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Oscillating Populations and Biodiversity Maintenance

JOHN VANDERMEER

Species persistence in the face of competitive or predatory pressure has long been assumed to be a consequence of either dynamic equilibrium or stochastic longevity. More recently, however, the complex intersection of nonlinear dynamics with elementary ecological interactions has provided a distinct platform for conceptualizing the problem of species coexistence. One well-known result from nonlinear dynamics is that oscillating systems will tend to coordinate with one another when coupled, even if the coupling is extremely weak. This elementary result yields remarkable insights in many fields of study. Here I summarize recent results showing that a particular structure emerging from a nonlinear analysis of the classic equations of ecology can be merged with more qualitative ideas to form a possible general framework for analyzing species diversity. As a specific example, I examine the case of two consumer–resource systems that, when coupled, inevitably produce some kind of phase coordination. Understanding the nature of that phase coordination provides a qualitative viewpoint for understanding exclusion and coexistence in this example. Finally, I discuss possible applications to other classical ecological questions.

Keywords: oscillations, competition, biodiversity, chaos, communities

The nature of biodiversity has long been a central focus in biology. This may not seem the case any longer, since the most visible and spectacular advances in biology have been with a very restricted set of organisms—the house mouse (*Mus musculus*), the fruit fly (*Drosophila* spp.), the nematode *Caenorhabditis elegans*, the plant *Arabidopsis*, the bacterium *Escherichia coli*, and a few others. Basic mechanisms of physiology, development, and genetics have been elucidated for these few species at many levels of organization, and an unprecedented cooperation among laboratories has restructured the science of biology such that a practitioner from Darwin's time would not recognize a biology lab today for what it is. Yet many biologists and paleontologists remain perplexed by questions that would not seem at all unusual for their 19th-century counterparts. Where do all the species come from? How is it that some localities have a great deal of biodiversity while others have little? What causes extinctions, and are they more or less balanced with speciation events? Darwin's "tangled bank" and Wallace's "plan of the mighty maze" are still alive and enigmatic, and still motivate a large number of biologists.

Darwin himself set out a dual approach to the problem: variation and the "force of selection." Selection acting on variation to produce adaptation has been the biologist's equivalent of Newton's laws ever since the widespread scientific acceptance of Darwin's theory. As Lewontin so perceptively described it in *The Triple Helix* (2000), a complete theory of diversity is, in a sense, provided by "adaptation" to

an "ecological niche." Adaptation results from the force of selection acting on variation. The problem of variation—potentially Darwin's Achilles' heel, given what he thought he understood about genetics—was solved by Mendel. But no Mendel came to clarify the force of selection; and the notion of the ecological niche, to which the organism adapts, remains obscure and poorly defined.

In modern terms, Darwin's force of selection has become identified with the field of ecology, but the specific problem of the ecological niche has never been resolved. And that problem has become considerably more complex than Darwin, Wallace, or other 19th-century biologists may have anticipated. Later biologists have gleaned significant insight by formulating the problem as one of the "construction" of niches by organisms, rather than adaptation into niches (Lewontin 2000, Odling-Smee et al. 2003). However, there is a far more important way in which niches relate to diversity: through their influence on species' interactions.

For example, a speciation event in which only reproductive function is altered would seem not to be sustainable in principle. That is, the two new species, even though they are true species in the sense that they are incapable of inter-

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breeding, continue occupying the same niche. Classical ecological theory suggests that these two species could not coexist in the same environment. However, a closer look at the theory that leads to that conclusion (Levins 1979, Armstrong and McGehee 1980) reveals that something more complicated may happen. Under certain circumstances, species can indeed occupy the same niche. And those circumstances are related to the oscillations that inevitably arise from patterns of consumption, which is to say the relationship between an organism and its natural enemies (predators, parasites, diseases, etc.). Could it be that such a conclusion represents a more general rule?

At the famous 1944 meeting of the British Ecological Society, the great geneticist J. B. S. Haldane was reported to query the assembled sages regarding the likelihood that competitors would, to some extent, share natural enemies. How might that affect the competitive exclusion principle, for example? We have only a short summary of that meeting (Anonymous 1944) and will never know for sure what Haldane actually said. But it appears that he had, to some extent, anticipated the problems associated with competitors oscillating as a consequence of trophic structure. It is those oscillations that cast a shadow of complexity on the issue of diversity (Armstrong and McGehee 1980). However, perhaps those oscillations, once investigated further, may shed light on the issue as well.

When can a third species invade?

I take as an example the standard textbook case of two species on a simple environmental gradient (figure 1). In a major insight into the science of biodiversity, MacArthur and Levins (1967) noted that if the niches of the two species overlapped too much, one species or the other would be excluded from the environment, and, more important, selection would operate most strongly on those individuals located in the zone of overlap. While these assumptions are complex and questionable, the basic idea is clear. Suppose there is heritable variation in niche use, where “use” is stipulated as a particular position on the gradient. If individuals in the population occupy only restricted positions along the gradient, selection would indeed favor the individuals not located in the intensely competitive zone where the niches overlap (figure 1a). The consequence would be a reduction in the breadth of the two niches (figure 1b). But this generates a new condition. The overlap of the niches becomes so small that a part of the niche space now becomes available for some other species to invade the system (figure 1c). The overall consequence is clear. With a new species inserted, niche overlap will again be large, and again selection will favor reduction in that overlap, which will provide a space for an invading species. But there must be some limit to the number that can squeeze into this niche space—the number of species that can be “packed” into an ecosystem—which leads to the idea of species packing, one of the central ideas, historically, in biodiversity science.

