

Litter and Plant Competition

Nicholas Kortessis

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Abstract

A model of plant competition between an annual and a perennial is presented where the annual produces litter that inhibits germination of both species. Invasion analysis shows that stable coexistence, priority effects, and exclusion are possible in the model. Coexistence is possible when the perennial is more sensitive to competition than the annual yet is less sensitive to litter than the annual. The size of the coexistence region in parameter space is determined by the difference between species in the factor that most influences population growth of the species. Flipping the tradeoff between species such that the annual is less sensitive to litter and more sensitive to competition than the perennial, cannot allow for stable coexistence. Exclusion on one species always results in this case, with contingent exclusion for some parameter combinations. I present a graphical depiction of direct and indirect effects on litter and resources and species' responses to these factors. All outcomes can be understood using the concept of density-dependent feedback loops and the general ecological principle that coexistence requires greater intraspecific density-dependence than interspecific density-dependence. I also briefly discuss the potential roles of pathogens in strengthening and disrupting these feedback loops to alter the outcome of competitive interactions.

1 Introduction

We are interested in the effect of an invasive grass, *Microstegium vimineum*, on the invaded plant community. Field studies of this system have used native perennial grasses in the genus *Elymus*, a dominant graminoid in the system, to understand the effects of invasion. Multiple possible mechanisms can contribute to competitive effects. These surely include resource and interference competition. In addition, *M. vimineum* can create a dense mat of dead vegetation at the end of the season following senescence, which is slow to decompose and can inhibit germination and growth of plants. Hence, there are possible indirect effects of *M. vimineum* on the native plant community through its role in generating and maintaining litter.

In addition to resource competition and possible negative effects mediated by litter, there is another important biotic player in the system. Fungal pathogens of the genus *Bipolaris* heavily infect *M. vimineum* in some portions of its invaded range. Evidence points to plant to plant transmission both between *M. vimineum* individuals but also pathogen transmission between *M. vimineum* and the native plant community. Unfortunately, little is known about host-specific pathogen effects and transmission. The goal of this study is to understand the role of litter in plant invasions and its possible interaction with disease. We do so first by modeling growth of an annual species (here representing invasion of a species like *M. vimineum*) and a perennial species (here representing a species like *Elymus sp.*) where the annual can produce some litter.

We characterize plant density-dependence into two effects: effects from competition for resources, C , and effects of litter, D . For resource competition, we

assume that individuals of both species decrease resources per-unit size identically. We show that the long-term outcomes of competition are solely determined by each species intrinsic rate of growth in isolation (akin to individual reproductive rate) and their responses to resource depletion α and their responses to litter β .

The model is developed in detail in section 2. Analysis of equilibrium conditions is messy with the inclusion of litter and so the approach of invasion analysis is used and is derived in detail in section 3. To do the invasion analysis, the equilibrium density of each species grown in isolation is needed. This is done for the perennial and annual in section 4. Equilibrium expression for annual and litter dynamics are complex and so some special cases are presented which greatly facilitate understanding. Long-term outcomes are presented in section 5 with a discussion of the importance of the assumptions of the model. Finally, potential pathogen effects on model parameters are discussed in section 6, with a more complete analysis of pathogen effects to come in another document.

2 The Model

Without any disease, the model has four state variables: N_A , the density of annual seeds; N_S , the density of perennial seeds; N_P , the density of perennial adults; and L , the density of litter. First, we begin with a factors governing changes in annual density N_A and litter L .

2.1 Annual Plant Dynamics

We model of the dynamics of the annual using the seed bank model. Population density is given by N_A , the seed density of the annual. Seed dynamics follow the recursion

$$N_A(t+1) = s_A(1 - G_A(t))N_A(t) + N_A(t)G_A(t)v_A Y_A(t), \quad (1)$$

where G_A is the germination rate of annuals in year t , s_A is the survival of dormant seeds in the seed bank, v_A is the final plant biomass per seed that germinates, and $Y_A(t)$ is the seed production per unit biomass in year t .

We assume that plant competition C reduces reproduction of growing plants such that Y_A is a continuous and monotonically decreasing function of C . The assumption of monotone effects of density excludes the possibility of any density-mediated facilitation in the model.

There are many stages in the model that can influence competition, although a reasonable starting point is that $N_T = G_A N_A + N_P$, the total density of growing plants in the system, comprises competition. Note that N_A is the density of annual seeds and so the density of growing plants is $N_A G_A$, the total number of seeds that germinate. We further stipulate that C is a monotonically increasing function of N_T . As a specific case of these assumptions, per-capita

seed yield can be written as

$$Y_A(t) = \frac{y_A}{C_A(t)} = \frac{y_A}{1 + \alpha_A N_T(t)}, \quad (2)$$

where y_A is the seed production in the absence of intraspecific competition and C_A is the strength of reproduction experienced by the annual. Throughout the analysis, we use this specific form for exact results, but at the same time evaluate if the qualitative conclusions are robust to alternative forms of competition. The response of the annuals to these growing plants is given by the competition coefficient α_A .

Germination is assumed to decrease as a function of the amount of litter, $L(t)$ present at the beginning of the growing season. This is justified by the intuition that germination requires light, and that light is restricted by the density of litter on the soil surface. I assume the following functional form of germination

$$G_A(t) = \frac{g_A}{D_A(t)} = \frac{g_A}{1 + \beta_A L(t)}. \quad (3)$$

Equation (3) indicates that a fraction of seeds g_A germinates in the absence of litter and declines with D_A , the effect of litter. A convenient form for D_A is used showing that germination declines to 0 in the limiting case of large density of litter (i.e. $\lim_{L \rightarrow \infty} G_A \rightarrow 0$). The larger the value of β_A , the per-capita litter effect on germination of the annual, the faster germination declines with increasing litter.

2.2 Litter Dynamics

To model litter, assume that only annual plant biomass at the end of the season and litter retention from the previous year comprise litter in the current year. Litter affects germination early in the growing season yet is produced at the end of the growing season in the previous year. Litter at the beginning of the growing season in year $t + 1$ can then be described by the equation

$$L(t + 1) = c \left[N_A(t) G_A(t) v_A + (1 - d) L(t) \right]. \quad (4)$$

The first term in Equation (4) represents production of litter from plant growth the previous year because final plant biomass in year t is $N_A(t) G_A(t) v_A$. The second term represents retention of litter from the previous year with litter decaying at a constant rate during the season. The fraction that decays is d with $1 - d$ being the fraction of litter present at the beginning of the season that has not degraded by the end of the growing season. Therefore, the litter that is present at the beginning of the growing season in year $t + 1$ is c times this sum. Note that germination of the annual also depends on litter, and so years of abundant litter may limit production of litter through low germination.

