

Coupled Oscillations in Food Webs: Balancing Competition and Mutualism in Simple Ecological Models

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ABSTRACT: As in other oscillating systems, oscillations of consumer resource pairs in ecological systems may be coupled such that complex behavior results. The form of that coupling may determine the nature and extent of this behavior. Two biologically significant forms of coupling are here investigated: first, where consumers consume each other's resources (CR coupling, representing competition between the two consumers), and second, where the resources are in competition with one another (RR coupling, potentially representing indirect mutualism between the two consumers). Interestingly, CR coupling leads to in-phase synchrony of the oscillations, whereas RR coupling leads to antiphase synchrony. With either form of coupling, if the coupling remains weak, synchronous behavior is generated in the two systems. At strong levels of coupling, when the two forms act simultaneously, a balance between competition and mutualism is generated, which is manifest differently at different levels of resource coupling.

Keywords: coupled oscillators, competition, mutualism, chaos.

Attempting to answer questions about nature by examining the structure of food webs has a long history, as summarized in several key volumes (Cohen 1978; Pimm 1982; DeAngelis et al. 1983; Kerfoot and Sih 1987; Carpenter 1988; Cohen et al. 1990; Higashi and Burns 1991; DeAngelis 1992; Polis and Winemiller 1995). Since May's (1973) counterintuitive result that increased species diversity leads to lowered community stability, many studies have sought to ferret out those aspects of food web structure that are at least partly determinant of various community features, ranging from stability and persistence to productivity (Winemiller and Polis 1995), and many key

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contemporary concepts have little meaning outside of the context of food webs (e.g., apparent competition [Holt 1977], indirect mutualism [Vandermeer 1980], or trophic cascades [Carpenter et al. 1987]). Most recently, there has been a great deal of activity aimed at understanding food web dynamics in the context of the theoretical constructs normally associated with the ideas of complexity theory. Examples are too numerous to mention but include the observation of chaos in a simple three-species food chain (Hastings and Powell 1991), generation of chaos in coupled predator-prey systems (Vandermeer 1993; Vandermeer et al. 2002), competitive chaos (Huisman and Weissing 2001a; Passarge and Huisman 2002), fractal basin boundaries (Vandermeer and Yodzis 1999; Huisman and Weissing 2001b), weak link stability (McCann et al. 1998), and complex patterns from environmental forcing (Kot and Schaffer 1984; Rinaldi et al. 1993; Pascual et al. 2000; Vandermeer et al. 2001).

In conceptualizing food webs, the most elementary unit is normally consumption (a consumer and its resource, a predator and its prey, a carnivore and a herbivore, and so on). It has long been known that this basic unit is oscillatory. If the elementary unit is oscillatory, when those elementary units are connected, the conceptual framework is one of a system of coupled oscillators. Systems of coupled oscillators have served as model frameworks for many applications in nature, including physical systems (van der Pol and van der Mark 1927; Pikovsky et al. 2001; Bennet et al. 2002), physiological systems (Winfree 1980), and many others (Strogatz 2003). Conceptualizing ecosystems as systems of coupled oscillators has been previously noted (Vandermeer 1993) at least in the context of consumer resource dynamics.

Despite the obvious fact that food webs are, by their basic definition, systems of coupled oscillators, the underlying nature of the coupling has not been systematically explored. From elementary ecological considerations, there are two obvious ways in which the coupling can occur (fig. 1). First, as conceptualized originally by MacArthur (1970), consumers can be thought of as specializing on a particular resource but consuming an alternative resource

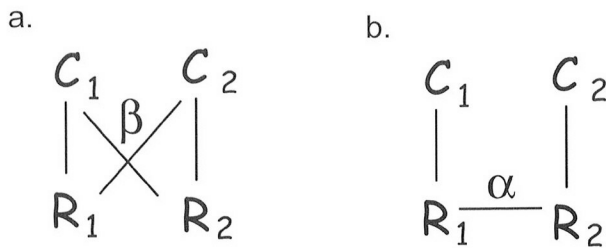


Figure 1: Diagrammatic illustration of the two coupling modes of two consumer/resource oscillators. Each pair of consumer and resource represents an oscillator; *a* represents the CR mode of coupling the two oscillators, whereas *b* illustrates the RR mode of coupling.

on which some other consumer specializes (fig. 1*a*). This form is frequently thought of as representing competition mechanistically, since the competition (between the two consumers) is reflected in their consumption rates, which represents the mechanism of the competition. This form has been analyzed in a variety of contexts (Abrams 1980, 1986; Vandermeer 1980; Chesson 1990) and is here referred to as CR coupling. Second, the resources themselves may be in competition with one another, which can be represented in a phenomenological fashion (fig. 1*b*). That is, the phenomenon of competition is defined with no reference to any underlying mechanism, which is the classic form for modeling competition. In the context of two consumer resource systems, when the resources are in competition, the consumers may be indirectly mutualistic with one another (Levine 1976; Vandermeer 1980). This form is referred to as RR coupling.

Here I describe the behavior of the system with CR coupling, with RR coupling, and, as must be the case with many if not most ecosystems, a combination of CR and RR coupling.

The Model

If the system illustrated in figure 1 is modeled using the standard form, we obtain

$$\frac{dC_i}{dt} = \frac{a\Psi_i C_i}{1 + b\Psi_i} - mC_i, \quad (1a)$$

$$\frac{dR_i}{dt} = r_i R_i \left(\frac{K - R_i - \alpha R_j}{K} \right) - aR_i \left(\frac{C_i}{1 + b\Psi_i} + \frac{\beta C_j}{1 + b\Psi_j} \right) \quad (1b)$$

for $i = 1, 2, j = 1, 2$, and $j \neq i$, where C_i is the i th consumer, R_i is the i th resource, r_i is the intrinsic growth rate of the i th resource, m is the death rate of the consumer, a is the resource consumption rate, K is the carrying capacity of the resource, α is the competition coefficient, b

is the parameter of the functional response, and Ψ_i is given as

$$\Psi_i = R_i + \beta R_j.$$

Model 1 conforms to the standard form with density dependence operating on the resources and a type II functional response acting on the consumers. If we set $\alpha = \beta = 0$, we have two independent oscillators, each corresponding to the standard model of resource/consumer (predator/prey) ecology. With $\alpha = 0$ and $\beta > 0$, the system is CR coupled (as in fig. 1*a*), and with $\beta = 0$ and $\alpha > 0$, the system is RR coupled (as in fig. 1*b*).

