



Hetero-chaos in a common ecological modality

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Abstract

Based on an example of a four dimensional ecological community composed of three ant species and a group of phorid flies, a simplified dynamic model is proposed and analyzed qualitatively. The model contains an intransitive triplet of ant species coupled with a predator/prey pair, where the prey is one of the ants in the intransitive competition, thus coupling a 3D oscillator with a 2D oscillator. Relaxing basic symmetries, a chaotic attractor emerges in which two distinct unstable modalities are recognizable, identifiable with the two biological processes involved. The unstable manifolds of each of the instabilities are of distinct dimensionalities, a characteristic known as hetero-chaos. It is suggested that the qualitative arrangement may be common as a modality within large ecological systems, thus proposing hetero-chaos as possibly common in ecosystems that have chaotic behavior.

Acceptance of chaos as a common form of population behavior in ecology has been slow. The important paper by Rogers and colleagues (2022) has accelerated that acceptance, perhaps leading to a new and interesting set of questions (Munch et al. 2022). An alternative literature, mainly in physics and mathematics, has been dealing with the complications that chaos implies for some time now (e.g., Blanchard 2008; Crutchfield 2012; Sander and Yorke 2015), suggesting a potential refitting of some applications in ecology. Especially important today, seemingly intractable problems such as global climate change and biodiversity loss require an articulation with the reality of the complications inherent in ecological systems, rivaling or even exceeding the similar issue in climatology (Lorenz 1963, 1993), and certainly generating the same concerns in relevant models (Patil et al. 2001). Confronting the chaotic behavior that is almost certain to exist in the complex models needed to deal with such large problems has given center stage to the general field of chaos studies.

Ecology's connection with the broader subject of environmental science and its frequent identification with popular notions of "the natural" have enriched (or burdened) it with powerful metaphors. The popular notion of the

balance of nature is an example, strongly suggesting that ecosystems in their natural state are in some sense stable, unless perturbed by a destabilizing force. Gause's experiments were closely tied to elementary dynamic theory, and the formalities of Lotka and Volterra tied that dynamic theory to the basic question of equilibrium – stable or not (Gause 1932; Lotka 1925; Volterra 1927). Tying these early results with popular notions of diversity and stability, MacArthur (1955) suggested that a natural equilibrium (implicitly a stable one) would emerge as a system became more diverse, already a popular idea among naturalists. In what remains as a central core of understanding, May pointed out that ecology's most basic equations suggested the opposite, that more diversity led to more instability (May 1971, 1972, 1973), a clear rejection of the popular notion that a "balance of nature" must be somehow central to our ecological understanding of the world. Nevertheless, the underlying framework continued to dominate ecology, tacitly setting the core question for the field as whether an ecosystem was stable or unstable, perhaps not unique to ecology (Ghys 2013). Yet acceptance of the stable/unstable dichotomy is an Achilles heel for theoretical ecology in light of the chaos revolution (e.g., a chaotic attractor likely contains an unstable equilibrium point yet is as persistent over time as any stable point).

Although Lorenz's classic paper (1963) likely initiated the modern interest in chaos, for ecology it was mainly May's exposition that the most basic of all ecological equations implied chaos. In the common discrete time

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model of population dynamics, the logistic map [$X_{t+1} = rX_t(1 - X_t)$], as long as the rate of population increase (r) was less than about 3.5, or greater than 4, the population would be either well-behaved or extinct. Perhaps ecologists had been inadvertently ignoring the 3.5–4 range of population growth since it led to confusing population behavior. That interregnum between good behavior (e.g., equilibrium population) and extinction, for ecology's most basic equation, turned out to be arguably the most interesting part, chaos. Failure to appreciate its importance in part stemmed from the early use of discrete maps (especially the logistic) to interrogate partial data sets, causing ecologists to focus on rate of population increase as the key variable distinguishing chaos from non-chaos (Munch et al. 2022), perhaps taking too literally what should have been treated as intended, as a toy model.

The logistic map style of chaos, while important, reflects only part of the more interesting complexity of what is now known to be a more extensive group of behaviors, collectively treated as “chaos.” Recent literature is extensive (e.g., Saiki et al. 2024; Strogatz 2024), especially in the mathematical and physical sciences. Yet it is in ecology that the implications may be most important. The growing complexity of chaotic forms being discovered theoretically (e.g., Desharnais et al. 2024; Sander and Yorke 2015; Saiki et al. 2021) suggests that a deeper look at particular ecological arrangements is warranted. In particular, hetero-chaos is one form of a chaotic pattern in which the complexity of chaos is understandable with a simple metaphor, unstable dimension variability (Dawson et al. 1994; Saiki et al. 2024), referring to the dimensions of various local outsets (unstable manifolds) of particular unstable points. A hetero-chaotic system is one in which the dimension of two or more instabilities is itself variable (e.g., as in the present work, explained in what follows, one unstable region is unidimensional the other bidimensional).

