

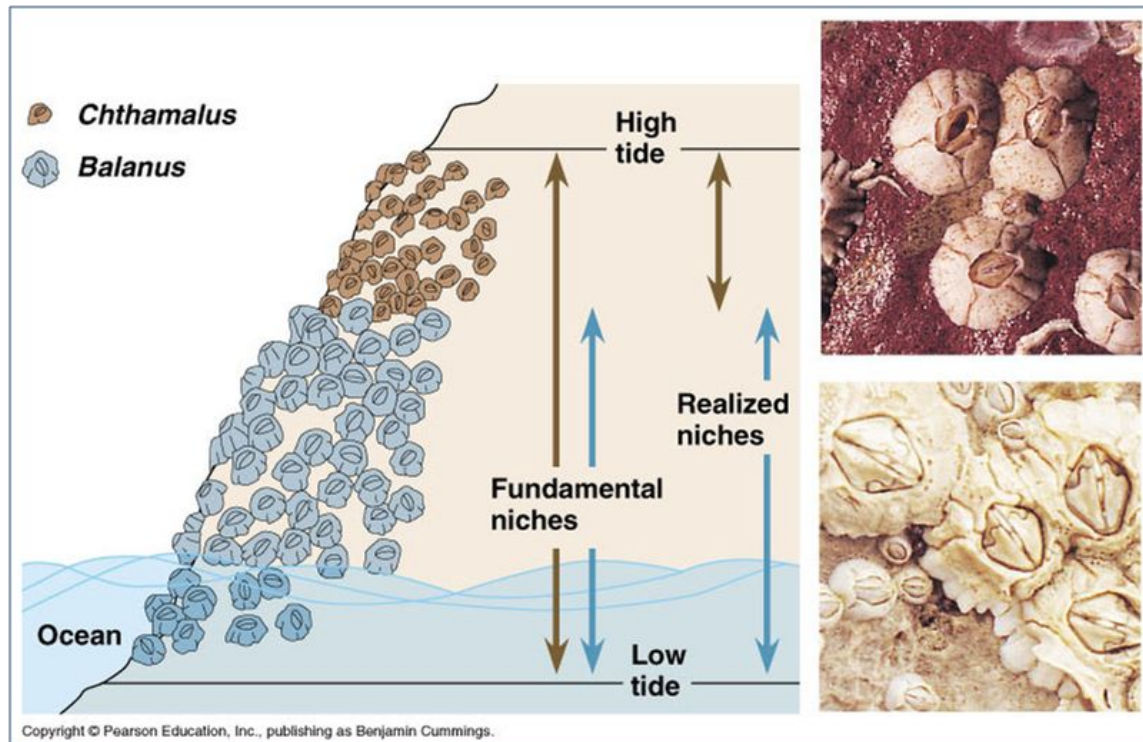
# Ecosystem Engineering

# Some questions

- Why do populations cycle?
- Why are habitat patches unoccupied?

# Effects of ecosystems on organisms

- Demography (growth, survival, reproduction)
- Density dependence (intraspecific competition)



# Effects of organisms on ecosystems



North American beaver *Castor canadensis*





# What population consequences come from the feedback of organisms on ecosystems?

Organism



Environment



## Stages of beaver-modified environment

Beaver active for (~4 years , range: 1-20)

Disintegration and drainage -> Beaver meadow (~70 year)

Conversion to forested riparian zone (~100s years)

# Ecosystem Engineering

*Ecosystem engineering* – the physical or chemical modification of habitats by organisms

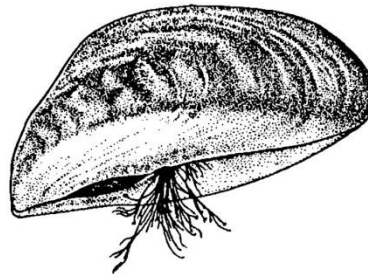
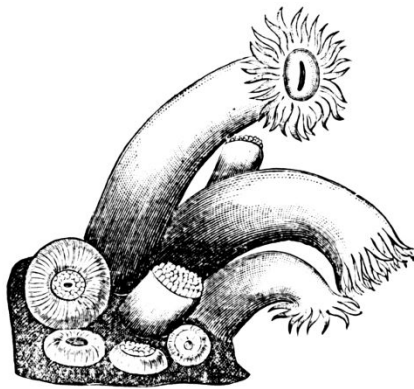