It is well known that the basic two-dimensional system has three fundamental modes, as originally articulated by Rosenzweig and MacArthur (1963). If the consumer isocline, which is $R = m/(a - bm)$, falls to the left of the peak of the hump of the resource isocline, which is $R^* = (Kb - 1)/2b$, the system is normally a limit cycle attractor (sustained oscillations). If it falls to the right of the carrying capacity of the resource, the consumer goes extinct, and if it falls between the carrying capacity of the resource and the peak of the hump of the resource isocline, the system is a focal point attractor (damped oscillations; May 1972).

For many parameter sets, the system exhibits oscillations in which one or more of the state variables approach ever closer to 0 (much like the system described by May and Leonard [1975]). From a biological point of view, even though all variables may never actually reach 0 and may approach it only asymptotically, that approach effectively means extinction. For biological reasons, I follow May and Leonard (1975) in assuming that a system in which very low population levels are approached, for all practical purposes, indicates exclusion of that population. Part of the argument that follows is dependent on the pattern in which rare values of the various populations are expressed.

The system's general typology with CR coupling and no RR coupling is one of interspecific competition between the two consumers. Thus, we would expect that as CR coupling increases, eventually the point of Gaussian exclusion will be reached. This is normally what happens with system (1), depending on the values of the other parameters in the system. However, the intermediate stages between little competition (small β) and competitive exclusion (large β) can be quite complicated (Vandermeer 1993, 1994), and it is also possible to choose the parameters a , b , and r_i in such a way that extinction does not occur, even with the largest value of $\beta = 1.0$. With RR coupling and no CR coupling, the magnitude of the competitive effect (α), if large enough, would be expected to remove one of the resources, which is indeed what happens. Again, the intermediate stages between little competition and com-

petitive exclusion (this time the exclusion of one of the resources) can be quite complicated.

If the parameter of functional response is set to 0, the system (1) reverts to a modification of MacArthur's classical system (Levine 1976) in which each isolated oscillator is a focal point attractor, exhibiting damped oscillations to extinction. With such a system, we know that if a is near 0, the RR coupling will tend to exclude one of the resources (through classic Gaussian extinction). If one of the resources is excluded, it is also the case that both of the consumers cannot survive, given that a single resource is available, a result strongly dependent on the assumption that $b = 0$. However, if $b > 0$, even if RR coupling is large and one of the resources is excluded, it is still possible for both consumers to persist (Armstrong and McGehee 1980). These preliminary observations suggest that the pattern of coexistence of the consumers is a complicated interplay of both CR and RR coupling.

Nearly Identical Oscillators and Weak Coupling

We begin with the system set such that the uncoupled oscillators generate an equilibrium point that is locally unstable but globally constrained; that is, the consumer isocline is to the left of the hump of the resource isocline. Thus, we study the system where $2bm$ is smaller than $Kab - Kmb^2 - a + bm$. Very weak coupling has a generally predictable effect, much like weak coupling in any system of coupled oscillators: synchrony. But here there is a very consistent pattern, obtained for a wide variety of parameter values: CR coupling leads to in-phase synchrony, while RR coupling leads to antiphase synchrony (fig. 2).

This generalization about the phase orientation in synchrony is reflected in the circle map (Vandermeer 1994). Construction of the circle map begins with the simple transformation

$$\Theta = \tan^{-1} \left(\frac{C_t - C^*}{R_t - R^*} \right)$$

for each of the CR oscillators, where C^* and R^* refer to the mean values of C and R over the whole time series. Then the value of Θ for one of the oscillators is used as a strobe variable, and observations are made of the Θ of the other oscillator. Thus, if Θ_1 is the value for the first CR system, we examine the value of Θ_2 at some particular recurring value of Θ_1 . This formulation is commonly used to study behavior of weakly coupled oscillators in both a physical context (Bak 1986) and a biological one (Vandermeer 1994; Vandermeer et al. 2001). The standard circle map is then given as

$$\Theta(t+1) = \Omega + \Theta(t) + \left(\frac{k}{2\Pi} \right) \sin [2\Pi\Theta(t)] \pmod{1}, \quad (2)$$

where Ω is the difference in the period of the two oscillators (which will be 0 in the case of identical oscillators) and k is proportional to the strength of the coupling. Given the observation that CR coupling leads to in-phase synchrony and RR coupling leads to antiphase synchrony, the circle map can reflect these two qualitatively distinct modes with a simple adjustment of the sign of the coupling parameter k . Set $\Omega = 0$ (i.e., the two oscillators are identical) and the strobe angle at .5 such that in-phase synchrony ($k > 0$) will result in the response variable Θ asymptotically approaching 0.5 (fig. 3a), while the antiphase synchrony ($k < 0$) will result in Θ gradually approaching 0 or 1.0 (fig. 3d). This is the case if $|k| < 1.0$.

Extensive simulations with system (1) with weak coupling suggest the behavior deduced from the circle map is a general rule. With CR coupling, the system always synchronizes in an in-phase fashion, and with RR coupling, it always synchronizes in an antiphase fashion. Furthermore, when the perfect symmetry is altered sufficiently (by changing the equality of any of the parameters), the behavior of the system tends to be quasi-periodic or quasi-periodic chaos, following qualitatively the predictions of the circle map, as has been reported for similar models elsewhere (Rinaldi et al. 1993; Vandermeer et al. 2001).

