

Competitive Exclusion and Coexistence of Species with Complex Life Cycles

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Complex life cycles are life histories in which abrupt ontogenetic transformations and niche shifts occur at the transition between stages. The effects of this niche differentiation between stages on coexistence between species are investigated using a simple discrete model of two-stage populations. The model incorporates exploitation competition for limiting resources within stages, between stages, and between species. While species with simple life cycles can never coexist at equilibrium, stable coexistence is shown to be possible between species with complex life cycles provided that (1) one species is more efficient in resource utilization at low resource abundance in the larval stage while the other is more efficient at low resource abundance in the adult stage; and (2) each species is mainly limited by that stage which is less efficient at low resource abundance. Stable coexistence is somewhat easier between a species with a simple life cycle and one with a complex life cycle. It requires that (1) the species with the simple life cycle should not be decidedly more efficient than that with the complex life cycle in utilizing the resource on which it lives; and (2) the main resource limitation for the species with a complex life cycle should occur in that stage which escapes competition with the species with a simple life cycle. Lastly, a complex life cycle can offer a decisive competitive superiority over a simple life cycle in interspecific competition, which suggests that competition can be a driving force of the evolution of complex life cycles. © 1994 Academic Press, Inc.

INTRODUCTION

Many organisms pass through several well-distinct stages during their ontogeny. The metamorphosis of holometabolous insects or amphibians is the most spectacular example of the ontogenetic transformations that may

accompany the transition from one stage to another. Life histories in which such abrupt ontogenetic changes occur are called complex life cycles (Wilbur, 1980). Complex life cycles have far-reaching implications for ecology because the various stages usually occupy quite distinct habitats or ecological niches. As such they are extreme cases of ontogenetic niche shifts, which are widespread in many taxonomic groups (Werner and Gilliam, 1984). Does niche differentiation between stages make coexistence between species easier? Do complex life cycles have an advantage over simple life cycles in the competition between species? Are complex life cycles more stable than simple ones? These are some of the basic questions ecology should answer.

Yet the theory of complex life cycles is still in its infancy. Most theoretical questionings have concerned the evolution of complex life cycles, and the emphasis has been laid diversely on resource use, spatial heterogeneity, or temporal variability of the environment (Istock, 1967; Bryant, 1969; Slade and Wassersug, 1975; Wilbur, 1980). But a solid foundation in theoretical ecology is still lacking.

This lack is due in part to the difficulty in producing analytically tractable models of structured populations. Recent efforts have been accomplished in that direction using continuous equations (Tognetti, 1975; Rotenberg, 1977; Cushing, 1980; Nisbet and Gurney, 1983; Gurney *et al.*, 1983; Metz and Diekmann, 1986). But the models produced this way are still fairly complicated, notably because of the time lag involved in the duration of stages. So far they have not been applied to elucidate the problem of competition and niche differences between stages.

An alternative to continuous models lies in discrete models, which generalize the classical approach of Leslie matrices for modeling age-structured populations (Leslie, 1945, 1948) by incorporating some form of density dependence (May *et al.*, 1974; Travis *et al.*, 1980). This approach has more restricted conditions of application since it implies a regular and synchronous development liable to be described by a discrete process at fixed time intervals, while the continuous approach can model an asynchronous development in which developmental stages have an arbitrary duration (Nisbet and Gurney, 1983; Gurney *et al.*, 1983). It is, however, convenient for stage-structured organisms whose development is tuned in to the seasonal cycle of the environment, thus making generations effectively discrete, such as many insects and amphibians. Because of its (relative) simplicity it also has a great heuristic value. It has been used successfully in theoretical investigations of intraspecific competition between stages (May *et al.*, 1974; Tschumy, 1982; Ebenman, 1987, 1988; Loreau, 1990) and interspecific competition between two-stage populations (Hassell and Comins, 1976; Travis *et al.*, 1980; Bellows and Hassell, 1984; Mittelbach and Chesson, 1987). Nonetheless, most functional forms of

density dependence lead to analytically untractable models, and none of the above works has considered within-stage, between-stage, and between-species competition simultaneously. To our knowledge, the only theoretical investigation of the general issue of competition and coexistence of complex life cycles is that by Haefner and Edson (1984), which relies entirely on simulation.

In this paper, we analyse a general discrete model of two-stage populations which incorporates all the kinds of competitive interactions (within stages, between stages, and between species). The form of competition, however, is limited to exploitation competition for a single resource at each stage. The issues we want to address specifically using this model are whether the competitive exclusion principle holds for complex life cycles just as for simple life cycles, and whether complexity of the life cycle provides any advantage or disadvantage in interspecific competition. Stable coexistence among several consumers of one resource is well known to be impossible when competition is purely exploitative (MacArthur and Levins, 1964; Levin, 1970). But since the various stages of complex life cycles use different resources, it is conceivable that several complex life cycles may coexist on the same resources if they are competitively superior at different stages (Ayala, 1972; Wilbur, 1980). On the other hand, when competition occurs through interference, coexistence is possible even among species that use one and the same resource (Vance, 1985), and complexity of the life cycle can only add to its potential.

