

Following 2003  
Chesson & Ellner 2004  
\* Gouda & Ellner 2004

$$N_j(t+1) = \underbrace{(1-d_j) N_j(t)}_{\substack{\text{survival} \\ \text{in seedbank} \\ = s_j(1-g_j)}} + \underbrace{R_j(t) N_j(t)}_{\substack{\text{germination} \\ \& \\ \text{death in seedbank} \\ = 0^*(1-g_j)(1-s_j) + g_j F_j}}$$

$$g_j F_j = \frac{\lambda_j}{1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t}}$$

see p.5  
this is a problem

operational def'n  $\left[ \begin{aligned} E_j(t) &= \ln R_j^0(t) \leftarrow \text{seedbank w/o comp} \\ C_j(t) &= \ln(R_j^0(t)/R_j(t)) \leftarrow \text{seedbank w/comp} \end{aligned} \right.$

$$R_j(t) = g_j F_j = \frac{g_j \lambda_j}{1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t}}$$

$$= \underbrace{\ln(g_j \lambda_j)}_{E_j(t)} - \underbrace{\ln(1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t})}_{-C_j(t)}$$

C2003  
Eqn 6

$$C_j(t) = \sum_{i=1}^n a_{ij} e^{E_i(t)} N_i(t)$$

$\downarrow$   
competitive effect of a sp*i* individual

$g_i N_i$  without competition  $g_i N_i$  indivs of sp*i* would recruit each year

Assume that the  $C_j$  does not depend on  $j$ .  $\rightarrow$

Can I write  $C$  in a general form like A.5

A.5.  $C = f(\sum_i a_i(N) e^{E_i} N_i)$

$f$  is increasing fcn  
as competitive effects of juveniles of sp*i*  
as a function of adult density  $N$

$$-C_j = -\ln F_j = \ln \left[ \frac{\lambda_j}{1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t}} \right]$$

$$= \ln \lambda_j - \ln \left( 1 + \sum_i \underbrace{\alpha_{ij} e^{E_i} N_{i,t}}_{= g_i(t)} \right)$$

\* Operational Definition of  $E, C$

$$E_j(t) = \ln(g_{j,t} \lambda_j)$$

$$C_j(t) = \ln \left[ \frac{g_{j,t} \lambda_j}{g_{j,t} \lambda_j / (1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t})} \right]$$

$$= \ln(1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t})$$

Question:

Should  $\lambda_j$  be a part of  $E_j$  or  $C_j$ ?

It seems to fall out naturally as part of  $E_j$

$\hookrightarrow$  see p.5 this changes when germination is removed from  $(1-d_j)$

## $C_t$ vs $C_{j,t}$

- Assumption: all species experience the same amount of competition  $\rightarrow C_j(t) = C(t)$
- More general situation:  $C_j$  are proportional between species (not sure what this means)
- $\rightarrow$  in both situations, equilibrium coexistence is excluded: in the absence of fluctuations, no coexist
- We don't really want to have to make this assumption, I don't think, which may make the calculation more challenging
- This comes down to an assumption that all  $\alpha_{ii}$  are equal. i.e. that intra & inter-specific competition coeffs are equal.
- We could make this assumption to start, and then break from that assumption.

## Relative Recruitment Variation

$$\begin{aligned} \text{Var}(\ln R_j(t)) &= \text{Var}(E_j(t)) + \text{Var}(C_j(t)) - 2 \text{Cov}(E_{j,t}, C_{j,t}) \\ &= \text{var}(\ln(g_{j,t} \lambda_j)) + \text{var}(\ln(1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t})) - 2 \text{Cov}(E, C) \\ &\quad \text{var}(\ln g_{j,t} + \ln \lambda_j) \\ &= \text{Var}(\ln g_{j,t}) + \text{Var}(\ln(1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t})) - 2 \text{Cov}(\ln g_{j,t}, \ln(1 + \sum_i \alpha_{ij} g_{i,t} N_{i,t})) \end{aligned}$$