Since there is an obvious and dramatic difference between CR and RR coupling, the question arises as to how this difference would be resolved if these two forms of coupling occur together, as they certainly must in nature. An a priori expectation might be that when CR coupling is large compared with RR coupling, there should be in-phase synchrony, while when RR coupling is large relative to CR coupling, there will be antiphase synchrony. This is what is found for all parameter values for which either simple antiphase or in-phase synchrony is involved, that is, for all cases of weak coupling. However, it might also be expected that between these two obvious extremes there will be some range in which there is effective competition between the two modes, perhaps generating chaos. With extensive simulation experiments, with weak coupling, this pattern is inevitably observed, albeit with some complications. The phase transition from the dominance of RR coupling (which gives antiphase synchrony) to CR coupling (which gives in-phase synchrony) is frequently characterized by complicated quasi periodicity and quasi-periodic chaos. For example, consider system (1) with the modification

$$\alpha = pw,$$

$$\beta = (1 - p)v,$$

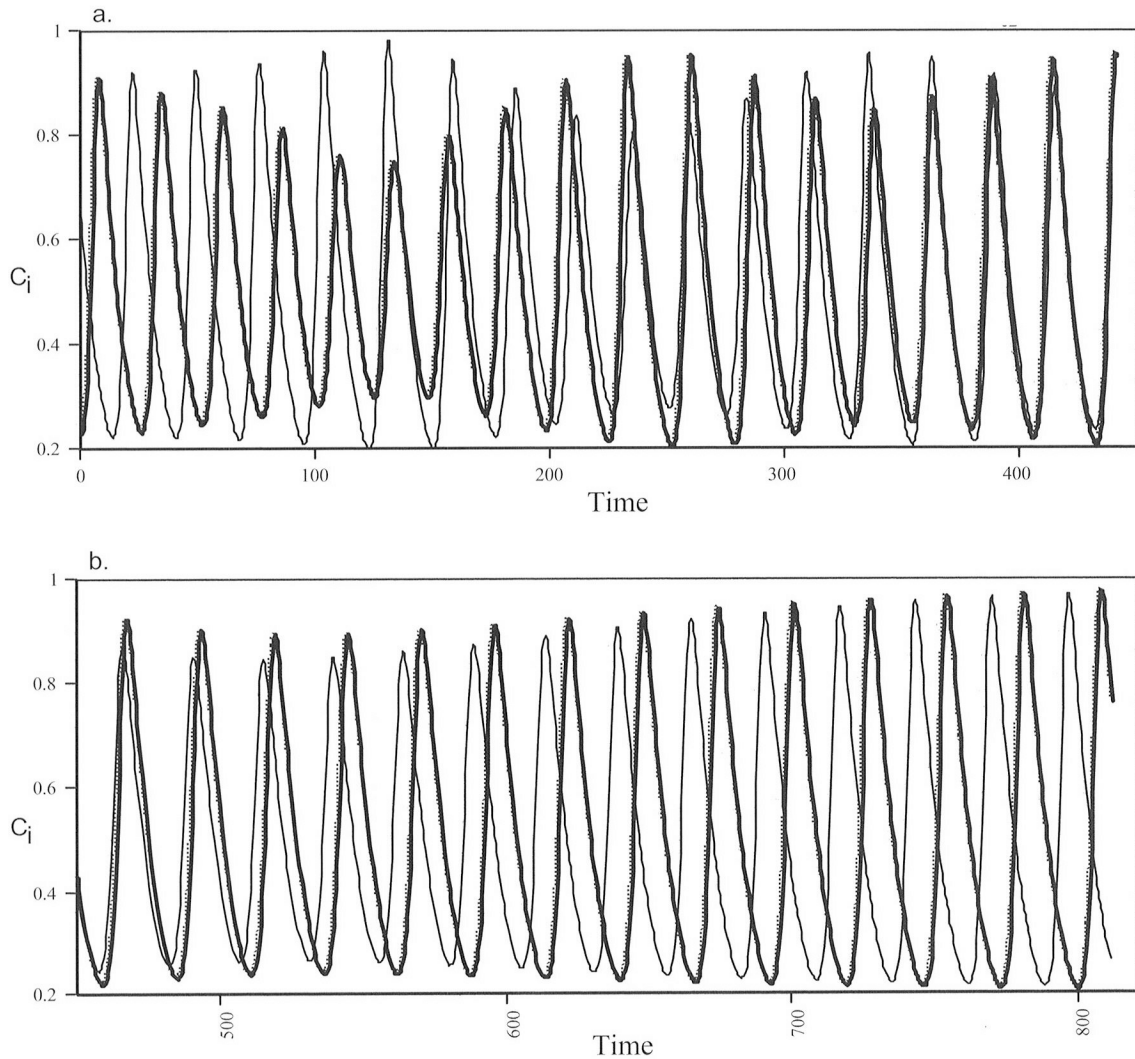


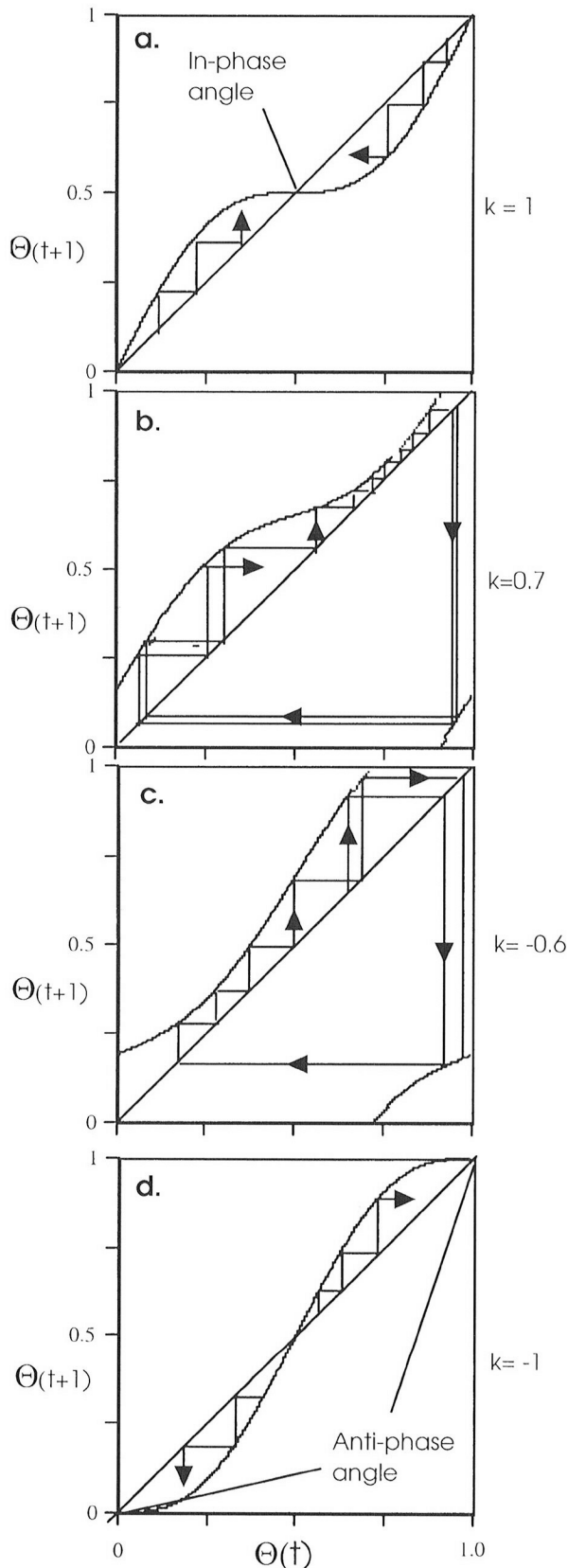
Figure 2: Time series of the two consumers with (a) CR coupling and (b) RR coupling, illustrating the distinct patterns of phase coordination. In the case of CR coupling (a), the coordination is synchronization (the peaks of the oscillations tend to occur together after transients have died down), while in the case of RR coupling (b), the coordination is phase reversal (the peaks of the oscillations are reversed, with the peak of one occurring at the valley of the other). The illustrated time series are transient, but the qualitative behavior of in-phase synchronization (a) or antiphase synchronization (b) remains constant for very long simulation runs. Parameter values were $a = 2$, $m = 0.1$, $b = 1.3$, $K = 1$, and $r_1 = r_2 = 1$. a, $\alpha = 0$, $\beta = 0.0015$. b, $\alpha = 0.075$, $\beta = 0$.

so that w and v can be set small (for modeling weak coupling generally) and their relative contribution modeled with p . For $w = 0.15$ and $v = 0.003$, a plot of the local maximum of either of the consumers yields the pattern illustrated in figure 4. It is also the case that the phase transition (in fig. 4) is characterized by either quasi periodicity or quasi-periodic chaos (note the invariant loop in the peak to peak map at two values of p in fig. 4b, 4c).

The quasi-periodic nature of this transition phase suggests that if the circle map is to be taken as an approximate model for this coupling, the parameter k in the standard

circle map must be thought of as a more complicated function modeling the process of coupling in this particular system, even at very low coupling values. For example, the following modified circle map,

