

Supplementary Material 2

Number of trophic levels supported in Uqbar (Simple System)

Some features of the outcomes of simulations can be obtained analytically, at least as approximations. This provides a quantitative basis for the persistence of trophic levels and a justification for recognizing high-input and low-input regimes.

Principle: abundance of members of a trophic level will tend to increase if net resource acquisition by members of that level is positive.

Vocabulary:

| | |
|---|--|
| I | Probability of input of single resource packet, value V , per move |
| D | Probability of spontaneous decomposition of resource packet, when packet is Agent, per move. |
| V | Value of resource packet, in resource units |
| V_P | mean value of resources held by a Producer |
| V_H | mean value of resources held by a Herbivore |
| C_P | metabolic cost of move by Producer, in resource units |
| C_H | metabolic cost of move by Producer, in resource units |
| C_K | metabolic cost of move by Producer, in resource units |
| a | probability of capture of resource packet encountered by Producer |
| b | probability of capture of Producer encountered by Herbivore |
| c | probability of capture of Herbivore encountered by Carnivore |
| R | abundance of Resources (number of slots occupied): r^* is steady-state frequency of Resources. |
| P | abundance of Producers: p^* is steady-state frequency of Producers. |
| H | abundance of Herbivores: h^* is steady-state frequency of Herbivores. |
| K | abundance of Carnivores: k^* is steady-state frequency of Carnivores. |
| R', P', H', K' are corresponding resource holdings (rather than abundance). | |
| M | number of slots in ecosystem |

1. Resources only.

When Resources are rare (ecosystem nearly empty) rate of input is IV . Thus resources begin to accumulate if $IV > 0$, i.e. $I > 0$.

As resources become more abundant, net input per move is $\Delta R' = IV - (R/M)DV$. Hence $\Delta R' > 0$ if $I > (R/M)D$. This will reach steady state when $\Delta R' = 0$, and $I = r^*D$, i.e. $r^* = I/D$.

2. Resources + Producers

When Producers are very rare, expected net rate of resource acquisition per move is $\Delta P' = a(R/M)V - C_p$. Hence $\Delta P' > 0$ if $ar^*V - C_p > 0$, i.e. $I > C_pD/aV$.

$G_p = aV/C_p$ is the benefit:cost ratio for a Producer: if this is less than 1 a Producer will get net resource gain from encountering a resource packet. Hence the condition is equivalent to $I/D > 1/G_p$.

As Producers grow more abundant, net input per move to Resources and Producers is

$$\Delta R' = IV - (R/M)DV - a(P/M)(R/M)V \text{ (noting that when Resource is Agent there is no Patient)}$$

$$\Delta P' = a(R/M)V - C_p$$

Hence $\Delta R' = 0$ when $(R/M)D + a(P/M)(R/M) = I$. i.e. $r^* = I/(D + ap^*)$. Likewise $\Delta P' = 0$ when $r^* = C_p/aV$.

Substituting,

$$r^* = C_p/aV$$

$$p^* = I(V/C_p) - (D/a)$$

3. Resources + Producers + Herbivores

When Herbivores are very rare, their expected net rate of resource acquisition per move is $\Delta H' = b(P/M)V_p - C_H$. Hence $\Delta H' > 0$ if $bp^*V_p > C_H$, or $b((IV/C_p) - (D/a)) > C_H/V_p$, i.e. $I > C_pD/aV + C_pC_H/bV_p$.

Note that $G_H = bV_p/C_H$ is the benefit:cost ratio for Herbivores: if this is greater than 1 they will have a net gain from encountering a Producer. The condition is thus $I/D > 1/G_p + 1/aG_pG_H$, or roughly $I/D > 1/G_p(1 + 1/G_H)$ if a Producer is more or less certain to consume a compatible resource it encounters.