2.3 Perennial Plant Dynamics

The perennial plant is assumed to consist of adults that persist across years and a seed bank. The density of seeds is denoted by N_S and the density of perennial adults N_P . The system of equation is given by

$$\mathbf{N}(t+1) = \mathbf{M}(t)\mathbf{N}(t) \quad (5)$$

where $\mathbf{N} = (N_S, N_P)^T$, with T indicating the transpose of a matrix or vector. The transition matrix for this population is

$$\mathbf{M} = \begin{bmatrix} s_S(1 - G_P(t)) & v_P Y_P(t) \\ G_P(t) & s_P \end{bmatrix}. \quad (6)$$

The first entry in the top row indicates survival of perennial seeds, $s_S(1 - G_P(t))$. Seeds may also germinate and turn into adults, given by the first entry in the second row of \mathbf{M} . Adults meanwhile, survive with probability s_P and produce $v_P Y_P(t)$ seeds per adult where v_P is perennial plant size and Y_P is the seed yield per unit biomass.

Similar to the assumptions above for the annual, I assume that germination declines with litter by a factor D_P and seed production of declines with the total density of growing plants by a factor C_P such that

$$G_P(t) = \frac{g_P}{D_P(t)} = \frac{g_P}{1 + \beta_P L(t)} \quad (7)$$

$$Y_P(t) = \frac{y_P}{C_P(t)} = \frac{y_P}{1 + \alpha_P N_T(t)}. \quad (8)$$

Analogous to the equations for germination and litter of the annual, g_P is the germination fraction of perennial seeds in the absence of litter and y_P is the seed yield per-unit biomass when plant density is near zero (i.e. $N_T \rightarrow 0$).

3 Invasion Analysis - Potential Mechanisms of Coexistence

One way to evaluate coexistence is by mutual invasibility. Using mutual invasibility, the perennial and the annual are said to coexist when (i) the perennial can invade the annual, given the annual single-species attractor for the system defined by equations (1) - (4), and (ii) the annual can invade the perennial at its single-species attractor for the system defined by equations (5) - (8).

Invasion analysis can accommodate any type of attractor, be they equilibrium points, periodic cycles, chaotic dynamics, or stationary distributions. However, it turns out that both the annual and the perennial settle on equilibrium points when growing alone (see section 4 below). It suffices for our purposes now to denote these equilibrium values with a star, such that N_A^* and L^* are the equilibrium points for annual seeds and litter with no perennials present and N_S^* and N_P^* are equilibrium densities of perennial seeds and adults when no annuals (and hence no litter) is present.

3.1 Invader growth rate for the perennial

Invasion growth of the perennial occurs when the annual seed density and litter equilibrates at the values N_A^* and L^* , respectively. Under these conditions, the growth rate of the perennial is determined by the eigenvalues of \mathbf{M} . These eigenvalues are

$$\lambda = \frac{s_S(1 - G_P^*) + s_P}{2} \pm \sqrt{\left[\frac{s_S(1 - G_P^*) - s_P}{2}\right]^2 + G_P^* v_P Y_P^*}. \quad (9)$$

Both terms inside the square root are positive and so neither of the roots is complex. Furthermore, since all terms are positive, the larger of the eigenvalues is the one for which the square root term adds.

For the perennial to invade, a necessary condition is that the dominant eigenvalue is greater than 1. The dominant eigenvalue operates as the growth rate at the stable stage distribution, given by the corresponding right eigenvector of \mathbf{M} . The growth rate of the perennial population will transiently deviate from the dominant eigenvalue until the stable age distribution is reached. However, with no influence of demographic stochasticity as assumed here, the dominant eigenvalue will ultimately determine long-term growth from low density. Simulations later will show that such a characterization of the invasion process is justified.

Conditions for the dominant eigenvalue to be greater than 1 can be written as

$$v_P Y_P^* G_P^* > [1 - s_S(1 - G_P^*)](1 - s_P). \quad (10)$$

The term on the left of the inequality of (10) is the seed production of the perennial per seed in the invasion state. On the right hand side of the inequality in (10) is the average mortality rate of an individual in the population in the invader state. Hence the inequality simply states that an individual perennial in the invader state must have fecundity greater than 1 in its lifetime to invade. This makes sense, but of course depends critically on how the annual affects aspects of reproduction and lifetime expectancy through competitive and litter effects. Equation (10) can be written more informatively as

$$R_0^P > C_P^{A*} [D_P^*(1 - s_S g_P) + s_S g_P], \quad (11)$$

where $R_0^P = v_P y_P g_P / (1 - s_S(1 - g_P))(1 - s_P)$ is the number of seeds produced in a generation of the perennial when growing in isolation, $D_P^* = 1 + \beta_P L^*$ signifies litter effects on the perennial with the annual at equilibrium, and $C_P^{A*} = 1 + \alpha_P G_A^* N_A^*$ is likewise the competitive effect on the perennial influenced by the annual at equilibrium. Note that, when the perennial is alone, D_P^{A*} and C_P^{A*} are both 1 and so the condition for invasion of the perennial naturally becomes the viability condition, $R_0^P > 1$. The RHS of this equation is increasing with both the strength of resource competition and litter density-dependence, indicating that both factors restrict invasion of the perennial.

3.2 Invader growth rate for the annual

When the annual is in the invader state, there is no litter produced in the system. Hence, germination is constant in the invader state, i.e. $G_A(t) = g_A$, and the growth rate of the annual is

$$\lim_{N_A \rightarrow 0} \frac{N_A(t+1)}{N_A(t)} = \frac{g_A v_A y_A}{C_A^{P*}} + s_A(1 - g_A), \quad (12)$$

where C_A^{P*} is the competition effect of the perennial on the annual when the perennial is at equilibrium. The annual can then increase in the invader state whenever its finite rate of increase exceeds 1, which can be written as

$$\frac{g_A v_A y_A}{1 - s_A(1 - g_A)} > C_A^{P*}. \quad (13)$$

Note again that the LHS of eqn (13) is the annual fecundity per generation, R_0^A . Eqn (13) says that the annual can invade when the number of offspring per generation is more than that reduced by interspecific competition from the perennial. Following similar reasoning to that above, Eqn (13) can be rewritten as

$$R_0^A > C_A^{P*}. \quad (14)$$

The question at hand is what conditions allow for both species to invade when rare, i.e. stably coexist. When stable coexistence is not possible, what are the competitive outcomes? To answer these questions, we need to derive explicit expression for C_A^{P*} , C_P^{A*} , and D_P^* . Operationally, this means finding expressions for the equilibrium values of the annual and litter when growing alone, as well as that for the perennial when growing alone.