$$\Theta(t+1) = \Phi(k+1)(k-1) + \Theta(t) + \left(\frac{k}{2\Pi}\right) \sin [2\Pi\Theta(t)] \pmod{1}, \quad (3)$$



results in the system slowly changing from phase synchrony (fig. 3a) at one extreme through phase reversal (fig. 3d) at the other extreme, with various forms of quasi-periodic and potentially quasi-periodic chaos forms in intermediate (fig. 3b, 3c). Further detailed analysis of this particular model is unwarranted here. It is only worth noting that, even for weak coupling of the CR and RR form, in transitioning from in-phase synchrony to anti-phase synchrony, quasi-periodic or quasi-periodic chaos may be encountered. As will be seen, this transition behavior can become extremely complicated with stronger coupling yet takes on a form that has distinct biological significance.

Strong Coupling of Identical Oscillators

The study of the system with weak coupling of identical oscillators was undertaken mainly to provide a foundation on which to build the more general study of coupling, to which we now turn. Since the process of interspecific competition between the two consumers is modeled with the CR coupling, we expect that an increase in the strength of CR coupling will eventually generate competitive exclusion of one or the other consumer, an expectation from classical ecological theory (i.e., Gause's principle). Indeed, this is the result normally encountered, as illustrated in figure 5a, where oscillations of C_1 become very large as the strength of CR coupling increases (here the logs of the local minima are plotted). While system (1) does not have formal equilibria precisely located at any of the $C_i = 0$ or $R_i = 0$, the oscillatory patterns generated are frequently heteroclinic cycles (May and Leonard 1975; Hofbauer and Sigmund 1989), in which the state variables, while never attaining the 0 value, become ever closer to 0 with each oscillatory cycle, whether chaotic or not. Thus, for biological realism, we must set some arbitrary lower limit below which the population is declared locally extinct or excluded. The horizontal line located at $\ln(C_1) = -2.6$ is positioned in figure 5, indicating the critical minimal value of C_1 below which the population is deemed excluded. In particular, for zero RR coupling, the pattern resulting from increased CR coupling (fig. 5a) may be very complicated (quasi-periodic, quasi-periodic chaos, period doubling cascades, intermittent chaos, and seemingly other forms [Vandermeer et al. 2001]) but leads to the qualitative result that at some critical value of CR coupling, the pop-

Figure 3: Graphs of circle maps for various values of oscillator coupling (parameter k). a, In-phase synchrony. b, In-phase quasi-periodic pattern. c, Antiphase quasi-periodic pattern. d, Antiphase synchrony.