Storage effect depends on how  $\text{cov}(E, C)$  depends on density

$$\bar{r}_i \approx \underbrace{\bar{r}_i'}_{\text{equilibrium means of coexistence}} + \underbrace{\Delta N_i}_{\text{net nonlin}} + \underbrace{\Delta I_i}_{\text{storage effect}}$$

Can we calculate the values in Table 1?

$$\bar{r}_i' / d_i = \delta \mu_i + \delta V_i + \langle \dots \rangle$$

→ revised post page 5 ←

Two Species

$$\frac{\bar{r}_i'}{d_i} = \delta \mu_i + \delta V_i$$

$$\mu_j = \langle E_j \rangle - \ln d_j$$

$$\delta \mu_i = \mu_i - \bar{\mu}_s^{(j \neq i)}$$

$$\delta \mu_i = \mu_i - \mu_r$$

$$\sigma_j^2 = V(E_j)$$

$$\delta V_i = \frac{1}{2}(1-d_i)\sigma_i^2 - \frac{1}{2}(1-d_s)\sigma_s^2$$

$$\delta V_i = \frac{1}{2}(1-d_i)\sigma_i^2 - \frac{1}{2}(1-d_r)\sigma_r^2$$

$$\langle E_j \rangle = \langle \ln g_{j,t} \rangle$$

$$\mu_j = \langle \ln g_{j,t} \rangle - \ln(1-s_j)$$

$$\delta \mu_i = \mu_i - \mu_r \text{ (OR) } \mu_i - \bar{\mu}_r \text{ where } \bar{\mu}_r \text{ is average over resident spp}$$

$$\text{var}(E_j) = V(\ln g_{j,t})$$

$$\delta V_i = \frac{1}{2} S_i V(\ln g_{i,t}) - \frac{1}{2} S_r V(\ln g_{r,t}) \text{ (OR) } \frac{1}{2} S_i V(\ln g_{i,t}) - \frac{1}{2} \overbrace{S_r V(\ln g_{r,t})}^{\text{avg over all residents}}$$

$$g_{j,t} = G_{\max} e^{-h(\tau_p - \tau_i)^2}$$

$$\tau_p \sim B(p, q)$$

$$\ln g_{j,t} = \ln G_{\max} - h(\tau_p(t) - \tau_i)^2$$

$$\langle \ln g_{j,t} \rangle = \ln G_{\max} - h \langle (\tau_p(t) - \tau_i)^2 \rangle$$

$$\begin{aligned} & (\tau_p(t) - \tau_i)(\tau_p(t) - \tau_i) \\ &= \tau_p(t)^2 - 2\tau_p(t)\tau_i + \tau_i^2 \end{aligned}$$

$$= \ln G_{\max} - h \left( \langle \tau_p(t)^2 \rangle - 2\tau_i \langle \tau_p(t) \rangle + \tau_i^2 \right)$$

$$= \ln G_{\max} - h \left( \text{var}(\tau_p(t)) + \langle \tau_p \rangle^2 - 2\tau_i \langle \tau_p \rangle + \tau_i^2 \right)$$

$$\text{var } \tau_p = E(\tau_p^2) - (E(\tau_p))^2$$

$$\text{var } \tau_p + E(\tau_p)^2$$

$$E(\tau_p) = \frac{p}{p+q}$$

$$V(\tau_p) = \frac{pq}{(p+q)^2(p+q+1)}$$

$$= \ln G_{\max} - h \left[ \sigma_{\tau_p}^2 + \mu_{\tau_p}^2 - 2\tau_i \mu_{\tau_p} + \tau_i^2 \right]$$

$$\frac{\Delta I_i}{d_i} = \overline{(1-d_s) \chi_s^{(-i)}}^{(s \neq i)} - (1-d_i) \chi_i^{(-i)}$$

→ fixed after p.5 ←

$$\chi_j^{(-i)} = \text{Cov}(E_j, C^{(-i)}) \quad \text{where } C^{(-i)} \text{ is competition when sp } i \text{ is invader}$$