A contentious complication of this framework is that niche overlap is poorly defined, and thus its articulation with com-

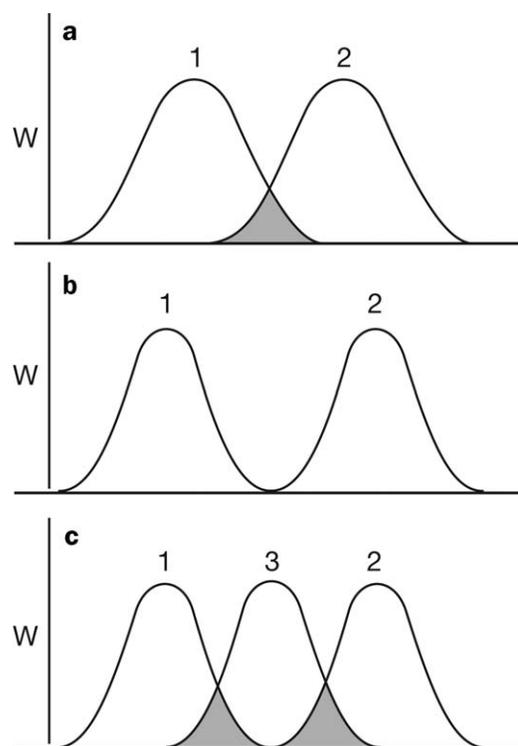


Figure 1. Elementary form of the Levins and MacArthur limiting similarity argument. The x-axis represents an arbitrary environmental gradient, and the y-axis represents some measure of fitness (W) for each of two species. The intersections (shaded areas) represent the areas of intense competition between neighboring species. (a) Selection favors the individuals that are not located in the intensely competitive zone where the niches overlap. (b) The result is a reduction in the breadth of the two niches. (c) As the overlap between the two niches shrinks, enough niche space becomes available to allow a third species to invade the system.

petition is questionable in the first place. But the basic problem can be formulated without this complication with a simple extension of Lotka–Volterra principles (MacArthur 1970). MacArthur’s original formulation can be shown in a graph, as in figure 2a. The two consumers are generalist in their eating habits but tend toward specialization. The degree of generalization is correlated with the intensity of competition between them. Since the joint use of resources is the mechanism of competition, this approach is appropriately referred to as a “mechanistic” approach, in contrast with the “phenomenological” approach in which the phenomenon of competition is simply written into the equations as a constant, usually referred to as the competition coefficient. The position on the resource gradient in the phenomenological sense is simply a connection between the two species (see box 1). However, adding Haldane’s effect, we note that all species have their natural enemies, hence the phenomenological formulation becomes similar to the mechanistic formulation (fig-

ure 2b). Thus, in either the mechanistic or the phenomenological approach, we have two consumer–resource (predator–prey, parasite–host) systems that are coupled (either through consumption by the predators, as in figure 2a, or through competition between the prey, as in figure 2b).

This formulation brings us face-to-face with the ideas of nonlinear dynamics and complexity theory. Recently published research suggests that this sort of quantitative theory, when applied to elementary ecological interactions, provides a distinct platform for conceptualizing the problem of species coexistence (Vandermeer 1989, 2004, Abrams et al. 1998, Huisman and Weissing 1999, 2001, Abrams and Holt 2002, Vandermeer et al. 2002, 2006, Koelle and Vandermeer 2005, Vandermeer and Pascual 2006). In particular, when the underlying biological force is consumption, as it is in the current example, the expected dynamical behavior is oscillatory. Thus a consumer–resource system (which includes herbivore–plant, predator–prey, and parasite–host) is oscillatory—perhaps controlled to the point where the oscillations damp out over time, or perhaps permanently oscillating in a limit cycle, but in one way or another an oscillating system. Consequently, in figure 2a and 2b, the system P_1, X_1 is oscillatory, as is the system P_2, X_2 .

A well-known result from nonlinear dynamics is that oscillating systems will tend to coordinate with one another when coupled, even if the coupling is extremely weak. This elementary result yields remarkable insights in many fields at vast scales of organization, from biochemical pathways to the dynamics of galaxies, as summarized in Stephen Strogatz’s popular book *Sync* (2000). One might even generalize that “it can be argued, such is the norm of nature and its importance cannot be over-emphasized” (Criminale et al. 2004). What might this general result from nonlinear dynamics have to do with the problem of species diversity? Specifically, when two consumer–resource systems are coupled, as they are in the elementary formulation of two species with overlapping niches on a resource gradient, some kind of phase coordination is inevitably produced. I contend that understanding the nature of that phase coordination could provide a new qualitative viewpoint for understanding exclusion and coexistence.

