Interspecific Competition

Intraspecific competition – Classic logistic model

Interspecific extension of density-dependence

- Individuals of other species may also have an effect on per capita birth & death rates

Interspecific Competition

Forms of competition

- Interference competition (directly affecting other species) also called contest competition
  - Interspecific territoriality, aggressive behavior, allelopathy
- Exploitation competition (mediated via limiting resources) also called scramble competition
  - Food, light, space, nutrients

Interspecific Competition

- Exploitation competition (mediated via limiting resources)
  - Food, light, space, nutrients
  - Resource dynamics
    - "falling fruit" resource supply rates not affected by consumption rate, although standing crop may be
      - More usefully thought of as resource competition, but can be approximate equivalent of interference competition
    - Dynamic resources (e.g., prey): consuming resource affects population growth rate of prey
      - More usefully thought of as 2 predator 1 prey systems

Competition

Lotka-Volterra Competition Model – classic set of models for basic biotic interactions.

Start with logistic growth model for intraspecific competition:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1}{K_1} \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2}{K_2} \right)$$

Competition

Now, add interspecific competition:

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1} \right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2} \right)$$

Where α and β are competition coefficients.

If these equal 1, the two spp are interchangeable,

α = 4 means each individual of sp 2 depresses growth of sp 1 as if 4 individuals of sp 1 were added (an individual of sp 2 uses 4x the resources as an individual of sp 1)

Competition

Thus, α and β are measures of relative importance *per individual* of interspecific competition (relative to intraspecific competition)

*If α>1, the *per capita* effect of interspecific competition is greater than the *per capita* effect of intraspecific competition

If α<1, intraspecific competition is greater than interspecific… adding one individual of sp 1 has greater impact than adding one of sp 2

→ α & β are measures of the per capita effect sp sp 2 on sp 1 in units of sp 1 (or vise versa)

Competition

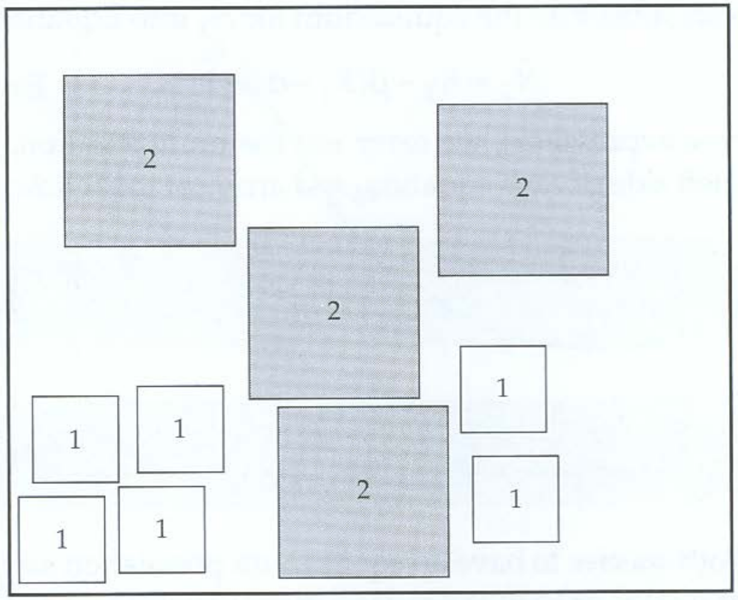


Figure 5.1 A graphical analogy for interspecific competition. The heavy square frame represents the carrying capacity for species 1 (K_1). Each individual consumes a portion of the limited resources available and is represented by a tile. Individuals of species 2 reduce the carrying capacity four times as much as individuals of species 1. Hence, the tiles for species 2 are four times larger than those for species 1, and $\alpha = 4.0$. (After Krebs 1985.)

Note 1: In this illustration, sp 2 reduces K greater than sp 1 (uses more resource *per capita*)

Note 2: This illustration assumes both species are limited by the single resource represented by the box; no alternative resources exist.