(i.e. competition from everyone except sp i)

$$\chi_s^{(-i)} = \text{Cov}(\ln g_{r,t}, \ln \left( \frac{\lambda_r}{1 + \sum_{r \neq i} \alpha_{rr} g_{r,t} N_{r,t}} - s_r \right)) \quad \text{for } z \text{ spp}$$

$$= \text{Cov}(\ln g_{r,t}, \ln \left( \frac{\lambda_r}{1 + \sum_{l \neq i} \alpha_{rl} g_{l,t} N_{l,t}} - s_r \right))$$

$r$  is all resident species

$$\chi_i^{(-i)} = \text{Cov}(\ln g_{i,t}, \ln \left( \frac{\lambda_i}{1 + \sum_{l \neq i} \alpha_{il} g_{l,t} N_{l,t}} - s_i \right))$$

$$\frac{\Delta N_i}{d_i} = \frac{1}{2} V(C^{(-i)}) (d_i - \bar{d}_s^{\{s \neq i\}})$$

$$V(C^{(-i)}) = \text{var} \left( \ln \frac{\lambda_i}{1 + \sum_{l \neq i} \alpha_{il} g_{l,t} N_{l,t}} - s_i \right)$$

$$\bar{d}_s^{\{s \neq i\}} = \frac{1}{n-1} \sum_{l \neq i} (1-s_l)$$

(5)

Potential problem: with current definition  $d$  varies with time

$$\begin{aligned}\frac{N_{j,t+1}}{N_{jt}} &= (1-d_j) N_{jt} + R_{jt} N_{jt} \\ &= \underbrace{s_j (1-g_{jt})}_{\text{surv did not germ}} N_{jt} + g_{jt} F_{jt} N_{jt}\end{aligned}$$

$$\begin{aligned}&= s_j N_{jt} + g_{jt} (F_{jt} - s_j) N_{jt} \\ &\quad + g_{jt} F_{jt} N_{jt} - g_{jt} s_j N_{jt}\end{aligned}$$

If we stick to a pre-season count, then

$$\begin{aligned}\frac{N_{j,t+1}}{N_{jt}} &= (1-d_j) N_{jt} - R_{jt} N_{jt} \\ &= s_j N_{jt} + g_{jt} (F_{jt} - s_j) N_{jt}\end{aligned}$$

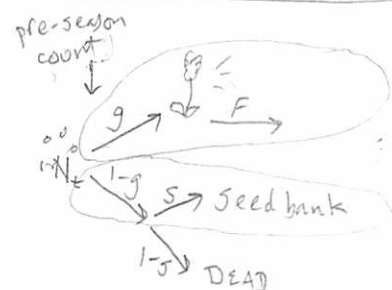
$$\begin{aligned}\ln R_{jt} &= \ln(g_{jt} (F_{jt} - s_j)) \\ &= \ln\left(g_{jt} \left(\frac{\lambda_j}{1 + \sum_k \alpha_{kj} g_{kt} N_{kt}} - s_j\right)\right) \\ &= \underbrace{\ln g_{jt}}_{E_{jt}} + \underbrace{\ln\left(\frac{\lambda_j}{1 + \sum_k \alpha_{kj} g_{kt} N_{kt}} - s_j\right)}_{-C_{j,t}}\end{aligned}$$

$$s(1-g) + gF_{\text{germ}}$$

$$s_j - s_j g_{jt} + g_{jt} F_{jt}$$

$$s_j - g_{jt} (F_{jt} - s_j)$$

how to conceptualize the  $-gs$  term?

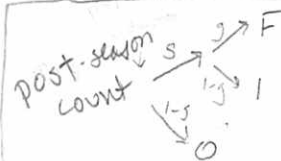


$$NgF + N(1-g)s + N(1-g)(1-s)0$$

$$gFN + s(1-g)N$$

$$sN - sgN + gFN$$

$$sN + g(F-s)N$$



$$sgFN_t + s(1-g)N_t + (1-s)N_t$$

$$sgFN_t + sN_t - sgN_t$$

$$sN_t + sg(F-1)N_t$$