

***Ecological Archives* E090-010-A4**

Jessica J. Kuang and Peter Chesson. 2009. Coexistence of annual plants: Generalist seed predation weakens the storage effect. *Ecology* 90:170–182.

Appendix D. Derivation of the invasion rate

Coexistence of annual plant species in presence of environmental fluctuations is studied in detail in Chesson (1994). The basic idea is to evaluate the invasion rate, and partition it into terms representing the different coexistence mechanisms and the fitness comparison discussed in the text. Although Chesson (1994) did not consider predation explicitly, its general results apply here by substituting the combination of competition and predation, $F = C + aP$, for competition, C , in Chesson (1994). These general results require certain technical assumptions, which are satisfied whenever temporal fluctuations are small and the parameter differences between species are comparable to the variances of the environmental responses. Although these assumptions are restrictive, we shall find that they point the way to the larger patterns. We specialize the results of Chesson (1994) to the present context where we assume that the log germination fractions, the $E_j(t)$'s, have the same probability distribution for all species as well as at different times.

Thus, $\bar{E}_j = \bar{E}_k$ (where \bar{E}_j means the expected value, $E[E_j(t)]$, of the random variable $E_j(t)$).

Also, $\text{var}(E_j) = \text{var}(E_k)$, and we denote the common value of this variance by σ^2 . For the approximations below, we need to assume that this variance is small. However, appendix E shows that the results are qualitatively correct even with large σ^2 .

Like Chesson (1994), we assume independence over time, but the $E_j(t)$'s are correlated between species with common correlation ρ . For simplicity, we assume also that the seed dormancy rate, and predator attack rate, are same for each species, i.e. $s_j = s_k$, $a_j = a_k$, for each j and k . Thus, it follows that the seed loss rate, β , is same for each species, i.e., $\beta_j = \beta_k$. Chesson (1994) uses a slightly different definition of β_j , replacing \bar{G} by $\exp(E_j^*)$, where E_j^* is defined below. However, the difference is $O(\sigma^2)$, which changes the results below by $O(\sigma^4)$. This difference is less than the accuracy of the approximations below as explained in Chesson (1994),

and so is of no significance. To achieve this outcome, however, we must assume that the Y 's for different species differ only by $O(\sigma^2)$. The final assumption that we make is that the variance in F over time is also $O(\sigma^2)$. This is to be expected when the underlying models would have stable equilibria in the absence of environmental fluctuations (e.g. Ripa and Ives 2003). That will be the case in some regions of parameter space, but not in others. Nevertheless, the formulae we obtain do give qualitatively correct results, at least for two species (appendix E).

To begin the analysis, we note that from equation (C.4) that we can write the growth rate of species j in the form

$$(D.1) \quad r_j(t) = \ln \left(s(1 - e^{E_j}) + Y_j e^{E_j - F} \right),$$

where t is suppressed on the right in E_j and F for notational convenience; and Y , but not s , is assumed to depend on j . This formula is just a special case of the general form used in Chesson (1994), where

$$(D.2) \quad r_j(t) = g_j(E_j, C_j),$$

g_j is an arbitrary continuously twice differentiable function, E_j is an environmental response satisfying the assumptions above, and C_j is the competitive response of species j , which is here simply F , the combination of competition and predation. Thus, here $r_j(t) = g_j(E_j, F)$.

The analysis in Chesson (1994) uses a quadratic-level two-variable Taylor expansion of r_j in E_j and F . This expansion is then averaged over time to get the invasion rate. By expanding the growth rate to quadratic order, it is possible to see the effects of means (from the linear part the Taylor expansion), and variances and covariances (from the quadratic terms of the Taylor expansion) on the invasion rate. Of special note here is the covariance between E_j and F , because it leads to the storage effect. It arises in the quadratic expansion from the product of E_j and F , which can be thought of as defining the interaction between E_j and F in determining r_j .

