



Viewing communities as coupled oscillators: elementary forms from Lotka and Volterra to Kuramoto

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Abstract

Ecosystems and their embedded ecological communities are almost always by definition collections of oscillating populations. This is apparent given the qualitative reality that oscillations emerge from consumer-resource interactions, which are the elementary building blocks for ecological communities. It is also likely always the case that oscillatory consumer-resource pairs will be connected to one another via trophic cross-feeding with shared resources or via competitive interactions among resources. Thus, one approach to understanding the dynamics of communities conceptualizes them as collections of oscillators coupled in various arrangements. Here we look to the pioneering work of Kuramoto on coupled oscillators and ask to what extent can his insights and approaches be translated to ecological systems. We explore the four ecologically significant coupling arrangements of the simple case of three oscillator systems with both the Kuramoto model and with the classical Lotka-Volterra equations. Our results show that the six-dimensional Lotka-Volterra systems behave strikingly similarly to that of the corresponding Kuramoto systems across all coupling combinations. This qualitative similarity in the results between these two approaches suggests that a vast literature on coupled oscillators may be relevant in furthering our understanding of ecosystem and community organization.

Keywords Coupled oscillators · Phase synchronization · Kuramoto · Lotka-Volterra · Community ecology

Introduction

Interacting species assemblages are composed of consumers and their resources. If pairs of consumer-resource systems are persistent in a given community, then the fundamentals of ecological theory suggest that these communities are, in principle, assemblages of oscillators. To the extent that the consumers tend to overlap in their diets, or the resources interact with one another, ecological communities may be thought of as systems of coupled oscillators. Although ecologists have long been interested in understanding large assemblages of interacting species, relatively little research in community ecology has drawn on the body of theory associated with coupled oscillators to conceptualize such systems. In many branches of science, coupled oscillators have been used as a key metaphor for developing general theory, from electronics to neurobiology (Norton et al. 2018;

Laing 2017; Fukuyama and Okugawa 2017). Here we suggest that consumer-resource oscillators can be thought of as the building blocks of ecological communities and the analogy of coupled oscillators can potentially be used as an abstraction for community ecology.

The inevitability of oscillatory dynamics in ecological systems stems from one of ecology's most foundational models of consumer-resource interactions, where the simplest assumptions of one population consuming another generate persistent oscillations (Lotka 1926; Volterra 1927). Adding Holling's functional response (Holling 1959), this basic framework can generate persistent oscillations in the form of stable limit cycles, a form that could be considered as a starting point for envisioning ecological communities, which is to say, as coupled oscillators (Vandermeer 1993, 1994, 2004, 2006). Restricting the analysis to the parameter space within which limit cycle solutions exist, while limiting from a complete ecological point of view, is potentially a useful simplification explored here.

In this work, we deal with three oscillators, which means three consumers and three resources. Since there are six variables with the only necessary restriction that resources

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get consumed by consumers, the number of ways one could couple the variables together is large. Conceptualizing the system as three oscillators (a consumer and one of the resources) restricts the possible combinations, but there are still many. Yet there is a way in which some ecological assumptions can make the landscape simpler and perhaps more intuitive. Suppose that oscillatory consumer-resource pairs function in two distinct and ecologically relevant ways (Vandermeer 2004). First, when two consumers share two resources they can be thought of as coupled with one another via trophic cross-feeding, the case of resource competition between the two consumers. Second, resources that are in direct competition with one another can be thought of as being coupled via competition for some external resource. Here we refer to these two qualitatively distinct forms as trophic-coupling and resource-coupling, respectively. When coupling is weak, surprising generalizations emerge in the phase dynamics for these arrangements. For weak trophic-coupling, the oscillators converge on a pattern of relative in-phase synchrony, and for weak resource-coupling, the oscillator pairs will converge on a pattern of relative anti-phase synchrony (Vandermeer 2004) (Fig. 1). It is almost certainly the case that consumer-resource pairs are not exclusively resource-coupled or trophic-coupled in nature, and incorporating both coupling types can lead to complicated dynamics such as chaotic oscillations (Vandermeer 2004). Even given these complications, Benincà et al. (2009) demonstrated that the insights from these particular forms of coupled oscillators can be successfully applied to complex empirical communities.