4 Single Species Dynamics

Here we analyze the dynamics of each species as single species in order to determine equilibrium conditions for the invasion analysis. This is straightforward for the perennial and so we begin there. Things are more complicated for the annual because of the role of litter. Despite the difficulties that arise from litter production of the annual, we can understand much of the qualitative behavior of the system from graphical analysis. Some special cases are also investigated that reinforce these graphical arguments.

4.1 Perennial Dynamics

4.1.1 Perennial Equilibrium

When the perennial grows alone, litter is not present and so $L = 0$ for all time points and $D_P = 1$. Resource competition is solely the result of intraspecific resource draw down from perennial adults, but not seeds. Therefore, $C_P(t) =$

$1 + \alpha_P N_P(t)$. These assumptions mean that the population projection matrix \mathbf{M} simplifies to

$$\mathbf{M} = \begin{bmatrix} s_S(1 - g_P) & v_P y_P / (1 + \alpha_P N_P(t)) \\ g_P & s_P \end{bmatrix}. \quad (15)$$

Using this matrix in equation (5) for perennial dynamics gives a system of two equations in two variables. At equilibrium, we stipulate that $N_S(t) = N_S(t+1) = N_S^*$ and $N_P(t) = N_P(t+1) = N_P^*$ for all t . Solving this system of equations for N_P^* and N_S^* yields

$$N_P^* = \frac{1}{\alpha_P} \left[\frac{y_P v_P g_P}{[1 - s_S(1 - g_P)](1 - s_P)} - 1 \right] \quad (16)$$

and

$$N_S^* = \frac{(1 - s_P)}{g_P} N_P^*. \quad (17)$$

Note that the same expressions can be derived by use of the eigenvalues and eigenvectors of the matrix \mathbf{M} given in (15). At equilibrium, the population has dominant eigenvalue equal to 1 and the stable stage distribution is given by the right eigenvector. These two expressions can be used to solve for N_P^* and N_S^* . Doing so yields expressions (16) and (17).

4.1.2 Equilibrium Stability

Despite stage structure of the perennial, the equilibrium density of adults is straightforward to understand. The equilibrium perennial density can be rewritten as

$$N_P^* = \frac{R_0^P - 1}{\alpha_P}, \quad (18)$$

where again $R_0^P = v_P y_P g_P / (1 - s_S(1 - g_P))(1 - s_P)$. Equation (18) shows that equilibrium population density of the perennial increases with its expected fecundity per generation (R_0^P) and decreases with the perennial's sensitivity to competition (α_P).

To evaluate stability of this single-species system with stage structure, we approximate the discrete-time system by a continuous-time system on the grounds that perturbations to the equilibrium are small and so continuous change in the population well approximates discrete change. Note that the change in one time step leads to the system

$$\Delta \mathbf{N}(t) = \begin{bmatrix} -(1 - s_S(1 - g_P)) & v_P y_P / (1 + \alpha_P N_P(t)) \\ g_P & -(1 - s_P) \end{bmatrix} \mathbf{N}(t), \quad (19)$$

where $\Delta \mathbf{N}(t) = \mathbf{N}(t+1) - \mathbf{N}(t)$. Given the assumptions above of small perturbations to equilibrium, this system can be approximated by the set of differential

equations

$$\frac{dN_S}{dt} = -(1 - s_S(1 - g_P))N_S + \frac{v_P y_P}{1 + \alpha_P N_P} N_P \quad (20)$$

$$\frac{dN_P}{dt} = g_P N_S - (1 - s_P)N_P. \quad (21)$$

The Jacobbian of this system of equations is

$$\mathbf{J} = \begin{bmatrix} -(1 - s_S(1 - g_P)) & v_P Y_P^* + N_P^* \frac{\partial Y_P^*}{\partial N_P^*} \\ g_P & -(1 - s_P) \end{bmatrix}, \quad (22)$$

where $Y_P^* = y_P/(1 + \alpha_P N_P^*)$ is the equilibrium seed yield. The sum of the eigenvalues of \mathbf{J} are given by the trace of \mathbf{J} , which here is negative because s_S , s_P , and g_P are all values between 0 and 1. Stability is then given if the determinant is positive, because then both eigenvalues have the same sign, implying based on their negative sum that both are negative. The determinant of \mathbf{J} is

$$\det(\mathbf{J}) = [1 - s_S(1 - g_P)](1 - s_P) - g_P(v_P Y_P^* + N_P^* Y_P'(N_P^*)). \quad (23)$$

Note that the first product is positive. Now consider the second term. This term includes the derivative of Y evaluated at equilibrium, which given the Beverton-Holt form is $Y_P'(N_P^*) = -Y_P^* \alpha_P / (1 + \alpha_P N_P^*)$. Hence, the determinant can be rewritten as

$$\det(\mathbf{J}) = [1 - s_S(1 - g_P)](1 - s_P) - g_P Y_P^* \left(v_P - \frac{\alpha_P N_P^*}{1 + \alpha_P N_P^*} \right). \quad (24)$$

The sign of this expression is difficult to evaluate but can be made simpler by recognizing that at equilibrium, $1 - s_S(1 - g_P) = v_P Y_P^* N_P^* / N_S^*$ and $1 - s_P = g_P N_S^* / N_P^*$. Using these identities in (24) yields

$$\det(\mathbf{J}) = \left[v_P Y_P^* \frac{N_P^*}{N_S^*} \right] \left[g_P \frac{N_S^*}{N_P^*} \right] - g_P Y_P^* \left(v_P - \frac{\alpha_P N_P^*}{1 + \alpha_P N_P^*} \right). \quad (25)$$

Simplifying this expression leads to the final result that

$$\det(\mathbf{J}) = v_P g_P Y_P^* - g_P v_P Y_P^* + \frac{g_P Y_P^* \alpha_P N_P^*}{1 + \alpha_P N_P^*} \quad (26)$$

$$= \frac{g_P Y_P^* \alpha_P N_P^*}{1 + \alpha_P N_P^*} > 0, \quad (27)$$

which implies stability of the system provided the continuous-time approximation holds.

