

Time Scale of Resource Dynamics and Coexistence through Time Partitioning

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The difference between the time scales of consumer and resource dynamics is a critical factor for the coexistence of consumers that occupy different temporal niches in a seasonal environment. Its significance is investigated using a general discrete cyclic model involving two consumers competing for the exploitation of one resource. Simulations confirm and extend previous analytical results. Temporal overlap and difference between consumer efficiencies play roles that are in general qualitatively similar to those of niche overlap and difference between carrying capacities in the classical theory of competition in a constant environment. But the relative time scale of resource dynamics plays a crucial role which does not have an analogue in the classical theory: coexistence at the consumer level is possible only above threshold values of both frequency and speed of dynamics at the resource level. © 1992 Academic Press, Inc.

INTRODUCTION

Three broad types of factors allow resource partitioning and hence coexistence among species: space, food, and time. Among these, time was traditionally regarded as the least important (Schoener, 1974). This view was influenced by—quite naturally—biases from early population ecologists towards large-sized vertebrates as study organisms and towards the autonomous differential systems of classical mechanics as mathematical tools. Many other organisms are so strongly dependent on the natural periodicities of the environment, especially the seasonal one, that their whole life cycle can be modeled on them. Organisms with a generation time of about 1 year, like univoltine insects or annual plants, often have regular annual life cycles, tightly and specifically synchronized with the annual cycle of seasons. In such organisms, time can be a major niche dimension allowing segregation of species (e.g., Loreau, 1986).

But time is a special niche dimension, to which the classical results of competition theory cannot be applied as they stand. First, these results were derived from autonomous models such as the classical

Lotka–Volterra equations. Introduction of time-dependent parameters in competitive systems is more than a mere refinement; it makes their analysis mathematically much more complex. Recent advances in this direction have been made for periodic (Cushing, 1980, 1986; Rosenblat, 1980; de Mottoni and Schiaffino, 1981; Smith, 1981; Namba, 1984) and stochastically varying (Chesson and Warner, 1981; Chesson, 1986) competitive systems. Second, time differs from other niche dimensions in that resource dynamics can mediate competition even between species whose temporal niches do not overlap. Consequently, when competition is of the exploitation type, it is generally not justified theoretically to abstract simple equations for competitors without specification of resource dynamics. Very few works have incorporated the latter into models of competition between species with different temporal niches (Stewart and Levin, 1973; Cushing, 1984; Loreau, 1989).

This brings in a critical potential element of complexity, i.e., the difference between time scales of interacting trophic levels. Multiple scales are commonplace in ecosystems (Levin, 1978), but have been little studied. The traditional approach is to assume that scales are different enough so that processes occurring on a time scale longer than the process under consideration may be reduced to mere parameters, while processes occurring on a shorter time scale may be described by moving equilibria (Lotka, 1925). The reality of ecosystems is more complex, since there is a continuum of possible scales. Loreau (1989), analyzing a simple discrete cyclic system in which consumers alternate seasonally, showed that the difference in the characteristic time scales of resource and consumer dynamics is a crucial factor for the coexistence of consumers.

This subject is investigated further in the present paper. In Loreau (1989), only the two borderline cases where resource dynamics occurs either on the same time scale as the consumers' or on a much shorter scale were analyzed fully. Here, the general case of an arbitrary time scale of resource dynamics is considered using a more general version of the model, for which simulation results will be given.

THE MODEL

The model developed in Loreau (1989) describes as simply as possible a system made up of two "consumers" C and C' , such as univoltine insects or annual plants, which have annual discrete generations and different seasonal occurrences, and which live on the same "resource" R . The consumers interact exclusively through the exploitation of the resource. Each is active and reproduces in the system during a given season, then disappears from it and completes its life cycle in another niche or habitat.

The resource flows through the system, without reproducing in it, during the whole annual cycle; it may be, e.g., nutrients for plants or various prey for ground beetles during their transit at the ground's surface.

In the general case considered here, the two consumers have partly overlapping periods of activity and thus determine three different seasons: one season during which consumer C alone is active; a second one during which both C and C' are active; and a third one during which C' alone is active. Resource dynamics is discrete, but its time step can be equal to or arbitrarily smaller than that of the consumers. Thus there are two time scales in the system: one, which is measured by τ , is characteristic of the resource and describes within-season dynamics; the other, which is measured by t , is characteristic of the consumers and describes between-season dynamics.