Competition

Reality Check

Real competition may be asymetrical which means that $\alpha \neq 1/\beta$ (they MAY be equal, but would be a special case)

In the last figure, 4 individuals of species 1 used the same resources as 1 individual of species 2, and vice versa.

However, in practice species use multiple resources and may be unequal in ability to shift use in response to presence of competitors. Thus, the impact of adding 4 individuals of sp 1 on sp 2 may affect sp 2 differently than adding 1 individual of sp 2 on sp 1 (for example if sp 1 has an alternative food resource and sp 2 does not).

Competition

Equilibrium solutions

Solve for $\hat{N}$ by setting dN/dt = 0 yields:

$$\hat{N}_1 = K_1 - \alpha N_2$$
$$\hat{N}_2 = K_2 - \beta N_1$$

But must solve with respect to each other

By substitution, you get:

$$\hat{N}_1 = K_1 - \alpha(K_2 - \beta\hat{N}_1)$$

$$\hat{N}_2 = K_2 - \beta(K_1 - \alpha\hat{N}_2)$$

Reduces to:

$$\hat{N}_1 = \frac{K_1 - \alpha K_2}{1 - \alpha\beta}$$

$$\hat{N}_2 = \frac{K_2 - \beta K_1}{1 - \alpha\beta}$$

Generally, the product $\alpha\beta < 1$ is necessary for coexistence

Competition

Can examine solutions to these simple models by graphs of state space, i.e., plots of sp1 vs sp2