4.2 Annual – Litter System

The dynamics of the equilibrium points, if they exist, satisfy

$$\left. \frac{N_A(t+1)}{N_A(t)} \right|_{N_A^*} = 1 \quad (28)$$

and

$$\left. \frac{L(t+1)}{L(t)} \right|_{L^*} = 1. \quad (29)$$

Solving these equations for equilibrium conditions in the general case requires that one solve a third-order polynomial (not shown). The expressions can be used to calculate the equilibrium values computationally for specific parameter values, but they provide no analytical insight. Instead, visualizing growth using isoclines can be helpful for understanding the qualitative behavior of the model, specifically whether the dynamics are likely to cyclic or chaotic, which we suspect might occur due to the feedbacks between annual plants and the litter they produce. If cyclic or chaotic dynamics are produced by this model, the invasion analysis presented above is not valid. We check here to see when this might occur.

4.2.1 Graphical Analysis of Isoclines

First, consider the equation for population growth of the annual, Eqn (1). The annual does not change in density for any combination of L and N_A such that Eqn (28) is satisfied. These combinations of values are given by the relationship:

$$N_A = \frac{1}{g_A \alpha_A} \left[\frac{g_A v_A y_A (1 + \beta_A L)}{s_A g_A + (1 - s_A)(1 + \beta_A L)} - 1 - \beta_A L \right], \quad (30)$$

which shows that the equilibrium density of annual seeds declines with litter. This equation isn't the easiest to interpret, but can be understood by investigation of it's general properties around critical point. First, note that N_A given $L = 0$ (i.e., no litter) can be written $N_A = (R_0^A - 1)/(g_A \alpha_A)$, which again recapitulates the idea of the equilibrium seed density from competition only a rescaling of $R_0^A - 1$ by the average number of *germinated seeds*. This is the point at which the annual growth isocline intersects the axis of N_A . Similarly, the isocline intersects the L axis, which can be seen because the Eqn (30) is negative in the limit of large L . Hence, for viable N_A , the iscline is in the positive region of (N_A, L) , but is negative for some L . The point where the isocline intersects the L axis is found by assuming Eqn (30) is zero, which yields

$$L = \frac{1}{\beta_A} \left[\frac{g_A v_A y_A + s_A (1 - g_A) - 1}{1 - s_A} \right], \quad (31)$$

which is positive for any viable population of the annual. This can be seen because the numerator of the solution is the per-capita growth rate of the annual in the absence of either interference or resource competition (i.e. $L = 0$ and $N_A = 0$). Hence, there is an overall negative relationship between equilibrium N_A and L . However, this need not always be locally negative.

is given by the derivative of (30) can be written

$$\frac{dN_A}{dL} = \frac{\beta_A}{g_A \alpha_A} \left[\frac{s_A g_A^2 v_A y_A}{[s_A g_A + (1 - s_A)(1 + \beta_A L)]^2} - 1 \right], \quad (32)$$

which may be positive for some values of L . The interest here is asking whether there is any possibility that the annual may increase at equilibrium with an increase in litter. A sufficient condition for this to occur is for the term in brackets to be positive when $L = 0$, which can be written as

$$R_0^A - 1 > \frac{1 - s_A}{s_A g_A}. \quad (33)$$

This condition is possible when seed survival of the annual is small.

Intuitively, more litter at equilibrium leads to lower equilibrium seed density. Interestingly, the rate of this change is proportional to β_A/α_A , the sensitivity of the annual to interference competition via litter relative to intraspecific resource competition.

In the absence of litter, $L = 0$, Eqn (30) simplifies to $N_A = (R_0^A - 1)/\alpha_A$.

Equation (30), when plotted as a function of N_A on a graph of L versus N_A gives the relationship of zero change in the annual. It is the solid line in Figure 1. Simulations show that, for most reasonable parameters, only the solution which adds the square root term in Eqn (30) is positive. Points to the left of the line indicate that seed density increases (i.e. N_A moves to the right on the figure). Values to the right of this solid line indicate seed density decreases (i.e. N_A moves to the left). The isocline intersects the vertical axis when $N_A = 0$, which from Eqn (30) corresponds to $L = \beta_A^{-1}(\lambda_A' - 1)/(1 - s_A)$. Eqn (30) is a decreasing function of N_A and reaches the horizontal axis at the point $N_A = (R_0^A - 1)/(\alpha_A g_A)$, which corresponds to the equilibrium density of seeds if litter were completely absent. Notice that the expression is nearly identical to that for the perennial (equation 18) when taken as the equilibrium density of *germinated seeds*, i.e. $g_A N_A = (R_0^A - 1)/\alpha_A$.

The isocline for litter dynamics can be found by solving for the combinations of L and N_A in the litter dynamics equation (4) when evaluated for equilibrium. The isocline can be written as

$$L = \frac{1}{2\beta_A} \left[\pm \sqrt{1 + \frac{4c\beta_A}{1 - c(1 - d)}(N_A g_A v_A) - 1} \right]. \quad (34)$$

There are two components to this isocline. The question is whether both are biologically feasible and need to be considered. In fact, only the solution with the positive part of the square root in (34) is biologically feasible. This can be seen by first noting that the terms inside the square-root are all positive for feasible N_A . Then, taking the square-root term as negative leads to a sum of two negative terms inside the brackets. Hence, this sum is negative for all feasible N_A and all values of L are negative.

The biologically feasible isocline increases indefinitely from 0, being unbounded by any finite value, i.e. $\lim_{N_A \rightarrow \infty} L \rightarrow \infty$. The rate at which this increases declines with N_A , and so is fastest as $N_A \rightarrow 0$. Provided that the isocline is not too steep, we can safely assume that the dynamics of the system lead to a stable equilibrium over the long-term. The maximum incline of the curve is given by the local derivative of the isocline at $N_A = 0$, which is

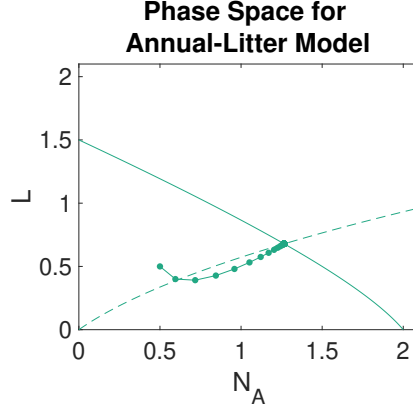


Figure 1: Isoclines and dynamics of the annual and litter. The isocline for annual growth is given by the solid line. The isocline for litter growth is given by the dashed line. Points connected by lines represent simulation of the model. The equilibrium is stable and convergent. Parameters: $\alpha_A = 0.5$, $\beta_A = 5$, $g_A = 0.5$, $v_A = 1$, $s_A = 0.5$, $y_A = 3$, $c = 0.9$, and $d = 0.5$.