THE BASIC MODEL

Consider an organism with two stages, larvae or juveniles (L) and adults (A). Larvae grow during one season (or year etc.), at the end of which they yield an average number (or biomass etc.) of adults per larva, $\mu(N_L)$, which is a function of the amount of resources available to larvae, N_L . Adults breed during the next season, and yield an average number of larvae per adult, $\rho(N_A)$, which is a function of the amount of resources available to adults, N_A . They die with probability $\alpha(N_A)$ after reproduction ($0 < \alpha \leq 1$); a proportion $1 - \alpha(N_A)$ of the adult population thus survives to the following season. Similarly, a proportion $1 - \beta(N_L)$ of the larval population is allowed to survive from season to season ($0 < \beta \leq 1$). Both mortality probabilities are allowed to vary with the amount of resources available to each stage. The model thus reads

$$\begin{aligned} A(t+1) &= \{1 - \alpha[N_A(t)]\} A(t) + \mu[N_L(t)] L(t) \\ L(t+1) &= \{1 - \beta[N_L(t)]\} L(t) + \rho[N_A(t)] A(t) \end{aligned} \quad (1)$$

or, more compactly

$$\mathbf{X}(t+1) - \mathbf{X}(t) = \mathbf{G}(t) \mathbf{X}(t), \quad (2)$$

where $\mathbf{X}(t)$ is the vector of adult and larval subpopulation sizes, and

$$\mathbf{G}(t) = \begin{bmatrix} -\alpha & \mu \\ \rho & -\beta \end{bmatrix}_{(t)}$$

is the matrix that governs the growth of the population.

The functions α , β , μ , and ρ may have any form, but for them to be biologically reasonable we shall assume that the mortality probabilities α and β decrease, while the recruitment rates μ and ρ increase, monotonically with increasing amounts of resources. Thus:

$$\begin{aligned} d\alpha/dN_A &\leq 0, & d\beta/dN_L &\leq 0, \\ d\mu/dN_L &\geq 0, & d\rho/dN_A &\geq 0. \end{aligned} \quad (3)$$

Resources are specified in the model only because they mediate exploitation competition between consumer populations. To avoid the additional complexity of resource dynamics, we shall assume that its time scale is shorter than that of the consumers' dynamics, so that resource abundance is some function of the consumer populations:

$$N_X(t) = f_X[A(t), L(t)] \quad (X = A \text{ or } L). \quad (4)$$

We shall further scale the functions α , β , μ , and ρ so that resource abundance in the absence of consumers is equal to 1, and make the biologically reasonable assumptions that N_X decreases monotonically with increasing consumer populations. Thus,

$$f_X(0, 0) = 1, \quad f_X(\infty, \infty) = 0, \quad \partial f_X / \partial X \leq 0. \quad (5)$$

Model (1) is more general than the models used by most authors (May *et al.*, 1974; Hassell and Comins, 1976; Tschumy, 1982; Bellows, 1982; Bellows and Hassell, 1984; Ebenman, 1987, 1988) in that it allows part of the adult and larval populations to survive from one season to the next. Adult survival, which was also included in Mittelbach and Chesson (1987), is frequent after the first breeding season in natural populations, as in ground beetles or amphibians. Larval survival is rarer, but occurs in some amphibians (e.g., Collins, 1979; Bruce, 1985) and has been included for theoretical completeness (the case when larval survival is absent is merely a special case of the model where $\beta = 1$). The specific feature of Model (1), however, is that the functions α , β , μ , and ρ depend directly only on some

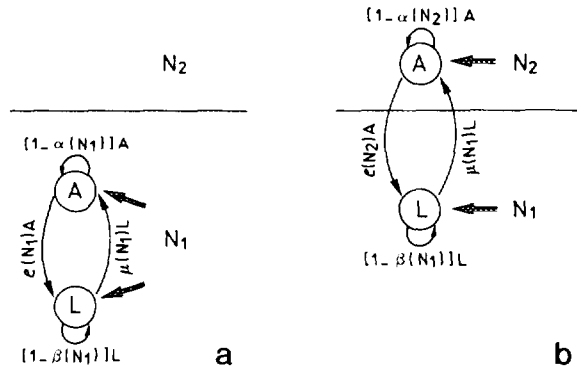


FIG. 1. Flow diagrams of a simple (a) and a complex (b) life cycle. The two resources N_1 and N_2 define two different niches (separated by the horizontal line). In the simple life cycle (a), the adult (A) and larval (L) stages occupy the same niche: they both consume N_1 (thick arrows). In the complex life cycle (b), the two stages occupy two different niches: larvae consume N_1 , and adults consume N_2 . Thin arrows show discrete population flows between two time units.

limiting resources which mediate exploitation competition among consumers, whether of the same stage, of different stages, or of different species.