We use a specific four-dimensional case studied for the past seven years in Puerto Rico, to construct a model that we propose suggests hetero-chaos. It is worth noting that the qualitative arrangement of an intransitive triplet coupled with a predator acting on one of the competitors is likely to be a common motif in natural systems, even if hidden within the complexity of further network connections. Using a knowledge of the dynamics of this example of this motif is thus of potentially broader interest than the actual natural system that motivates the analysis.

A low-dimensional, yet complex, tropical system: qualitative network structure and a toy model

Observations of a small component of the insect community on a coffee farm in Puerto Rico suggests a network pattern that seems self-contradictory in a spatial context. On a plot of approximately 120×30 m, for the past seven years we have monitored the detailed spatial patterns of three non-native species of ants (*Solenopsis invicta*, *Wasmannia auropunctata*, and *Monomorium floricola* – which we refer to by their generic names henceforth), and conducted supportive laboratory studies. These experimental and observational studies revealed that the three species form an intransitive loop (much as in the game of rock, scissors, paper) (Vandermeer and Perfecto 2023, 2024; Vandermeer et al. 2022). A complicating feature of this arrangement is the presence of a group of parasitoid flies in the family Phoridae (*Pseudacteon curvatus*, *P. tricuspidis*, and *P. obtusus*) that are all specialists on *S. invicta*. In addition to their basic predatory effects (each one consumes the brain of a worker ant), their presence notably affects the behavior of the ant, with reduced foraging activity and a behavioral response of remaining motionless, teleologically suggesting “fear” of the marauding flies (Vandermeer and Perfecto 2020, 2024).

When initiating the study of this system in 2019, there was an overwhelming preponderance of *Wasmannia* in the sampling plot. The replacement by *Solenopsis* proceeded for the next two to three years, with *Monomorium* replacing *Solenopsis* periodically (as expected from the intransitive nature of their competition). The phorids were discovered in a spatially explicit form in 2021, and have been increasing in one part of the sampling area since then, evidently increasing and weakening the expansion of *Solenopsis* by reducing its competitive effect against *Wasmannia*, leading to a current preponderance of *Wasmannia* on the plot. In the summer of 2025 the permanent plot was divided between the two oscillatory processes: to the west, the intransitive competition still dominated the dynamics while to the east (at a distance of approximately 100 m), the predator/prey system seemed to dominate. Thus, overall, the system appears as a collection of sections, on a gradient from west to east, of the two oscillatory mechanisms – to the west oscillations of the intransitive triplet, to the east, predator and prey. It makes sense, then, to view the overall system in a philosophically mean field framework, describing the dynamics as an intersection of two oscillatory dynamic modes – intransitive competition and predator prey interaction.

Interactions among all four species are contingent on environmental and other biological forces, dependent on particularities of spatial extent, either from background conditions or autonomously generated, influenced by migrations from other sites, and much more. Yet, the basic features are, as we deduce from a decade of studying the system directly in the field, three species compete in an intransitive fashion and one of the intransitive species is attacked by a predator (Vandermeer and Perfecto 2020, 2023, 2025). The dynamics inherent in these two fundamental ecological forms (intransitive competition and predator/prey interaction) form the foundation of a simple model of the network structure of the system.

A completely “stripped down” version of the basic natural history is represented by the four dimensional system:

$$\frac{dP}{dt} = P \left(\frac{1}{1 + fS} - m \right) \tag{1a}$$

$$\frac{dS}{dt} = S \left(1 - S - \alpha_o M - \frac{1}{1 + fS} P \right) \tag{1b}$$