Let us first define the dynamical equations of the system on the resource time scale. Let φ be the input flow of the resource, ρ its disappearance rate in the absence of consumers, and κ and κ' its removal rates by individuals of C and C' , respectively, on this time scale. Since the consumers have annual generations, their population changes are assumed to occur at the end of their period of activity. Each grows in proportion to the average quantity of resource it has consumed during its whole period of activity, at a rate r or r' , respectively, and suffers death at a rate θ or θ' . Finally, let n_1 , n_2 , and n_3 denote the numbers of time units in the three successive seasons, and τ_0 denote the time at the start of the cycle. The dynamical equations of the system then are

$$\begin{aligned}
 R_{\tau+1} &= \varphi + (1 - \rho - \kappa C_\tau) R_\tau & (\tau_0 \leq \tau \leq \tau_0 + n_1 - 1) \\
 R_{\tau+1} &= \varphi + (1 - \rho - \kappa C_\tau - \kappa' C'_\tau) R_\tau & (\tau_0 + n_1 \leq \tau \leq \tau_0 + n_1 + n_2 - 1) \\
 R_{\tau+1} &= \varphi + (1 - \rho - \kappa' C'_\tau) R_\tau & (\tau_0 + n_1 + n_2 \leq \tau \leq \tau_0 + n_1 + n_2 + n_3 - 1) \\
 C_{\tau+1} &= C_\tau & (\tau \neq \tau_0 + n_1 + n_2 - 1) \\
 C_{\tau+1} &= \left(1 + \frac{r}{n_1 + n_2} \sum_{i=\tau_0}^{\tau_0 + n_1 + n_2 - 1} R_i - \theta \right) C_\tau & (\tau = \tau_0 + n_1 + n_2 - 1) \\
 C'_{\tau+1} &= C'_\tau & (\tau \neq \tau_0 + n_1 + n_2 + n_3 - 1) \\
 C'_{\tau+1} &= \left(1 + \frac{r'}{n_2 + n_3} \sum_{i=\tau_0 + n_1}^{\tau_0 + n_1 + n_2 + n_3 - 1} R_i - \theta' \right) C'_\tau & (\tau = \tau_0 + n_1 + n_2 + n_3 - 1).
 \end{aligned}
 \tag{1}$$

It is convenient to change from the resource to the consumer time scale, both because it makes the model more tractable and because we are interested in letting the number of time intervals within the seasons vary while keeping the length of the latter constant. To slightly simplify the problem,

we shall consider the case where the two consumers have periods of activity of equal lengths, so that these can be set to unity on the new time scale and their overlap can be measured by the single parameter γ ($0 \leq \gamma \leq 1$). Thus let us define

$$n = n_1 + n_2 = n_2 + n_3$$

$$\gamma = n_2/n$$

$$\Delta t = \Delta \tau/n,$$

and rescale the dynamical parameters of the resource to $\Phi = n\phi$, $p = n\rho$, $q = n\kappa$ and $q' = n'\kappa'$. Let us also define $T_i = n_i/n$ as the length of season i , and $L = \sum_i T_i = 2 - \gamma$ as the period of the annual cycle, on the consumer time scale. Finally, for notational convenience, let us denote by $t(i)$ the time at the end of season i (hence $t(3) = t(0) + L$), and let

$$y_1 = p + qC_{t(0)}$$

$$y_2 = p + qC_{t(0)} + q'C'_{t(0)}$$

$$y_3 = p + q'C'_{t(0)}$$

$$x_i = 1 - y_i/n.$$

The equations describing between-season resource dynamics can be developed by iteration of the equations for within-season dynamics. Model (1) then turns into

$$R_{t(i)} = \frac{\Phi}{y_i} + x_i^n \left(R_{t(i-1)} - \frac{\Phi}{y_i} \right) \quad (i = 1, 2, 3)$$

$$C_{t(0)+L} = \left\{ 1 - \theta + r \sum_{i=1}^2 \left[\frac{\Phi T_i}{y_i} + \frac{1 - x_i^n}{y_i} \left(R_{t(i-1)} - \frac{\Phi}{y_i} \right) \right] \right\} C_{t(0)} \quad (2)$$

$$C'_{t(0)+L} = \left\{ 1 - \theta' + r' \sum_{i=2}^3 \left[\frac{\Phi T_i}{y_i} + \frac{1 - x_i^n}{y_i} \left(R_{t(i-1)} - \frac{\Phi}{y_i} \right) \right] \right\} C'_{t(0)}$$

Note that resource dynamics becomes continuous in the limit $n \rightarrow \infty$. In this case, $x_i^n \rightarrow e^{-y_i T_i}$.