In this model, simple and complex life cycles will be distinguished ecologically very sharply (Fig. 1): a simple life cycle will be defined as a life cycle in which the two stages occupy the same niche—they use the same resource $N_A = N_L = N_1$ (Fig. 1a)—and a complex life cycle as one in which the two stages occupy completely different niches—they use two different resources $N_L = N_1$ and $N_A = N_2$ (Fig. 1b).

The various cases we shall investigate below will differ from each other merely in the number of consumer populations that use resources N_1 and N_2 . We shall first briefly envisage the basic behaviour of single-species models, as a preliminary to the investigation of coexistence in models for two-species competition.

SINGLE-SPECIES DYNAMICS

A general isocline analysis of Model (1) without survival from one generation to the next was carried out by Tschumy (1982). When these survival terms are nonlinear, they reinforce the nonlinearity of the isoclines but do not change their shape qualitatively; thus the analysis of Tschumy need not be repeated here. Tschumy showed that there is generally one intrinsically stable equilibrium point, but multiple equilibria are possible, and equilibrium points can be unstable due to the time lag involved in discrete models.

Some general properties of the system described by Eqs. (1) and of its equilibria, however, are worth investigating in more detail because they can be used conveniently in the analysis of two-species competition. The equilibrium levels A^* and L^* reached by the adult and larval populations, respectively, are obtained by setting $A^* = A(t+1) = A(t)$ and $L^* = L(t+1) = L(t)$ in Eqs. (1). An equilibrium thus satisfies the two relations:

$$\alpha(N_A^*)A^* = \mu(N_L^*)L^* \quad (6.a)$$

$$\beta(N_L^*)L^* = \rho(N_A^*)A^*. \quad (6.b)$$

These can be combined to give the condition:

$$P(N_A^*, N_L^*) = \mu(N_L^*) \rho(N_A^*) / [\alpha(N_A^*) \beta(N_L^*)] = 1. \quad (7)$$

The quantity $P[N_A(t), N_L(t)]$ has a definite biological meaning: because $\rho[N_A(t)]$ is the average number of larvae yielded per adult in season t and $1/\alpha[N_A(t)]$ is the expected number of seasons an adult would live under the conditions prevailing at time t , $\rho[N_A(t)]/\alpha[N_A(t)]$ is the average number of larvae an adult would yield over its lifetime as an adult under those conditions; similarly, each of these larvae is expected to yield $\mu[N_L(t)]/\beta[N_L(t)]$ adults during its larval life under those conditions. Therefore $P[N_A(t), N_L(t)] = \{\rho[N_A(t)]/\alpha[N_A(t)]\} \{\mu[N_L(t)]/\beta[N_L(t)]\}$ is the expected number of offspring yielded by an individual over its whole lifetime under the conditions prevailing at time t ; it represents the *net reproductive rate* under those conditions. Equation (7) makes sense biologically; the net reproductive rate has to be equal to 1 for the population to keep steady.

Because of Conditions (3), P increases monotonically with N_A and N_L , and thus, because of (5), $P > 1$ when the population is under its equilibrium level, while $P < 1$ when the population is above its equilibrium level. Therefore the isocline $P(N_A, N_L) = 1$ in the (N_A, N_L) -square delimits two zones: one above the line where resources are abundant enough to allow further population growth ($P > 1$ means that on average parents leave more offspring than is necessary for their replacement), and another under the line where resources are too scarce to allow the population to keep steady ($P < 1$, and the population tends to decrease). This property will be used to analyse two-species competition graphically. A formal proof of the fact that $P - 1$ determines the sign of population growth is provided in the Appendix.

A corollary of the foregoing is that a feasible equilibrium exists if and only if $P > 1$ when resources are at their maximum abundance ($N_A = N_L = 1$):

$$P(1, 1) = \mu(1) \rho(1) / [\alpha(1) \beta(1)] = R > 1 \quad (8)$$

which is the condition for the population to invade the environment. R is known as the *basic reproductive rate* in the population dynamics of infectious diseases (Anderson, 1981), and represents the average number of offspring produced by an individual over its lifetime in a very small population (in which density dependence is negligible). Clearly the basic reproductive rate has to be greater than 1 for a population to invade and persist in a given environment.

We shall therefore assume in what follows that Condition (8) is fulfilled for any species. We shall also assume that the single-species equilibrium is stable. It is well known that the competitive exclusion principle does not necessarily hold under non-equilibrium conditions (Levins, 1979; Armstrong and McGehee, 1980), but the analysis is here restricted to the conditions in which the competitive exclusion principle applies to populations without a complex life cycle, that is, equilibrium conditions.

TWO-SPECIES COMPETITION

When two species compete, their population dynamics is still described by Model (1), but all variables, functions and parameters will now have a subscript which associates them with species 1 or 2. We shall further denote by $N_j^{(i)}$ the equilibrium abundance of resource j with the single species i present ($i, j = 1$ or 2).

Three qualitatively different cases are possible, depending on whether the two species are both species with a simple life cycle, both species with a complex life cycle, or one species with a simple life cycle and the other with a complex life cycle. We shall examine these cases successively.