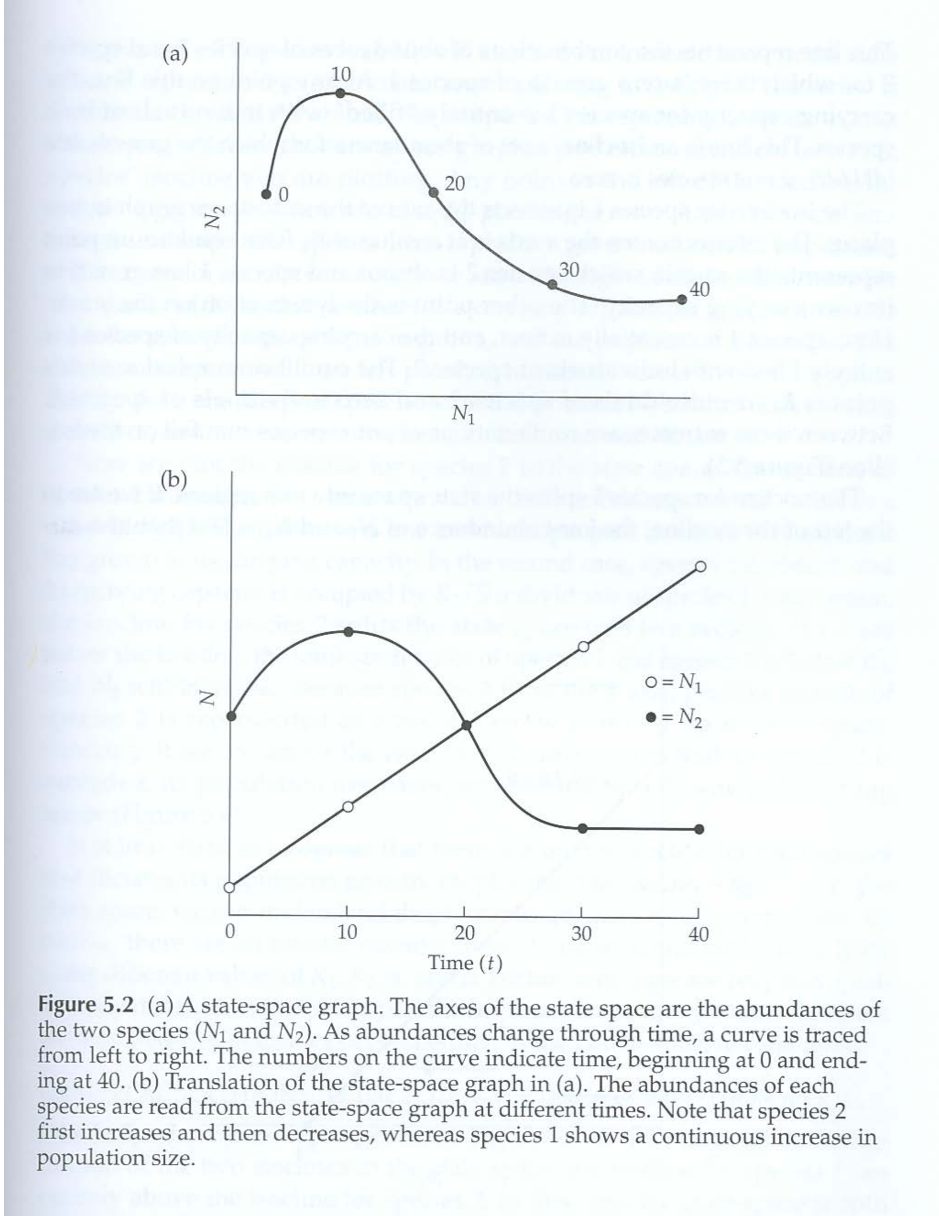


Figure 5.2 (a) A state-space graph. The axes of the state space are the abundances of the two species (N_1 and N_2). As abundances change through time, a curve is traced from left to right. The numbers on the curve indicate time, beginning at 0 and ending at 40. (b) Translation of the state-space graph in (a). The abundances of each species are read from the state-space graph at different times. Note that species 2 first increases and then decreases, whereas species 1 shows a continuous increase in population size.

Competition

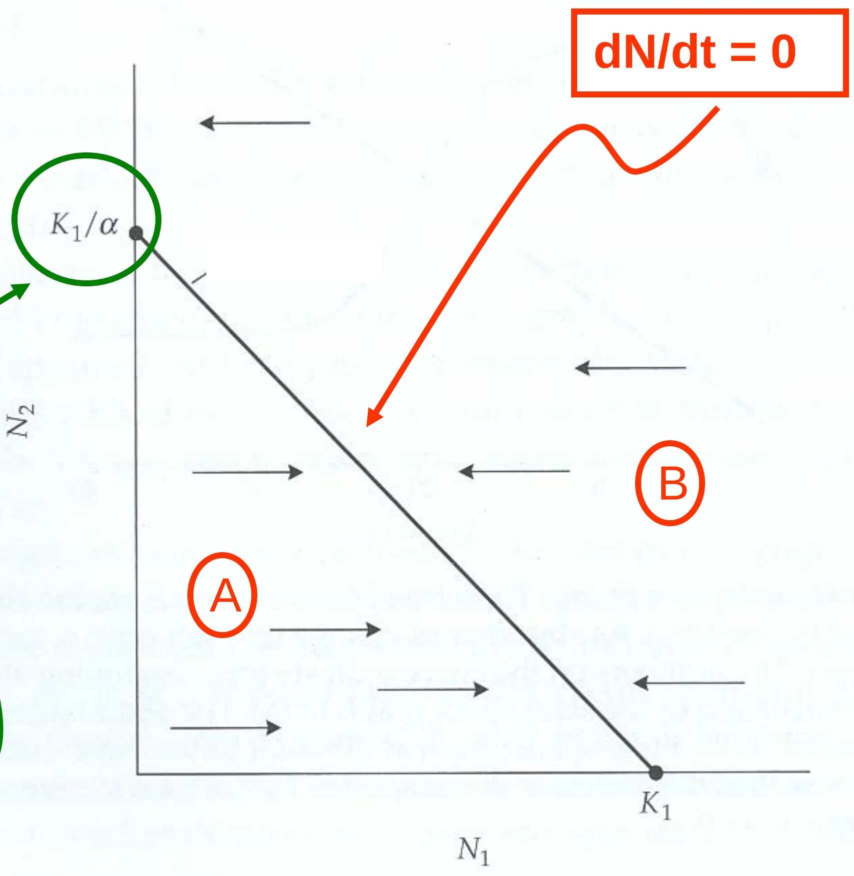
Models yield linear solutions indicating combinations of abundances for which one of the species is at equilibrium

