

different dimensional parameter changes. For example, doubling the carrying capacity K is exactly equivalent to halving the predator response parameter D . The dimensionless parameters are the important bifurcation ones to determine.

3.5 Competition Models: Principle of Competitive Exclusion

Here two or more species compete for the same limited food source or in some way inhibit each other's growth. For example, competition may be for territory which is directly related to food resources. Some interesting phenomena have been found from the study of practical competition models; see, for example, Hsu et al. (1979). Here we discuss a very simple competition model which demonstrates a fairly general principle which is observed to hold in Nature, namely, that when two species compete for the same limited resources one of the species usually becomes extinct.

Consider the basic 2-species Lotka–Volterra competition model with each species N_1 and N_2 having logistic growth in the absence of the other. Inclusion of logistic growth in the Lotka–Volterra systems makes them much more realistic, but to highlight the principle we consider the simpler model which nevertheless reflects many of the properties of more complicated models, particularly as regards stability. We thus consider

$$\frac{dN_1}{dt} = r_1 N_1 \left[1 - \frac{N_1}{K_1} - b_{12} \frac{N_2}{K_1} \right], \quad (3.29)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left[1 - \frac{N_2}{K_2} - b_{21} \frac{N_1}{K_2} \right], \quad (3.30)$$

where $r_1, K_1, r_2, K_2, b_{12}$ and b_{21} are all positive constants and, as before, the r 's are the linear birth rates and the K 's are the carrying capacities. The b_{12} and b_{21} measure the competitive effect of N_2 on N_1 and N_1 on N_2 respectively: they are generally not equal. Note that the competition model (3.29) and (3.30) is not a conservative system like its Lotka–Volterra predator–prey counterpart.

If we nondimensionalise this model by writing

$$\begin{aligned} u_1 = \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \\ a_{12} = b_{12} \frac{K_2}{K_1}, \quad a_{21} = b_{21} \frac{K_1}{K_2} \end{aligned} \quad (3.31)$$

(3.29) and (3.30) become

$$\begin{aligned} \frac{du_1}{d\tau} &= u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2), \\ \frac{du_2}{d\tau} &= \rho u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2). \end{aligned} \quad (3.32)$$

The steady states, and phase plane singularities, u_1^*, u_2^* , are solutions of $f_1(u_1, u_2) = f_2(u_1, u_2) = 0$ which, from (3.32), are

$$\begin{aligned}
 u_1^* = 0, u_2^* = 0; \quad u_1^* = 1, u_2^* = 0; \quad u_1^* = 0, u_2^* = 1; \\
 u_1^* = \frac{1 - a_{12}}{1 - a_{12}a_{21}}, u_2^* = \frac{1 - a_{21}}{1 - a_{12}a_{21}}.
 \end{aligned}
 \tag{3.33}$$

The last of these is only of relevance if $u_1^* \geq 0$ and $u_2^* \geq 0$ are finite, in which case $a_{12}a_{21} \neq 1$. The four possibilities are seen immediately on drawing the null clines $f_1 = 0$ and $f_2 = 0$ in the u_1, u_2 phase plane as shown in Figure 3.10. The crucial part of the null clines are, from (3.32), the straight lines

$$1 - u_1 - a_{12}u_2 = 0, \quad 1 - u_2 - a_{21}u_1 = 0.$$

The first of these together with the u_2 -axis is $f_1 = 0$, while the second, together with the u_1 -axis is $f_2 = 0$.