1. Two Simple Life Cycles

When two species with simple life cycles occupy the same niche (Fig. 2.1), we have

$$N_{A_1}(t) = N_{L_1}(t) = N_{A_2}(t) = N_{L_2}(t) = N_1(t) = f_1[A_1(t), L_1(t), A_2(t), L_2(t)]. \quad (9)$$

Since both species live on the same single resource, they each reach an equilibrium for a unique equilibrium resource abundance, which is, from Condition (7),

$$N_1^{(i)} = P_i^{-1}(1), \quad (10)$$

where P_i^{-1} is the inverse of the function P_i . These vertical isoclines do not cross, and the species that lowers the equilibrium level of N_1 most (species 1 in Fig. 3) outcompetes the other, in accordance with the competitive exclusion principle (MacArthur and Levins, 1964; Levin, 1970).

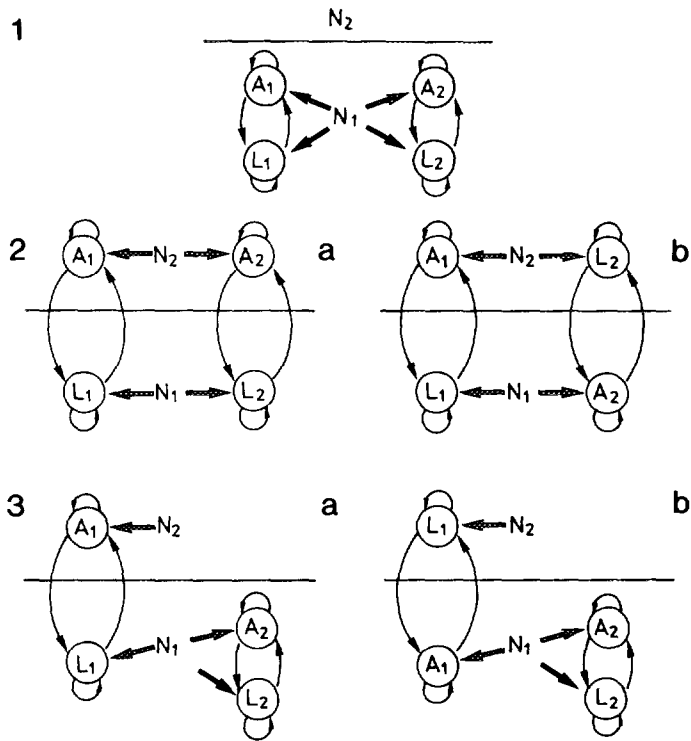


FIG. 2. Flow diagrams of two-species competition. 1: two simple life cycles; 2: two complex life cycles, niches similar (a) or niches inverted (b); 3: one simple and one complex life cycle, adults (a) or larvae (b) escape interspecific competition.

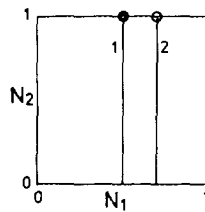


FIG. 3. Graphical analysis of competition between two species with simple life cycles. The lines 1 and 2 are the isoines $P_i(N_1, N_2) = 1$ of species $i = 1$ and 2. Open circles indicate unstable equilibria, while full circles indicate stable equilibria.

2. Two Complex Life Cycles

When the two species have complex life cycles, two symmetrical cases are theoretically possible: either both species occupy the same niche at each stage (Fig. 2.2a), or the adults of each species occupy the same niche as the larvae of the other species (Fig. 2.2b) (although the latter case is admittedly implausible). In the first case,

$$\begin{aligned} N_{L_1}(t) = N_{L_2}(t) = N_1(t) &= f_1[L_1(t), L_2(t)] \\ N_{A_1}(t) = N_{A_2}(t) = N_2(t) &= f_2[A_1(t), A_2(t)]. \end{aligned} \quad (11)$$

In the second case,

$$\begin{aligned} N_{L_1}(t) = N_{A_2}(t) = N_1(t) &= f_1[L_1(t), A_2(t)] \\ N_{A_1}(t) = N_{L_2}(t) = N_2(t) &= f_2[A_1(t), L_2(t)]. \end{aligned} \quad (12)$$

Since these two cases are symmetrical, we need only consider the first one. A graphical analysis (Fig. 4) shows that four qualitatively different outcomes are possible. If the isoclines do not cross, the species that lowers equilibrium resource abundance most (species 1 in Fig. 4a) outcompetes the other, as in the case of two simple life cycles. A necessary condition for coexistence is that the two isoclines cross, which occurs when one species is more efficient at low N_1 (species 1 in Figs. 4b–4d) while the other is more efficient at low N_2 (species 2 in Figs. 4b–4d). Three outcomes are then possible depending on the positions of the two single-species equilibrium points in relation to the intersection point of the isoclines. For each species i the position of its equilibrium point on the isocline is determined by one of Eqs. (6), say (6.a), which can be expressed in terms of resource abundance using (4):

$$\alpha_i(N_2^{(i)}) f_2^{-1}(N_2^{(i)}) = \mu_i(N_1^{(i)}) f_1^{-1}(N_1^{(i)}) \quad (13)$$

where f_j^{-1} is the inverse of the function f_j .