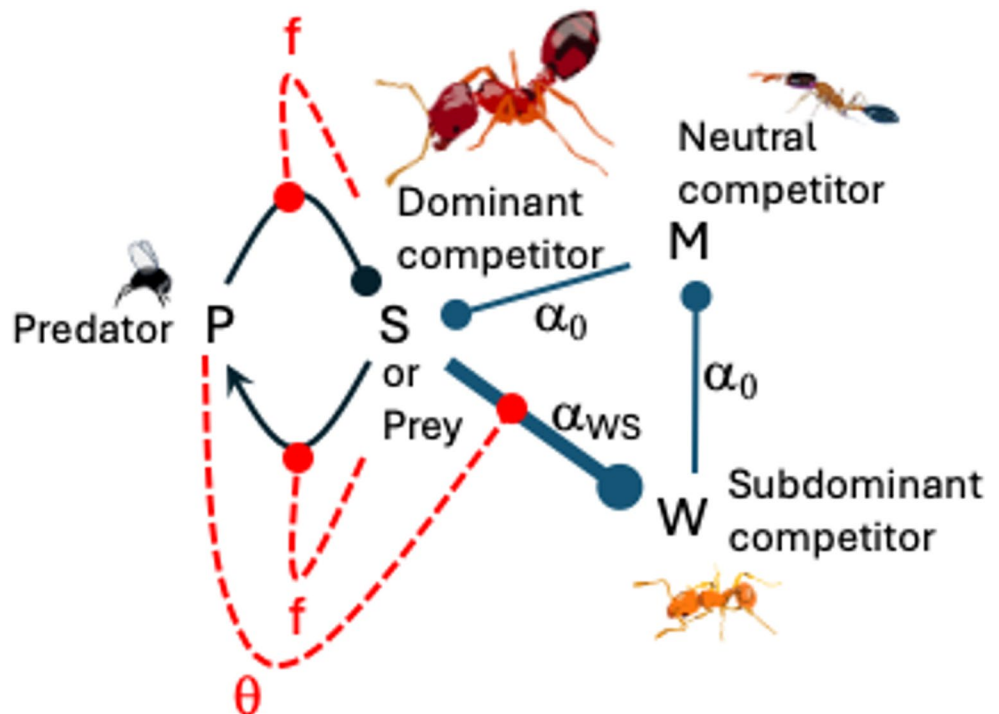
$$\frac{dM}{dt} = M (1 - M - \alpha_o W) \tag{1c}$$

$$\frac{dW}{dt} = W \left(1 - W - \frac{\alpha_{ws}}{1 + \theta P} S \right) \tag{1d}$$

where $S = \textit{Solenopsis}$, $P = \textit{phorids}$, $M = \textit{Monomorium}$, $W = \textit{Wasmannia}$. We refer to *Solenopsis* as the dominant competitor since it is the species affected by the predator, and is referred to as such in older literature on predator-mediated coexistence (Caswell 1978). Its strongest competitive effect is directed at *Wasmannia* which we refer to as the subdominant competitor, leaving *Monomorium* as the “neutral” competitor (all such monikers are arbitrary). The system has been simplified to include only parameters that previous experimental or observational information suggest may be important, at least sometimes. There are only four relevant parameters: The base-line competition coefficient, α_o , the competitive effect of S on W, α_{WS} , the predator functional response, f , and the trait-mediated effect, θ , which is the effect the phorid predators have on the behavior of S. Other evident parameters have effectively been set to either 0 or 1.0 and do not emerge as interesting interlocutors in the system. All parameters have been qualitatively established in the field, although any pretense at accurately stating their quantitative values would be, indeed, pretense, except at the extremes (the competition coefficients are all positive real numbers, the predation coefficients are positive real numbers, etc...). In Fig. 1 is a diagram of equation system 1, using general ecological categories, illustrating the four parameters involved (α_o , α_{WS} , f , and θ).

Isolating the two subsystems (the intransitive triplet and the predator/prey pair), base elements of stability are evident. The predator subsystem (S, P) zero growth isoclines are:

Fig. 1 Diagram of the four dimensional system, with the studied parameters indicated. S=*Solenopsis invicta*, M=*Monomorium floricola*, W=*Wasmannia auro-punctata*, P=the phorid species complex, *Pseudacteon tricuspis*, *P. curvatus*, and *P. obtusus*. M is referred to as a neutral competitor because it is neither dominant nor subdominant, not because it does not exert and respond to competition. Small filled circles at the ends of connectors indicate a negative effect, arrowheads indicate a positive effect. Connections that connect with other connectors represent higher order indirect effects (e.g. θ reduces α_{WS} in proportion to the value of P), making the graph, formally, a hypergraph (Golubski et al. 2016). Connection between S and W is thicker than the other two meaning that when competition is not symmetrical, α_{WS} is the larger coefficient



$$P = 1 - S + f S(1 - S) \tag{2}$$

and

$$S = m / (1 - mf) \tag{3}$$

both of which are diagrammed in Fig. 2a. If the prey isocline is less than the Hopf bifurcation point, the local equilibrium will be unstable, if to the right of the point it will be stable. The critical point separating the stable from unstable occurs when,

$$m = (f - 1) / (f^2 + f) \tag{4}$$

a graph of which is shown in Fig. 2b.

