$  is  $dh/dt = \alpha u + \beta n u - \delta h = (\alpha + \beta n)u - \delta h$ .

How does  $u$  change with respect to time? First, we will rearrange equation 1 to give the total quantity of degraded habitat  $d = \phi - h - u$  and assume a constant rate  $\rho$  for the conversion of degraded habitat to unimproved habitat. Since the only “loss” of unimproved habitat is by conversion to usable habitat (and from the argument above we know that this occurs at rate  $(\alpha + \beta n)un$ ), we now have for the total rate of change  $du/dt = \rho(\phi - h - u) - (\alpha + \beta n)u$ . Altogether, we know have a *system* of three mutually dependent equations:

$$dn/dt = rn(1 - n/h) \quad (2)$$

$$dh/dt = (\alpha + \beta n)un - \delta h \quad (3)$$

$$du/dt = \rho(\phi - h - u) - (\alpha + \beta n)un. \quad (4)$$

When one of  $n$ ,  $h$ , or  $u$  changes then the rates  $dn/dt$ ,  $dh/dt$ , and  $du/dt$  all change as well, which of course feeds back to affect  $n$ ,  $h$ , and  $u$ . So, the abundance of ecosystem engineers and the state of the habitat is inseparably intertwined, just as the concept of ecosystem engineering insists that they ought to be.

What are the dynamical consequences of this feedback? As before, we will seek to identify equilibria. Although the full description of these equilibria involves equations for the quantities of usable and unimproved habitat as well, we will focus on just the abundance of the ecosystem engineer. Concerning these, there are a few possibilities. First, if

$$\alpha\phi < \left(\frac{\beta\phi^2(1 + \delta/\rho)}{4}\right) \left(\frac{1}{1 + \delta/\rho} + \frac{\alpha}{\beta\phi}\right)^2 < \delta \quad (5)$$

only the extinct state  $n^* = 0$  is stable. Indeed, if  $\alpha T < \delta$  then extinction is a stable equilibrium, regardless of what else may occur. This inequality expresses the condition where a lone individual working in an unimproved ecosystem cannot improve habitat faster than it degrades. It is intuitive that under this condition the environment cannot be made habitable, at least by the introduction of a single individual. However, if  $\alpha\phi > \delta$ , meaning that a single engineer can replenish habitat faster than it degraded, then there are two equilibria. The first involves  $n^* = 0$ , which we already know is extinction.

This equilibrium is unstable. The second equilibrium is given by the equation

$$n^* = \frac{\phi}{2} \left( \frac{1}{\delta/\rho} - \frac{\alpha}{\beta\phi} + \sqrt{\left( \frac{1}{\delta/\rho} + \frac{\alpha}{\beta\phi} \right)^2 - \frac{4\delta}{\beta(1+\delta/\rho)\phi^2}} \right). \quad (6)$$

Interesting, this “upper finite equilibrium” may be either stable or unstable. If it is stable, it functions like carrying capacity, as an attracting state that the number of ecosystem engineers tends to. If it is unstable, it is a *repellor* (in contrast to the *attractor* we have seen before) and when the population gets too close to this size it is kicked away. Since extinction is also unstable, the net effect is that the population is bounced back and forth in persistent cycles as shown in Figure 3.

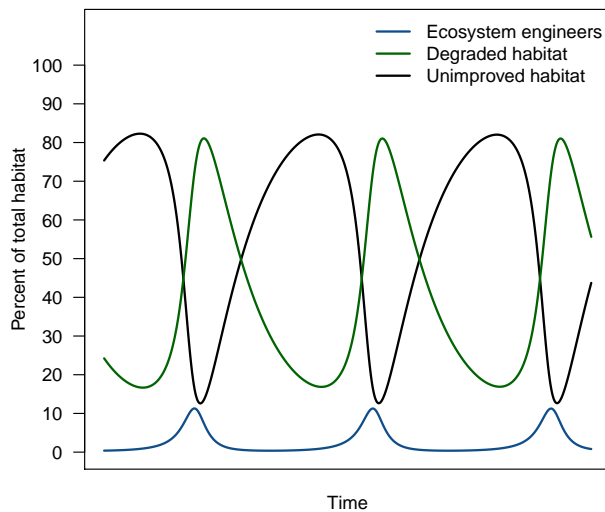


Figure 3: Quantity of degraded and unimproved habitat and abundance of ecosystem engineers in time series of the Gurney-Lawton model. Parameters values in this example are  $r = 1$ ,  $\alpha = 2$ ,  $\phi = 1$ ,  $\beta = 50$ ,  $\delta = 1.5$ , and  $\rho = 0.1$ .