The three possible outcomes are shown in Figs. 4b–4d:

(1) If the equilibrium point of each species lies on that side of the intersection where that species is less efficient, each single-species equilibrium lies in the zone where the population of the other species grows, and the intersection point is a point of stable coexistence (Fig. 4b). Another way to put this is that stable coexistence is achieved when each species is mainly limited by that stage which is less efficient at low resource abundance (compared with the other species).

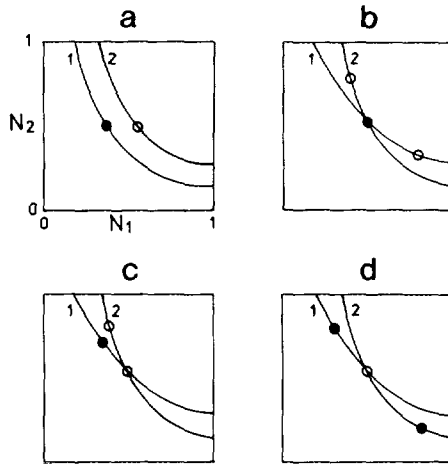


FIG. 4. Graphical analysis of the four qualitatively different outcomes of competition between two species with complex life cycles. Legend as in Fig. 3.

(2) If both single-species equilibrium points lie on the same side of the intersection, that species which is more efficient on that side (species 1 in Fig. 4c) outcompetes the other. The conclusion is of course identical in the case symmetrical to that shown in Fig. 4c when both single-species equilibrium points lie on the other side of the intersection (species 2 would then win).

(3) If the equilibrium point of each species lies on that side of the intersection where that species is more efficient, or, in other words, if each species is mainly limited by that stage which is more efficient at low resource abundance, the intersection point is unstable, and there are two alternative stable single-species equilibria depending on the initial conditions (Fig. 4d).

As an illustration of these qualitative conclusions, let us consider an example using simple specific functions. Assume that mortality is density independent in both stages and both species, and that recruitment rates follow the widely used Michaelis-Menten or Holling type-II function, that is,

$$\begin{aligned} \alpha_i(N_2) &= a_i, & \beta_i(N_1) &= b_i, \\ \mu_i(N_1) &= m_i N_1 / (k_i + N_1), & \rho_i(N_2) &= r_i N_2 / (s_i + N_2), \end{aligned} \quad (14)$$

where a_i and b_i are the constant mortality probabilities at the adult and larval stages, respectively, m_i and r_i are the maximum recruitment rates to

the adult and larval stages, respectively, and k_i and s_i are half-saturation constants which determine the efficiency of resource use at low resource abundance (the lower the half-saturation constant, the more efficient the resource use at low resource abundance).

Then

$$\begin{aligned} P_i(N_1, N_2) &= m_i r_i N_1 N_2 / [a_i b_i (k_i + N_1)(s_i + N_2)] \\ R_i &= m_i r_i / [a_i b_i (k_i + 1)(s_i + 1)]. \end{aligned} \quad (15)$$

If the two species do not differ by their half-saturation constants ($k_1 = k_2 = k$ and $s_1 = s_2 = s$), the equations of the two isoclines are

$$N_1 N_2 (k + 1)(s + 1) / [(k + N_1)(s + N_2)] = 1/R_i. \quad (16)$$

The isoclines have the same equation except for the constant R_i ; therefore they never cross and the species with the higher basic reproductive rate outcompetes the other as in Fig. 4a. This is the case more generally whenever two species do not differ by some nonlinear coefficient.

In general, the more different the basic reproductive rates of the two species, the more difficult an intersection of the isoclines. To illustrate the outcomes described in Figs. 4b–4d, let us consider the situation most favourable for an intersection of the isoclines, that is, when the basic reproductive rates of the two species are equal ($R_1 = R_2 = R$). From the graphs in Figs. 4b–4d it is readily seen that the two isoclines intersect if and only if the isocline of species 1 intersects the line $N_2 = 1$ at a smaller value of N_1 , but intersects the line $N_1 = 1$ at a higher value of N_2 , than does the isocline of species 2 (these inequalities must of course be reversed in the symmetrical case when the two isoclines are inverted compared with Fig. 4). When the two species have identical basic reproductive rates, these conditions reduce to

$$\begin{aligned} k_1 &< k_2 \\ s_1 &> s_2 \end{aligned} \quad (17)$$

which is precisely the condition derived qualitatively above, that is, species 1 must be more efficient at low resource abundance in the larval stage while species 2 must be more efficient at low resource abundance in the adult stage (or vice versa in the symmetrical case).