Arrows refer to sp 1

A – joint abundance of sp 1 and 2 below K, sp1 increases; **B** is above K for sp1, so it decreases

Sp 1 is extinct and K of sp1 is filled by individuals of sp2

Graph of results for sp 1



dN/dt = 0

Figure 5.3 The linear isocline for species 1 in the Lotka–Volterra competition model. The isocline defines the combination of abundances for which species 1 shows zero growth. For points to the left of this line, the population of species 1 increases, indicated by the right-pointing horizontal arrow. For points to the right, the joint abundance of species 1 and species 2 exceeds the isocline for species 1, so its population decreases, indicated by the left-pointing arrows.

Competition

Same graph as last page, but for species 2

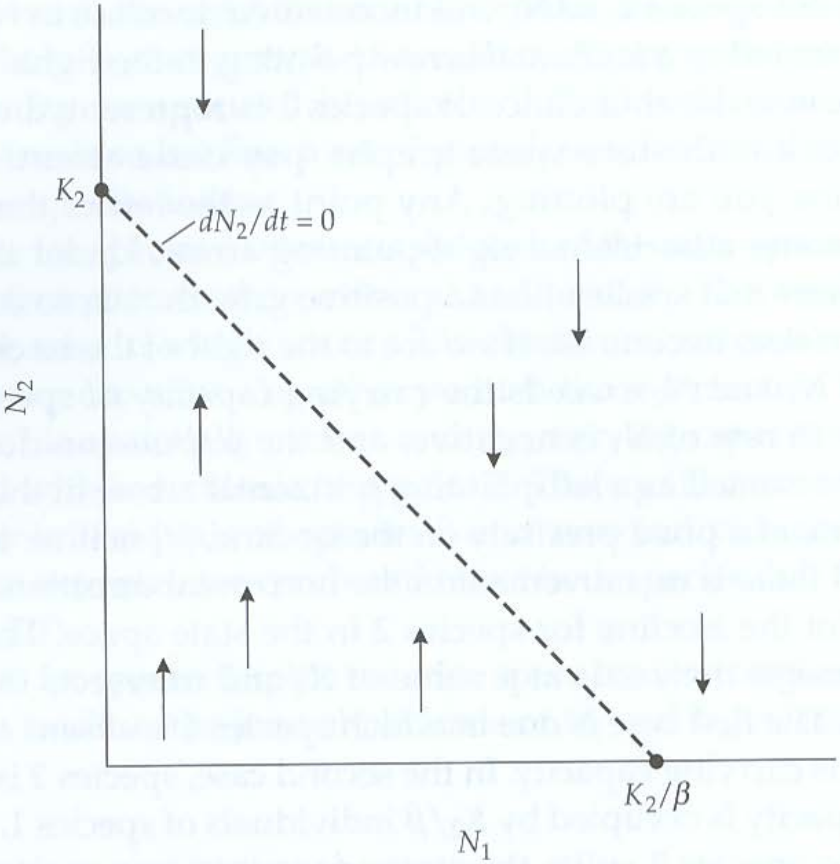


Figure 5.4 The isocline for species 2 in the Lotka–Volterra competition model. Note that the arrows point vertically for species 2, because its abundance is measured on the *y* axis of the state space graph.