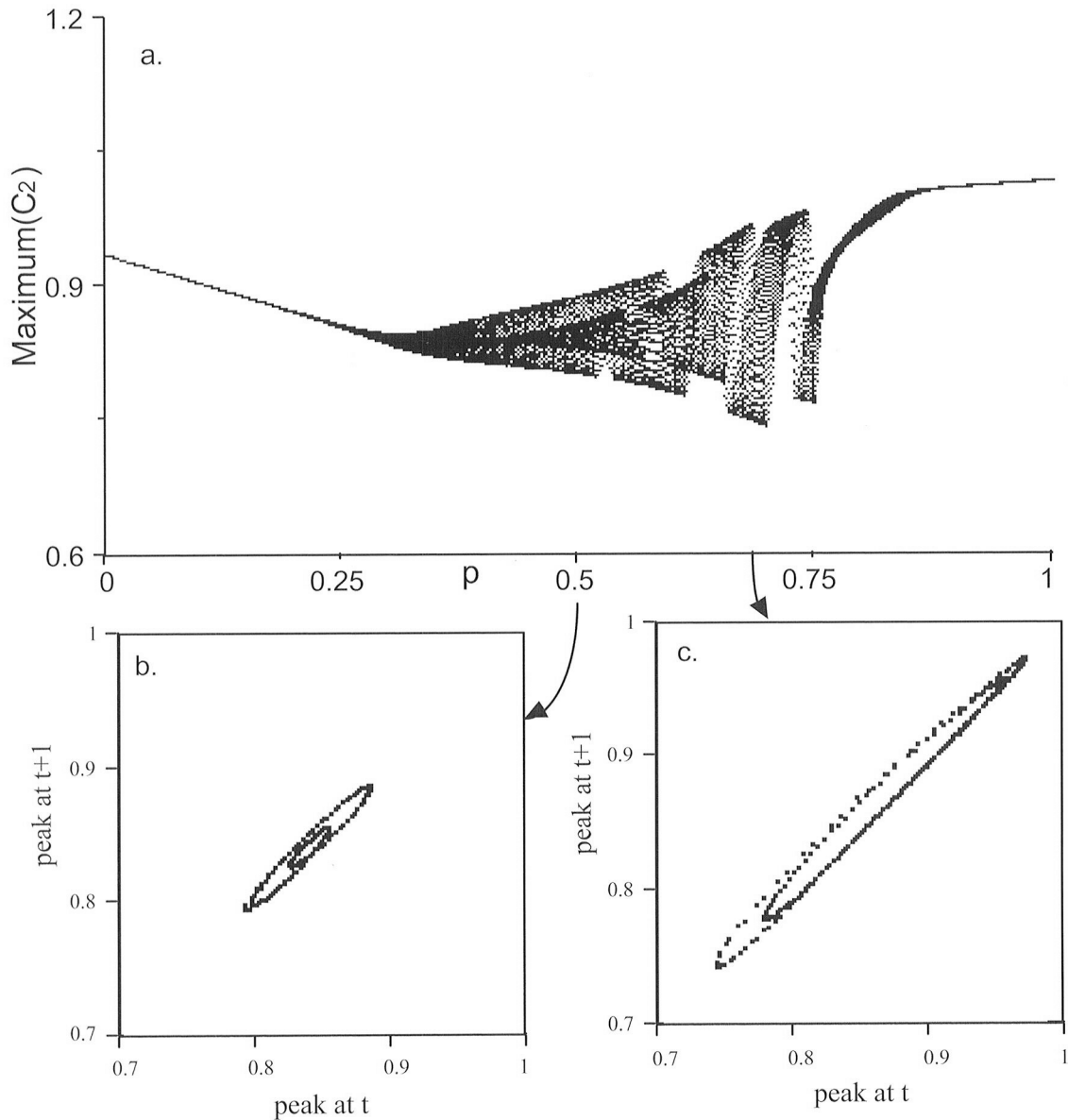


Figure 4: *a*, Local maxima of C_2 as a function of the balance between CR and RR coupling (p) for weak coupling. Parameters as in figure 2, with $w = 0.15$ and $v = 0.003$. Values toward the origin (p small) are where the system is in strict in-phase coordination, while values toward the right (p large) are where the system is in strict antiphase coordination. Intermediate values of p generate a zone of quasi periodicity, as illustrated by the trace of invariant loops in *b* and *c*.

ulation will be driven to exclusion, as indicated by the dashed vertical line in figure 5*a*.

While RR coupling alone leads to antiphase synchrony, elementary biological considerations allow us to engage the a priori expectation that eventually one of the resources will be eliminated from the system (since RR coupling is competition between the two resources), which then would result in either the maintenance of two consumers

on a single resource (Armstrong and McGehee 1980) or the elimination of one of the consumers. For a variety of particular parameter settings, the changes in C_1 resulting from increasing RR coupling to its ultimate exclusion from the system may be quasi-periodic, quasi-periodic chaotic, or other forms of extreme oscillatory behavior (not illustrated here), ultimately leading to the transcendence of the lower limit of one of the state consumers in the system.