It must be noted that the model has a structural constraint due to the linear form of the x_i , which limits its range of validity towards small n . Its consistency requires $x_i \geq 0$ (otherwise the quantity of resource disappearing from the system would be greater than the quantity present in it—see the equations for R in (1), where x_i represents the bracketed term), which in turn sets a limit on the quantity of resource consumed. The form of this constraint, which relaxes as n increases, is shown below.

Model (2) was analysed numerically. In each simulation run, its dynamics was followed until an asymptotic behaviour was reached, i.e., no change in variable values during at least 50 generations at the precision level chosen. No cyclic or chaotic behaviour was detected. The outcomes were classed as either coexistence (all three variables positive) or no coexistence (at least one consumer population equal to zero). The model was declared inadequate when the constraint $x_i \geq 0$ ($i = 1, 2,$ or 3) was violated. For each of the cases considered below, the sensitivity of the outcome to the parameters was first examined. The model was then simulated for various values of the relevant parameters, until the parameter regions corresponding to the various outcomes were delimited.

RESULTS

Two distinct aspects characterize the time scale of a discrete process: its *frequency*, i.e., the number of times the process is repeated in a time unit, and its *speed*, determined by the rate of change of the dynamical variable (Loreau, 1989). The former is specific to discrete processes, while the latter is common to both discrete and continuous processes. In the context of the present model, the frequency of resource dynamics is measured by n , while speed can be measured by Φ and p . The difference between the time scales of resource and consumer dynamics can thus arise from either increased frequency or increased speed of resource dynamics.

To illuminate the effect of this difference between scales, we first reduce the number of parameters under consideration by concentrating on the case of two like consumers ($r = r', \theta = \theta', q = q'$). A partial analytical treatment of this case when the two consumers are completely separated in time ($\gamma = 0$) (Loreau, 1989) showed that a necessary condition for the coexistence of the two consumers to be stable then is

$$(y + 2)[(1 - y/n)^n + 1] > 4, \quad (3)$$

where $y = y_1 = y_3 = E\Phi$, and the ratio $E = r/\theta$ is defined as a consumer's efficiency. Numerical simulations confirmed that this inequality does bound the region of stable coexistence from below (Fig. 1). This condition shows that there is a critical value of frequency of resource dynamics ($n = 2$) up to which stable coexistence is impossible. Above this critical value, coexistence is possible provided that the speed of resource dynamics (as measured here by Φ) and consumer efficiency (E) are high enough. But the minimum value of the product $E\Phi$ required for coexistence tends itself to zero as n tends to infinity.

This condition, however, only guarantees the stability of the periodic

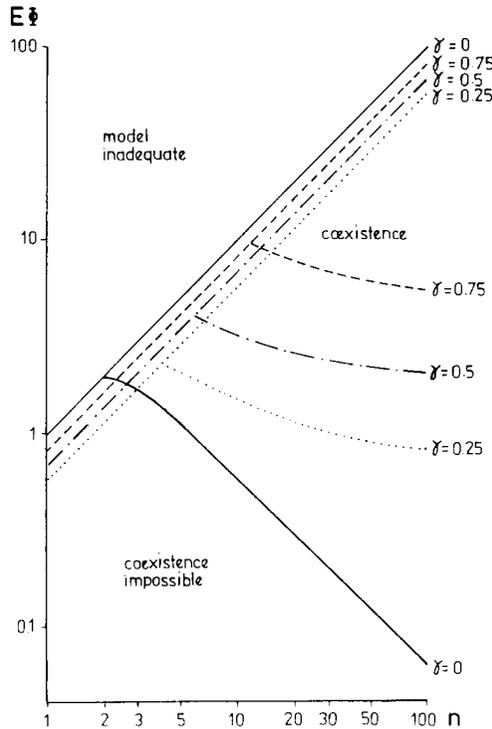


FIG. 1. Effect of time scale of resource dynamics on the potential for stable coexistence of two like consumers: curves of $E\Phi$ (product of consumer efficiency and resource input flow) as a function of n (frequency of resource dynamics) delimiting the region of stable coexistence, for various values of γ (temporal overlap) (log scales). In the upper region, the structural constraint $x \geq 0$ is violated. Simulation results.