# Universality of ecosystem engineering

Kingdom	Engineering process
Eubacteria & Archaeobacteria	<ul style="list-style-type: none"> <li>•Decomposition</li> <li>•Production of products of metabolism (oxygen, ammonia)</li> <li>•Nitrogen fixation</li> <li>•Bacterial allelopathy</li> </ul>
Protista	<ul style="list-style-type: none"> <li>•Physical/chemical weathering</li> <li>•Soil production</li> <li>•Photosynthetic and metabolic products</li> <li>•Oxygen production</li> </ul>
Fungi	<ul style="list-style-type: none"> <li>•Decomposition</li> <li>•Physical/chemical weathering</li> <li>•Soil production</li> <li>•Moisture retention</li> <li>•Mineral extraction</li> <li>•Creation of environmental structure</li> </ul>
Plantae	<ul style="list-style-type: none"> <li>•Photosynthetic and metabolic products</li> <li>•Physical/chemical weathering</li> <li>•Alteration of hydrology</li> <li>•Soil stabilization</li> <li>•Microclimate modulation</li> <li>•Nutrient retention and modification of nutrient cycles</li> <li>•Allelopathy</li> <li>•Scattering and absorption of light; creation of shade</li> <li>•Modification of wind speed</li> </ul>
Animalae	<ul style="list-style-type: none"> <li>•Construction of nests, burrows, cases, food caches, dens</li> <li>•Provision and protection of nursery environments</li> <li>•Nutrient retention and modification of nutrient cycles</li> <li>•Soil compaction</li> <li>•Decomposition of coarse organic matter</li> </ul>

# Kinds of ecosystem engineering


- Habitat creation (North American beaver)
- Habitat stabilization (*Spartina alterniflora*)
- Biomixing/Bioturbation (mussels)
- Habitat complexity (corals, trees)





# Population dynamics in organism-modified environments (Gurney model)

Rate of change of ecosystem engineer


$$\frac{dE}{dt} = rE(1 - E/H)$$

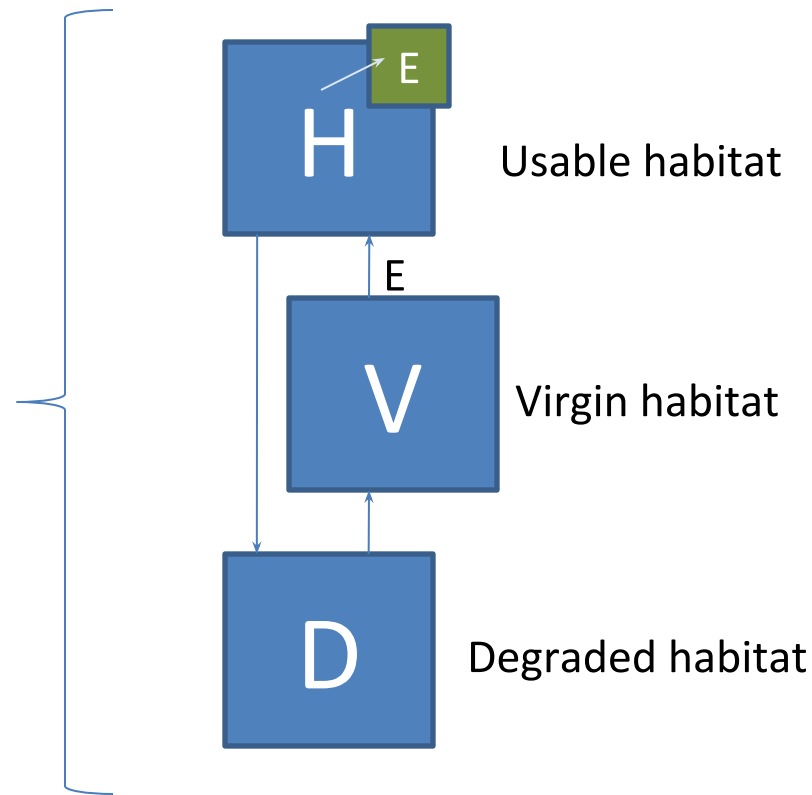


Abundance of limiting resource

# Population dynamics in organism-modified environments

Total stock ( $T$ ) of habitats is composed of usable habitat ( $H$ ), degraded habitat ( $D$ ), and virgin habitat ( $V$ )