For example, simply asking whether two oscillatory systems are correlated positively or negatively—that is, whether their oscillatory coordination is in phase or out of phase—could have obvious biological meaning. If two consumer–resource

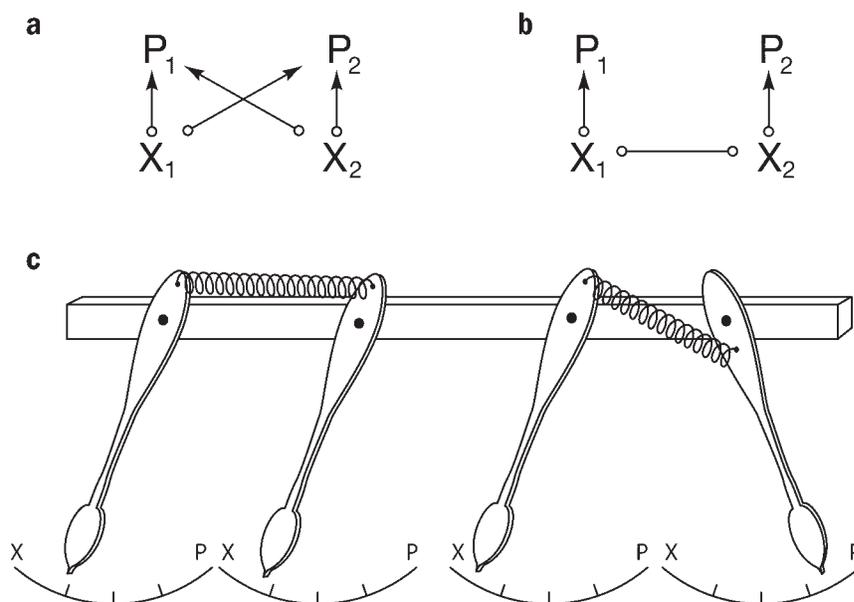


Figure 2. The elementary coupling of consumer–resource systems and the qualitative outcomes. (a, b) Two predators (consumers), P_1 and P_2 , eat two resources (prey), X_1 and X_2 , with arrowheads indicating a positive effect and small circles a negative effect. The form of coupling is (a) that the predators eat each other’s prey (and thus become competitors with one another) or (b) that the prey items compete with one another. (c) Physical metaphor of coupled pendulums, with metaphorical springs connecting them in two different ways, one corresponding to the predators consuming one another’s resource (left-hand pair) and the other corresponding to the prey in competition with one another (right-hand pair). The scale at the bottom illustrates how the metaphorical pendulums oscillate between numerical dominance of predator and numerical dominance of prey. The two forms of coupling generally result in either in-phase (bottom left) or antiphase (bottom right) coordination of the oscillators.

oscillators are coordinated in phase with one another, might this not provide a periodic opportunity for another species to enter the system, parallel to the case of the niche gradient with two species sufficiently spaced on the gradient to permit entry of a third species in the classic limiting similarity scenario (MacArthur and Levins 1967)? For example, if the lion and leopard populations are simultaneously at low values (which they would be repeatedly if they were coordinated in phase), might the cheetah population be able to invade at that point? So obvious is this point that it is hardly recognizable as something to be noted. For instance, since diurnal cycles coordinate the daily activities of many animals, having a “night niche” or “day niche” can be thought of as avoiding competition or predation. The same could be said for seasonal cycles, and there are many other examples. Coordination of the oscillations of some species may represent an opportunity for other species to invade their niche space.

However, the dynamic coordination of a species invading the environment of two consumer–resource oscillators represents a special situation. The invading species is, by definition, coupled to the two original oscillators and thus is

Box 1. Derivation of the model system.

The model system follows the classical equations of Lotka and Volterra as follows:

$$dX_1/dt = X_1(1 - X_1 - c_1\alpha X_3) - aX_1(P_1f_1 + c_2P_3f_3),$$

$$dX_2/dt = X_2(1 - X_2 - c_1\alpha X_3) - aX_2(P_2f_2 + c_2P_3f_3),$$

$$dX_3/dt = X_3 [1 - X_3 - c_1\alpha(X_1 + X_2)],$$

$$dP_1/dt = aP_1f_1X_1 - mP_1,$$

$$dP_2/dt = aP_2f_2X_2 - mP_2,$$

$$dP_3/dt = c_2aP_3f_3(X_1 + X_2) - mP_3,$$

$$f_i = 1/(1 + b_iX_i) \text{ for } i = 1, 2, \text{ and}$$

$$f_3 = 1/[1 + c_2b_3(X_1 + X_2)],$$

where X_i is the population density or biomass of the i th resource species, P_i is the population density or biomass of the i th consumer species, a is the consumption coefficient, m is the mortality rate of the consumers, c_1 is the coupling through resource competition (figure 2a), c_2 is the coupling through predation (figure 2b), α is the competition coefficient, and b is the parameter of the functional response. Unless indicated otherwise, for all examples in this article, $\alpha = 1.1$, $m = 0.8$, and $b = 2$. When $c_1 = 0$ and $c_2 > 0$, coupling is through predation (figure 2b); when $c_2 = 0$ and $c_1 > 0$, coupling is through resource competition (figure 2a).

For the example of weakly coupled resources with P_3 as an invader (figure 5), the resource equations are

$$dX_1/dt = X_1(1 - X_1 - \beta X_2 - c_1\alpha X_3) - aX_1(P_1f_1 + c_2P_3f_3) \text{ and}$$

$$dX_2/dt = X_2(1 - X_2 - \beta X_1 - c_1\alpha X_3) - aX_2(P_2f_2 + c_2P_3f_3),$$

where β is the coupling/competition coefficient connecting the two resources.

implicated in the nature of their coordination. So the dilemma is that, while oscillations between two consumer–resource systems may make conditions ripe for the invasion of a third species, the third species is necessarily implicated in the making or breaking of those ripe conditions. Sorting out this dilemma could be important for understanding the consequences of particular patterns of connections in food webs more generally.