Since the three outcomes described in Figs. 4b–4d depend on the positions of the equilibrium points determined by Eq. (13), the form of the functions f_1 and f_2 needs to be further specified. For the sake of simplicity, the following form may be used for each species i in isolation:

$$\begin{aligned} N_1(t) &= f_1[L_i(t)] = 1/[1 + d_i L_i(t)] \\ N_2(t) &= f_2[A_i(t)] = 1/[1 + c_i A_i(t)]. \end{aligned} \quad (18)$$

Equation (13) then provides the equation of a second line along which the equilibrium point of each species i must lie:

$$N_2 = a_i d_i (k_i + N_1) / [a_i d_i (k_i + N_1) + m_i c_i (1 - N_1)]. \quad (19)$$

It is not difficult to verify that this line has the following properties:

$$\begin{aligned} 0 < N_2 < 1 & \quad \text{for } N_1 = 0 \\ N_2 = 1 & \quad \text{for } N_1 = 1 \\ dN_2/dN_1 > 0 & \\ d^2N_2/dN_1^2 = C(m_i c_i - a_i d_i) & \quad \text{where } C > 0. \end{aligned} \quad (20)$$

From this it results that this line remains above the diagonal in the (N_1, N_2) -square when $m_i c_i \leq a_i d_i$. Assuming that the isoclines intersect not too far from the diagonal, $m_i c_i < a_i d_i$ ensures that the equilibrium point of species i lies to the left of the intersection point, while a more or less strong concavity of the curve (19), that is, $m_i c_i \gg a_i d_i$, is necessary for the equilibrium point to lie to the right of the intersection point. Since c_i and d_i measure the strength of the dependence of resource abundance on the adult and larval density, respectively, their ratio indicates at which stage the main resource limitation occurs. The three qualitative outcomes analysed graphically above are thus recovered here:

(1) When $m_1 c_1 \gg a_1 d_1$ and $m_2 c_2 < a_2 d_2$, the main limitation occurs in each species at that stage which is less efficient at low resource abundance (adult stage for species 1, larval stage for species 2), and the situation described in Fig. 4b is recovered.

(2) When $m_1 c_1 < a_1 d_1$ and $m_2 c_2 < a_2 d_2$, the main limitation occurs at the larval stage in both species, and the situation described in Fig. 4c is recovered.

(3) When $m_1 c_1 < a_1 d_1$ and $m_2 c_2 \gg a_2 d_2$, the main limitation occurs in each species at that stage which is more efficient at low resource abundance (larval stage for species 1, adult stage for species 2), and the situation described in Fig. 4d is recovered.

3. One Simple and One Complex Life Cycle

When a species with a complex life cycle competes with one with a simple life cycle, one of its stages occupies a niche on its own and escapes inter-specific competition. Again two symmetrical cases are possible. Either the adults escape competition (Fig. 2.3a), in which case

$$\begin{aligned} N_{L1}(t) = N_{A2}(t) = N_{L2}(t) = N_1(t) &= f_1[L_1(t), A_2(t), L_2(t)] \\ N_{A1}(t) = N_2(t) &= f_2[A_1(t)] \end{aligned} \quad (21)$$

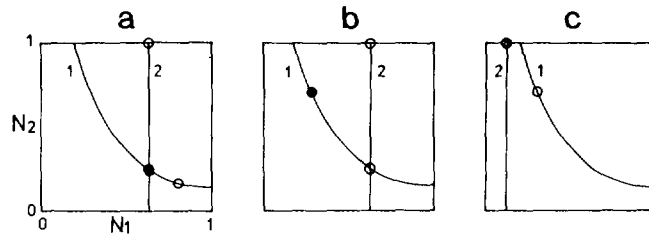


FIG. 5. Graphical analysis of the three qualitatively different outcomes of competition between a species with a complex life cycle and a species with a simple life cycle. Legend as in Fig. 3.

or the larvae escape competition (Fig. 2.3b), and then

$$\begin{aligned} N_{A_1}(t) = N_{A_2}(t) = N_{L_2}(t) = N_1(t) &= f_1[A_1(t), A_2(t), L_2(t)] \\ N_{L_1}(t) = N_2(t) &= f_2[L_1(t)] \end{aligned} \quad (22)$$

The analysis being similar in both cases, let us consider the first one. Three qualitatively different outcomes are possible (Fig. 5). Intersection of the isoclines occurs easily in this case because the isocline of the species with a simple life cycle is vertical while that of the species with a complex life cycle is curved. The condition for the isoclines to cross is simply that the species with the complex life cycle lower N_1 more than does the species with a simple life cycle when N_2 is at its maximum ($= 1$) (Figs. 5a and 5b). Note that this does not require that the species with the complex life cycle be more efficient than the species with the simple life cycle, because its net reproductive rate is also a function of N_2 ; when N_2 is abundant, the species with the complex life cycle can yield many larvae which may lower N_1 more than would the species with the simple life cycle even though the latter may be intrinsically more efficient at utilizing N_1 .