Although oscillations emerge from many nonlinear systems, oscillators themselves have been the focus of understanding systems. One elegant perspective on coupled

oscillators is the abstraction of Yoshiki Kuramoto (1975, 1984), which was partially inspired by the pioneering work by Arthur Winfree on biological oscillators (1967). Kuramoto envisioned collections of coupled oscillators as weakly coupled limit cycles on the circle and the oscillator conditions indicated as the angle Θ made by the point of resource and consumer on the unit circle, taken to represent the limit cycle of the oscillator. Presuming that synchronization will occur, Kuramoto writes

$$\frac{d\Theta_i}{dt} = \omega_i + \frac{K}{N} \sum_j \sin(\Theta_i - \Theta_j) \quad (1)$$

where ω_i is the intrinsic frequency of oscillator i (the rate of advancement on the circle dictated by the inherent oscillations), K is the intensity of coupling, and N is the number of oscillators. Clearly, the intent of the model is to view the phase of the oscillations (not the amplitude) as the key dynamical variable. All oscillators are identical (with the possible exception of the intrinsic frequency), and couplings are taken to be universal (all to all). A rather remarkable result emerges from this simple model—with random initiations, no synchrony occurs when coupling strengths are small, but a critical point of coupling intensity is reached where rapid attainment of synchrony of all oscillators is achieved. There is now a large technical literature on this model, as well as a long history, both of which are summarized in a reader-friendly way by Strogatz (2000).

In an ecological context, Kuramoto's limit-cycle oscillators could be thought of as resource-consumer pairs in the parameter regimes that generate limit cycle behavior. Although it is apparent to ecologists that oscillations are an essential feature that results from the most elementary of ecological interactions, approaches used in the field of complex systems, like those

Fig. 1 The two qualitatively distinct coupling arrangements for consumer-resource oscillators and their dynamical outcomes (Vandermeer 2004). Resource coupling (competition between resources) leads to asynchrony, and trophic coupling (cross-feeding) leads to synchrony. Circles represent negative effects, arrows positive effects, and dotted lines oscillator coupling

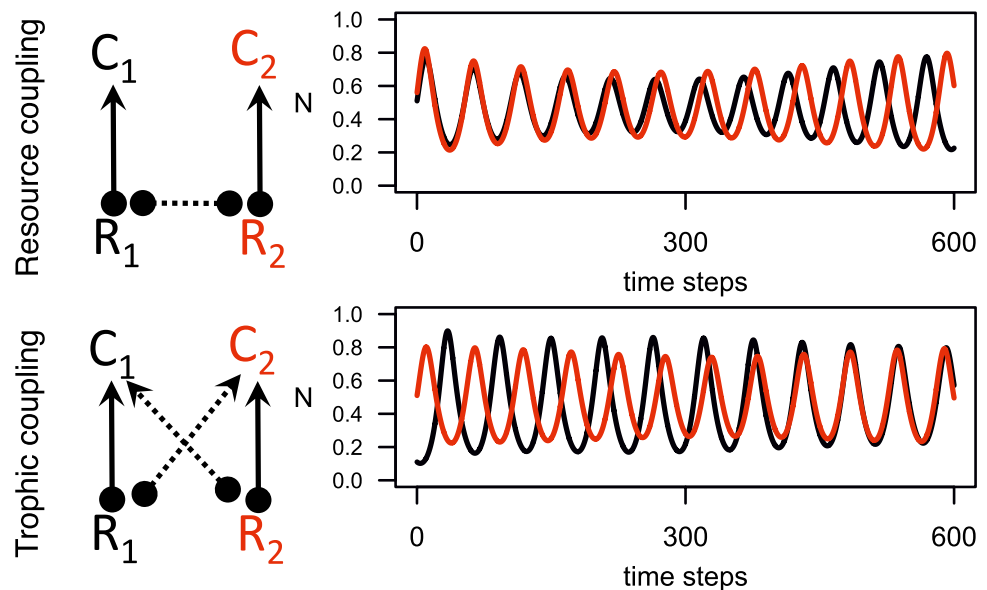


Fig. 2 Diagrammatic representation of the analogous forms of Lotka-Volterra and Kuramoto for three oscillator communities. Lotka-Volterra diagram illustrates the core idea of three consumer/resource coupled oscillators, C_i is the biomass of the i th consumer, and R_i is the biomass of the i th resource. Connectors indicate a positive effect with an arrowhead and a negative effect with a closed circle. Kuramoto diagram illustrates the three oscillators as nodes in a graph and their connections, edges, with the elements of the adjacency matrix ($+ = 1$ or $- = -1$) indicated near the edges. $\frac{1}{2} \sum \Gamma$ shows the sum of the elements of half of the adjacency matrix to simply represent the four unique coupling arrangements. Note that the coloring scheme of the oscillators is consistent throughout the article