$cg_A v_A / [1 - c(1 - d)]$. This suggests that nonlinear dynamics are the most likely when an individual's contribution to litter is large (large $cg_A v_A$) and when the loss of litter each year ($1 - c(1 - d)$) is small. Figure 2 shows a case where the input to litter $g_A v_A$ is large, almost all litter is retained $c(1 - d) \approx 1$, and litter has strong feedback to annual germination $\beta_A = 10$. In this case, the annual and litter system exhibits damped oscillations to a point equilibrium.

Indeed, stable equilibrium points are the only long-term state observed in simulations across a large range of parameters (see Figure 3). Naturally, these figures show that equilibrium L and N_A decline with both α_A and β_A . Density-dependence, either occurring directly via density (α) or indirectly through changes in litter (β), increases with both parameters and therefor limits equilibrium population growth of the annual. Interestingly, a fixed increase in competitive effect has larger effect when β_A is small than when it is large. This shows that density-dependent processes are not additive, similar to conclusions about the roles of resources and natural enemies in limiting species (Chesson and Kuang (2009)).

Now we turn to some special cases.

4.2.2 Case 1. No effect of litter

When litter has no effect on annual plant growth, the system can be solved quite simply as a single-species population growth model, where the per-capita growth rate of the annual is

$$\frac{N_A(t+1)}{N_A(t)} = \frac{g_A v_A y_A}{1 + \alpha_A g_A N_A(t)} + s_A(1 - g_A). \quad (35)$$

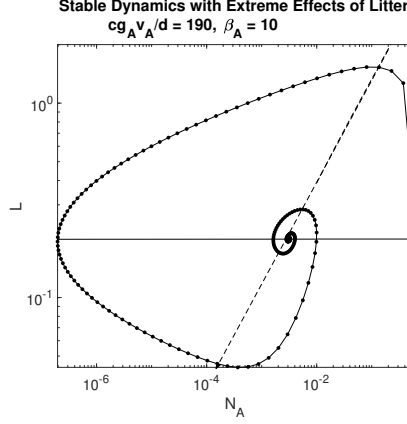


Figure 2: Dynamics of annual seed density and litter density in the case of strong per-capita contributions to litter ($g_A v_A = 10$), strong per-capita responses to litter ($\beta_A = 10$), and strong litter retention ($c/d = 19$). These conditions make the system strongly non-linear, which we expect to be more likely to produce sustained cycles. Nonetheless, the system exhibits damped oscillations to a stable equilibrium point. Note that the axis are on the log-scale.

The equilibrium population density of growing plants is $g_A N_A^* = [R_0^A - 1]/\alpha_A$, which is the same as the solution from the isocline analysis assuming no litter. Hence, any viable annual in this simplified model must have $R_0^A > 1$.

Despite annual plant dynamics occurring independently of accumulation of litter, litter itself depends on the density of annuals and their total biomass. Solving for equilibrium litter density yields

$$L^* = v_A g_A N_A^* \left(\frac{c}{1 - c(1 - d)} \right) = v_A \left(\frac{R_0^A - 1}{\alpha_A} \right) \left(\frac{c}{1 - c(1 - d)} \right). \quad (36)$$

This equation simply says that the density of litter at equilibrium is a constant times $v_A g_A N_A^*$, the total biomass of growing annual plants at equilibrium. This constant is given by the ratio of litter retention over the winter c relative to the total loss over a year $1 - c(1 - d)$. If loss is near 1, this constant is small and litter density at equilibrium is also small. If the loss is very small, the constant is large and there is abundant litter at equilibrium. This matches the simulation results above.

This system can be described in terms of absolute change as

$$\begin{bmatrix} \Delta N_A(t) \\ \Delta L(t) \end{bmatrix} \begin{bmatrix} s_A(1 - g_A) + \frac{g_A v_A y_A}{1 + \alpha_A g_A N_A(t)} - 1 & 0 \\ c g_A v_A & -(1 - c(1 - d)) \end{bmatrix} \begin{bmatrix} N_A(t) \\ L(t) \end{bmatrix}. \quad (37)$$

At equilibrium, assuming changes are small for each time step, this system can be approximated by the set of differential equations

$$\dot{x} = \mathbf{F}x \quad (38)$$

where $\dot{x} = (dN_A/dt, dL/dt)^T$, $x = (N_A, L)^T$, and \mathbf{F} is the matrix given in Eqn (37). The Jacobbian of this system evaluated at equilibrium is the matrix

$$\begin{bmatrix} N_A^* \frac{\partial \lambda}{\partial N_A} & 0 \\ cg_A v_A & -[1 - c(1 - d)] \end{bmatrix}. \quad (39)$$

Note that for a feasible equilibrium, $N_A^* > 0$ and by the definition of competition, $\partial \lambda / \partial N_A < 0$. Hence, the Jacobbian has negative elements along the diagonal and non-negative values for the off-diagonal elements. This means that the trace of the Jacobbian is negative, the determinant of the matrix is positive, and so both eigenvalues of the Jacobbian are negative. Hence, the system is locally stable.

4.2.3 Case 2. Litter effects only

We may also consider the case of just density-dependence that arises from the litter, assuming perhaps that the annual is sufficiently sparsely populated across space that plant-plant competition is weak. The question is whether litter is sufficient alone to cause density-dependent annual plant dynamics?