solution of the system, which in this case reduces to the equilibria $R^* = 1/E$ and $C^* = C'^* = (E\Phi - p)/q$ (Loreau, 1989). The feasibility of these equilibria further requires $E\Phi > p$, which in fact is simply the condition for the consumers to be able to live on the resource (i.e., to invade a system composed of the resource alone). This lower bound on $E\Phi$ is not shown in Fig. 1 because it depends on the additional parameter p .

On the other hand, the constraint $x \geq 0$, which amounts to $E\Phi \leq n$, sets an upper bound on $E\Phi$, beyond which the model becomes inadequate to describe the system (upper region in Fig. 1).

Similar curves delimiting the region of stable coexistence were obtained by simulation for other values of γ (Fig. 1). The only two outcomes of the system's dynamics are always either stable equilibrium coexistence of the two consumers, or exclusion of one or both consumers, and $E\Phi$ and n remain the only two parameters determining the stability of coexistence. Clearly, increasing γ has the effect of closing the parameter window of

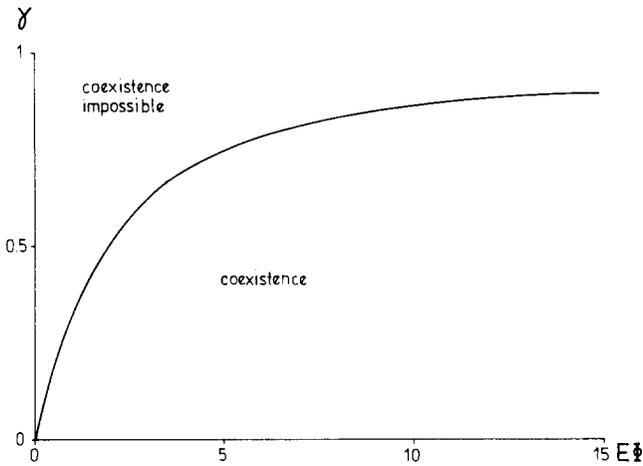


FIG. 2. Increased temporal overlap (γ) between two like consumers made possible by increased values of $E\Phi$, in the case of continuous resource dynamics ($n \rightarrow \infty$). Simulation results.

stable coexistence. The increase in $E\Phi$ required for coexistence with increased γ is further illustrated in Fig. 2 for the case of a continuous resource dynamics.

When the temporal overlap between the consumers is zero, the case of two like consumers considered so far is most favourable for coexistence because the resource is kept at a constant equilibrium level. Any difference between consumer efficiencies drives the system into periodic trajectories which tend to destabilize the equilibrium between the consumers. Therefore an increased ratio E'/E between consumer efficiencies requires larger values of $E\Phi$ to compensate for this destabilizing factor, as simulations confirm (Fig. 3). On the other hand, when $\gamma > 0$, the second consumer, C' , suffers more from competition with C than C does from C' because it is active after the second season during which the two species cooccur and thus depress the resource level most. Consequently, coexistence is easiest for a ratio $E'/E > 1$, as shown in Fig. 3. However, this most favourable ratio was found to be very close to 1; even quite moderate differences between consumer efficiencies again require increased values of $E\Phi$ for stable coexistence to be possible. Note that the curves in Fig. 3 also depend on p : large p increase the threshold value of $E\Phi$ allowing coexistence. This effect, however, becomes negligible for p small ($p \sim 0.1$, as in Fig. 3).