Stable coexistence is then achieved when the equilibrium point of species 1 lies to the right of the intersection point (Fig. 5a), that is, when the species with the complex life cycle is mainly limited by that stage which escapes competition with the species with the simple life cycle (adult stage in Fig. 5); otherwise the species with the complex life cycle outcompetes the other (Fig. 5b). Lastly the species with the simple life cycle wins if it is very efficient in utilizing N_1 so that its isocline lies entirely to the left of the other (Fig. 5c). Thus there is a strong asymmetry in the outcome of competition for the two species; unless the species with the simple life cycle is decidedly more efficient at utilizing resources, a complex life cycle appears to provide a competitive advantage because it can persist under a wide range of conditions, either alone or in coexistence with the simple life cycle.

To illustrate these conclusions, let us again consider a simple example using specific functions. Assume again that mortality is density independent in both stages and both species, and that recruitment rates are simply proportional to resource abundance:

$$\begin{aligned}\alpha_i(N_j) &= a_i, & \beta_i(N_1) &= b_i, \\ \mu_i(N_1) &= m_i N_1, \\ \rho_1(N_2) &= r_1 N_2, & \rho_2(N_1) &= r_2 N_1.\end{aligned}\tag{23}$$

Then

$$\begin{aligned}R_i &= m_i r_i / (a_i b_i) \\ P_1(N_1, N_2) &= R_1 N_1 N_2 \\ P_2(N_1) &= R_2 N_1^2.\end{aligned}\tag{24}$$

The isoclines intersect if and only if the isocline of species 1 intersects the line $N_2 = 1$ at a smaller value of N_1 than does the isocline of species 2 (Fig. 5). This condition reduces to

$$R_1 > \sqrt{R_2}.\tag{25}$$

The two outcomes depicted in Figs. 5a–5b further depend on the position of the equilibrium point of species 1 in relation to the isocline of species 2. Coexistence requires

$$N_1^{(1)} > 1/\sqrt{R_2},\tag{26}$$

otherwise species 1 excludes species 2.

Using the same functions f_1 and f_2 as defined by (18) for species 1, $N_1^{(1)}$ is easily determined from Equation (13). Condition (26) then becomes

$$\sqrt{R_2} > (a_1 d_1 R_1 + m_1 c_1) / (a_1 d_1 + m_1 c_1).\tag{27}$$

Conditions (25) and (27) confirm the competitive advantage of a complex life cycle over a simple one, since in this example the former needs only have a basic reproductive rate greater than the square root of that of the latter to persist (Condition 25), while the conditions for the persistence of the species with a simple life cycle are much more stringent (Condition 27). In particular, the species with a complex life cycle always persist when the basic reproductive rates of the two species are equal ($R_1 = R_2 = R$).

In the latter case, Condition (27) reduces to

$$\sqrt{R} < m_1 c_1 / (a_1 d_1)\tag{28}$$

which shows clearly that the main resource limitation (as indicated by the ratio c_1/d_1) must occur in that stage which escapes interspecific competition (the adult stage in this case), in order to prevent the complex life cycle from gaining a decisive advantage in the competition for the resource its other stage shares with the simple life cycle.

DISCUSSION

The discrete model of two-stage populations analysed in this paper is completely general, and thus allows some general conclusions to be drawn on the coexistence or competitive exclusion between species with complex life cycles when competition has the form of exploitation competition for a single resource at each stage. A complex life cycle was here defined ecologically by a complete niche differentiation between the two stages, which use different resources, as opposed to a simple life cycle in which the two stages occupy the same niche. It is worth recalling that the analysis was restricted to the conditions in which the competitive exclusion principle applies to populations without a complex life cycle, that is, equilibrium conditions. It is well known that the competitive exclusion principle in its classical formulation does not necessarily hold under non-equilibrium conditions (Levins, 1979; Armstrong and McGehee, 1980) even for simple populations. Clearly, relaxing these restrictions would generate more varied and more complex situations than those considered in this work. Our analysis of two-species competition also did not consider multiple single-species equilibria which may occur under some circumstances (Tschumy, 1982). However, multiple equilibria lend themselves so the same graphical analysis as simple equilibria; thus they do not modify the conclusions of the analysis but make several of the outcomes described separately possible for different initial conditions.

Three major conclusions emerge from this work. First, while species with simple life cycles can never coexist at equilibrium, stable coexistence is possible between species with complex life cycles provided that two conditions are met:

- (1) one species must be more efficient in resource utilization at low resource abundance in the larval stage while the other must be more efficient at low resource abundance in the adult stage;
- (2) each species must be mainly limited by that stage which is less efficient at low resource abundance.

Failure to meet one of these conditions results either in the exclusion of one species or in alternative single-species stable equilibria depending on the initial conditions. The first condition is not trivial because it concerns only

a restricted class of parameters. Any interspecific differences in density-independent parameters which intervene in linear terms in the model in no way contribute to the potential for coexistence. For instance, whatever differences in maximum recruitment rates or density-independent mortality probabilities in the two stages do not prevent competitive exclusion. This is explained by the fact that the various stages of a species are mutually interdependent through the life cycle that unites them. A species' overall competitive ability is determined by its net reproductive rate, which is a function of the whole set of parameters over the life cycle. Therefore only differences in parameters responsible for nonlinearities in the response to resource abundance can make one species more efficient than the other in a particular stage, and hence create conditions for coexistence. The second condition above is equivalent to the standard condition that the two species must be limited by different factors to coexist (Levin, 1970), with the additional requirement that the limitation must occur in that stage which is less efficient at low resource abundance. If this requirement is not met, each species tends to outcompete the other in that stage which is more efficient, which results in alternative single-species stable equilibria.