The stability of the steady states is again determined by the community matrix which, for (3.32), is

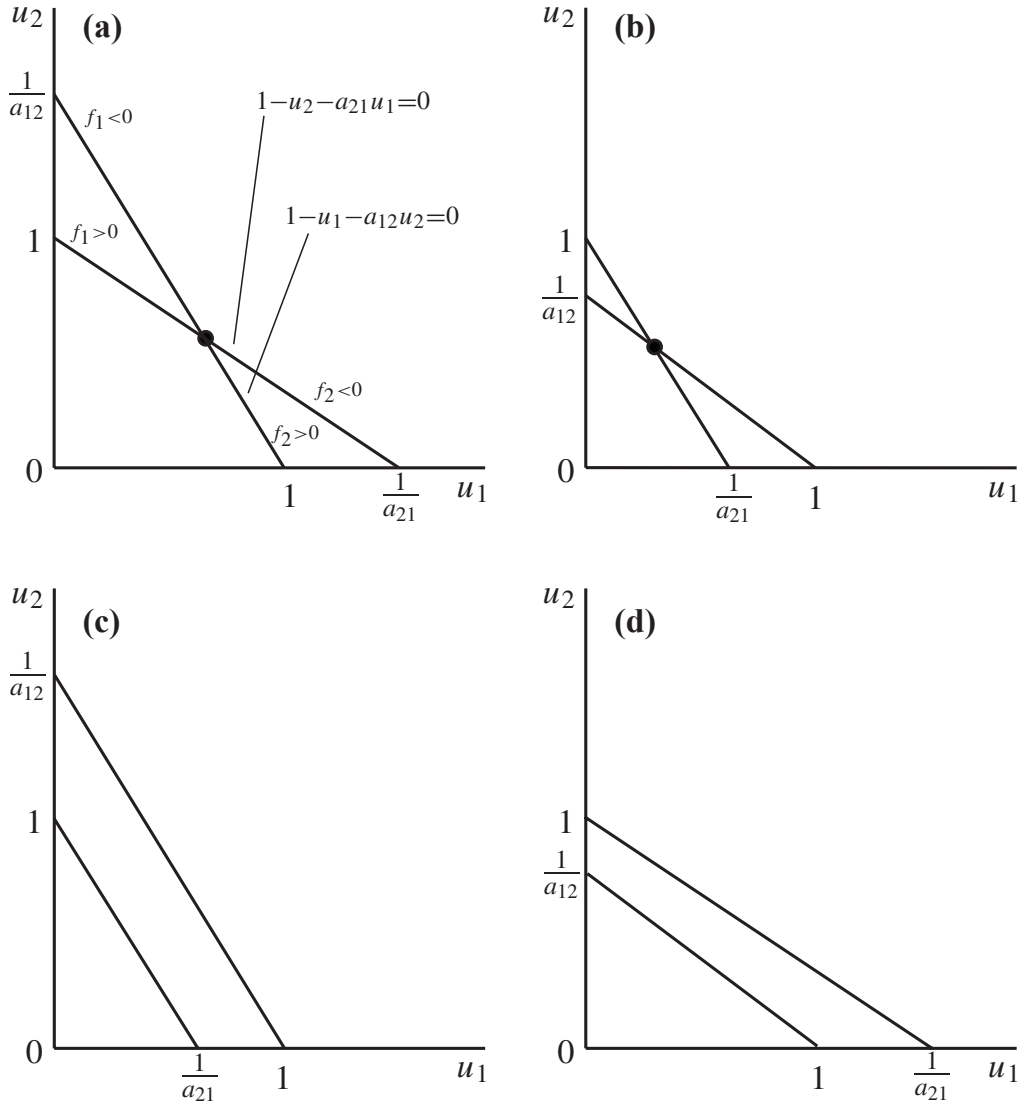


Figure 3.10. The null clines for the competition model (3.32). $f_1 = 0$ is $u_1 = 0$ and $1 - u_1 - a_{12}u_2 = 0$ with $f_2 = 0$ being $u_2 = 0$ and $1 - u_2 - a_{21}u_1 = 0$. The intersection of the two solid lines gives the positive steady state if it exists as in (a) and (b); the relative sizes of a_{12} and a_{21} as compared with 1 for it to exist are obvious from (a) to (d).