$$T = D + H + V$$



# Population dynamics in organism-modified environments

Cooperative engineering

$$\frac{dE}{dt} = rE(1 - E/H)$$

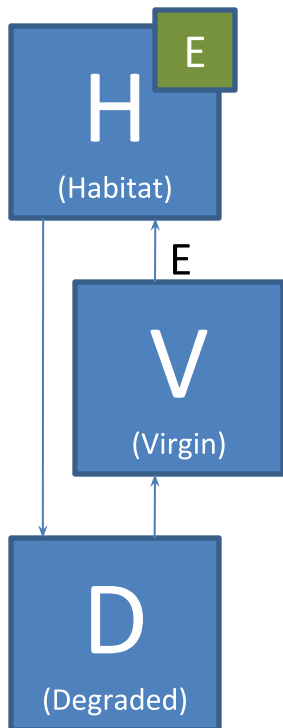
Degradation through use

$$\frac{dH}{dt} = (\alpha + \beta E)V - \delta H$$

$$\frac{dV}{dt} = \rho(T - V - H) - (\alpha + \beta E)V$$

Recovery to virgin state

Conversion through engineering



# Equilibria

A single engineer can replenish habitat faster than it degrades

- If  $\alpha T > \delta$  then there are two equilibria

Unstable  $E^* = 0$  "ZE" state (zero engineer)

Stable or unstable  $E^* = \frac{T}{2} \left[ \frac{1}{1 + \delta/p} - \frac{\alpha}{\beta T} \right] + \sqrt{\left( \frac{1}{1 + \delta/p} + \frac{\alpha}{\beta T} - \frac{4\delta}{\beta(1 + \delta/p)T^2} \right)}$

Upper "FE" state (finite engineer)

- If  $\alpha T < \delta < \frac{\beta T^2(1 + \delta/\rho)}{4} \left( \frac{1}{1 + \delta/\rho} + \frac{\alpha}{\beta T} \right)^2$  then three equilibria

Stable  $E^* = 0$

Unstable  $E^* = \frac{T}{2} \left[ \frac{1}{1 + \delta/p} - \frac{\alpha}{\beta T} \right] - \sqrt{\left( \frac{1}{1 + \delta/p} + \frac{\alpha}{\beta T} - \frac{4\delta}{\beta(1 + \delta/p)T^2} \right)}$