So far we have focused on the threshold value of $E\Phi$ allowing coexistence, which implies a threshold of speed of resource dynamics as embodied in the parameter Φ . At the other extreme, if resource dynamics becomes very fast compared with consumer dynamics, we can investigate

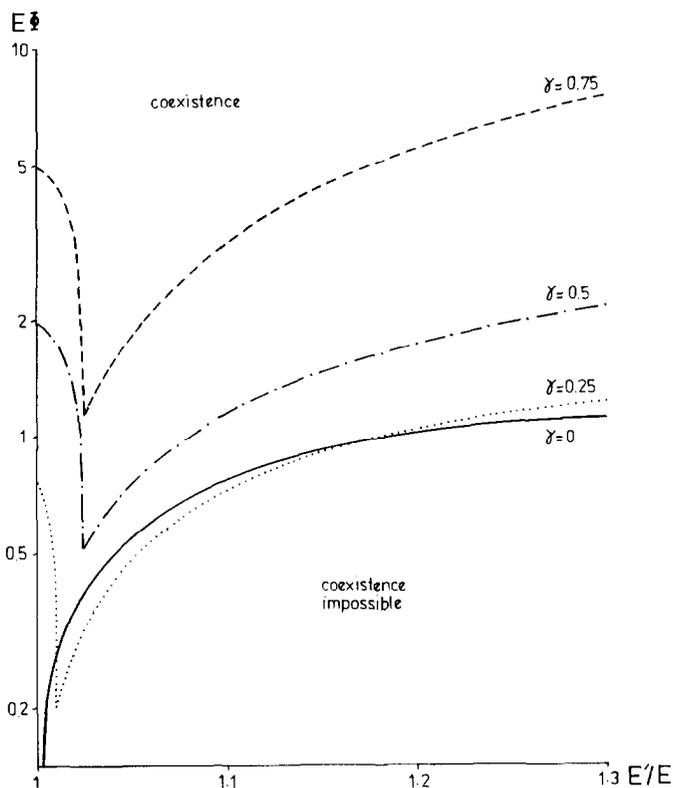


FIG. 3. Threshold values of $E\Phi$ (log scale) allowing stable coexistence between consumers as a function of the ratio between consumer efficiencies, in the case of continuous resource dynamics. Simulation results, with $p = 0.1$.

the most favourable conditions for coexistence. This case comes down to letting Φ and p go to infinity while their ratio $M = \Phi/p$ —which is the carrying capacity of the resource in the absence of consumers—remains finite. The resource can then be regarded as being in a moving equilibrium with the consumers, which allows one to describe the system by autonomous equations for the consumers alone. This case was fully analyzed in Loreau (1989), who showed that the necessary and sufficient condition for stable coexistence is

$$\gamma < \frac{EM - 1}{EM - E/E'}, \quad (4)$$

where E is arbitrarily defined as the efficiency of the less efficient species. This condition is illustrated in Fig. 4. Coexistence is now always possible

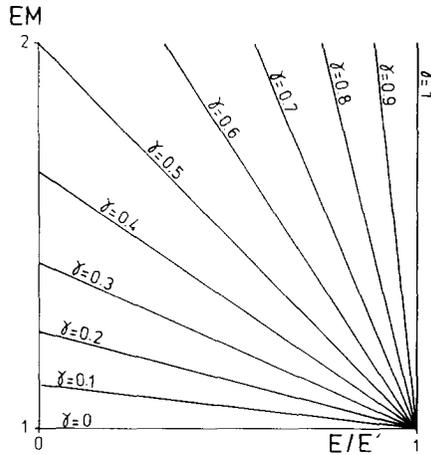


FIG. 4. Graphical representation of the analytical condition (4) for stable coexistence in the case where the time scale of resource dynamics is very short compared with that of the consumers.

when $\gamma = 0$ (provided of course that each species can live on the resource, i.e., $EM > 1$), but gets increasingly difficult with increasing γ . As long as $\gamma < 1$, it is facilitated by increased consumer efficiency (E), resource abundance (M), and similarity between consumer efficiencies (E/E').

DISCUSSION

Extensive investigation of Model (2) fully confirms and extends the analytical results achieved by Loreau (1989) using a less general version of the model. Five parameters (as compared with the 10 original parameters) determine the conditions for the stable coexistence of the consumers: the frequency of resource dynamics (n), the product of consumer efficiency (E) and resource input flow (Φ), the resource disappearance rate (p), the temporal overlap between consumers (γ), and the ratio between consumer efficiencies (E/E').