$$\begin{aligned}
 A &= \left(\begin{array}{cc} \frac{\partial f_1}{\partial u_1} & \frac{\partial f_1}{\partial u_2} \\ \frac{\partial f_2}{\partial u_1} & \frac{\partial f_2}{\partial u_2} \end{array} \right)_{u_1^*, u_2^*} \\
 &= \left(\begin{array}{cc} 1 - 2u_1 - a_{12}u_2 & -a_{12}u_1 \\ -\rho a_{21}u_2 & \rho(1 - 2u_2 - a_{21}u_1) \end{array} \right)_{u_1^*, u_2^*}.
 \end{aligned} \tag{3.34}$$

The first steady state in (3.33), that is, $(0, 0)$, is unstable since the eigenvalues λ of its community matrix, given from (3.34) by

$$|A - \lambda I| = \begin{vmatrix} 1 - \lambda & 0 \\ 0 & \rho - \lambda \end{vmatrix} = 0 \Rightarrow \lambda_1 = 1, \lambda_2 = \rho,$$

are positive. For the second of (3.33), namely, $(1, 0)$, (3.34) gives

$$|A - \lambda I| = \begin{vmatrix} -1 - \lambda & -a_{12} \\ 0 & \rho(1 - a_{21}) - \lambda \end{vmatrix} = 0 \Rightarrow \begin{array}{l} \lambda_1 = -1, \\ \lambda_2 = \rho(1 - a_{21}) \end{array}$$

and so

$$u_1^* = 1, u_2^* = 0 \text{ is } \begin{cases} \text{stable} \\ \text{unstable} \end{cases} \text{ if } \begin{cases} a_{21} > 1 \\ a_{21} < 1 \end{cases}. \tag{3.35}$$

Similarly, for the third steady state, $(0, 1)$, the eigenvalues are $\lambda = -\rho, \lambda_2 = (1 - a_{12})$ and so

$$u_1^* = 0, u_2^* = 1 \text{ is } \begin{cases} \text{stable} \\ \text{unstable} \end{cases} \text{ if } \begin{cases} a_{12} > 1 \\ a_{12} < 1 \end{cases}. \tag{3.36}$$

Finally for the last steady state in (3.33), when it exists in the positive quadrant, the matrix A from (3.34) is

$$A = (1 - a_{12}a_{21})^{-1} \begin{pmatrix} a_{12} - 1 & a_{12}(a_{12} - 1) \\ \rho a_{21}(a_{21} - 1) & \rho(a_{21} - 1) \end{pmatrix}$$

which has eigenvalues

$$\begin{aligned}
 \lambda_1, \lambda_2 &= [2(1 - a_{12}a_{21})]^{-1} [(a_{12} - 1) + \rho(a_{21} - 1) \\
 &\quad \pm \{[(a_{12} - 1) + \rho(a_{21} - 1)]^2 - 4\rho(1 - a_{12}a_{21})(a_{12} - 1)(a_{21} - 1)\}^{1/2}].
 \end{aligned} \tag{3.37}$$

The sign of λ , or $\text{Re } \lambda$ if complex, and hence the stability of the steady state, depends on the size of ρ, a_{12} and a_{21} . There are several cases we have to consider, all of which have ecological implications which we come to below.

Before discussing the various cases note that there is a confined set on the boundary of which the vector of the derivatives, $(du_1/d\tau, du_2/d\tau)$, points along it or inwards: here it is a rectangular box in the (u_1, u_2) plane. From (3.32) this condition holds on the u_1 - and u_2 -axes. Outer edges of the rectangle are, for example, the lines $u_1 = U_1$ where $1 - U_1 - a_{12}u_2 < 0$ and $u_2 = U_2$ where $1 - U_2 - a_{21}u_1 < 0$. Any $U_1 > 1, U_2 > 1$ suffice. So the system is always globally stable.