With no direct intraspecific competition from resources, any density-dependence in the model must emerge from the dynamics of litter and its effects on plant germination. Annual and litter dynamics in this case follow the system of equations

$$\begin{aligned} N_A(t+1) &= N_A(t) \left(\frac{v_A y_A g_A}{1 + \beta_A L(t)} + s(1 - g_A) \right) \\ L(t+1) &= c \left(\frac{N_A(t) g_A v_A}{1 + \beta_A L(t)} + (1 - d)L(t) \right). \end{aligned} \quad (40)$$

The equilibrium litter in the system can be found using the equation for annual growth, which yields

$$L^* = \frac{R_0^A - 1}{\beta_A}. \quad (41)$$

Naturally, a condition for litter to persist in the system is for the annual to be viable, i.e. $R_0^A > 1$, and the amount of litter at equilibrium decreases with β_A , the annual's sensitivity to litter. The equilibrium expression for the annual is

$$N_A^* = \frac{1 - c(1 - d)}{cg_A v_A} L^*. \quad (42)$$

This equation shows that equilibrium density of the annual is proportional to the equilibrium level of litter. This proportion decreases with $cg_A v_A$, the biomass contribution of an individual seed to litter the following year, and increases with $1 - c(1 - d)$, the amount of litter lost each year. Notice that this exactly reflects the isocline analysis above in the limiting case of $N_A \rightarrow 0$, reflecting the fact that annual density does not matter for the dynamics in this case due to the absence of intraspecific competition.

We evaluate the stability of this equilibrium following the same approach as before by approximating the discrete-time system by a continuous-time system

at its equilibrium. The Jacobbian for the continuous-time system evaluated at equilibrium is

$$\begin{bmatrix} 0 & v_A y_A \frac{\partial G_A}{\partial L} \Big|_{L^*} \\ v_A G_A^* & N_A^* c v_A \frac{\partial G_A}{\partial L} \Big|_{L^*} - (1 - c(1 - d)) \end{bmatrix}. \quad (43)$$

Assuming that a viable population of the annual, $L^* > 0$ and $N_A^* > 0$. Furthermore, our assumption that litter only reduces germination means that $\partial G / \partial L < 0$. The two elements in the left column of the matrix are non-negative and the two elements in the right column of the matrix are negative. Thus, the trace of the matrix is negative and the determinant is positive. These two together indicate that both eigenvalues of the matrix are negative and the system is locally stable.

An interesting extension is to ask what happens if litter has some positive effects on germination. This simple analysis suggests that stability is determined by the sign of $v_A y_A \partial G_A / \partial L$. When this is positive, the local equilibrium is unstable. This issue will be taken up a later time.

5 Outcomes of Competition Between Species: Coexistence, Exclusions, and Priority Effects Mediated by Litter

In principle, we have shown conditions where coexistence is possible, in particular when the annual germination is highly sensitive to litter. This is mainly because it causes strong intraspecific density-dependence in the annual, which subsequently can allow the perennial to invade. By contrast, the annual does not have to deal with any litter in the invasive state and so must simply be a better competitor than the perennial in order to invade as well.

To investigate this trade-off, we plotted isoclines of the low-density growth rate as a function of the R_0 for each species. We first consider the case of identical responses of each species to competition, i.e. $\alpha_A = \alpha_P$, but different responses to litter. Remember that our model assumes no contribution of the perennial to litter.

Figure 4 shows an example where the annual is more sensitive to litter than the perennial $\beta_A / \beta_P = 2$. Three outcomes are possible in this case. Exclusion of each species by the other is possible, but also stable coexistence of both species. Notice from Figure 4(a) that stable coexistence requires that $R_0^A > R_0^P$, meaning that the annual must grow better in the absence of litter than the perennial. The perennial is at an automatic advantage over the annual due to its relatively low sensitivity to litter. For the two to coexist, the annual must make up this disadvantage with greater reproductive capacity.

Consider now the case where the annual is less sensitive to litter than the perennial. The potential outcomes of competition are shown in Figure 5(a).

Here, there is an area where the invader growth rates of both species are negative, meaning that neither can invade the other. This is not because the species are non-viable. In fact, all parameter values presented in Figure 5(a) are viable. Instead, this region corresponds to a priority effect. Both species can grow from low density in isolation, but neither can grow from low density when the other is at high density.

The priority effect occurs because each species is limited more by the a factor that is affected most by its competitor. For the annual, this is competition. Notice that the region lies above the 1:1 line, meaning that it requires the perennial to have higher lifetime reproduction than the annual. Hence, the perennial contributes more to competition. By contrast, the perennial is more affected by litter, which is solely produced by the annual. In both cases, the competitor, when at its equilibrium density, degrades conditions enough to limit the growth of the competitor. For R_0 values given by the black dot in Figure 5(a), panels (b), (c), and (d) show different outcomes based on initial species densities. In 5(c), the annual excludes the perennial. In 5(d), the perennial excludes the annual.

Clearly, a trade-off between sensitivity to litter and competition is required for coexistence. But the above special cases show that the trade-off must be in one configuration for coexistence to occur; the annual must be more sensitive to litter. The alternative leads to priority effects. The reason for this difference is that the species do not equally affect competition and litter. Only the annual can affect litter. Density-feedbacks mediated by litter, as exemplified in Figure 7, occur within-species for the annual, but between-species for the perennial. Stable coexistence only occurs when within-species density-feedbacks are stronger than between-species. Between-species feedbacks are stronger than within-species feedbacks when the trade-off is such that the perennial is more sensitive than the perennial, explaining why stable coexistence is not possible in such a case. Instead, contingent exclusion is the result.

Finally, consider the relative overall effects of α and β . Multitrophic diversity maintenance theory suggests that coexistence via differential resource use can be weakened by strong effects of generalist natural enemies (Chesson and Kuang 2009). Similarly, the diversity maintenance effects of specialist natural enemies can be weakened when a single, shared resource is critical to growth. In general, the strength of a trade-off promoting coexistence should be relative to its effect on per-capita growth of species. Hence, this body of theory predicts that increasing the overall strength of resource-based density-dependence, i.e. increasing the absolute magnitude of α , could weaken the diversifying effects of differences in sensitivity to litter. We check this prediction by fixing the trade-off between β across species while increasing the absolute magnitude of α .

Figure 6 shows the prediction bears out in this model. For a fixed trade-off in responses to litter and competition, the coexistence region increases as β/α increases, indicating that more opportunities for coexistence are possible when β is more important for growth.

5.1 Effect of Assumptions

- Different life histories - probably doesn't matter much (life histories outcomes just summarized by R_0). Possibly the details matter
- Competition based on plant density, not biomass density. Probably doesn't matter much because we just rescale N by Nv , where v is a constant.
- Competition affects seed production. Competition could effect plant growth throughout the year instead. There is the possibility that this contributes greatly to litter production, because high competition effects reduce litter production. This suggests that competition and litter density-dependence interfere to a greater extent. Worth looking into.