As Herbivores grow more abundant, expected net resource acquisition by Resources, Producers and Herbivores is

$$\Delta R' = IV - (R/M)DV - a(P/M)(R/M)V$$

$$\Delta R' = 0 \text{ when } r^* = i/(D + ap^*) \text{ or } p^* = (I/r^*) - D/a$$

$$\Delta P' = a(P/M)(R/M)V - 2b(P/M)(H/M)V_P - (P/M)C_P$$

$$\Delta P' = 0 \text{ when } r^* = (2bh^*V_P + C_P)/aV$$

$$\Delta H' = 2b(P/M)(H/M)V_P - (H/M)C_H$$

$$\Delta H' = 0 \text{ when } p^* = C_H/2bV_P$$

Substituting,

$$r^* = 2abIV_P / (2bDV_P + aC_H)$$

$$p^* = C_H / 2bV_P$$

$$h^* = (a^2IV - DC_P - (a/b)C_P C_H / 2V_P) / (2bDV_P + aC_H)$$

4. Resources + Producers + Herbivores + Carnivores

When Carnivores are very rare, their expected net rate of resource acquisition per move is

$$\Delta K' = c(H/M)V_H - C_K. \text{ Hence } \Delta K' > 0 \text{ if } h^* > C_K/cV_H. \text{ From previous result, this requires } (a^2IV - DC_P - (a/b)C_P C_H / 2V_P) / (2bDV_P + aC_H) > C_K/V_H, \text{ i.e. } I > (C_P D/aV) + (a/b)(C_H C_P / 2aV V_P) + C_K(aC_H + 2bV_P D)/(acV V_H).$$

Here, $G_K = C_K/cV_H$ is the net gain to a Carnivore from encountering a Herbivore.

Summary

Conditions that a trophic level is occupied:

$$R \quad I > 0$$

$$\begin{array}{lll}
R + P & I > C_p D / a V & I / D > G_p \\
R + P + H & I > C_p D / a V + C_p C_H / b V V_p & I / D > G_p + a G_p G_H \\
R + P + H + K & I > C_p D / a V + C_p C_H / b V V_p + [C_H C_K V_p + 2(b/a) C_K V_p^2 D - \frac{1}{2} (c/b) C_p C_H V_H] / c V V_p V_H &
\end{array}$$

To draw a graph, simplify by setting: $a = b = c = 1$; $V = 1$; $V_p = V_H$; $C = C_p = C_H = C_K$. Then conditions are:

$$\begin{array}{ll}
R & I > 0 \\
R + P & I > CD \\
R + P + H & I > CD + C^2 / V_p \\
R + P + H + K & I > 3CD + (3/2)C^2 / V_p
\end{array}$$

Dynamic regimes

Critical value of resource supply rate and immigration in Uqbar Simple System, using very rough approximations.

For resource input this depends on the supply rate (I), the decomposition rate (D) and the benefit/cost ratio for a Producer encountering a resource packet (G_p) and for a Herbivore encountering a Producer (G_H): the critical value is at $I/D = (1/G_p) (1 + 1/G_H)$, assuming that a Producer always consumes any compatible resource packet it encounters.

In Uqbar Simple System $G_p = 150/4 \approx 40$; $G_H = 75/4 \approx 20$; $D = 0.5$. Hence $I \approx 0.01$.

For immigration, we set the critical value at $W = 1$ individual entering the community per generation. Generation time depends on the quantity of resources that must be acquired in order to reproduce and the net resource gain per move, equal to $rV - C$, where r is the resource density, V is the value of the resource packet and C is the maintenance cost. Since $G_p = V/C$ the critical value for a system with M sites is $W = (1/M) (rG_p - 1) / Z$ where Z is the cost of reproduction relative to the cost of maintenance.

In Uqbar Simple System $G_p = 150/4 \approx 40$; $G_H = 75/4 \approx 20$; $r \approx 0.25$; $Z = 40$. Hence $W \approx 0.0001$.

This value has two shortcomings. First, it applies to Producers only. Secondly, it assumes that all immigrants are permitted, which is not the case in Uqbar Simple System because fully occupied webs cannot be invaded. Both will increase W , so $W = 0.001$ is more realistic.

These are no more than rough rules of thumb, but do seem to correspond with regimes in which Herbivores first become abundant in simulations.