Lotka-Volterra diagram	Kuramoto diagram	$\frac{1}{2} \sum \Gamma$
		1
		-1
		-3
		3

pioneered by Kuramoto, have gained relatively little traction in the field of ecology. It is most frequently the practice in ecology, especially in the food web literature, to couple together large networks of ordinary differential equations (e.g., Lotka-Volterra)

representing individual populations of consumers and resources. Although this approach has been fruitful, it sometimes leads to unwieldy parameterization, limiting analytical questions to those amenable to linear stability analyses. To explore the

potential usefulness of employing approaches such as those of Kuramoto, here we study the concordance between his model and the classical Lotka-Volterra models used in ecology, for the most elementary formulation of an ecological community.

Methods

Modifying Kuramoto's model, we write the following:

$$\frac{d\Theta_i}{dt} = \omega_i + \frac{K}{N} \sum_j \Gamma_{ij} \sin(\Theta_i - \Theta_j) \quad (2)$$

where Kuramoto's mean field approach has been disaggregated with the adjacency matrix Γ stipulating the coupling of each pair of oscillators. Note that $\Gamma_{ij} > 0$ indicates the oscillators i and j will synchronize "in phase" while $\Gamma_{ij} < 0$ indicates they will synchronize "anti-phase." If we stipulate that $|\Gamma_{ij}| = 1.0$, the sum of the upper triangle of the adjacency matrix $[\frac{1}{2} \sum (\Gamma_{ij})]$ can be -3 , -1 , 1 , or 3 for a three-oscillator system. Figure 2 illustrates the basic combinations of a three oscillator system with the expected outcomes of oscillator phases based on coupling dynamics from Vandermeer (2004).

Taking the classic Lotka-Volterra consumer resource equations, we write the following:

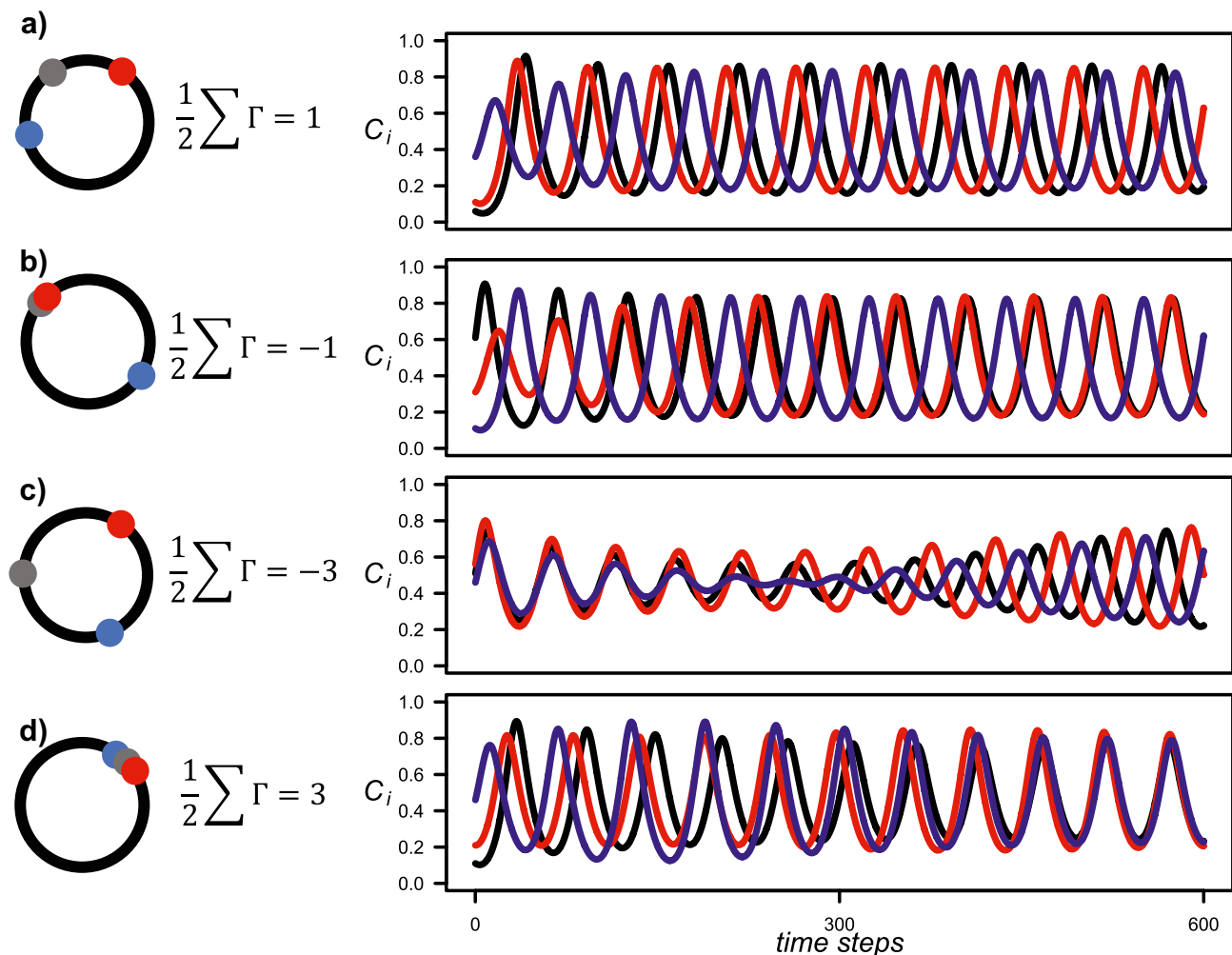


Fig. 3 Time series from the four separate coupling configurations of the three-dimensional Kuramoto and six-dimensional Lotka-Volterra systems. (a)–(d) show the oscillator phases from the Kuramoto systems and the time series for the analogous six dimensional Lotka-Volterra systems. The clear concordance between the Lotka-Volterra time series and the Kuramoto oscillator phases is evident by the end of the Lotka-Volterra time series plots. Note that only the consum-

ers are plotted in the time series to more clearly illustrate the correspondence in oscillatory dynamics between LV and Kuramoto. The parameters for all Lotka-Volterra simulations are as follows: $a = 0.7$, $m = 0.1$, $h = 3.0$, $b = 0.3$, $\beta = 0.01$, and $\alpha = 0.1$. For the Kuramoto model simulations, $K = 0.01$, $\omega = 0.01$, and the model was run for 200 time steps

$$\frac{dC_i}{dt} = \frac{aC_i \sum_{j=1}^3 \beta_{ij}R_j}{1 + h \sum_{j=1}^3 R_j} - mC_i \quad (3a)$$

$$\frac{dR_i}{dt} = bR_i \left(1 - \sum_{j=1}^3 \alpha_{ij}R_j \right) - \frac{aC_i \sum_{j=1}^3 \beta_{ij}R_j}{1 + h \sum_{j=1}^3 R_j} \quad (3b)$$

where C and R denote “consumers” and “resources” respectively and i ranges from 1 to 3. The basic parameters of the model are as follows: a = the attack rate of the consumers, m = the mortality rate of the consumers, h = the functional response term of the consumer, b = the birth rate of the resource, α_{ij} = the competitive effect of resource j on resource i (note, $\alpha_{ii} = 1$), and β_{ij} = the strength of cross feeding (note, $\beta_{ij} = 1$). The parameter α represents the strength of competition (resource coupling) between resources, and β represents the strength of cross-feeding (trophic coupling).

In the spirit of Kuramoto’s model, we first located parameter space where individual consumer-resource pairs oscillate in limit cycles (equation set 3). For all simulations presented here, those parameters are as follows: $a = 0.7$, $m = 0.1$, $h = 3.0$, and $b = 0.3$. Given a persistent oscillator in the Lotka-Volterra formulation, we then couple them in four paradigmatic combinations outlined in Fig. 2, where trophic-coupling implies eventual synchrony and resource-coupling implies asynchrony. Manipulating α_{ij} and β_{ij} in equation set 3, we create the parameter states for all four coupling arrangements depicted in Fig. 2 (see Appendix for long form equations for each coupling scenario). For all simulations presented here, we used low values of coupling coefficients ($\beta = 0.01$ and $\alpha = 0.1$).