The various cases are: (i) $a_{12} < 1, a_{21} < 1$, (ii) $a_{12} > 1, a_{21} > 1$, (iii) $a_{12} < 1, a_{21} > 1$, (iv) $a_{12} > 1, a_{21} < 1$. All of these are analyzed in a similar way. Figures 3.10(a) to (d) and Figures 3.11(a) to (d) relate to these cases (i) to (iv) respectively. By way of example, we consider just one of them, namely, (ii). The analysis of the other cases is left as an exercise. The results are encapsulated in Figure 3.11. The arrows in-

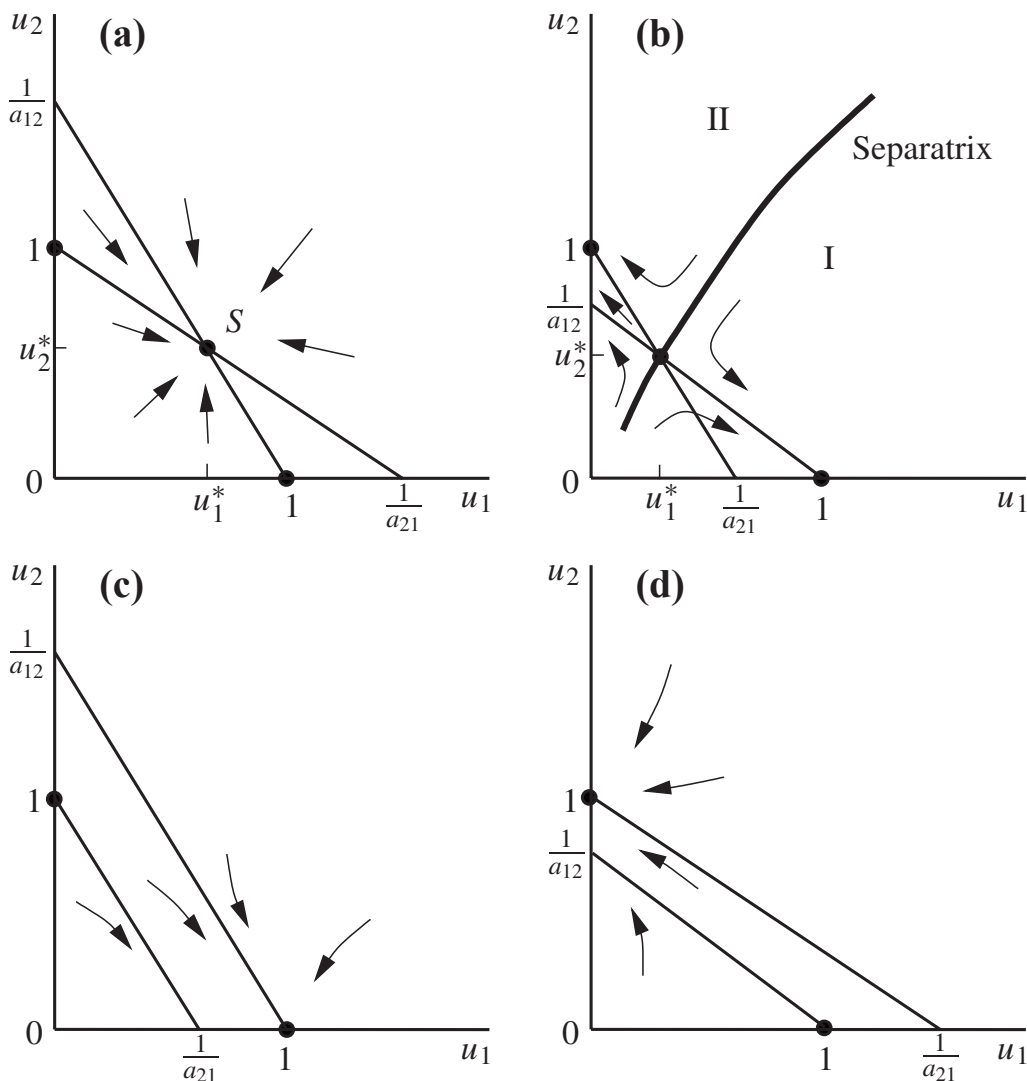


Figure 3.11. Schematic phase trajectories near the steady states for the dynamic behaviour of competing populations satisfying the model (3.32) for the various cases. (a) $a_{12} < 1, a_{21} < 1$. Only the positive steady state S is stable and all trajectories tend to it. (b) $a_{12} > 1, a_{21} > 1$. Here, $(1, 0)$ and $(0, 1)$ are stable steady states, each of which has a domain of attraction separated by a separatrix which passes through (u_1^*, u_2^*) . (c) $a_{12} < 1, a_{21} > 1$. Only one stable steady state exists, $u_1^* = 1, u_2^* = 0$ with the whole positive quadrant its domain of attraction. (d) $a_{12} > 1, a_{21} < 1$. The only stable steady state is $u_1^* = 0, u_2^* = 1$ with the positive quadrant as its domain of attraction. Cases (b) to (d) illustrate the competitive exclusion principle whereby 2 species competing for the same limited resource cannot in general coexist.

dicating the direction of the phase trajectories. The qualitative behaviour of the phase trajectories is given by the signs of $du_1/d\tau$, namely, $f_1(u_1, u_2)$, and $du_2/d\tau$ which is $f_2(u_1, u_2)$, on either side of the null clines.

Case $a_{12} > 1, a_{21} > 1$. This corresponds to Figure 3.10(b). From (3.35) and (3.36), $(1, 0)$ and $(0, 1)$ are stable. Since $1 - a_{12}a_{21} < 0$, (u_1^*, u_2^*) , the fourth steady state in (3.33), lies in the positive quadrant and from (3.37) its eigenvalues are such that $\lambda_2 < 0 < \lambda_1$ and so it is unstable to small perturbations: it is a saddle point. In this case, then, the phase trajectories can tend to either one of the two steady states, as illustrated in Figure 3.11(b). Each steady state has a *domain of attraction*. There is a line, a *separatrix*, which divides the positive quadrant into 2 nonoverlapping regions I and II as in Figure 3.11(b). The separatrix passes through the steady state (u_1^*, u_2^*) : it is one of the saddle point trajectories in fact.

