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Species coexistence mechanisms involving spatial and temporal variation

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Species Coexistence Mechanisms involving Spatial and Temporal Variation

Peter Chesson

The next figure shows stable coexistence of three species as a consequence of different responses of the three species to temporal environmental fluctuations. These are the thick lines. The thin lines are the situation when the environment is constant, and shows competitive exclusion.

Next is coexistence due to spatial environmental variation. Here we have two annual plants competing with each other and there are gradients across the landscape defining favorability of germination conditions for each of the two species. In the figure, these gradients are orthogonal, and defined by the line spacing for a given direction, and color for the species responding to that gradient. Each dot on the figure represents the location of a single seed, color-coded by species. In the graph that follows these we see fluctuating total abundances of the two species. It shows stable coexistence that results from the two species having different germination responses to the physical environment as it varies in space. These figures are not printed as they make the file too large.

Now we want to put together a general theoretical framework to help us understand species coexistence in a variable environment. We focus on spatial environmental variation, which is actually a little complicated than temporal environmental variation, and includes all the same concepts. We start out with defining a spatially dependent fitness of an individual.

General formulation of spatial population models in discrete time

$\lambda_{jx}(t)$	fitness
j, i, r	species: general, invader, resident
x	spatial location
t	time

I illustrate spatially varying fitness using an example of annual plant community, with the following parameters
s: survival of dormant seeds
G: germination fraction
V: mean size of a seedling at flowering--includes survival and growth
Y: yield in new seeds per unit size
U: survival of seed from production to incorporation in the soil seed bank.
C_x is reduction in actual yield due to competition. It can be defined operationally in the field, but here I give an example of what it would be like in a model. η is the density of seeds of a species in a competitive neiighbourhood of the given individual plant at location x.

This particular example is just one model in which λ can be wriitten as a function of its response to the physical environment through a parameter E, and response to competition C. In this example, E is chosen to be one of the parameters above, depending on which parameter we think is most likely to vary in space and to discriminate between species. The function F is abitrary in this theory, but is given by the formula for λ above for the special case of this annual plant model, with a given choice for E.

E.g. General annual plant model

$\lambda_{jx}(t)N_{jx}(t)$:local contribution to next generation

$$\lambda_{jx}(t) = s_j(1 - G_j) + \frac{U_j Y_j V_j}{C_x} G_j$$

$$C_x = 1 + \sum_j a_j V_j G_j \eta_{jx}(t)$$

General formula:

$$\lambda_{jx}(t) = F_j(E_{jx}(t), C_{jx}(t))$$

Next we consider the general theory of dynamics at the landscape level. This involves individual average fitness, which defines population dynamics, and which is then split into spatial average fitness and fitness-density covariance. The function F is in general nonlinear, and coexistence mechanisms arise from averaging it in space. Other mechanisms arise from the fitness-density covariance.

$\tilde{\lambda}_j(t)$: Individual average fitness

$\bar{\lambda}_j(t)$: Spatial average fitness

$\mathrm{cov}(\lambda_{jx}, \nu_{jx})$: Fitness-density covariance

From Monday's lecture we know that

$$\bar{N}_j(t+1) = \tilde{\lambda}_j(t)\,\bar{N}_j(t)$$

I.e. Landscape-level dynamics given by $\tilde{\lambda}$

$$\tilde{\lambda}_j = \bar{\lambda}_j + \mathrm{cov}(\lambda_{jx}, \nu_{jx})$$

$$= \overline{F_j(E_j, C_j)} + \mathrm{cov}(\lambda_{jx}, \nu_{jx})$$

Point mechanisms + variation-nonlinearity interactions

Fitness-density covariance

Invasibility criterion

$$\tilde{\lambda}_i > 1, \ \forall i$$

Analysis of the invasion rate:

Interactions between environment and competition

$$\bar{\lambda}_i = \overline{F_i(E_i, C_i)}$$

$$= \text{(e.g.)}\ \overline{s_i(1-E_i) + Y_i E_i / C_i}$$

$$= s_i(1-\bar{E}_i) + Y_i \bar{E}_i \cdot \overline{(1_i / C_i)} + Y_i \operatorname{cov}(E_i, 1/C_i)$$

Add fitness-density covariance to get $\tilde{\lambda}$

Next we define a general approximation which shows the critical features of averaging the fitness in space. To do this, we transform E and C to curl E and curly C, which then provide a generic representation of the model, bringing out the interaction between environment and competition as a product whose sign and magnitude is controlled by the constant γ. This constant is usually negative in these models. This product, when averaged in space introduces the covariance between the E and C variables into the spatial average fitness.

We can understand best how the fitness of a low density invader behaves by comparing it to the fitnesses of residents. These fitnesses of residents are always 1, and so that is why the equation at the bottom of the next page is correct. Using that equation to compare components the fitnesses of the different species then helps us define the spatial coexistence mechanisms that follow. The constants q, relate the sensitivities of the different species to competition and allow accurate comparisons to be made.

The slide after the next one then partitions the individual average λ into contributions from the different coexistence mechanisms whose mathematical form is given in subsequent slides.