Results

Employing the Kuramoto model (Eq. 2) if $\frac{1}{2} \sum \Gamma_{ij} = 3$, the system synchronizes in-phase (i.e., all oscillators are effectively on the same point in circle space, as in Fig. 3d); if it is -3 , the system synchronizes precisely anti-phase (each oscillator separated from each other by $2\pi/3$ radians, as in Fig. 3c); if it is -1 , two oscillators are in-phase and the third is anti-phase against the two in-phase oscillators (Fig. 3b). However, if the sum is 1 a situation emerges in which oscillator 3 is in-phase synchrony with oscillator 1, oscillator 1 is in-phase synchrony with oscillator 2, while oscillator 2 is anti-phase synchronous with oscillator 3, but, qualitatively stable. The three oscillators are separated from one another by $\Theta_{1,2} = \Theta_{1,3} = \pi/3$ and $\Theta_{2,3} = 4\pi/3$ (Fig. 3a). In all four cases (Fig. 3), while all oscillators retain the same relative position with respect to one another, they all together progress around the state space according to the intrinsic frequency.

Employing the Lotka-Volterra model (Eqs. 3a and 3b), typical time series results of all four ODE simulations are presented in Fig. 3. It is clear that the Lotka-Volterra predictions for all four qualitatively distinct cases (Fig. 2) are precisely what we get from the simpler Kuramoto approach. It is worth noting that the Lotka-Volterra simulations are quite robust as long as the coupling is not strong. As reported elsewhere (Vandermeer, 1993, 1994, 2004, 2006) as coupling becomes stronger, frequently complicated behavior, including chaos and quasiperiodicity, typically emerges from these structures. Regarding the Kuramoto simulations, the results are seemingly completely robust in that we found no examples of coupling (in the range 0–1) that did not yield the same qualitative results as visualized in Fig. 3.

Discussion

The ubiquity of oscillatory dynamics in ecology has long been appreciated (Platt and Denman 1975; Huisman and Weissing 2001; Blasius et al. 2020). Empirically, across a range of spatiotemporal scales from large scale dynamics of the hare-lynx system (Blasius et al. 1999) to the microcosm experiments of Huffaker (1958), and theoretically emerging from the simplest conceptualizations of consumer-resource interactions (Lotka 1926; Volterra 1927), synchronization of coupled consumer-resource oscillators is well-known, both from an implied spatial coupling (e.g., predator or prey migrating among habitat patches (Koelle and Vandermeer 2005) and direct energy transfer (e.g., different predators coupling among different prey in the same habitat (Vandermeer 2006)). Here we demonstrate that for the four most obvious qualitatively distinct yet ecologically significant coupling patterns in a six-species community (three oscillators), weak coupling leads to precisely the pattern predicted by Kuramoto’s phase coupled system. These results suggest a wholly distinct vision of ecological communities in which the “agents” are not population densities, but rather oscillators.

There are evident limitations in the analysis as presented here, but, we argue, those limitations suggest that the approach holds much potential. For example, the introduction of dissipating oscillators into the mix is an evident expansion of the system, one that has not been examined, at least not in the context of the Lotka-Volterra and Kuramoto connection. Another important element is the possibility of studying coupled chaotic oscillators with the Kuramoto framework, certainly a challenging possibility. Blasius and colleagues (1999) have already indirectly entered this topic with their UPCA pattern (uniform phase chaotic amplitude), which is, in a sense, putting chaotic dynamics in a Kuramoto-like framing (although chaotic, the lynx/hare cycle synchronizes

phases across Canada). Contrarily, one might ask what a UACP pattern (uniform amplitude, chaotic phase) would look like and how it could be generated, perhaps a more direct application of the Kuramoto metaphor since amplitudes are fixed and the interest is in the dynamics of the phases. On the other hand, the existence of chimeric elements (individual oscillators that refuse to synchronize in any way with synchronous groups of oscillators) may already be examples of chaos or chaos-like behavior in the Kuramoto framing (Kotwal et al. 2017; Laing 2009).

There is a rich and diverse literature on synchronization, popularly summarized for a generalist audience by Steven Strogatz in his book “Sync.” (2012). Ecological applications are less common but the field is growing. For example, some authors have examined correlations with external forcing, either regular or stochastic (Vasseur and Fox 2007; Reuman et al. 2008) in driving or sometimes quenching synchronized systems, and spectral analysis (Vasseur and Gaedke 2007) recalls the original insights of Platt and Denman (1975). And, of course, it has long been acknowledged that a metapopulation in which subpopulations oscillate in sync is far more likely to undergo global extinction (Matter 2001).