Competition

Can overlay these isoclines to predict outcome of competition. There are four general outcomes:

1. Sp 1 wins: If isocline of sp 1 is entirely above that of sp2

2. Sp 2 wins: If isocline of sp 2 is entirely above that of sp 1

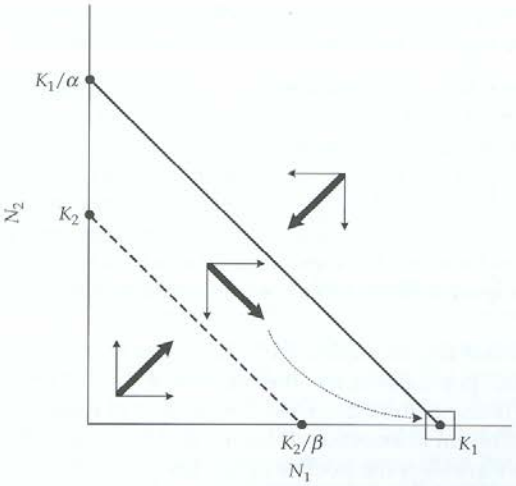


Figure 5.5 Case 1: Competitive exclusion of species 2 by species 1. The thin arrows show the trajectories of each population, and the thick arrow is the joint vector of movement. Competition results in the exclusion of species 2 and an equilibrium for species 1 at carrying capacity. The box indicates a stable equilibrium point.

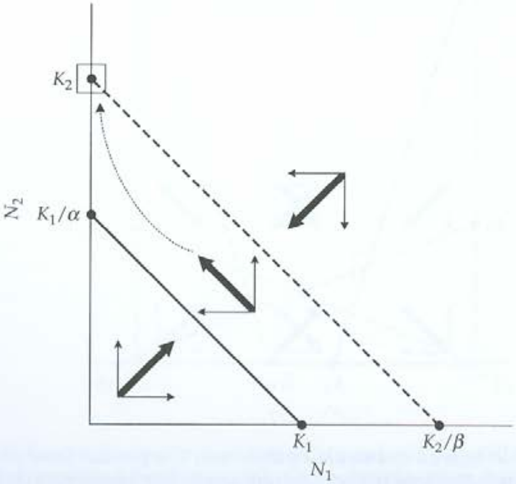


Figure 5.6 Case 2: Competitive exclusion of species 1 by species 2.

Competition

3. Stable Coexistence: Isoclines of species cross such that K for sp2 alone is less than its abundance in units of sp1 if sp 1 were absent, and vice versa (if its resource use is translated into units of sp2, it would have a higher K than it does in its actual use)

4. Unstable Coexistence: Isoclines of species cross such that K for sp2 alone is greater than its abundance in units of sp1 if sp 1 were absent, and vice versa (if its resource use is translated into units of sp2, it would have a lower K than it does in its actual use)

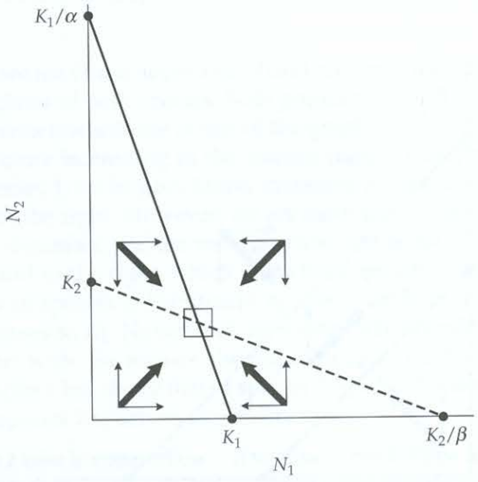


Figure 5.7 Case 3: Coexistence in a stable equilibrium. The two isoclines cross, and the joint vectors point in towards the equilibrium point. The equilibrium is stable because if the populations are displaced, they will always return to their equilibrium sizes.