The second subsystem (S, W, M), has been the subject of a great deal of analysis (see esp., May and Leonard 1975; Zeeman and Zeeman 2002). The analysis begins with the neutral case, for the more general competitive system, $x_i = x_i (1 - x_i - \alpha_{ij}x_j - \alpha_{ik}x_{jk})$, where the matrix A with elements α_{ij} is circulant, which is to say, $\alpha_{ij} > \alpha_{ji}, \alpha_{jk} > \alpha_{kj}, \alpha_{ki} > \alpha_{ik}$. Following May and Leonard, a special case (herein called the “neutral” case) is when $\alpha_{ij} = \alpha_{ji} = 2.0$, which in the case of Eq. 1a, 1b, 1c, 1d, with $\theta = 0$, is $\alpha_o = \alpha_{WS}$ (average competition = 2.0). Under these parameter settings all initial conditions merge rapidly to a stable manifold defined as $S + W + M = 1.0$. The metric,

$$C = \frac{S_o W_o M_o}{[S_o + W_o + M_o]^3} \tag{5}$$

stipulates a particular permanent oscillation located on the carrying simplex. If initial conditions are such that $S_o + W_o + M_o = 1.0$, then $S_t + W_t + M_t = 1.0$ for all $t > 0$, and $C = S_o W_o M_o$, defines a unique cycle on the carrying simplex, of which there are thus an infinite number. Furthermore, by definition (of the carrying simplex), $S_o + W_o + M_o$ will always approach 1.0, which means that no matter where in 3D space the initial conditions lie, some cycle on the carrying simplex will be approached, meaning that in the 3D space there exist an infinite number of limit cycles (all, in the limit, located on the carrying simplex, or manifold).

It is useful to consider two forms of stability in the context of this model. If we restrict the analysis to $\alpha_o = \alpha_{WS} = 2$, the background condition of $P=0$ insures that some limit cycle will occur on the carrying simplex, that, no matter the initial conditions, the carrying simplex is an attractor for an unlimited number of limit cycles. This behavior seems unusual in the context of the actual trajectories on the carrying simplex which are “centers” in the sense that any particular initial conditions, if on the carrying simplex, will repeat after one oscillation, from M to W to S to M. If we allow $2\alpha_o + \alpha_{WS} = 6$ (an average competition of 2.0), all $\alpha_o > 0$ result in either the unlimited number of limit cycles (if $\alpha_o = \alpha_{WS} = 2$) or a stable focal point. Thus, $2\alpha_o + \alpha_{WS} = 6$ can be considered as a stable form. It is, in another sense, similar to a Hopf bifurcation in that if $2\alpha_o + \alpha_{WS} > 6$ the carrying simplex itself is distorted (Zeeman and Zeeman 2002) such that a single heteroclinic cycle (provided the difference between α_o and α_{WS} is not too large, always approaching the cycle, 0,0,1; 0,1,0; 1,0,0) occurs as opposed to $2\alpha_o + \alpha_{WS} < 6$ in which the carrying simplex is distorted in the opposite direction such that a focal point attractor is ultimately approached, an equilibrium at,