By reorienting the focus of ecological analogy from individual populations to collections of oscillators, the dynamical nature of the system becomes the central focus rather than questions of stability or persistence. As in other sciences, the collective dynamics of coupled oscillators can provide a useful heuristic for exploring the general properties of large and complex systems of the sort that ecologists have long cited with awe (Hutchinson 1961; Lawton 1999; Vellend 2010). Furthermore, by highlighting the ability to move between classical models in ecology and classical models in the coupled oscillator literature, we suggest that both approaches can be used in tandem and exploited for their strengths. Approaches to Kuramoto effectively increase the tractability of large complex systems by halving the dimensionality and providing an elegant and intuitive way to visualize the oscillatory dynamics, while approaches to Lotka-Volterra permit investigation of how basic biological parameters influence dynamics. The most obvious utility of such an approach is where synchronous dynamics are the focus of investigation (e.g. Earn et al. 1998; Blasius et al. 1999; Liebhold et al. 2004) and may have practical implications for the management of fisheries (Kaemingk et al. 2018), the planning complex biological control systems in agroecosystems (Vandermeer et al. 2019), or conservation (Earn et al. 2000).

The once popular idea that ecosystems are at, or moving towards, Lyapunov stability is considered passé (e.g., Morozov et al. 2019). The growing appreciation among ecologists that ecosystems and communities are dominated by nonlinear processes often outside of equilibrium (DeAngelis and Waterhouse 1987) suggests

that our tool kits to understand ecosystems need to evolve along with our analogies of them, as suggested long ago (Platt and Denman 1975). We suggest that networks of oscillators, rather than networks of populations, represent a potentially new paradigm for the examination of ecological communities.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflicts of interest.

Appendix

$\frac{1}{2} \sum \Gamma = 1$ for the Lotka-Volterra system of ordinary differential equations has C_1 with trophic-coupling on R_2 and R_3 , C_2 with trophic-coupling on R_1 , C_3 with trophic-coupling on R_1 , and R_2 and R_3 resource coupled. Initial conditions for Fig. 2 are as follows: $R_1 = 0.05$, $R_2 = 0.10$, $R_3 = 0.35$, $C_1 = 0.06$, $C_2 = 0.11$, and $C_3 = 0.36$.

$$\dot{R}_1 = bR_1(1 - R_1) - \frac{aR_1C_1}{1 + ahR_1} - \beta \frac{aR_2C_2}{1 + ahR_2} - \beta \frac{aR_3C_3}{1 + ahR_3} \quad (4a)$$

$$\dot{C}_1 = \frac{aR_1C_1}{1 + ahR_1} - mC_1 + \beta \frac{aR_2C_1}{1 + ahR_2} + \beta \frac{aR_3C_1}{1 + ahR_3} \quad (4b)$$

$$\dot{R}_2 = bR_2(1 - R_2 - \alpha R_3) - \frac{aR_2C_2}{1 + ahR_2} - \beta \frac{aR_1C_1}{1 + ahR_1} \quad (4c)$$

$$\dot{C}_2 = \frac{aR_2C_2}{1 + ahR_2} - mC_2 + \beta \frac{aR_1C_2}{1 + ahR_1} \quad (4d)$$

$$\dot{R}_3 = bR_3(1 - R_3 - \alpha R_2) - \frac{aR_3C_3}{1 + ahR_3} - \beta \frac{aR_1C_1}{1 + ahR_1} \quad (4e)$$

$$\dot{C}_3 = \frac{aR_3C_3}{1 + ahR_3} - mC_3 + \beta \frac{aR_1C_3}{1 + ahR_1} \quad (4f)$$

for $\frac{1}{2} \sum \Gamma = -1$ for the Lotka-Volterra system of ordinary differential equations has C_1 with trophic-coupling on R_2 ; C_2 with trophic-coupling on R_1 , R_2 , and R_3 with

resource-coupling; and R_1 and R_3 with resource-coupling. Initial conditions for Fig. 2 are as follows: $R_1 = 0.60$, $R_2 = 0.30$, $R_3 = 0.10$, $C_1 = 0.61$, $C_2 = 0.31$, and $C_3 = 0.11$.