Now consider some of the ecological implications of these results. In case (i) where $a_{12} < 1$ and $a_{21} < 1$ there is a stable steady state where both species can exist as in Figure 3.10(a). In terms of the original parameters from (3.31) this corresponds to $b_{12}K_2/K_1 < 1$ and $b_{21}K_1/K_2 < 1$. For example, if K_1 and K_2 are approximately the same and the interspecific competition, as measured by b_{12} and b_{21} , is not too strong, these conditions say that the two species simply adjust to a lower population size than if there were no competition. In other words, the competition is not aggressive. On the other hand if the b_{12} and b_{21} are about the same and the K_1 and K_2 are different, it is not easy to tell what will happen until we form and compare the *dimensionless* groupings a_{12} and a_{21} .

In case (ii), where $a_{12} > 1$ and $a_{21} > 1$, if the K 's are about equal, then the b_{12} and b_{21} are not small. The analysis then says that the competition is such that all three nontrivial steady states can exist, but, from (3.35) to (3.37), only $(1, 0)$ and $(0, 1)$ are stable, as in Figure 3.11(b). It can be a delicate matter which ultimately wins out. It depends crucially on the starting advantage each species has. If the initial conditions lie in domain I then eventually species 2 will die out, $u_2 \rightarrow 0$ and $u_1 \rightarrow 1$; that is, $N_1 \rightarrow K_1$ the carrying capacity of the environment for N_1 . Thus competition here has eliminated N_2 . On the other hand if N_2 has an initial size advantage so that u_1 and u_2 start in region II then $u_1 \rightarrow 0$ and $u_2 \rightarrow 1$ in which case the N_1 -species becomes extinct and $N_2 \rightarrow K_2$, its environmental carrying capacity. We expect extinction of one species even if the initial populations are close to the separatrix and in fact if they lie on it, since the ever present random fluctuations will inevitably cause one of $u_i, i = 1, 2$ to tend to zero.