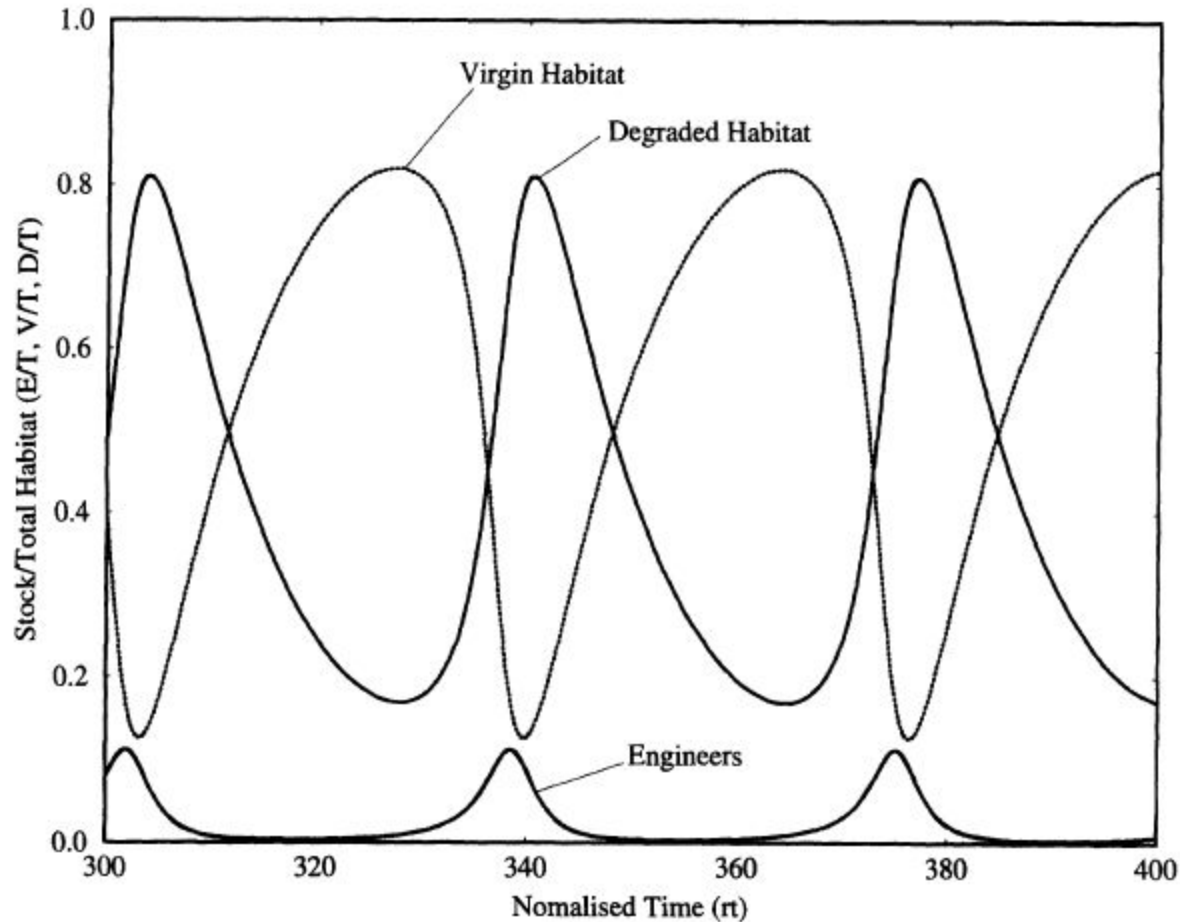
Lower "FE" state

Stable or unstable  $E^* = \frac{T}{2} \left[ \frac{1}{1 + \delta/p} - \frac{\alpha}{\beta T} \right] + \sqrt{\left( \frac{1}{1 + \delta/p} + \frac{\alpha}{\beta T} - \frac{4\delta}{\beta(1 + \delta/p)T^2} \right)}$