However, for the example of two consumer–resource systems coupled through either consumption or competition (figure 2a, 2b, box 1), it has been shown (Vandermeer 1989, 2004) that if there is weak coupling through consumption (figure 2a), the two systems will come into complete synchrony, with peaks in the oscillations of P_1 occurring at close to the same time as peaks in the oscillations of P_2 . However, if coupling is mainly through competition between the resource species (figure 1b), an antiphase coordination will be effected. A useful metaphor for this phenomenon is the cou-

pled oscillating pendulum model, in which it is easy to see how either in-phase or antiphase coordination is driven by the specific nature of the coupling (figure 2c).

The form of phase coordination will, to some extent, determine whether other species can invade an ecosystem, and as such could be a major force in determining species diversity. Here I consider the most elementary case, formally equivalent to the limiting similarity argument: that of a third species invading a system composed of two consumer–resource systems. There are two interesting ways in which the problem can be conceptualized (figure 3). On the one hand, there may be a third resource species acting as a competitor with the other resource species (X_3 in figure 3a). On the other hand, there may be a third consumer species (P_3 in figure 3b), acting as a predator on the two resource species and consequently a competitor with the other two predators. Either of these invasions represents the underlying ecological structure of one subordinate and two dominant competitors, the difference being in the phenomenological versus mechanistic approach to the competitive process. In the phenomenological approach (figure 3a), a third species (X_3) enters through the phenomenon of competition, without stipulating the underlying details of that competition. In the mechanistic approach (figure 3b), a third species (P_3) enters through the phenomenon of consumption and becomes an indirect competitor with the other two consumer species (P_1 and P_2). Thus, in either the phenomenological or the mechanistic case, the third species is a subdominant competitor, in the sense that it must compete with two other competitors. (Of course, if the new species is an extremely good competitor it could simply eliminate one or both of its competitors; this obvious result is not considered further here.)

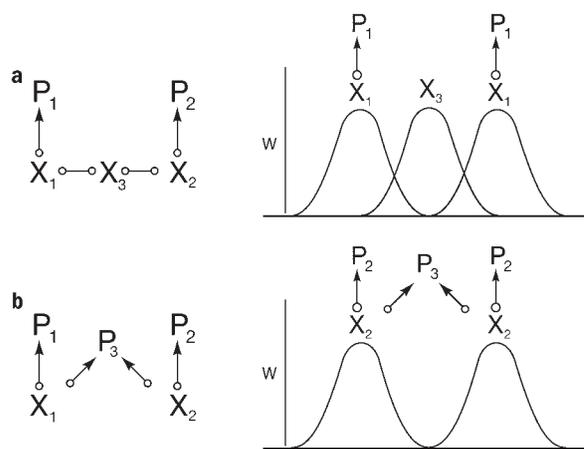


Figure 3. The two ways in which a third species can enter the ecosystem of two independent oscillators such that they are coupled through the third species. (a) The invading species (X_3) is a competitor with the two other resource species. (b) The invading species (P_3) is a predator on the prey of the other two species, and thus indirectly a competitor with them.

Mechanistic coupling

Consider first the mechanistic case (figure 3b). Phase coordination will normally be in the direction of in-phase coordination with systems 1 and 2, thus producing an especially strong competitive effect, since both P_1 and P_2 reach their peak values together and simultaneously with P_3 as a result of the inevitable phase coordination with P_3 . If we take the perfectly symmetrical case (all parameters identical for the independent subsystems, P_1, X_1 and P_2, X_2), the overall five-dimensional system reduces mathematically to a three-dimensional one with the three variables $2P_1, 2X_1$, and P_3 (or, equivalently, $2P_2, 2X_2$, and P_3 , since the two subsystems are identical and in phase). The dynamics of that three-dimensional system are well known (Armstrong and McGehee 1980). So, for example, if the uncoupled systems 1 and 2 are set in antiphase motion and later P_3 is added, the effect is first to push systems 1 and 2 into in-phase coordination, probably driving P_3 to extinction (figure 4). Paradoxically, even though systems 1 and 2 are completely independent of one another, together they are resistant to the invasion of P_3 because of the latter's tendency to push them into an in-phase coordinated state. Although these are not the only dynamics possible, the tendency for P_3 to act as a coordinating force to push the two parent subsystems toward in-phase coordination is general.

We might think of this system as representing ecosystem resistance to an invasive species (with the two uncoupled oscillators as the base ecosystem and P_3 as the invading species). The phenomenon of synchrony, then, explains one

way in which a community can resist an invasive species (i.e., first the invasive acts to synchronize the oscillations of the previously independent oscillators, and subsequently the coordinated behavior of those oscillators drives the invader to extinction). If the original system, after the extinction of the invader, went back to its original state of antiphase coordination, then the invader could again colonize. And if there is the slightest connection between the two resources, say through very weak competition, the system would be driven back into its antiphase-coordinated state (Vandermeer 2004). Adding the weak connection between the resources to the basic equations (the coupling/competition coefficient, β ; see box 1) generates an attractor, which in this case is chaotic, with very predictable long-term behavior (figure 5). As expected, the invader first acts to synchronize the two parent oscillators, the result of which is to drive the invader to very low levels. This generates an antiphase coordination, which allows the invader to invade once again, but that new invasion again results in synchronization, and the cycle repeats itself (figure 5).