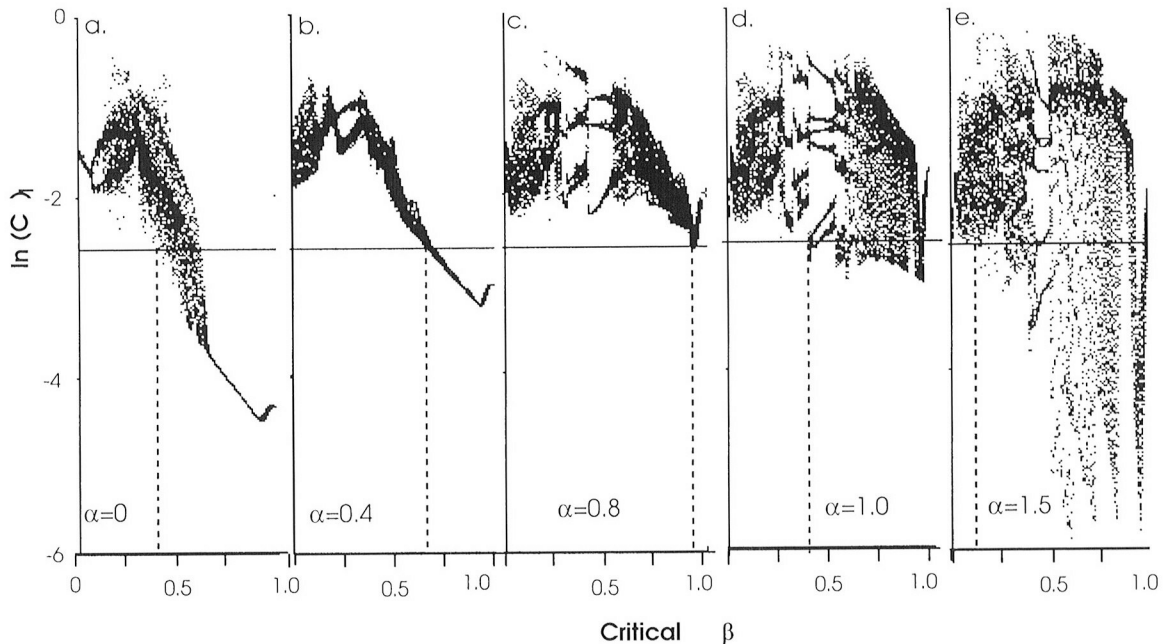


Figure 5: Local minima of the log of C_1 as a function of the CR parameter (β) for various values of the RR parameter (α). As the CR parameter increases, the variable C_1 exceeds the lower threshold of -2.6 , reflecting competitive exclusion (the C_2 variable persists). Immediately before the exclusion event, the system exhibits some form of chaotic behavior. The critical CR (β) value for which exclusion occurs (indicated by the intersection of the dashed line on the abscissa) changes nonmonotonically with changes in the RR (α) parameter. Parameter values as in figure 2, and initial values $C_1 = 0.1353$, $C_2 = 0.1877$, $R_1 = 0.2886$, and $R_2 = 0.5019$.

Thus, there are effectively two distinct bifurcation patterns: eventual elimination of one of the consumers because of increased CR coupling (fig. 5a) and eventual elimination of one of the consumers because of increased RR coupling (not illustrated). Both bifurcation patterns are commonly observed over a broad range of parameter values. One can encounter situations in which the consumer reaches the point of extinction without going through the chaotic phase, situations in which the chaotic phase has more of the character of period doubling chaos than of quasi-periodic chaos, and situations in which the chaotic phase is in a much broader zone of the coupling parameter. But the general pattern seems to be consistent over a very broad range of parameter values.

However, a rather remarkable behavior is sometimes encountered when CR and RR coupling are combined in the same model, reflecting the complications discussed for weak coupling above. Typically, as the parameter β is increased, the system eventually reaches the point of competitive exclusion (i.e., when competition becomes too intense, as explained earlier). Usually the system enters a chaotic zone just before the exclusion event (fig. 5a). However, the value of β at which that exclusion occurs depends on the value of α . That is, we have an unusual result in which RR coupling affects the degree to which CR coupling

(classic consumer competition) causes competitive exclusion (fig. 5). A biological explanation of this result is suggested below.

The pattern whereby RR coupling affects CR coupling is not a monotonic one as suggested from an examination of the intersection of the vertical dashed lines in figure 5 for different values of RR coupling (α). At low values of α (low RR coupling), the critical value of β (i.e., that which generates the extinction event) increases with more RR coupling; that is, species coexistence is enhanced by competition between the resources (see, e.g., fig. 5a–5c). However, there is a reversal of this pattern at an intermediate value of RR coupling (fig. 5c–5e), whereby further increases in α result in a lowering of the critical value of CR coupling. Thus, when RR competition is small, increasing it raises the critical level of CR competition that leads to exclusion. In contrast, when RR coupling is large, increasing it lowers the critical level of CR competition that leads to exclusion.

The general pattern is qualitatively understandable as a complication of the pattern described above for weak coupling. For any individual bifurcation diagram in figure 5, the left-hand side of the diagram is dominated by the influence of RR coupling (since CR coupling is small), while the right-hand side of the diagram is dominated by

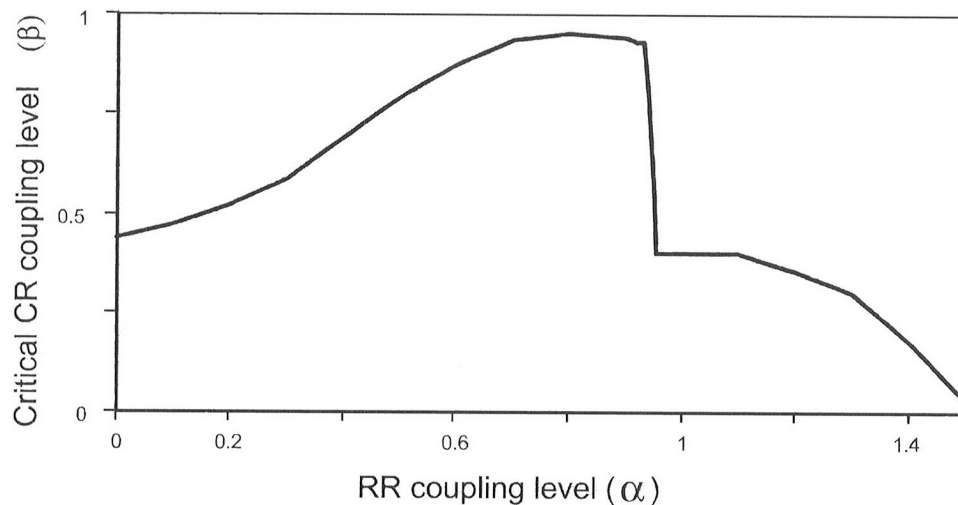


Figure 6: Relationship between level of RR coupling and the critical value of CR coupling; parameter set and initial conditions as in figure 5

the influence of CR coupling. However, as RR coupling increases, the distinction between the two forms is lost and, ultimately, the RR coupling pattern dominates. The consequence of this intermingling of the two chaotic patterns is the general pattern shown in figure 6; where at low levels of RR coupling the critical value of CR coupling that leads to exclusion increases when RR coupling is small and increasing but decreases when RR is large and increasing.