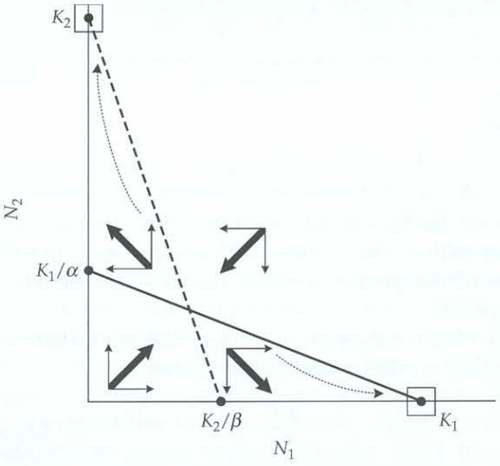


Figure 5.8 Case 4: Competitive exclusion in an unstable equilibrium. The two isoclines again cross and form an equilibrium point. However, the joint vectors point away from this equilibrium. If the populations are displaced, one species or the other will win in competition, depending on the starting abundances.

Competition

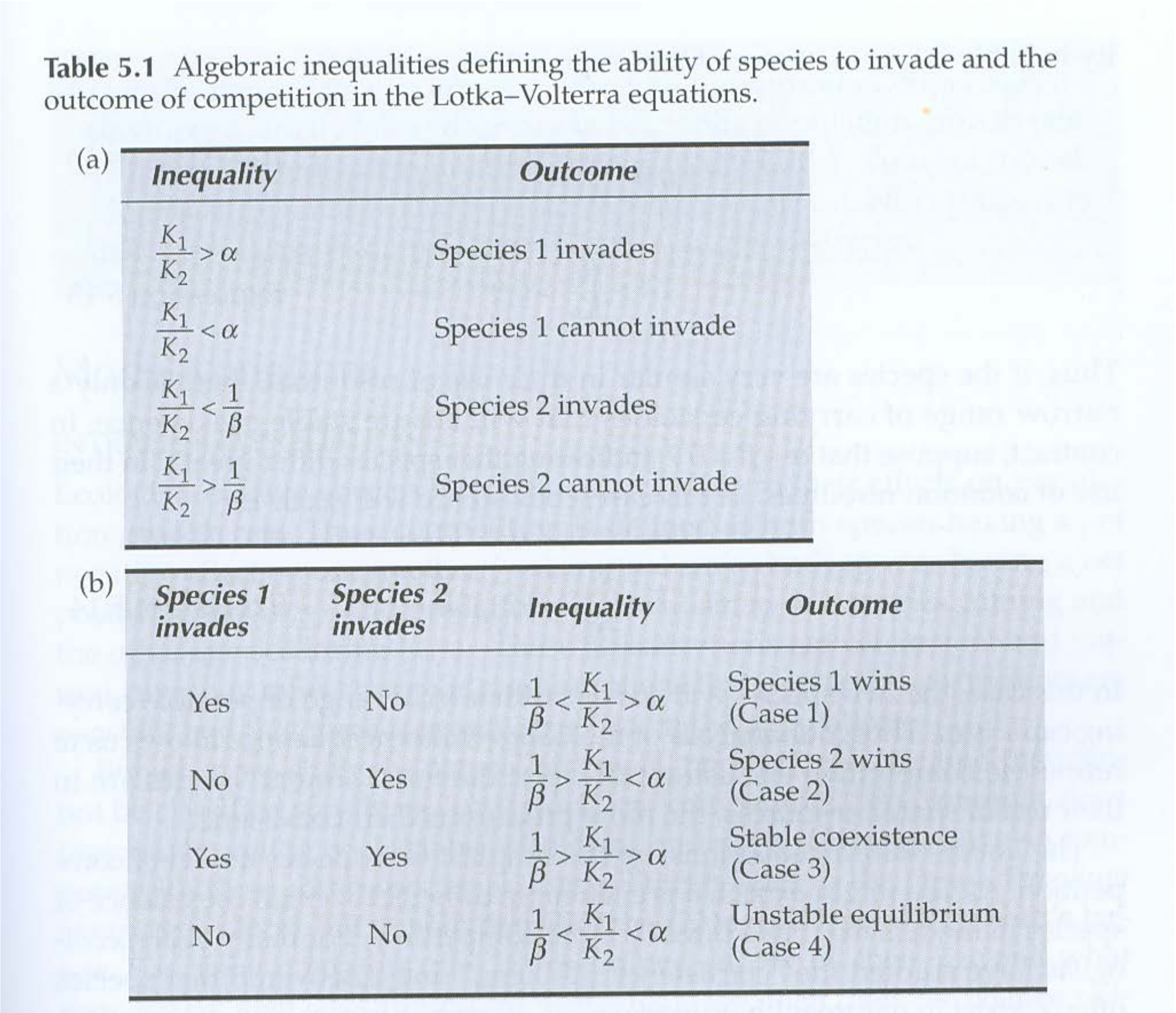


Table 5.1 Algebraic inequalities defining the ability of species to invade and the outcome of competition in the Lotka–Volterra equations.

(a)

Inequality	*Outcome*
$\frac{K_1}{K_2} > \alpha$	Species 1 invades
$\frac{K_1}{K_2} < \alpha$	Species 1 cannot invade
$\frac{K_1}{K_2} < \frac{1}{\beta}$	Species 2 invades
$\frac{K_1}{K_2} > \frac{1}{\beta}$	Species 2 cannot invade

(b)

Species 1 invades	*Species 2 invades*	*Inequality*	*Outcome*
Yes	No	$\frac{1}{\beta} < \frac{K_1}{K_2} > \alpha$	Species 1 wins (Case 1)
No	Yes	$\frac{1}{\beta} > \frac{K_1}{K_2} < \alpha$	Species 2 wins (Case 2)
Yes	Yes	$\frac{1}{\beta} > \frac{K_1}{K_2} > \alpha$	Stable coexistence (Case 3)
No	No	$\frac{1}{\beta} < \frac{K_1}{K_2} < \alpha$	Unstable equilibrium (Case 4)

Competition

Lotka-Volterra results lead to the

Principle of Competitive Exclusion (Gause's Principle): complete competitors can not coexist; two species must differ in resource use to coexist at a stable equilibrium.

If we observe coexistence of species with no clear differences in resource use, probably violate assumptions of this simple model.