An Allee effect



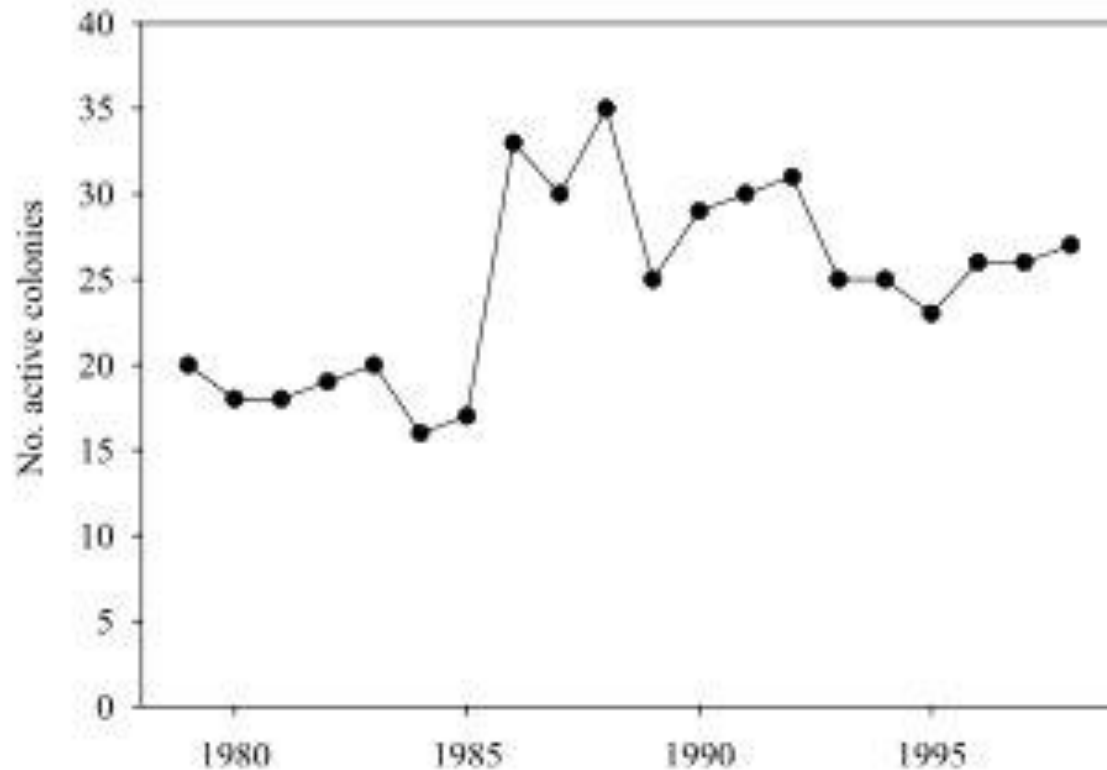
# Unstable upper FE state



Unstable if: (1)  $\beta$  too small (little cooperation), (2)  $\delta$  large (degradation too fast), or (3)  $\rho$  too small (environmental recovery slow)

# Population dynamics

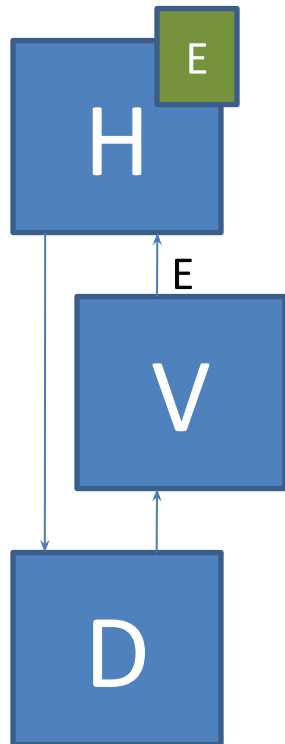
Active beaver colonies in Huntington Wildlife Forest



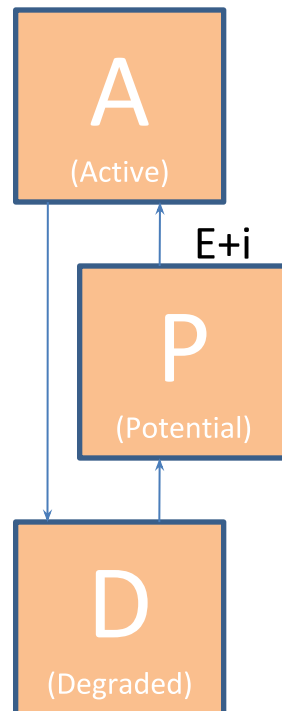
“The only mammal known not to have a cycle is the beaver” (Christian 1950)

# Population dynamics in organism-modified environments (Wright model)

Gurney et al. model



Wright et al. model



## Two key differences

- (1) Organism abundance doesn't just depend on habitats, but is equivalent to it
- (2) Habitat construction can be by "local colonists" from within the system and immigrants who arrive from outside (a landscape effect)

# Steady state solution

$$\left(n\left[1 + \delta/\rho\right]\right) A^{*2} + \left(i\left[1 + \delta/\rho\right] + \delta - n\right) A^* = 0$$

$n$  – per patch production rate of colonists

$\delta$  – decay rate of patches from active to degraded ( $A \rightarrow D$ ); inverse of occupancy duration

$\rho$  – recovery rate from degraded to potential ( $D \rightarrow P$ ); inverse of duration degraded

$i$  – immigration rate

## Steady state fraction of sites occupied ( $A^*$ )

- Decreases with  $\delta$  (the faster a site degrades the fewer active sites there will be at equilibrium)
- Increases with  $\rho$  (the faster a site becomes habitable again the more active sites there will be at equilibrium)
- Increases with  $n$  (the more productive the existing sites are at producing new colonists the more active sites there will be at eq'm)

Steady state fraction of sites occupied ( $A^*$ ) typically less than 50%

Change of model results in a single finite steady state, at which a large fraction of sites may be unoccupied (like metapopulation dynamics)



# Effects of ecosystem engineering on populations: Conclusions

- Can give rise to intrinsic cycling without interacting with another species
- Can give rise to a lower unstable equilibrium (an Allee effect)
- Can give rise to a substantial fraction of available habitat occupied at any one time

# Summary

- *Ecosystem engineering* is the physical or chemical modification of habitats by organisms
- Ecosystem engineering can result in
  - Population cycles
  - Allee effects
  - Vacant habitats