Phenomenological coupling

Turning to the phenomenological case (figure 3a), the qualitative nature of the system is such that X_2 and X_1 have a net indirect positive effect on one another (on the principle that "the enemy of my enemy is my friend"). Thus systems 1 and 2 are coupled through the resource species, but not in the competitive way shown in figure 2b. Rather, the indirect positive coupling between X_1 and X_2 (by coupling through X_3) should

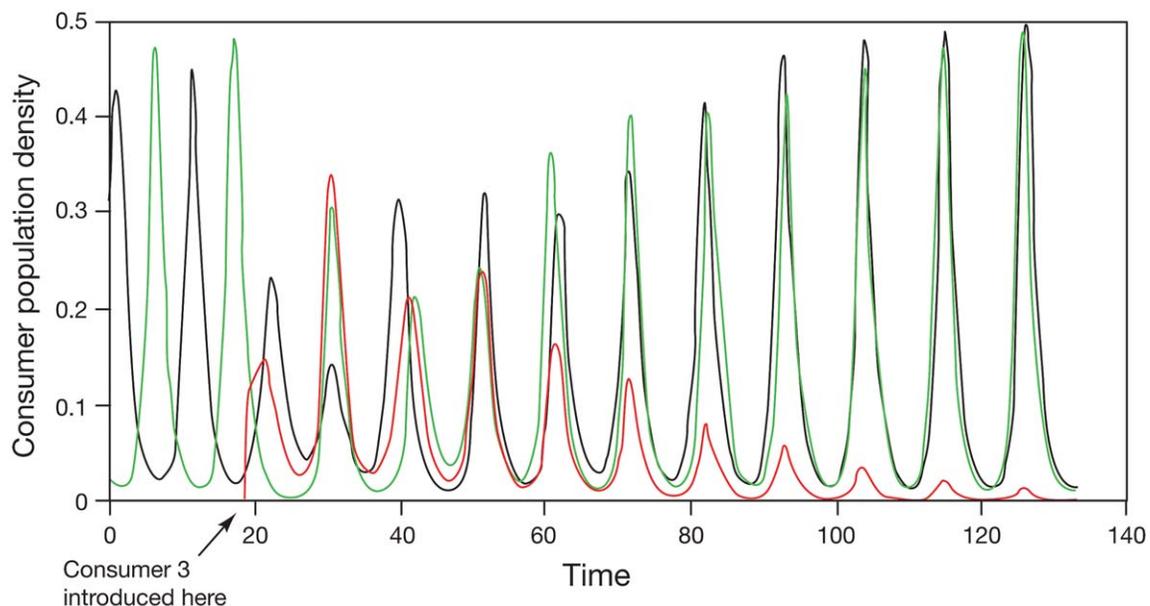


Figure 4. Population density of all three predators (P_1, P_2, P_3) under the situation of consumer coupling ($c_1 = 0$; figure 2b), and small predatory effect from P_3 . Black and green curves are P_1 and P_2 , and red curve is P_3 . Note how the main oscillators begin antiphase but rapidly are pushed into an in-phase coordination by the presence of P_3 . P_3 then is excluded (asymptotically approaches zero) as a result of the coordinated competitive pressure from P_1 and P_2 . Parameters are $a = 8$, $c_2 = 0.45$, $c_1 = 0$, $\alpha = 1.5$, $b_1 = b_2 = b_3 = 2$, $m = 0.8$.

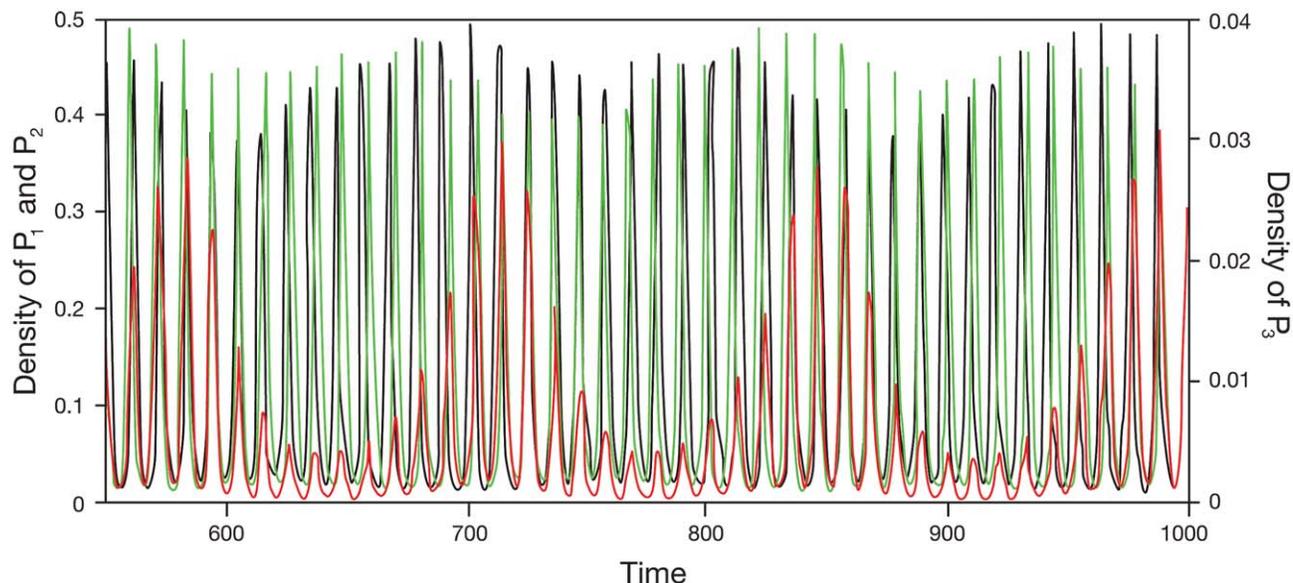


Figure 5. Chaotic control of an invasive species through an alternation of in-phase and antiphase coordination of the two predators. Time series shows long-term effects of invasive (red) and permanent (black and green) residents. Even though the system is chaotic, an obvious pattern with an obvious underlying biological mechanism is apparent. Parameters are $a = 8$, $c_2 = 0.45$, $c_1 = 0$, $\alpha = 1.5$, $b_1 = b_2 = b_3 = 2$, $m = 0.8$, $\beta = 0.1$.