This interaction, in biological terms, measures buffered population growth, as discussed in the text.

To perform a Taylor expansion, we must first choose fixed values, E_j^* and F^* , of E_j and F , about which to perform the expansion. The standard choice (Chesson 1994) is fixed values with the property

$$(D.3) \quad g_j(E_j^*, F^*) = 0 \text{ (i.e. } \ln(s(1 - e^{E_j^*}) + Y_j e^{E_j^* - F^*}) = 0),$$

i.e. these are values at which the growth rate (D.1) would be zero. A natural choice for F^* is the average over species of η because η_j is the value of F that gives species j zero growth in a constant environment. However, it does not matter exactly what F^* is so long as it is within $O(\sigma^2)$ of the constant-environment equilibrium F values of all species (Chesson 1994). Having chosen F^* , E_j^* is chosen as the solution to equation (D.3).

We wish to understand the effects that E_j and F , and their interaction, have on the growth rate r_j . The first part of this process is to transform the variables E_j and F into variables \mathcal{E}_j and \mathcal{F}_j representing their direct effects on r_j , with the other variable held fixed respectively at F^* and E_j^* , as follows:

$$(D.4) \quad \mathcal{E}_j = g_j(E_j, F^*), \text{ i.e. } \mathcal{E}_j = \ln \left\{ s \left[1 - e^{E_j} \right] + Y_j e^{E_j - F^*} \right\},$$

and

$$(D.5) \quad \mathcal{F}_j = -g_j(E_j^*, F), \text{ i.e. } \mathcal{F}_j = -\ln \left\{ s \left[1 - e^{E_j^*} \right] + Y_j e^{E_j^* - F} \right\}.$$

In these standard forms, \mathcal{E}_j and \mathcal{F}_j have the property that they are increasing functions respectively of E_j and F , but are in the same units as r_j . We can thus use these variables to partition out the direct effects of environment and competition on r_j , leaving behind their interaction. For example, averaging \mathcal{E}_j over time gives the average effect of the environment on the growth of species j , at a fixed level of the density dependent factor F , and is used below to

derive the fitness comparison measure $\eta_i - \bar{\eta}$, which then is a distinct element of the invasion rate, separate from the storage effect.

To proceed, Chesson (1994) uses these standard variables, rather than E_j and F directly, for the quadratic expansion of r_j . Averaging the resulting approximation over time then shows that the invasion rate can be expressed in terms of three generic components, \bar{r}_i' , ΔN , and ΔI , which correspond to different coexistence mechanisms, as follows:

$$(D.6) \quad \bar{r}_i = \bar{r}_i' - \Delta N + \Delta I,$$

(Chesson 1994, equation 52). The quantity \bar{r}_i' represents the effects of average fitness differences and coexistence mechanisms that do not rely on fluctuations over time. The term ΔN is the fluctuation-dependent mechanism called relative nonlinearity (see Chesson 1994), and ΔI is the storage effect. The relative nonlinearity term depends on differences between species in the shape of $g_j(E_j, F)$ as a function of F , and the variance of F . Here those shape differences depend on the differences between the Y_j , but as we assume these differences to be $O(\sigma^2)$, and $\text{var}(F)$ is also assumed to be $O(\sigma^2)$, those shape differences are too small to be important in the final result, and so ΔN can be ignored here.

Because there is only one limiting factor, $F = C + aP$, there is no fluctuation-independent coexistence mechanism, and so the term, \bar{r}_i' , consists only of average fitness differences. These fitness differences are written as ΔE in Chesson (1994). Thus, (D.1) reduces to the formula

$$(D.7) \quad \bar{r}_i = \Delta E + \Delta I.$$

Next we show that ΔE can be approximated as $\beta (\eta_i - \bar{\eta})$. The formal definition of ΔE is

$$(D.8) \quad \Delta E = E[\mathcal{E}_i] - \sum_{r \neq i}^n q_{ir} E[\mathcal{E}_r],$$