Another useful picture is obtained by plotting  $h$ , the quantity of usable habitat, against time (Figure 4). This figure shows that the abundance of ecosystem engineers is always very tightly correlated with the quantity of usable habitat. Nevertheless there do appear *lags* as engineers must construct a habitat before occupying it. Once fully occupied, degradation happens swiftly and the habitat and population of engineers become locked into a cycle of growth and decline. Another way these patterns can be visualized is with a *phase portrait* in which the state variables are plotted against each other and time goes around in an endless loop (Figure 5). These plots show better the geometry

of the engineer cycles, allowing one to see the rise and fall of the population together with the available habitat. All the state variables are inextricably linked – they are connected to each other through the system of equations – but the strength of connection varies. The very thin teardrop on the left shows that the quantity of usable habitat and abundance of engineers are indeed tightly correlated. In contrast, the larger loop in the right hand panel shows that the quantity of unimproved habitat is less tightly coupled to engineer abundance.

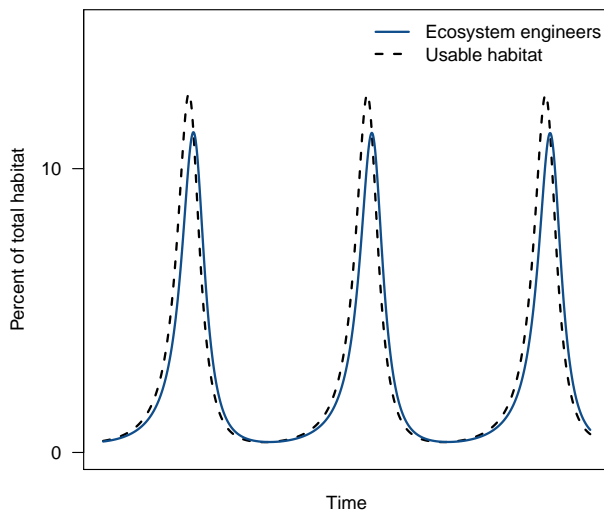


Figure 4: Quantity of usable habitat and abundance of ecosystem engineers in time series of the Gurney-Lawton model. Parameters values in this example are  $r = 1$ ,  $\alpha = 2$ ,  $\phi = 1$ ,  $\beta = 50$ ,  $\delta = 1.5$ , and  $\rho = 0.1$ .

One outcome of this model is that the maximum proportion of total habitat actually used at any one time is just under 12.7%. Put differently, peak usable habitat ( $h$ ) is never very high. This is important because although many ecological theories allow for vacant spaces and recolonization, there are few in which such low levels habitat occupancy arise. Interestingly, Naiman et al. (1988) estimated that the fraction of the total area of the Kabetogama Peninsula, Minnesota impounded by beaver dams in 1986 was 13%.<sup>4</sup> Also, interesting, however is the comment by Clarke<sup>5</sup> that the beaver is the only mammal that does not exhibit periodic cycles. Christian<sup>6</sup> observes that this might be a result of harvesting. As with pink salmon, it has not been determined if the species would exhibit cycles if harvesting were ceased. In any event, there is currently no evidence that beavers exhibits population cycles.

Returning to the case where  $\alpha\phi < \delta$  (a single individual cannot replenish habitat sufficiently fast), it is possible that a group of en-

<sup>4</sup> Robert J. Naiman, Carol A. Johnston, and James C. Kelley. Alteration of north american streams by beaver. *BioScience*, 38(11):753–762, 1988

<sup>5</sup> C. H. D. Clarke. Fluctuations in populations. *Journal of Mammalogy*, 30(1):21–25, 1949

<sup>6</sup> John J. Christian. The adreno-pituitary system and population cycles in mammals. *Journal of Mammalogy*, 31(3):247–259, 1950

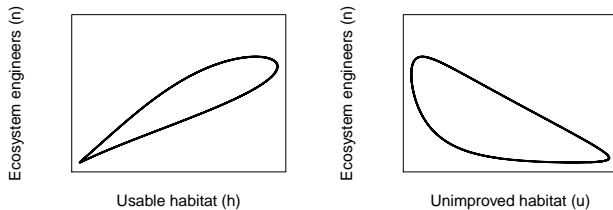


Figure 5: Phase portraits of the Gurney-Lawton model. Parameters values in this example are  $r = 1$ ,  $\alpha = 2$ ,  $\phi = 1$ ,  $\beta = 50$ ,  $\delta = 1.5$ , and  $\rho = 0.1$ .

gineers, working cooperatively, can maintain a sufficient quantity of usable habitat to ensure persistence. Specifically if  $\alpha\phi < \delta < \frac{\beta\phi^2(1+\delta/\rho)}{4} \left( \frac{1}{1+\delta/\rho} + \frac{\alpha}{\beta\phi} \right)^2$ , then the population of ecosystem engineers has an additional equilibrium. The equilibria at  $n^* = 0$  (extinction) and given by equation 6 remain. In between, a new equilibrium appears at

$$n^* = \frac{\phi}{2} \left( \frac{1}{\delta/\rho} - \frac{\alpha}{\beta\phi} - \sqrt{\left( \frac{1}{\delta/\rho} + \frac{\alpha}{\beta\phi} \right)^2 - \frac{4\delta}{\beta(1+\delta/\rho)\phi^2}} \right). \quad (7)$$

In this case, the extinct equilibrium is stable, the new equilibrium given by equation 7 is an unstable point, and the upper most equilibrium given by equation 6 may either stable or unstable as before. Some trajectories representative of this last possibility are shown in Figure 6. We have seen something like this before – a stable equilibrium at extinction and a stable equilibrium at carrying capacity separated by an unstable equilibrium – an Allee effect. Thus, we conclude that in at least some cases the Allee effect may be induced by the cooperation of ecosystem engineers, mediated by their effects on their environment. This is in contrast to the direct effects on fitness that result from such activities as cooperative foraging and defense. Finally, one might ask what causes the upper equilibrium to lose its stability and result instead in a cycle. The answer to this is not at all obvious, but numerical analysis shows that having any of  $\beta$  too small (too little cooperation),  $\delta$  large (degradation too fast), or  $\rho$  too small (environmental recovery slow) is destabilizing to this equilibrium.