cause the two underlying systems to become in-phase coordinated. There is no inherent reason why X_3 needs to be either in-phase or antiphase coordinated with either X_1 or X_2 , which leads to the possibility that the two main systems could be in-phase coordinated, thus leaving a space for the third species to invade. A particularly interesting case of this pattern is illustrated in figure 6. The two independent subsystems are set in antiphase motion to begin with, and then X_3 is introduced at about repetition 35 of the cycle. Coupling through X_3 causes in-phase coordination, as expected. However, the coupling also causes the two subsystems to be chaotic (figure 6). Because of the coupling, the chaos is in phase, leading to synchronized chaos (Winful and Rahman 1990, Vandermeer and Kaufmann 1998).

The curious form of synchronized chaos provides the invading species with unpredictable windows of opportunity to invade: It effectively takes advantage of the periodic and simultaneous lowering of the predator density, thus permitting the species to enter the system (figure 6). Thus, even though the two main competitors (X_1 and X_2) are very strong competitors against X_3 (competition coefficients = 1.1), all three coexist with the combination of the chaotic in-phase coordination of the dominants and the antiphase coordination of the subdominant. This case is quite complicated and is explored in detail elsewhere (Vandermeer et al. 2006).

Community structure through coupled oscillators

The coordination of oscillatory consumer–resource systems can have an important impact on the persistence of species, and consequently on the general problem of species diversity.

Despite the fact that underlying standard parameters such as competition coefficients and predation coefficients may indicate instability through traditional stability analysis, in-phase and antiphase coordination may allow for persistence stemming from the behavior of coupled oscillators. Thus, analyzing the balance between different forms of phase coordination, in addition to standard methods of stability analysis, may on the one hand be a useful tool, yet on the other hand provide a cautionary tale. Knowing how the coupling between two oscillators occurs may allow researchers to predict the general form of coherence and thus suggest biological interpretations of what that coherence means. However, knowing that two species are connected to one another, absent the details of that connection, may turn out to be of limited utility. Examining recent research on ecological networks in the light of the complex behavior of coupled oscillators, one must wonder whether knowing only the number of connections a species has with other species can illuminate understanding.

While the overall thrust of this article is a general examination of ecological interactions as coupled oscillators, the specific example used is that of competitive interactions along a gradient, the classical MacArthur–Levins formulation. When the study of ecological interactions as coupled oscillators is expanded to larger systems, a number of interesting questions emerge (or sometimes reemerge, with a modified tone owing to the frequently surprising dynamics associated with coupled oscillators). An example is the “paradox of the plankton.” Even before Levins and MacArthur presented their elegant theory, MacArthur’s mentor, G. E. Hutchinson (1961),

had recognized a problem. Assuming Gause's principle of competitive exclusion, Hutchinson noted that many communities contain species that would be difficult to characterize as having distinct niches. The phytoplankton community in a given lake or a given section of ocean will contain many species, all of which more or less passively float, photosynthesize, and use, for all practical purposes, the same nutrients. That is, plankton all seem to do the same thing, which is to say they all occupy the same niche. According to the classical theory, this means that they cannot coexist. Yet many of them do.

A variety of explanations for the paradox have been offered, but the hypothesis that seems to have gained the most currency is that of "intermediate disturbance," proposed more or less simultaneously (although in slightly different forms) by Connell (1978) and Huston (1979). They assumed that, indeed, the competitive interaction among species would result in all but one species being eliminated from an area, as the classical theory would have it, except that some outside event continually delays this otherwise inevitable outcome. So, for example, in the mowed fields of Darwin—it might be argued that Darwin was the actual originator of the hypothesis—the plants that were competing with one another would eventually have resulted in a single plant species competitively displacing all others, but the periodic disturbance of mowing reduced all the species to the same level of competition. Thus, competition would proceed to the elimination of all but the best competitor, but some sort of external disturbance periodically reduces the community to the point where the competitive process starts all over again. It is not an exceptionally long stretch to conceptualize this problem as one of periodic imposition of noncompetitive conditions resulting from particular patterns of coupling of consumer–resource oscillators, thus creating endogenous rhythms that act as if they were periodic disturbances.