where q_{ir} is the partial derivative of \mathcal{E}_i with respect to \mathcal{E}_r . This particular quantity q_{ir} serves the purpose of adjusting the comparisons between species due to differences in their sensitivities to competition (here, read F). For example, a less sensitive species is not harmed so easily by a more sensitive species, leading to a low q_{ir} for that comparison. In more general models, q_{ir} also has the effect of partitioning out fluctuation-independent mechanisms. For this model, table II of Chesson (1994) gives $q_{ir} = \beta_i / \beta_r (n - 1)$. Because the β 's are the same here, as explained above, $q_{ir} = 1/(n - 1)$. Hence

$$(D.9) \quad \Delta E = E[\mathcal{E}_i] - \frac{1}{n-1} \sum_{r \neq i}^n E[\mathcal{E}_r],$$

which is a comparison of mean invader and resident environmental responses. This quantity can be evaluated to sufficient accuracy following the techniques of Chesson (1994). First \mathcal{E}_j is expanded as a second order Taylor approximation about the value E_j^* to give

$$(D.10) \quad \mathcal{E}_j \approx (1-s)(E_j - E_j^*) + \frac{1}{2}s(1-s)(E_j - E_j^*)^2,$$

where “ \approx ” means with an $O(\sigma^4)$ error. Taking expected values gives

$$(D.11) \quad E[\mathcal{E}_j] \approx (1-s)(E[E_j] - E_j^*) + \frac{1}{2}s(1-s)\sigma^2,$$

using the fact (Chesson 1994) that $E[(E_j - E_j^*)^2] = \sigma^2 + O(\sigma^4)$. Because $E[E_j]$ is the same for all species, we see that

$$(D.12) \quad \Delta E \approx -(1-s)(E_i^* - \bar{E}^*),$$

where the bar on E^* means the average over resident species. The equilibrium relationship (D.3) allows Y_j and hence η_j to be written as a function of E_j^* . Differentiating this relationship shows that $d\eta_j/dE_j^* = -(1-s)/(1-s[1 - \exp(E_j^*)])$, which equals $-(1-s)/\beta + O(\sigma^2)$. By assumption, the E^* 's differ between species by $O(\sigma^2)$, and so linearly approximating the E^* difference (D.12) in terms of η differences gives

$$(D.13) \quad \Delta E \approx \beta(\eta_i - \bar{\eta}).$$

Table 2 of the text follows the convention of (Chesson 2008) and lists ΔE in natural units (per seed life time) as simply $\eta_i - \bar{\eta}$, i.e. (D.13) divided by β . Note that $\bar{\eta}$ is the average of the η 's of resident species, not the average η of all species, and thus differs slightly from the nominal F^* value suggested here. In the absence of environmental fluctuations, ΔE would be the only term in \bar{r}_i , and only species with higher than average η could invade. In fact, in that case, the growth rates of the species are ranked uniformly in magnitude according to the value of η , which directly reflects Y , and thus only the species with largest η value can persist in the long run. Its long-term growth rate must be zero as a resident. All other species have negative long-term growth rates and so are excluded.

The second term in the formula (D.7) for \bar{r}_i , is the storage effect, ΔI . To define it, we need a formal measure of the interaction between environment and competition (buffered population growth discussed in the text), which for species j is the quantity γ_j given as

$$(D.14) \quad \gamma_j = \frac{\partial^2}{\partial \mathcal{E}_j \partial \mathcal{C}_j} \bigg|_{\mathcal{E}_j = \mathcal{C}_j = 0}.$$