6 Pathogen Effects on Plant Competition

More related to the EEID project is the role of plant pathogens in mediating competition. Here the litter may also play a critical role in transmission and infection both within and between species. Fungal pathogens can have myriad effects. Included in these are density-independent effects, assuming that the fungus is largely maintained by factors other than the focal annual and perennial plants. Density-independent pathogens will have little to no effect on the feedbacks themselves, but instead will modify the relative values of R_0 between species. Hence, we predict that the outcome of competition will be different, but will not qualitatively change the types of outcomes possible. Furthermore, pathogens that proportionally affect both species should have no quantitative effect of the outcome of competition.

Density-independent pathogens might be the least biologically relevant for our system. Infected plants that senesce leave behind infected litter and the litter may be an important mediator of transmission. This is the simplest form of density-dependent pathogen dynamics. The functional effect of such an assumption is to increase the impact of litter. Thus, we expect that pathogens should shift potentially weak coexistence to stronger ones, similar to that shown in Figure 6. However, note that this will also increase the range of priority effects if the trade-off is in the incorrect configuration.

Species-specific density-dependent infection is likely to also be important. The basic expectation is that species-specific infection can create new trade-offs between species that allow for coexistence. However, the interaction with litter remains an important component that can make outcomes complex.

7 Thoughts from meeting with EEID Theory Group

- Relevance to invasive species effects on extinction? Might the introduction of an invader shift the relative importance of pathogen-based and

resource-based competition? Depending on the context of the coexistence in the community before invasion, the invader might have huge effects by weakening the relative importance of the stabilizing effect facilitating diversity.

- What happens to litter in along a gradient of different factors like litter retention?
- Couch in terms of effect and responses. We can make these explicit in a stripped down version of the model, which would also show that this isn't a model-specific result, but should apply in many scenarios.
- Is stability always likely for a suite of models related to litter and the annual? For example, one could conceive of a case where litter facilitates germination at low densities.
- What are other plausible biological scenarios? What are the other processes of most interest?
- Results probably apply to plant-soil feedbacks and allelopathy and such.
- Coexistence bandwidth: how robust are the results to perturbations? This can be done in a number of ways. One is by the size of the coexistence region (note that the difference between invasion boundaries is approximately constant on the log scale). Another is for the amount of mortality that each species can tolerate. Some of that is done in this model using R_0 s.
- Valuable to write out the exact predictions of how the pathogen might affect coexistence.

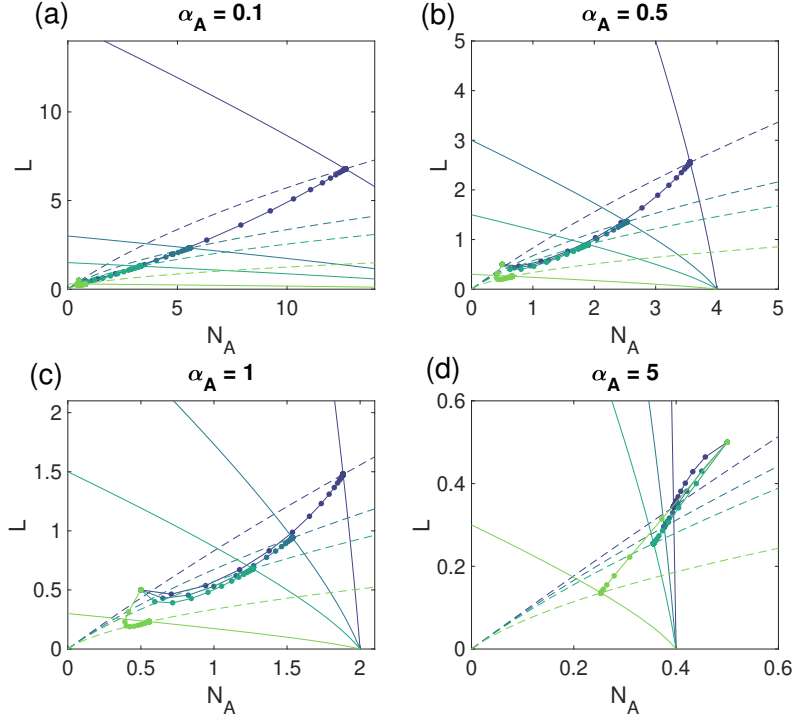


Figure 3: Isoclines and dynamics of the annual and litter. The isocline for annual growth is given by the solid line. The isocline for litter growth is given by the dashed line. The strength of litter effects, β_A increase from purple to light green in all figures. The strength of resource competition, α_A , increases from (a) to (b). Notice that changes in litter have smaller effect when resource competition is strong. Points connected by lines represent simulation of the model. In all cases, the equilibrium is stable and convergent. Parameters: $g_A = 0.5$, $v_A = 1$, $s_A = 0.5$, $y_A = 3$, $c = 0.9$, and $d = 0.5$.

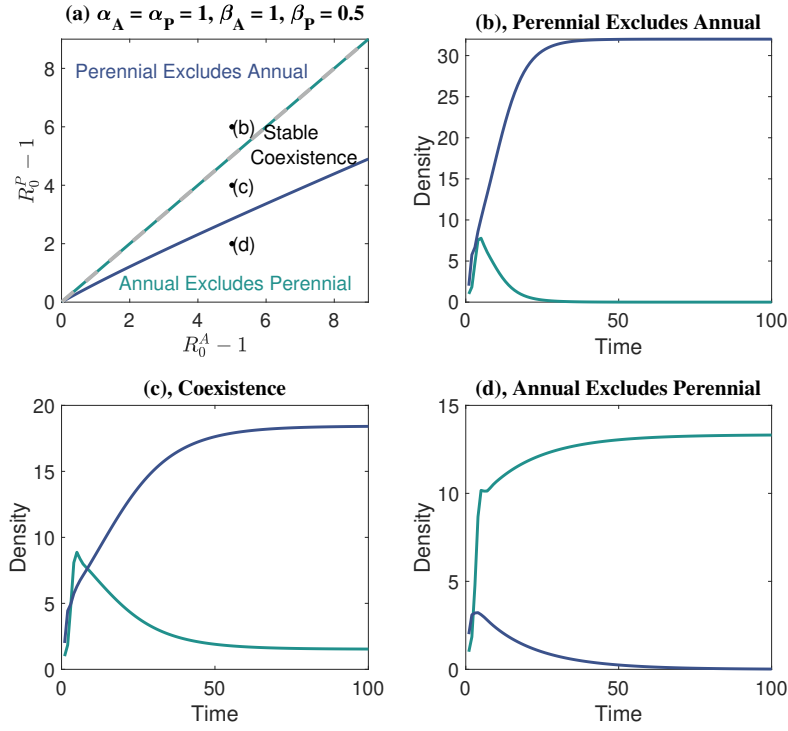


Figure 4: (a) Isoclines for invasion of perennial (blue) and annual (green). In this example, both species respond to competition identically, and so species average fitness is given by the relative value of λ' across the species. Species do not respond to litter identically; the annual responds more strongly than the perennial. Points lying above the blue line indicate invasion of the perennial. Points lying below the green line indicate invasion of the annual. Coexistence (mutual invasibility) occurs in the region between the lines. Examples of (b) exclusion of the annual, (c) stable coexistence, and (d) exclusion of the perennial are given with their respective parameter values shown in panel (a). In (b) - (d), green lines represent annual density and blue lines represent annual density.