The last two parameters are analogous to the parameters of the classical theory of competition and limiting similarity in a constant environment (MacArthur and Levins, 1967; MacArthur, 1972; May, 1974), namely, niche overlap and the difference between carrying capacities. In general, their effects are also qualitatively similar, namely, coexistence gets easier when temporal niche overlap and the difference between consumer efficiencies decrease. But this is true only *in general*; as illustrated in Fig. 3, a slight difference between consumer efficiencies can be favourable to coexistence for a given overlap, and conversely, a moderate amount of overlap too can

be favourable to coexistence for a given efficiency ratio. These distortions arise because of the finite time scale of resource dynamics; they vanish when the latter is infinitely short (Fig. 4).

The first three parameters highlight the crucial role of the time scales in the system, of which no account is taken in the classical theory. In particular, the difference between the frequencies of resource and consumer dynamics is a critical element, since there is a threshold relative frequency of resource dynamics below which coexistence is impossible, whatever the values of the other parameters, and this threshold increases with increased temporal overlap between consumers. The lumped parameter $E\Phi$ may be viewed as a measure of the characteristic speed of the time scale of the system as a whole. For any combination of parameter values, there is again a threshold speed below which coexistence is impossible. On the other hand, increasing the resource disappearance rate p , which also determines the speed of resource dynamics, has a negative effect on coexistence. But the latter is weaker than the positive effect of increasing Φ , and thus, for a given ratio $M = \Phi/p$, increasing the speed of resource dynamics is always favourable for coexistence. One can understand intuitively why increasing the difference between the time scales of the two trophic levels has such a favourable effect on coexistence at the higher level: the higher the frequency and the speed of resource dynamics, the greater the within-season regulation of the system and hence the smaller the between-season competitive effects mediated between consumers by the resource (Loreau, 1989). In a more general setting, this difference in time scale may be interpreted as a form of "storage effect" at the consumer level, of which the positive contribution to coexistence is well known from stochastic competition models (Chesson and Warner, 1981; Warner and Chesson, 1985; Chesson, 1986). Decreasing θ and increasing r and Φ , and hence increasing $E\Phi$, all contribute to enhance the growth rate of the consumer during the season favourable for it, and allow it to resist the more unfavourable seasons. Another form of storage is also involved in the acquisition of resources within a season when the frequency of resource dynamics is increased.

The present model has an important limitation for low-frequency resource dynamics due to the linear form of the x_i , which was chosen for simplicity and analytic tractability. The model then is consistent only for relatively low consumption levels, hence for relatively low values of $E\Phi$. Thus it must be considered a suitable linear approximation in the case of a slow system. To describe high consumption levels in this case, the interaction term should include some non-linear negative dependence on the consumer populations (such as the familiar negative exponential function in parasitoid-host models: Hassell, 1978). This in turn would introduce self-interaction terms in the equations for the consumers and hence the possibility of stable coexistence (Loreau, 1989). On the other hand, highly

non-linear terms could also lead to more complex behaviours like cycles of longer periods and chaos. Thus the region labeled "model inadequate" in Fig. 1 is open to several unexplored possibilities. However, since these possibilities pertain to the region of high-speed dynamics, the existence of lower thresholds of frequency and speed of resource dynamics allowing stable coexistence should be robust—at least when competition is of the exploitation type (it need not be true when there is interference within consumer populations).

The present findings have important implications for competition theory and its application to the interpretation of patterns of temporal niche overlap. One of the reasons why classical competition theory based on Lotka–Volterra equations has been so appealing is that these can approximate not only the dynamics of competition in simple experimental systems, but also the asymptotic dynamics of consumers embedded in intricate networks of interactions through their resources (MacArthur, 1972). When time itself is a significant niche dimension, a single-level description of competition between consumers cannot in general be abstracted from the whole system comprising the consumers and their resources, even as an approximation of its asymptotic behaviour. Thus there is no simple relationship between temporal niche overlap and competition; data on the lower trophic level are necessary to interpret patterns at the higher trophic level. Despite this complexity, the present work suggests that a rough evaluation of the relative time scale of resource dynamics may be sufficient to make at least qualitative comparisons between consumer communities.

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