The storage effect is defined in Chesson (1994, equation 23) as

$$(D.15) \quad \Delta I = \gamma_i \text{cov}(\mathcal{E}_i, \mathcal{C}_i^{\{-i\}}) - \sum_{r \neq i}^n q_{ir} \gamma_r \text{cov}(\mathcal{E}_r, \mathcal{C}_r^{\{-i\}}),$$

where the superscript $\{-i\}$ specifies a calculation with species i in the invader state. Table II of Chesson (1994) gives the γ 's here as identical, and equal to $1 - (1-s)^{-1}$. Moreover, Chesson (1994) shows that \mathcal{E}_j can be linearly approximated as $(1-s)(E_j - E_j^*)$, and \mathcal{C}_j can be linearly approximated as $\beta(F - F^*)$. (All these results from Chesson (1994) can be easily verified directly from expressions (D.1), (D.4) and (D.5), above, with a little calculus and algebra.) It follows that

$$(D.16) \quad \text{cov}(\mathcal{E}, \mathcal{C}) = (1-s)\beta \text{cov}(E, F) + O(\sigma^4).$$

Recalling that $q_{ir} = \beta_i/\beta_r(n-1) = 1/(n-1)$, it follows that

$$(D.17) \quad \Delta I \approx s\beta \left\{ \frac{1}{n-1} \sum_{r \neq i} \left[\text{cov}(E_r, F^{\{-i\}}) - \text{cov}(E_i, F^{\{-i\}}) \right] \right\}.$$

Since $F = C + aP$, only C is directly a function of the E_j 's, and the E_j 's are not correlated over time, $P(t)$ has zero covariance with $E_j(t)$ — predator density does depend on past values of E_j , but does not depend on the current one. Thus, (D.13) reduces to

$$(D.18) \quad \Delta I \approx s\beta \left\{ \frac{1}{n-1} \sum_{r \neq i} \left[\text{cov}(E_r, C^{\{-i\}}) - \text{cov}(E_i, C^{\{-i\}}) \right] \right\},$$

which is reported in natural units in table 2 (i.e. divided by β following the convention of Chesson 2008).

Further simplification of this formula is possible by using expression (80) of Chesson (1994), which shows that (D.18) can be written as

$$(D.19) \quad \Delta I \approx \beta \bar{a}(-\gamma)(1-\rho)\alpha^2\sigma^2,$$

where α is $1-s$ (Table II of Chesson 1994 — it is just the linear coefficient in the expansion (D.6) of \mathcal{E}_j in terms of E_j), and here \bar{a} is not the attack rate, but the average over resident species of the quantity

$$(D.20) \quad a_r = E \left[\partial C^{\{-i\}} / \partial \mathcal{E}_r \right].$$

(The quantity a_r arises because it defines the slope in the linear approximation of $C^{\{-i\}}$ in terms of \mathcal{E}_r , and thus allows the covariance to be approximated.). A little calculus shows that $a_r =$

$\bar{G}E[N_r]/(1-s)$, and so (D.19) becomes

$$(D.21) \quad \Delta I \approx \beta s(1-\rho)\sigma^2 \bar{G} \sum E[N_r]/(n-1) .$$

In the absence of predation, Chesson (1994, appendix II) shows that $E[C]$ must be within $O(\sigma^2)$

of F^* . However, $E[C] = E[G] \cdot \sum_r E[N_r] = \bar{G} \sum_r \bar{N}_r$. Hence, as the number of species, n , increases, total resident density cannot change greatly.

Literature Cited

- Chesson, P. 1994. Multispecies Competition in Variable Environments. *Theoretical Population Biology* **45**:227-276.
- Chesson, P. 2008. Quantifying and testing species coexistence mechanisms. Pages 119-164 *in* F. Valladares, A. Camacho, A. Elosegui, C. Gracia, M. Estrada, J. C. Senar, and J. M. Gili, editors. *Unity in Diversity: Reflections on Ecology after the Legacy of Ramon Margalef*. Fundacion BBVA, Bilbao.
- Ripa, J., and A. R. Ives. 2003. Food web dynamics in correlated and autocorrelated environments. *Theoretical Population Biology* **64**:369-384.