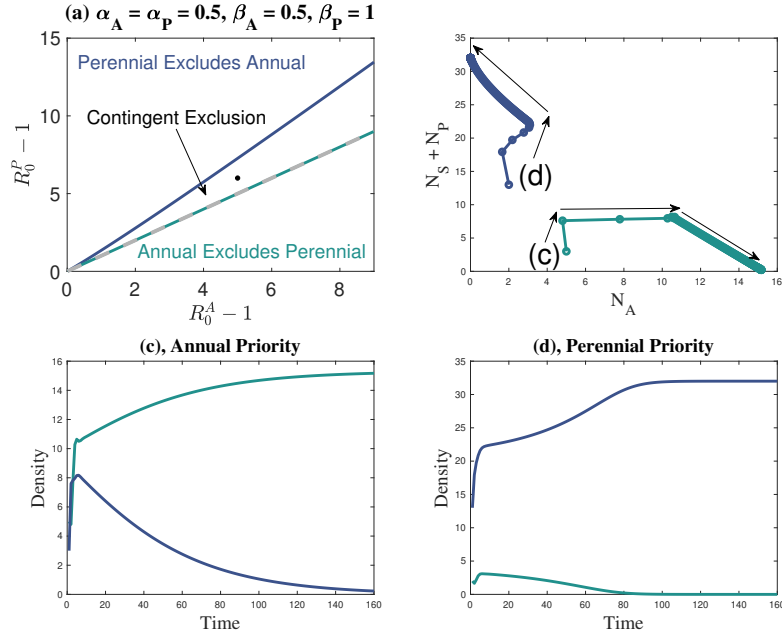


Figure 5: Priority effects possible when perennial is less sensitive to competition than the annual. Phase space in (a) as in Figure 4. Black point indicates values of R_0^A and R_0^P used in simulations of (b) - (d). (b) Dynamics of priority effects with two initial starting conditions. The blue line shows dynamics when the perennial initially is at higher density. The green line shows the same for the annual with higher initial density. Dynamics over time of these two examples are plotted in (c) and (d).

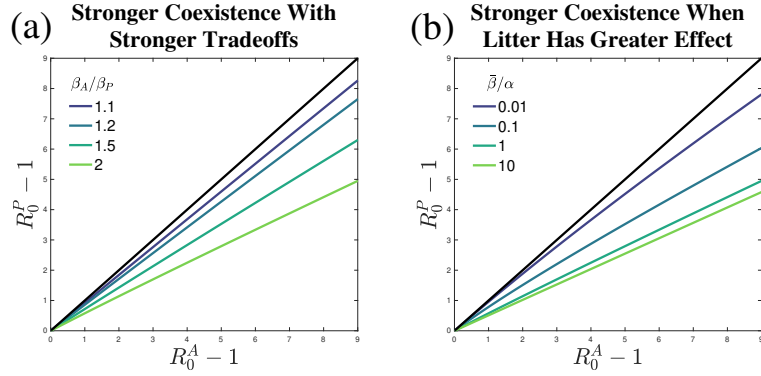


Figure 6: Tradeoffs necessary for coexistence. (a) Size of coexistence region increases with the strength of the difference between species in their sensitivity to litter. Stable coexistence occurs in the region between the black line and each colored line. Lighter colors indicate larger difference between species. (b) Differences between species in litter sensitivity creates more opportunities for coexistence when litter has stronger effects on population growth as indicated by the relative strength of β compared to α . Brighter colors indicate greater overall sensitivity to litter relative to resource competition. Parameters the same as in other figures, except $c = 0.9$ and $d = 0.1$.

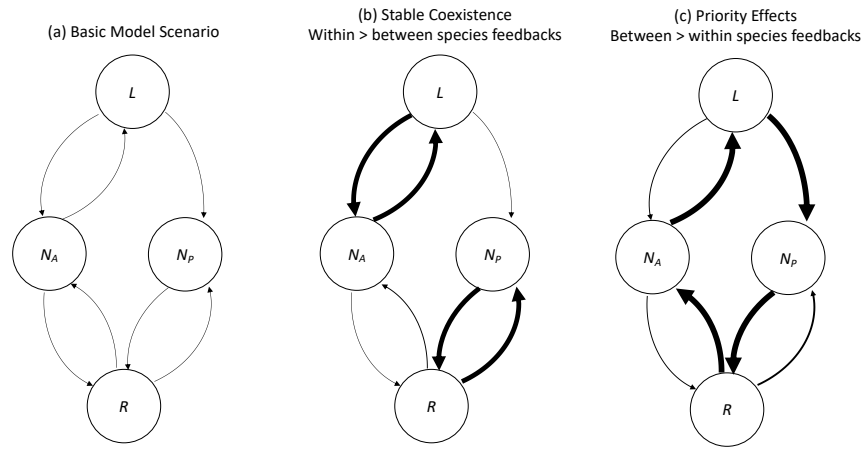


Figure 7: Explanation of coexistence and priority effects through feedback loops. (a) Per-capita effects and responses of annuals (N_A) and perennials (N_P) on litter (L) and competition via a shared resource (R). Note that the resource is not specified in the model but species effects are related to R_0 and per-capita responses are given by α s. (b) Configuration found in Figure 4 inside the coexistence region. Within-species feedbacks ($N_A \rightarrow L \rightarrow N_A$ and $N_P \rightarrow R \rightarrow N_P$) are strong relative to between-species feedbacks. (c) Configuration representing parameters in Figure 5, where between-species feedbacks ($N_A \rightarrow L \rightarrow N_P$ and $N_P \rightarrow R \rightarrow N_A$) are stronger than within-species feedbacks.