$$\dot{R}_1 = bR_1(1 - R_1 - \alpha R_3) - \frac{aR_1C_1}{1 + ahR_1} - \beta \frac{aR_2C_2}{1 + ahR_2} \quad (5a)$$

$$\dot{C}_1 = \frac{aR_1C_1}{1 + ahR_1} - mC_1 + \beta \frac{aR_2C_2}{1 + ahR_2} \quad (5b)$$

$$\dot{R}_2 = bR_2(1 - R_2 - \alpha R_3) - \frac{aR_2C_2}{1 + ahR_2} - \beta \frac{aR_1C_1}{1 + ahR_1} \quad (5c)$$

$$\dot{C}_2 = \frac{aR_2C_2}{1 + ahR_2} - mC_2 + \beta \frac{aR_1C_1}{1 + ahR_1} \quad (5d)$$

$$\dot{R}_3 = bR_3(1 - R_3 - \alpha R_2 - \alpha R_1) - \frac{aR_3C_3}{1 + ahR_3} \quad (5e)$$

$$\dot{C}_3 = \frac{aR_3C_3}{1 + ahR_3} - mC_3 \quad (5f)$$

for $\frac{1}{2} \sum \Gamma = -3$ has pairwise resource-coupling between all resources and no trophic-coupling. Initial conditions for Fig. 2 are as follows: $R_1 = 0.50$, $R_2 = 0.55$, $R_3 = 0.45$, $C_1 = 0.51$, $C_2 = 0.56$, and $C_3 = 0.46$.

$$\dot{R}_1 = bR_1(1 - R_1 - \alpha R_2 - \alpha R_3) - \frac{aR_1C_1}{1 + ahR_1} \quad (6a)$$

$$\dot{C}_1 = \frac{aR_1C_1}{1 + ahR_1} - mC_1 \quad (6b)$$

$$\dot{R}_2 = bR_2(1 - R_2 - \alpha R_1 - \alpha R_3) - \frac{aR_2C_2}{1 + ahR_2} \quad (6c)$$

$$\dot{C}_2 = \frac{aR_2C_2}{1 + ahR_2} - mC_2 \quad (6d)$$

$$\dot{R}_3 = bR_3(1 - R_3 - \alpha R_1 - \alpha R_2) - \frac{aR_3C_3}{1 + ahR_3} \quad (6e)$$

$$\dot{C}_3 = \frac{aR_3C_3}{1 + ahR_3} - mC_3 \quad (6f)$$

for $\frac{1}{2} \sum \Gamma = 3$ has pairwise trophic-coupling between all consumers and resources and no resource-coupling. Initial conditions for Fig. 2 are as follows: $R_1 = 0.10$, $R_2 = 0.20$, $R_3 = 0.45$, $C_1 = 0.11$, $C_2 = 0.21$, and $C_3 = 0.46$.

$$\dot{R}_1 = bR_1(1 - R_1) - \frac{aR_1C_1}{1 + ahR_1} - \beta \frac{aR_2C_2}{1 + ahR_2} - \beta \frac{aR_3C_3}{1 + ahR_3} \quad (7a)$$

$$\dot{C}_1 = \frac{aR_1C_1}{1 + ahR_1} - mC_1 + \beta \frac{aR_2C_2}{1 + ahR_2} + \beta \frac{aR_3C_3}{1 + ahR_3} \quad (7b)$$

$$\dot{R}_2 = bR_2(1 - R_2) - \frac{aR_2C_2}{1 + ahR_2} - \beta \frac{aR_1C_1}{1 + ahR_1} - \beta \frac{aR_3C_3}{1 + ahR_3} \quad (7c)$$

$$\dot{C}_2 = \frac{aR_2C_2}{1 + ahR_2} - mC_2 + \beta \frac{aR_1C_1}{1 + ahR_1} + \beta \frac{aR_3C_3}{1 + ahR_3} \quad (7d)$$

$$\dot{R}_3 = bR_3(1 - R_3) - \frac{aR_3C_3}{1 + ahR_3} - \beta \frac{aR_1C_1}{1 + ahR_1} - \beta \frac{aR_2C_2}{1 + ahR_2} \quad (7e)$$

$$\dot{C}_3 = \frac{aR_3C_3}{1 + ahR_3} - mC_3 + \beta \frac{aR_1C_1}{1 + ahR_1} + \beta \frac{aR_2C_2}{1 + ahR_2} \quad (7f)$$

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