The second conclusion is that stable coexistence is somewhat easier between a species with a simple life cycle and one with a complex life cycle. This requires two conditions:

(1) the species with the simple life cycle must not be decidedly more efficient than that with the complex life cycle in utilizing the resource on which it lives;

(2) the main resource limitation for the species with a complex life cycle occurs in that stage which escapes competition with the species with a simple life cycle, thus making it possible for the two species to be effectively limited by two different resources.

The simulation results by Haefner and Edson (1984) were qualitatively in agreement with the second condition. However, Haefner and Edson in their simulations failed to identify the first condition and thus the potential for a species with a simple life cycle to outcompete a species with a complex life cycle when this condition is not met. Also, Haefner and Edson found asymmetrical results for the two cases where either adults or larvae escape interspecific competition, with a greater potential for coexistence in the latter case. Since their model is structurally symmetrical, this asymmetry in all likelihood rests on the break of symmetry introduced by the implicit assumptions that $\mu < 1$ and $\rho > 1$, which in turn rest on the choice of the number of individuals as unit, and would vanish if one were to use other ecological units such as biomass or energy content, as Loreau (1990) showed for other models.

The third conclusion is that a complex life cycle can offer a decisive competitive superiority over a simple life cycle in interspecific competition because it can take advantage of a second niche free of competitors. For instance, in the specific example which was examined in detail, it was found in essence that the competitive ability of a species with a complex life cycle is measured by its basic reproductive rate while that of a species with a simple life cycle is measured by the square root of its basic reproductive rate. Thus, in an evolutionary perspective, even though the acquisition of a complex life cycle can entail evolutionary costs in the form of immobilization time, loss of energy and additional mortality during metamorphosis, these costs can be more than offset by an increased competitive ability as long as they do not reduce the species' reproductive rate too much. If in addition the stage that escapes competition with the simple life cycle opens up a new niche that is productive enough, the complex life cycle can out-compete the simple life cycle. The simulation results by Haefner and Edson (1984) suggested a qualitatively similar conclusion.

Although the present model was not intended to describe evolutionary processes (in particular because of the crude division between simple and complex life cycles), it does suggest that, even in a constant and homogeneous environment, competition can be a driving force of the evolution of complex life cycles. Whether it really is or other factors like temporal and spatial variability of the environment predominate (Bryant, 1969; Slade and Wassersug, 1975), is a matter that clearly requires more theoretical and empirical investigation. It is worth noting, however, that the above only concerns competition between a complex life cycle and a single simple life cycle. If the niches of both its stages are occupied by different simple life cycles, a complex life cycle is likely to lose any competitive advantage (Haefner and Edson, 1984), just as a generalist usually loses in the face of several complementary specialists (Levins, 1968). Also, the above is dependent upon the definition of simple and complex life cycles as ones occupying a single niche and two niches, respectively. If one were instead to compare a complex life cycle as defined here and a simple life cycle in which each stage used two resources, the conditions favouring the complex life cycle would be more stringent. But the definition used here and in other works (like Haefner and Edson, 1984) seems more to the point since the two stages of many species with complex life cycles in nature occupy quite distinct niches or habitats (e.g., freshwater or soil habitats as larvae, aerial habitats as adults in many insects), which a single stage would not be able to occupy simultaneously.

APPENDIX

The growth of a population obeying Eq. (2) hinges on the eigenvalues of the matrix $\mathbf{G}(t)$, which are given by the solutions of the characteristic equation of $\mathbf{G}(t)$, i.e.,

$$\lambda_1 = 1/2[T + (T^2 - 4D)^{1/2}]$$

$$\lambda_2 = 1/2[T - (T^2 - 4D)^{1/2}]$$

where T is the trace of $\mathbf{G}(t)$ and D is its determinant.

Since $T < 0$, $\lambda_2 < 0$, and the sign of population growth is determined by the sign of the single dominant eigenvalue λ_1 . This has a sign opposite to that of D . But $D = \alpha\beta(1 - P)$, which has the sign of $1 - P$. Therefore population growth is determined by the sign of $P - 1$.

It is important to note that since $\mathbf{G}(t)$ is a function of time via N_A and N_L and hence A and L , this eigenvalue analysis only indicates the trend of population growth under the conditions prevailing at time t . It is insufficient for a full stability analysis at equilibrium because it ignores the possibility of overcompensation, and thus cyclic or chaotic dynamics, around the equilibrium due to the time lag involved in discrete models. It is, however, appropriate for an analysis of intrinsic stability (*sensu* Levin and Udovic, 1977).

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