General approximation

$$\lambda_{jx} - 1 \approx \mathscr{E}_{jx} - \mathscr{C}_{jx} + \gamma_j \mathscr{E}_{jx} \mathscr{C}_{jx}$$

$$\mathscr{E}_{jx} = F_j(E_{jx}, C_j^*), \quad \mathscr{C}_{jx} = -F_j(E_j^*, C_{jx})$$

$$\bar{\lambda}_j - 1 \approx \overline{\mathscr{E}_j} - \overline{\mathscr{C}_j} + \gamma_j \overline{\mathscr{E}_j} \bullet \overline{\mathscr{C}_j} + \gamma_j \operatorname{cov}(\mathscr{E}_j, \mathscr{C}_j)$$

Invader-resident comparison:

$$\tilde{\lambda}_i - 1 = \tilde{\lambda}_i - 1 - \sum_r q_{ir} (\tilde{\lambda}_r - 1)$$

Spatial Recovery Rate

$$\tilde{\lambda}_i \approx \tilde{\lambda}_i' - \Delta N + \Delta I + \Delta \kappa$$

Point
mechanisms

Nonlinear
competitive
variance

Storage
effect

Fitness
density
covariance

Next we see the storage effect mechanism, whose magnitude is ΔI, in terms of resident and invader covariance between environment and competition, χ, and interaction γ. The diagram gives a scatter plot for these covariances in the situation where the species have independent responses to the varying physical environment. The red species has been perturbed to low density, and is therefore an "invader." The green species is a "resident." Note that in these circumstances the invader has zero covariance between environment and competition, while the resident has positive covariance. More generally, when species have correlated responses to the varying physical environment, the invader simply has a lesser covariance than the resident. The formula compares the two covariances, and in the usual case of negative γ and positive q, this formula tends to give a positive result, promoting recovery of the invader from low density, and hence species coexistence.

Components of the Storage Effect

$$\Delta I = \gamma_i \chi_i - \sum_{r \neq i} q_{ir} \gamma_r \chi_r$$

Invader: *i*

Resident: *r*

C

Scatter plot removed as it makes the file too large

E

γ : Buffering

χ : covariance

Relative sensitivity to competition: q_{ir}

Storage effect in simple symmetric models

$$\Delta I \approx \frac{b_i(1-\rho)(-\gamma)\sigma^2}{n-1}$$

This is just an example of a particular analytical formula available for the storage effect when the assumptions made are simple enough

Next we consider the mechanism called relatively nonlinear competitive variance. In this mechanism, each species has a different nonlinear response to common fluctuating competition (C). ΔN measures the different effects of Jensen’s inequality on the growth of two different species, and this difference allows coexistence in some circumstances.

Relatively nonlinear competitive variance

$F_i(E_i,C)$

Graph not printed

C

$$\Delta N \approx \tfrac{1}{2} b_i(\tau_i - \tau_r)\,\mathrm{var}\left(C^{\{-i\}}\right)$$

where

$$\frac{F_a''(C)}{F_a'(C)} - \frac{F_b''(C)}{F_b'(C)} = \tau_a - \tau_b$$

The next mechanism, fitness-density covariance, measures the differences in the tendencies of the species to build up in favorable locations. Invaders often find building up in favorable locations easier as they experience less intraspecific competition. This effect promotes coexistence

Fitness-Density Covariance

$$\Delta\kappa =$$

$$\operatorname*{cov}_{x}(\lambda_{ix},\nu_{ix}) - \sum_{r\neq i} q_{ir} \operatorname*{cov}_{x}(\lambda_{rx},\nu_{rx})$$

λ_{jx} : fitness of *j* at locality *x*

ν_{jx} : relative density of *j* at locality *x* $\left(N_{jx}/\bar{N}_{j}\right)$

Back to the general annual plant model

$\lambda_{jx}(t)N_{jx}(t)$:local contribution to next generation

$$\lambda_{jx}(t) = s_j(1 - G_j) + \frac{U_j Y_j V_j}{C_x} G_j$$

$$C_x = 1 + \sum_j a_j V_j G_j \eta_{jx}(t)$$

Any or all of *s*, *G*, *U*, *Y*, or *V* might vary in space

Do they all give the same results?

Analysis of a simple scenarios with a patch model approximation:

Only one parameter varies by space or species--independent variation between species

Environmental variation is either pure spatial or pure spatio-temporal

Dispersal is either widespread or widespread with local retention

Invasion rate

$$\tilde{\lambda}_i \approx \Delta E + \Delta I + \Delta\kappa$$

$$\Delta E = \overline{\mathscr{E}_i} - \overline{\mathscr{E}_r}$$

mean fitness difference

$$\Delta I = (-\gamma)(\chi_r - \chi_i)$$

buffering × cov(E,C) difference

$$\Delta\kappa = \mathrm{cov}_x(\lambda_{ix}, \nu_{ix}) - \mathrm{cov}_x(\lambda_{rx}, \nu_{rx})$$

fitness-density covariance difference

The table that follows considers signs (-, 0 or +) of invader and resident covariance between environment and competition, and fitness-density covariance. Coexistence is affected by invader-resident differences in these covariances. A positive value of Cov(E_r,C_r) -Cov(E_i,C_i), or a postive value of Cov(λ_i,ν_i) - Cov(λ_r,ν_r) will promote coexistence, and in many cases in the table that follows it is possible to tell the sign of this difference and whether coexistence is promoted. These patterns vary with the nature of the variation, the nature of dispersal, and the population parameters that vary. The issues involved are whether C is a function of E, and whether there is a memory at a site of the past state of the environment. Considering these, the signs of the covariances are in many cases undertandable intuitively.

Results of the annual plant competition model

parameter	E variation	dispersal mode	Cov(E, C)		Cov(λ, ν)	
			resident	invader	resident	invader
V	spatio-temporal (st)	wide-spread (w)	+	0	0	0
	st	local retention (l)	+	0	-	+
	Pure spatial (ps)	w	+	0	0	0
	ps	l	+	0	+	+
G	st	w	+	0	-	0
		l	+	0	-	?
	ps	w	+	0	-	-
		l	+	0	?	?
YU	st	w	0	0	0	0
		l	0	0	-	+
	ps	w	0	0	0	0
		l	+	0	+	+

Key References

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