Competition

Assumptions:

1. Resources are in limited supply;
2. All individuals of each species randomly interact with all individuals of the other species
3. Competition coefficients (α and β) and carrying capacities (K_1 and K_2) are constant (variation difficult to measure and cloud ability to predict outcome);
4. Density dependence is linear (adding an individual of either species has the same effect at all densities).

Competition

Other concepts in this area:

1. Liebig’s Law of the Minimum (p45) and Redfield Ratios
2. Forms of competition:
    a. Resource competition (scramble) … indirect
    b. Interference competition (contest)… direct
    c. Intraspecific vs interspecific
3. Niche concepts (p54-59)
    a. Role of orgs in community (Elton)
    b. Range of environments where found (Grinnell)… fundamental and realized niches
4. Hutchinson’s Paradox of the Plankton (p319)
5. Character displacement (p31)
6. Apparent competition (p 59, 208)
7. Intraguild predation (p118)
8. HSS models (125-127)
9. Ghost of competition past

Competition

Competitive Exclusion Principle – complete competitors can not coexist (Hardin 1960; but from Gause's classic experiments with protists)

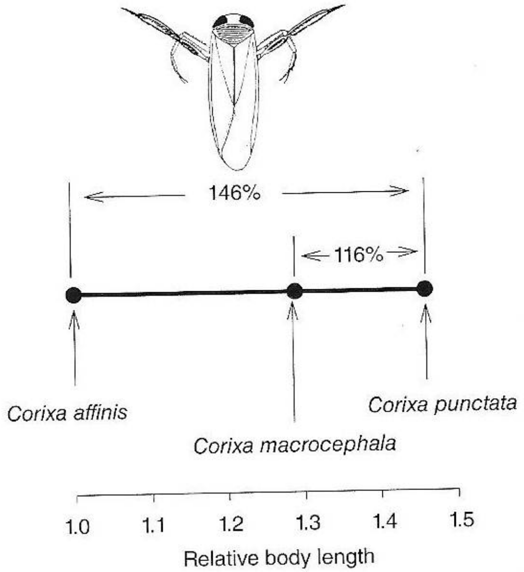
Note: Priority effects - initial conditions determine outcome of an interaction (spp already present inhibits or facilitates other spp success) fig 5.8, case 4

Limiting similarities

Caveat Emptor!