The pattern shown in figure 6 seems to be common for many parameter sets, although many variants on that pattern are possible. Furthermore, it is hardly worth mentioning that certain parameter values can generate a completely monotonic graph of critical β versus α , either positive or negative. Such will occur when the parameter values favor the dominance of either RR coupling or CR coupling exclusively. Clearly, the point of interest is in that collection of parameter values that do not generate such monotonicity, such as those explored here.

Discussion

The results reported have certain parallels to the more general literature on coupled oscillators (a popular summary of which appears in the recent book by Strogatz [2003]). The seventeenth century observations of Christian Huygens were foundational for everything from electrical oscillators to physiological rhythms. As has been so frequently reported, two pendulum clocks affixed to the wall of his study were repeatedly observed with their pendula in antiphase synchrony. Even when set in motion with identical phase oscillations, in time they came to oscillate with an antiphase coordination. It turns out that the wall

on which the clocks were mounted acted as a connection between them. The subtle vibrations set off by the oscillations mutually affected the motion of both pendula through that wall (Pikovsky et al. 2001; Bennet et al. 2002).

Synchronization of coupled oscillators can take on a variety of forms (Pikovsky et al. 2001) dependent mainly on the coupling between oscillators being weak and the oscillators being nearly identical. One form of particular interest for this work is due to the work of Blekhnman (as reported in Pikovsky et al. 2001), in which one particular formulation of Huygens's clocks generates both antiphase and in-phase synchrony. For oscillators with very different amplitudes and/or phases or for larger coupling strengths, the situation becomes far more complicated, with various dynamical behaviors appearing and disappearing, strongly depending on the details of the model. Nevertheless, in the case of consumer/resource (CR) models, there is regular and predictable qualitative behavior of even very different oscillators with strong coupling (Vandermeer 1993, 1994). Of particular importance, as in the case of physical oscillators, the general qualitative behavior depends on the details of how the coupling is manifest, the key point in the present work.

One of the most basic of all building blocks for ecological communities (consumption of resources) is an oscillator, most generally stated as a consumer population oscillating with a resource population (or a predator/prey or host/parasite combination). Furthermore, it has not escaped the attention of ecologists that the physical metaphor of coupled oscillators could also provide a kernel for further theoretical development in ecology (Vandermeer 1993; Blasius et al. 1999). The result that different forms of coupling of these ecological oscillators can gen-

erate dramatically different population behavior is new to the literature and demands, on the one hand, an intuitive grasp of its origin (if possible) and, on the other hand, a discussion of its possible significance for ecology.

Regarding an intuitive explanation of the results, an approximate way of looking at the system is as a balance between mutualism and competition. With reference to figure 1*b*, the indirect effect of C_1 on C_2 (and the reverse) may be mutualistic, since the reduction in a competitor for the food is a positive effect (the enemy of my enemy is a friend), corresponding to the well-known idea of indirect mutualism (Levine 1976; Vandermeer 1980). Thus, the RR coupling can be, in essence, a positive benefit to the consumers through the operation of the food web. However, the CR coupling is always competitive, which is to say, CR coupling is detrimental to both consumers. At low levels of RR coupling, the mutualistic effect overwhelms the competitive effect, and the system is less prone to extinction. However, when RR coupling is large, the competitive pressure exerted on both resources becomes severe, effectively adding to the pressure already exerted by the consumers. The peak of the curve (fig. 6) represents a break point from one type of behavior (where mutualism trumps competition) to another type of behavior (where two forms of competition exert a combined pressure on the system). This interpretation might be applied to food webs more generally, examining the degree to which positive indirect effects (mutualism) may be dominant over the negative indirect effects (competition), which is effectively the framework, loop analysis, suggested long ago for looking at complex systems at equilibrium (Levins 1974).

Regarding the general significance of these results, envisioning ecological systems as coupled oscillators has, directly or indirectly, generated notable patterns in the theoretical literature, as discussed in the first section of this article. It is likely that a deep study of any of those patterns will be affected to one degree or another by the results reported herein. Consider, for example, the work of McCann et al. (1998), which specifically notes that system stability tends to be promoted by the action of a stabilizing oscillator on a destabilizing one in several food web contexts, leading to the important conclusion that weak interactions can have an overriding effect on stabilizing ecosystems. This conclusion, as in the other cited cases, derives from the conceptualization of the ecosystem as a system of coupled oscillators. However, in the specific case of stabilization of food webs by the action of one oscillator on another (McCann et al. 1998), the results herein are particularly instructive. If the extra connection represented by RR coupling is weak, its increase represents a stabilizing influence: it takes a larger "competition coefficient" (CR coupling) to cause competitive exclusion of one of the consumers. However, if the RR coupling is strong (greater

than about 0.8 for the parameter set leading to fig. 6), increasing the strength of the RR coupling has the opposite effect. Thus, it could be said that increasing the strength of the weak coupling has a stabilizing effect, contrary to an increase in the strength of the strong coupling. While this may have nothing to do with the actual number of weak interactions in a complex food web (McCann et al. 1998), it is clearly an example of the way in which a strong web connection can have the opposite effect of a weak one.

At a more general level, it might be noted that many, perhaps most, studies of food webs are concerned with the way in which various populations interact with one another. Diagrams of food webs thus typically have nodes that are populations with the connections between them representing either interaction types (e.g., competition, predation) or energy transfer. The results herein actually suggest a slightly different framework for representing food webs. If we consider CR and RR coupling to be the major two forms of coupling and a consumer/resource system to be the key unit (the "atom" of construction), then the nodes in the web will be oscillators rather than populations, and the connections will be either in-phase or anti-phase coherent (CR or RR couplers). While the behavior of a simple two node system (eqq. [1]) has been discussed here, we can perhaps expect new insights about the structure of food webs with this new framework applied to larger webs.