### *Population dynamics in organism modified environments*

One strong assumption of the Gurney-Lawton model is that ecosystem engineers *act on* the environment, but do not themselves constitute the environment. In this sense, the environment exists independently of the ecosystem engineers, which are then catalysts for the

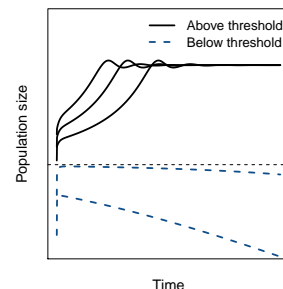


Figure 6: Trajectories of the Gurney-Lawton model with initial population size just above and below the lower equilibrium given by equation 7. Other parameters are  $\alpha = 2$ ,  $\phi = 1$ ,  $\beta = 50$ ,  $\delta = 2.005$ , and  $\rho = 0.1$ .

conversion of available habitat to a useable form. In contrast, many ecosystem engineers, particularly those that are structurally complex such as trees, kelp, and corals, may themselves be considered to be the habitat. Wright *et al.*<sup>7</sup> therefore proposed to modify the Gurney-Lawton model in two ways. First, the catalytic activity of the ecosystem engineers was removed from the model. Second, habitat construction could result from either the local reproduction of the ecosystem engineer or the immigration of engineering individuals from outside. Wright *et al.* further propose to consider not the total number of engineers as such, but rather then fraction of potential patches that are occupied. This model is considered to be a better representation of the ecology of, for instance, the North American beaver, which are organized into social units consisting of a monogamous pair and their offspring. The Wright model may be written as

$$dh/dt = (rh + v)u - \delta h \quad (8)$$

$$du/dt = \rho(1 - h - u) - (rh + i)u \quad (9)$$

where  $r$  is interpreted as the per patch production of new colonists and  $v$  is the immigration rate from outside the system. Unlike the Gurney-Lawton model, the Wright model does not result in cycles. When  $r < 0$  there is no positive stable steady state because (as before) patch creation by the engineer cannot keep up with degradation. Steady states only appear when  $r > \delta > 0$ . Particularly, when  $v = 0$  (no immigration) this model has two equilibria: an unstable equilibrium at  $n^* = 0$  (extinction) and a stable equilibrium at  $n^* = (1 - \delta/r)(1 - \delta/\rho)$ . When  $v > 0$  (immigration of engineers from the surrounding landscape), extinction is no longer a steady state. (Any temporary extinction will be reversed by the arrival of the next colonist.) Instead, all that remains is a single stable positive equilibrium which is a solution to

$$g(h) = (r(1 + \delta/\rho)h^{*2} + (v(1 + \delta/\rho) + \delta - r)h^* - 1 = 0. \quad (10)$$

Figure 7 shows a graph of this function for the values  $r = 1$ ,  $\delta = 1.5$ ,  $\rho = 0.1$ , and  $v = 0.1$  (so that immigration is small, one tenth of the rate of local reproduction  $r$ ). Evidently, under these conditions slightly less than 20% of potential habitat is actually in the improved condition and occupied. What this shows is that even without the cooperative effects of the Gurney-Lawton model the effect of ecosystem engineering on a population can be to severely reduce its size when compared with the total available habitat. The chief difference is that there is no longer a lower unstable equilibrium. Without cooperation there is no Allee effect.

<sup>7</sup> Justin P. Wright, William S. C. Gurney, and Clive G. Jones. Patch dynamics in a landscape modified by ecosystem engineers. *Oikos*, 105(2): 336–348, 2004

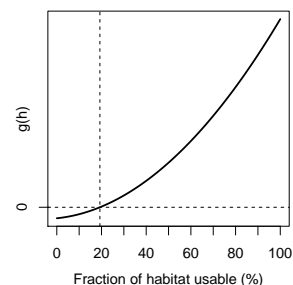


Figure 7: Function  $g(h)$  that gives the equilibrium fraction of patches occupied in the Wright model of an ecosystem engineer with immigration from the surrounding landscape.



*Test yourself*

- What are some of the ways that ecosystem engineers modify their environments?
- If the upper finite equilibrium in the Gurney-Lawton model is unstable, what kind of dynamics does the population ecosystem engineers exhibit?
- What dynamical behaviors are possible when ecosystem engineering is additive, but not cooperative?



## *Bibliography*

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