The intermediate disturbance hypothesis brings up an issue closely related to coupled oscillators, that of forced oscillations. An oscillating pendulum will normally come to rest as a result of friction. However, if every time the low point in the oscillation is reached, a force is applied to push the pendulum back into its oscillations, the gradual damping of the oscillations will not occur and the pendulum will oscillate forever. If we conceive of an oscillating biological popu-

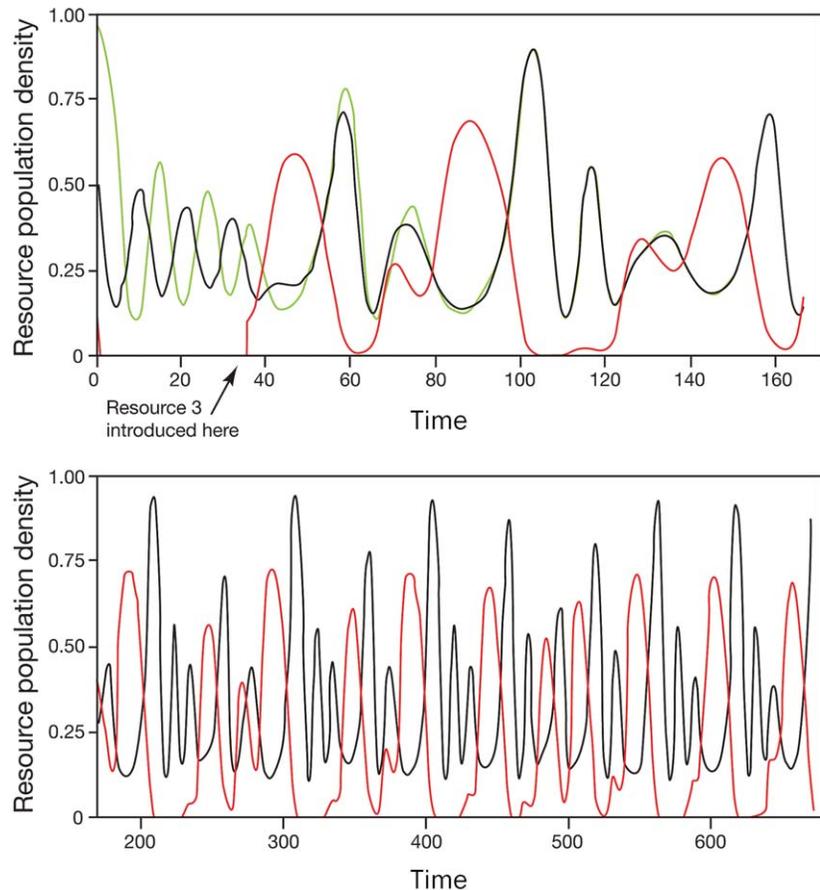


Figure 6. Population density of all three consumers (X_1 , X_2 , X_3) in the situation of resource competition ($c_2 = 0$; figure 2a). Black and green curves represent X_1 and X_2 , respectively; red curve represents X_3 . Note how the main oscillators begin anti-phase but rapidly are pushed into in-phase oscillations (this time chaotic), and how the subdominant competitor (X_3 , red curve) is able to persist by effectively occupying the space when the other two competitors are at a low point. Parameters are $a = 4.3$, $m = 0.8$, $b_3 = b_1 = b_2 = 2$, $\alpha = 1.1$, $c_1 = 1$, $c_2 = 0$.

lation subject to some sort of regular disturbance, we can think of the whole system as a forced oscillator, which is to say the regular disturbance periodically resets the system. Biological populations that oscillate synchronously are frequently thought to do so because of this mechanism, sometimes called the "Moran effect" (Hudson and Cattadori 1999). However, it is not the case that periodic forcing of biological oscillators always leads to coordination of the oscillations. Sometimes complicated and enigmatic oscillatory behavior is the result (Rinaldi and Muratori 1993, Rinaldi et al. 1993, Vandermeer 1996, King and Schaffer 1999, Vandermeer et al. 2001), a fact that cries out for further investigation.

The general line of reasoning that gave rise to the intermediate disturbance hypothesis (the paradox of the plankton) has been referred to as the "non-niche" approach, while that based on the underlying assumptions of the competitive exclusion principle has been referred to as the "niche" approach. This debate has been most active among researchers

working in tropical rainforests, one of the most speciose systems in the world. From the important paper by Hubbell and Foster (1986) through the influential book by Hubbell (2001), the “non-niche” or “neutral” theory of community structure has gained many adherents, even as it has generated much controversy (Wills et al. 1997).

The two schools of thought become intimately interconnected when the non-niche idea is coupled with the so-called Janzen–Connell hypothesis (Janzen 1970, Connell 1971). The fundamental idea originally focused on seed dispersal and seed predation (although herbivory or pathogens easily substitute for seed predation). One of the key forces driving terrestrial ecosystems is the dispersal of seeds. If there were no mechanisms for getting seeds away from the canopy of a tree, all seedlings would be clumped around the adult tree. Janzen and Connell noted that the probability of being attacked by a seed predator, or, in the case of seedlings, an herbivore, would be highest where the seeds were most concentrated, which would be mainly near the base of the mother tree. And the reason they would be so concentrated would be that they had not been dispersed. Thus, they suggested that the importance of dispersal was avoidance of these seed predators, or, more generally, avoidance of the natural enemies of the seeds and seedlings. Since the publication of this idea, there have been many studies confirming the existence of this phenomenon in nature, and it has become a part of the standard lore of tropical rainforest ecology that the Janzen–Connell hypothesis is true, at least for some species at least some of the time. While this idea has been enormously influential in discussions of rainforest dynamics, recent manifestations have actually placed it into a slightly different context than its original intent, and perhaps consequently elevated its importance even further.