- Hutchinson’s (1959) concept of limiting morphological similarity from famous Homage to Santa Rosalia paper

Fig. 1.8 Corixids, a kind of common aquatic hemipteran insect, inspired Hutchinson’s (1959) concept of limiting morphological similarity of coexisting species. Relative sizes of the three species considered by Hutchinson are indicated by their positions along a scale that corresponds to relative body size.



- Led to claim of minimum ratio of some aspect of size tied to resource partitioning of 1.3
- Unfortunately, this concept has not proven helpful and was a big distraction in the literature.

Character displacement

- Differences in morphology of ecologically similar species is greater in sympatry than allopatry
    - Evidence mixed and controversial
    - Mostly descriptive, important in development of null model concept
    - Some descriptive/experimental support in specific systems; Galapagos finches during times of drought stress (Grant and Grant)

Competition – Paradox of the Plankton

From: Hutchinson, GE. 1961. The Paradox of the Plankton. AmNat 95:137-145

“The principle of **competitive exclusion** has recently been under attack from a number of quarters. Since the principle can be deduced mathematically from a relatively simple series of postulates, which with the ordinary postulates of mathematics can be regarded as forming an axiom system, it follows that if the objections to the principle in any cases are valid, some or all the biological axioms introduced are in these cases incorrect. Most objections to the principle appear to imply the belief that equilibrium under a given set of environmental conditions is never in practice obtained. Since the deduction of the principle implies an equilibrium system, if such systems are rarely if ever approached, the principle though analytically true, is at first sight of little empirical interest.” Pp 137-138

Proposed the solution to diversity of phytoplankton in seemingly homogenous waters is mixing and **non-equilibrium conditions**.

Competition – Paradox of Plankton

Consider:

t_c = time to complete competitive replacement of one species by another

t_e = time taken for a significant seasonal change in the environment.

1. $t_c << t_e$ competitive exclusion at equilibrium complete before the environment changes significantly.
2. $t_c \approx t_e$ no equilibrium achieved.
3. $t_c >> t_e$ competitive exclusion occurring in a changing environment to the full range of which individual competitors would have to be adapted to live alone (i.e., large long-lived species integrate over short-term environmental change and exclude small short-lived ones that can't keep up with environmental change)

Chesson and Huntly (1997) showed that species must differ in their responses to environmental change to co-exist (i.e., for environmental fluctuation to maintain species diversity)

THE ROLES OF HARSH AND FLUCTUATING CONDITIONS IN THE DYNAMICS OF ECOLOGICAL COMMUNITIES

Peter Chesson and Nancy Huntly

Abstract.—Harsh conditions (e.g., mortality and stress) reduce population growth rates directly; secondarily, they may reduce the intensity of interactions between organisms. Near-exclusive focus on the secondary effect of these forms of harshness has led ecologists to believe that they reduce the importance of ecological interactions, such as competition, and favor coexistence of even ecologically very similar species. By examining both the costs and the benefits, we show that harshness alone does not lessen the importance of species interactions or limit their role in community structure. Species coexistence requires niche differences, and harshness does not in itself make coexistence more likely. Fluctuations in environmental conditions (e.g., disturbance, seasonal change, and weather variation) also have been regarded as decreasing species interactions and favoring coexistence, but we argue that coexistence can only be favored when fluctuations create spatial or temporal niche opportunities. We argue that important diversity-promoting roles for harsh and fluctuating conditions depend on deviations from the assumptions of additive effects and linear dependencies most commonly found in ecological models. Such considerations imply strong roles for species interactions in the diversity of a community.

Am. Nat. 1997. Vol. 150, pp. 519–553