Cases (iii) and (iv) in which the *interspecific* competition of one species is much stronger than the other, or the carrying capacities are sufficiently different so that $a_{12} = b_{12}K_2/K_1 < 1$ and $a_{21} = b_{21}K_1/K_2 > 1$ or alternatively $a_{12} > 1$ and $a_{21} < 1$, are quite definite in the ultimate result. In case (iii), as in Figure 3.11(c), the stronger dimensionless interspecific competition of the u_1 -species dominates and the other species, u_2 , dies out. In case (iv) it is the other way round and species u_1 becomes extinct.

Although all cases do not result in species elimination, those in (iii) and (iv) always do and in (ii) it is inevitable due to natural fluctuations in the population levels. This work led to the *principle of competitive exclusion* which was mentioned above. Note that the conditions for this to hold depend on the *dimensionless* parameter groupings a_{12} and a_{21} : the growth rate ratio parameter ρ does not affect the gross stability results, just

the dynamics of the system. Since $a_{12} = b_{12}K_2/K_1$, $a_{21} = b_{21}K_1/K_2$ the conditions for competitive exclusion depend critically on the interplay between competition and the carrying capacities as well as the initial conditions in case (ii).

Suppose, for example, we have 2 species comprised of large animals and small animals, with both competing for the same grass in a fixed area. Suppose also that they are equally competitive with $b_{12} = b_{21}$. With N_1 the large animals and N_2 the small, $K_1 < K_2$ and so $a_{12} = b_{12}K_2/K_1 < b_{21}K_2/K_1 = a_{21}$. As an example if $b_{12} = 1 = b_{21}$, $a_{12} < 1$ and $a_{21} > 1$ then in this case $N_1 \rightarrow 0$ and $N_2 \rightarrow K_2$; that is, the large animals become extinct.

The situation in which $a_{12} = 1 = a_{21}$ is special and, with the usual stochastic variability in nature, is unlikely in the real world to hold exactly. In this case the competitive exclusion of one or the other of the species also occurs.

The importance of species competition in Nature is obvious. We have discussed only one particularly simple model but again the method of analysis is quite general. A review and introductory article by Pianka (1981) deals with some practical aspects of competition as does the book of lectures by Waltman (1984). A slightly simpler competition model (see Exercise 2) was applied by Flores (1998) to the extinction of Neanderthal man by Early Modern man. Flores' model is based on a slightly different mortality rate of the two species and he shows that coexistence is not possible. He estimates the relevant parameter from independent sources and his extinction period is in line with the accepted palaeontological data of 5000 to 10,000 years. In Chapters 1 and 14, Volume II we discuss some practical cases of spatial competition associated with squirrels, wolf–deer survival and the release of genetically engineered organisms.

3.6 Mutualism or Symbiosis

There are many examples where the interaction of two or more species is to the advantage of all. Mutualism or symbiosis often plays the crucial role in promoting and even maintaining such species: plant and seed dispersal is one example. Even if survival is not at stake the mutual advantage of mutualism or symbiosis can be very important. As a topic of theoretical ecology, even for two species, this area has not been as widely studied as the others even though its importance is comparable to that of predator–prey and competition interactions. This is in part due to the fact that simple models in the Lotka–Volterra vein give silly results. The simplest mutualism model equivalent to the classical Lotka–Volterra predator–prey one is

$$\frac{dN_1}{dt} = r_1N_1 + a_1N_1N_2, \quad \frac{dN_2}{dt} = r_2N_2 + a_2N_2N_1,$$

where r_1 , r_2 , a_1 and a_2 are all positive constants. Since $dN_1/dt > 0$ and $dN_2/dt > 0$, N_1 and N_2 simply grow unboundedly in, as May (1981) so aptly put it, ‘an orgy of mutual benefaction.’