In its more recent manifestation, the hypothesis has been recognized as a subcomponent of an extensive literature on the control over competition by natural enemies. This literature is very large, probably originating with Darwin’s famous experiment with a mowed field, but essentially says that as one species begins to dominate in a non-niche community, its natural enemies tend to build up and effectively cancel its competitive dominance. This effect turns out to be more complicated than one might expect. It is a more complex version of the simple five-dimensional system in the examples offered in this article. That is, rather than ask how a single species can invade a system of two oscillators, the fundamental question is how a species can invade a system composed of a large number of oscillators that are already coupled in complex ways. Initial forays into this question have yielded interesting, albeit complicated, results (Vandermeer et al. 2002, Vandermeer and Pascual 2006).

The literature deriving from the paradox of the plankton, the intermediate disturbance hypothesis, and the Janzen–Connell effect constitutes, in effect, a multidimensional extension of the basic idea of two species on a gradient (figure 1), an extension that would appear open to a great deal of theoretical and empirical research. However, an alternative view

is also evident and relevant to the coupled-oscillator approach—a focus on higher-level trophic structures. An important example is the demonstration of complex chaotic cycles evolving from the formulation of a simple tritrophic system with the classical equations (Hastings and Powell 1991). Hastings and Powell identified the resulting chaotic attractor as a complex combination of two cycles, effectively the cycle involving the carnivore and the herbivore coupled with the cycle involving the herbivore and the plant.

This basic idea has an antecedent in the classic work of Hairston, Smith, and Slobodkin (1960) in which they noted that the effects of predators on herbivores would be such that plants would have to be controlled from below. That is, if predators control the population densities of herbivores, the latter could not possibly control the population densities of the plants, which means that the plants must be controlled through their own overutilization of their resources (commonly called “control from below”). A large literature on trophic cascades subsequently evolved (Pace et al. 1999, Schmitz et al. 2004). However, here, as in the case of competitive communities, most attention is focused on the effective linear connections among species (who eats whom), rather than the underlying oscillatory nature of consumer–resource connections. Here, too, a reformulation of the problems from the point of view of coupled oscillators, as pioneered by Hastings and Powell, may provide important insights.

Casting the tritrophic problem as one of coupled oscillators automatically brings up the question of omnivory (McCann and Hastings 1997, Vandermeer 2006), and ties trophic structure naturally to the fundamental structure of competition. Consider, for example, a system of herbivore, carnivore, top carnivore (H–C–T). One might imagine, for example, flies, spiders, and spider-eating birds. As long as the birds are strict top carnivores (eat only spiders), this is a tritrophic system. However, one might also imagine a system of flies, spiders, and fly-eating birds, in which case the basic competitive structure of fly-eating birds in competition with spiders corresponds to the examples analyzed in this article. The question of whether the birds can eat both spiders and flies naturally arises, in which case we have omnivory as an intermediate situation between tritrophic and competitive systems, between the two oscillators {T,C}, {C,H} and the two oscillators {T,H}, {C,H}. This implies that the coupling may be at both levels and raises the question of whether the insights afforded by the tritrophic case (e.g., Hastings and Powell 1991) can be combined with the insights afforded by the competitive case (Vandermeer 1989, 2004) to provide insight through looking at the system as a complex of coupled oscillators. This theme is complicated and is discussed more fully elsewhere (Vandermeer 2006).

The transfer of energy from one population to another has long been regarded as an elementary part of ecology, the closest thing ecologists have to an atomic theory. Yet the bulk of the literature seems to sidestep a fundamental feature of this elementary structure—our “atoms” (consumer and resource organisms) are inherently oscillatory. In seeking to understand

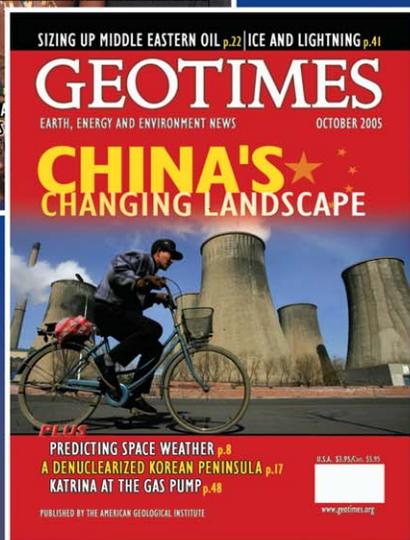
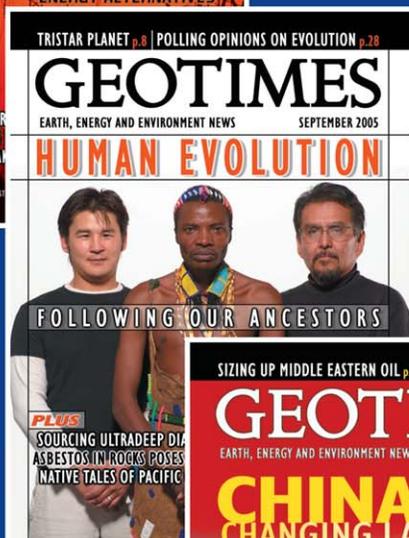
the complexity of nature, it does not seem wise to ignore this fundamental property—that we are working with coupled oscillators. In this article I use the classical example of the invasion of a species into an environment in which two other species have overlapping niches. The expected long-term behavior of the system is not straightforward when even the most elementary nonlinearities are introduced. Yet casting the problem in terms of coupled oscillators makes it possible to interpret that behavior in terms of various forms of coherence for the oscillators. I suggest that other classical phenomena in ecology, such as species packing, intermediate disturbance, the Janzen–Connell effect, trophic cascades, and omnivory, might also benefit from being cast in this framework.

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