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Literature Cited

- Abrams, P. A. 1980. Consumer functional response and competition in consumer-resource systems. *Theoretical Population Biology* 17:80–102.
- . 1986. Character displacement and niche shift analyzed using consumer-resource models of competition. *Theoretical Population Biology* 29:107–160.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* 115:151–170.
- Bak, P. 1986. The devil's staircase. *Physics Today* 1986:39–45.
- Bennet, M., M. F. Schatz, H. Rockwood, and K. Wiesenfeld. 2002. Huygens's clocks. *Proceedings of the Royal Society of London A* 458:563–579.
- Blasius, B., A. Huppert, and L. Stone. 1999. Complex dy-

- namics and phase synchronization in spatially extended ecological systems. *Nature* 399:354–359.
- Carpenter, S. R., ed. 1988. *Complex interactions in lake communities*. Springer, New York.
- Carpenter, S. R., J. F. Kitchell, J. R. Hodgson, P. A. Cochran, J. J. Elser, M. M. Elser, D. M. Lodge, D. Kretchmer, X. He, and C. N. von Ende. 1987. Regulation of lake primary productivity by food-web structure. *Ecology* 68:1863–1876.
- Chesson, P. 1990. MacArthur's consumer-resource model. *Theoretical Population Biology* 37:26–38.
- Cohen, J. 1978. *Food webs and niche space*. Princeton University Press, Princeton, N.J.
- Cohen, J. E., F. Briand, and C. M. Newman. 1990. *Community food webs: data and theory*. Springer, New York.
- DeAngelis, D. L. 1992. *Dynamics of nutrient cycling and food webs*. Chapman & Hall, New York.
- DeAngelis, D. L., W. M. Post, and G. Sugihara, eds. 1983. *Current trends in food web theory: report on a food web workshop*. Technical Report 5983. Oak Ridge National Laboratory, Oak Ridge, Tenn.
- Hastings, A., and T. Powell. 1991. Chaos in a three-species food chain. *Ecology* 72:896–903.
- Higashi, M., and T. P. Burns, eds. 1991. *Theoretical studies of ecosystems: the network perspective*. Cambridge University Press, Cambridge.
- Hofbauer, J., and K. Sigmund. 1989. On the stabilizing effect of predators and competitors on ecological communities. *Journal of Mathematical Biology* 27:537–548.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- Huisman, J., and F. J. Weissing. 2001a. Biological conditions for oscillations and chaos generated by multi-species competition. *Ecology* 82:2682–2695.
- . 2001b. Fundamental unpredictability in multi-species competition. *American Naturalist* 157:488–494.
- Kerfoot, W. C., and A. Sih, eds. 1987. *Predation: direct and indirect impacts on aquatic communities*. University of New England Press, Hanover, N.H.
- Kot, M., and W. M. Schaffer. 1984. The effects of seasonality on discrete models of population growth. *Theoretical Population Biology* 26:340–360.
- Levine, S. 1976. Competitive interactions in ecosystems. *American Naturalist* 110:903–910.
- Levins, R. 1974. Qualitative analysis of partially specified systems. *Annals of the New York Academy of Sciences* 231:123–138.
- MacArthur, R. H. 1970. Species packing and competitive equilibria for many species. *Theoretical Population Biology* 1:1–11.
- May, R. M. 1972. Limit cycles in predator-prey communities. *Science* 177:900–902.
- . 1973. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, N.J.
- May, R. M., and W. J. Leonard. 1975. Nonlinear aspects of competition between three species. *SIAM (Society for Industrial and Applied Mathematics) Journal of Applied Mathematics* 29:243–253.
- McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. *Nature* 395:794–798.
- Pascual, M., X. Rodó, S. P. Ellner, R. Colwell, and M. J. Bouma. 2000. Cholera dynamics and El Niño–Southern Oscillation. *Science* 289:1766–1769.
- Passarge, J., and J. Huisman. 2002. Competition in well-mixed habitats: from competitive exclusion to competitive chaos. Pages 7–42 in U. Sommer and B. Worm, eds. *Competition and coexistence*. Springer, Berlin.
- Pikovsky, A., M. Rosenblum, and J. Kurths. 2001. *Synchronization: a universal concept in nonlinear sciences*. Cambridge University Press, Cambridge.
- Pimm, S. L. 1982. *Food webs*. Chapman & Hall, London.
- Polis, G. A., and K. O. Winemiller, eds. 1995. *Food webs: integration of patterns and dynamics*. Kluwer Academic, London.
- Rinaldi, S., S. Muratori, and Y. Kuznetsov. 1993. Multiple attractors, catastrophes and chaos in seasonally perturbed predator-prey communities. *Bulletin of Mathematical Biology* 55:15–35.
- Rosenzweig, M. L., and R. H. MacArthur. 1963. Graphical representation and stability conditions of predator-prey interactions. *American Naturalist* 97:209–223.
- Strogatz, S. 2003. *Sync: the emerging science of spontaneous order*. Hyperion, New York.
- Vandermeer, J. H. 1980. Indirect mutualism: variations on a theme by Stephen Levine. *American Naturalist* 116:440–448.
- . 1993. Loose coupling of predator prey cycles: entrainment, chaos, and intermittency in the classic MacArthur consumer-resource equations. *American Naturalist* 141:687–716.
- . 1994. The qualitative behavior of coupled predator prey oscillations as deduced from simple circle maps. *Ecological Modelling* 73:135–148.
- Vandermeer, J. H., and P. Yodzis. 1999. Basin boundary collision as a model of discontinuous change in ecosystems. *Ecology* 80:1817–1827.
- Vandermeer, J. H., L. Stone, and B. Blasius. 2001. Categories of chaos and fractal basin boundaries in forced predator-prey models. *Chaos Solitons and Fractals* 12:265–276.
- Vandermeer, J. H., M. A. Evans, P. Foster, T. Höök, M. Reiskind, and M. Wund. 2002. Increased competition may promote species coexistence. *Proceedings of the*

- National Academy of Sciences of the USA 99:8731–8736.
- van der Pol, B., and J. van der Mark. 1927. Frequency demultiplication. *Nature* 120:64–80.
- Winemiller, K. O., and G. A. Polis. 1995. Food webs: what can they tell us about the world? Pages 1–22 *in* G. A. Polis and K. O. Winemiller, eds. *Food webs: integration of patterns and dynamics*. Kluwer Academic, London.
- Winfrey, A. T. 1980. *The geometry of biological time*. Springer, New York.

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