Realistic models must at least show a mutual benefit to both species, or as many as are involved, and have some positive steady state or limit cycle type oscillation.

Some models which do this are described by Whittaker (1975). A practical example is discussed by May (1975).

As a first step in producing a reasonable 2-species model we incorporate limited carrying capacities for both species and consider

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1 \left(1 - \frac{N_1}{K_1} + b_{12} \frac{N_2}{K_1} \right) \\ \frac{dN_2}{dt} &= r_2 N_2 \left(1 - \frac{N_2}{K_2} + b_{21} \frac{N_1}{K_2} \right),\end{aligned}\tag{3.38}$$

where $r_1, r_2, K_1, K_2, b_{12}$ and b_{21} are all positive constants. If we use the same nondimensionalisation as in the competition model (the signs preceding the b 's are negative there), namely, (3.31), we get

$$\begin{aligned}\frac{du_1}{d\tau} &= u_1(1 - u_1 - a_{12}u_2) = f_1(u_1, u_2), \\ \frac{du_2}{d\tau} &= \rho u_2(1 - u_2 - a_{21}u_1) = f_2(u_1, u_2),\end{aligned}\tag{3.39}$$

where

$$\begin{aligned}u_1 &= \frac{N_1}{K_1}, \quad u_2 = \frac{N_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_2}{r_1}, \\ a_{12} &= b_{12} \frac{K_2}{K_1}, \quad a_{21} = b_{21} \frac{K_1}{K_2}.\end{aligned}\tag{3.40}$$

Analysing the model in the usual way we start with the steady states (u_1^*, u_2^*) which from (3.39) are

$$\begin{aligned}(0, 0), \quad (1, 0), \quad (0, 1), \\ \left(\frac{1 + a_{12}}{\delta}, \frac{1 + a_{21}}{\delta} \right), \quad \text{positive if } \delta = 1 - a_{12}a_{21} > 0.\end{aligned}\tag{3.41}$$

After calculating the community matrix for (3.39) and evaluating the eigenvalues λ for each of (3.41) it is straightforward to show that $(0, 0)$, $(1, 0)$ and $(0, 1)$ are all unstable: $(0, 0)$ is an unstable node and $(1, 0)$ and $(0, 1)$ are saddle point equilibria. If $1 - a_{12}a_{21} < 0$ there are only three steady states, the first three in (3.41), and so the populations become unbounded. We see this by drawing the null clines in the phase plane for (3.39), namely, $f_1 = 0$, $f_2 = 0$, and noting that the phase trajectories move off to infinity in a domain in which $u_1 \rightarrow \infty$ and $u_2 \rightarrow \infty$ as in Figure 3.12(a).

When $1 - a_{12}a_{21} > 0$, the fourth steady state in (3.41) exists in the positive quadrant. Evaluation of the eigenvalues of the community matrix shows it to be a stable equilibrium: it is a node singularity in the phase plane. This case is illustrated in Figure 3.12(b). Here all the trajectories in the positive quadrant tend to $u_1^* > 1$ and $u_2^* > 1$; that is, $N_1 > K_1$ and $N_2 > K_2$ and so each species has increased its steady state population from its maximum value in isolation.

This model has certain drawbacks. One is the sensitivity between unbounded growth and a finite positive steady state. It depends on the inequality $a_{12}a_{21} < 1$, which from

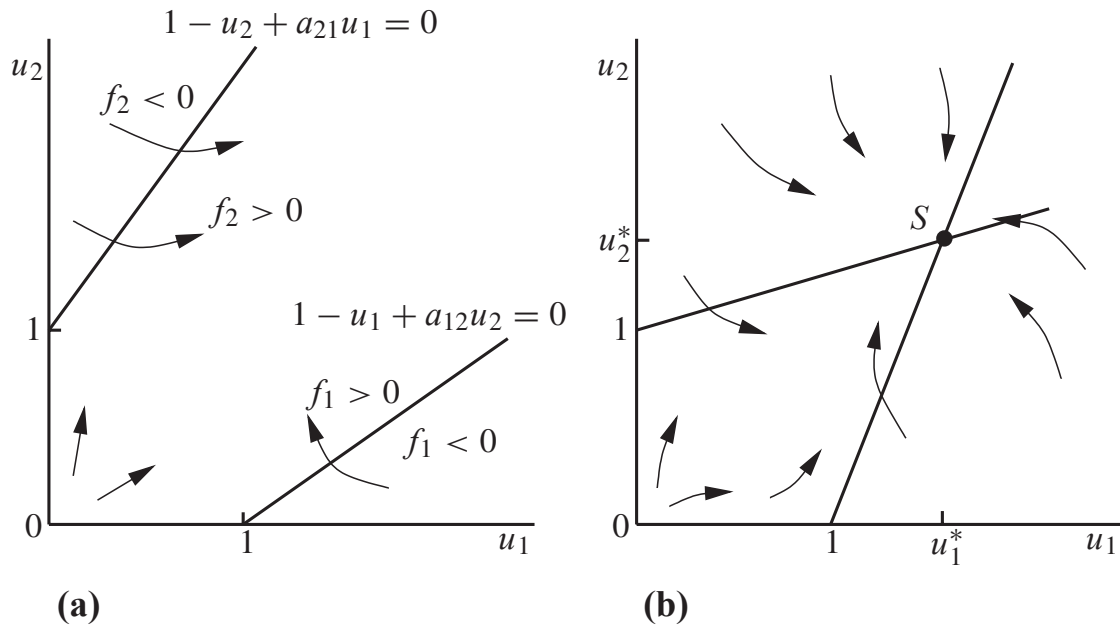


Figure 3.12. Phase trajectories for the mutualism model for two species with limited carrying capacities given by the dimensionless system (3.39). **(a)** $a_{12}a_{21} > 1$: unbounded growth occurs with $u_1 \rightarrow \infty$ and $u_2 \rightarrow \infty$ in the domain bounded by the null clines—the solid lines. **(b)** $a_{12}a_{21} < 1$: all trajectories tend to a positive steady state S with $u_1^* > 1, u_2^* > 1$ which shows the initial benefit that accrues since the carrying capacity for each species is greater than if no interaction were present.

(3.40) in terms of the original parameters in (3.38) is $b_{12}b_{21} < 1$: the b 's are dimensionless. So if symbiosis of either species is too large, this last condition is violated and both populations grow unboundedly.

3.7 General Models and Some General and Cautionary Remarks

All of the models we have discussed in this chapter result in systems of nonlinear differential equations of the form

$$\frac{dN_i}{dt} = N_i F_i(N_1, N_2, \dots, N_n), \quad i = 1, 2, \dots, \quad (3.42)$$

which emphasises the fact that the vector of populations \mathbf{N} has $\mathbf{N} = 0$ as a steady state. The two-species version is sometimes referred to as the Kolmogorov model or as the *Kolmogorov equations*.

Although we have mainly considered 2-species interactions in this chapter, in nature, and in the sea in particular, there are many species or *trophic levels* where energy, in the form of food, flows from one species to another. That is, there is a flow from one trophic level to another. The mass of the total number of individuals in a species is often referred to as its *biomass*, here the population times the unit mass. The ultimate source of energy is the sun, and in the sea, for example, the trophic web runs through plankton, fish, sharks up to whales and finally man, with the myriad of species in between. The species on one trophic level may predate several species below it. In general, models involve interaction between several species.