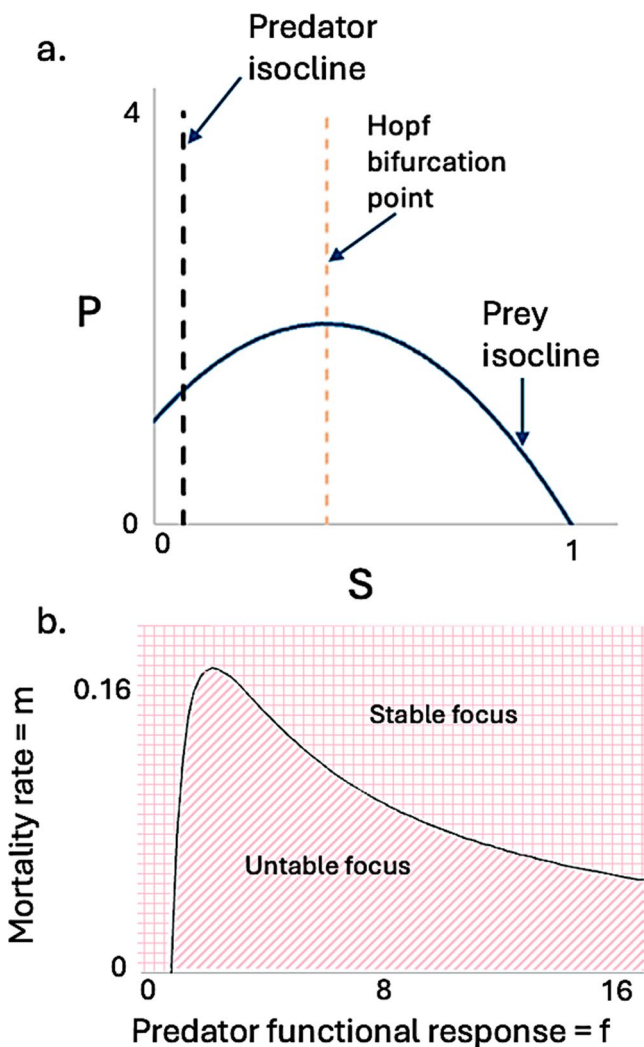


Fig. 2 Basic phase plane dynamics of the predator/prey component of the system. (a) isoclines when $f=5.6, m=0.05$. (b) Equation 4, separating the stable versus unstable foci of the equilibrium point. Note that there is a unique maximum for the mortality rate

$$\begin{aligned}
 S^* &= \frac{1 - \alpha_o + \alpha_o^2}{1 + \alpha_o^2 \alpha_{ws}}; \\
 W^* &= \frac{1 - \alpha_o + \alpha_o \alpha_{ws}}{1 + \alpha_o^2 \alpha_{ws}}; \\
 M^* &= \frac{1 - \alpha_{ws} + \alpha_o \alpha_{ws}}{1 + \alpha_o^2 \alpha_{ws}}; .
 \end{aligned}
 \tag{6}$$

Designating total competition as T_c , the equation $T_c = 2\alpha_o + \alpha_{ws}$ separates the stable parameter combinations when $T_c < 6$, from the more complicated situations where total competition is larger, specifically when $T_c > 6$. In this case the asymmetry of competition (the difference between α_o and α_{ws}) determines whether the system is heteroclinic or a stable focus (or, indeed, if one of the species is excluded).

Thus, the overall system is biologically composed of two subsystems, both of which are inherently oscillatory, the S, W, M system which is intransitive and three dimensional, and the S, P system which is predator/prey and two dimensional. From this characterization of the biological system only, the dynamic system (Eq. 1) can thus be qualitatively thought of as initially composed of a system of non-homogenous dimensional coupled oscillators (a 2D and a 3D oscillator).

We begin with an exploration of the intransitive subsystem symmetrical ($\alpha_o = \alpha_{ws}$) with neutral stability ($\alpha_o = 2.0$) coupled with the predator/prey subsystem at its Hopf point (a “neutral” state). From Eq. 4 (Fig. 2), m is maximized when $f = 2.4$ (whence $m = 0.172$), which we take as the two parameters ($f = 2.4$ and $m = 0.172$) for the “symmetrical/neutral system.” The system in this parameter space, if set at an arbitrary point on the carrying simplex ($S_o + W_o + M_o = 1.0$) with the predator very small, the SWM system moves toward a limit cycle (it’s precise position depending on the exact initial condition). At this particular parameter setting it is not possible for the predator to persist in the system. Since the motivation for this toy model is the real system of three ants and a parasitoid, it is worth noting that most biologists who work with phorids agree that the direct predatory effect is small compared to the indirect effect of changing the ant’s behavior (i.e. q) (Feener and Brown 1992; Morrison et al. 1997; Morrison and Gilbert 1999). Increasing θ might be expected to switch the system from one in which a stable oscillation of the SMW intransitivity (in limit cycle form) switches to the extinction of *Monomorium* and a dominance of the predator prey system. An example is illustrated in Fig. 3a.

As the predator increases, the system rapidly oscillates to the extinction of M and an oscillatory 3D system of SWP, as would be suggested by a qualitative look at the graph of the system (Fig. 2). Initiating the system off of the carrying simplex for the intransitive component, changes nothing. It seems a generalization that with the symmetry of $\alpha_{ws} = \alpha_o$, the addition of even a small population of P into the system relieves some of the competitive pressure

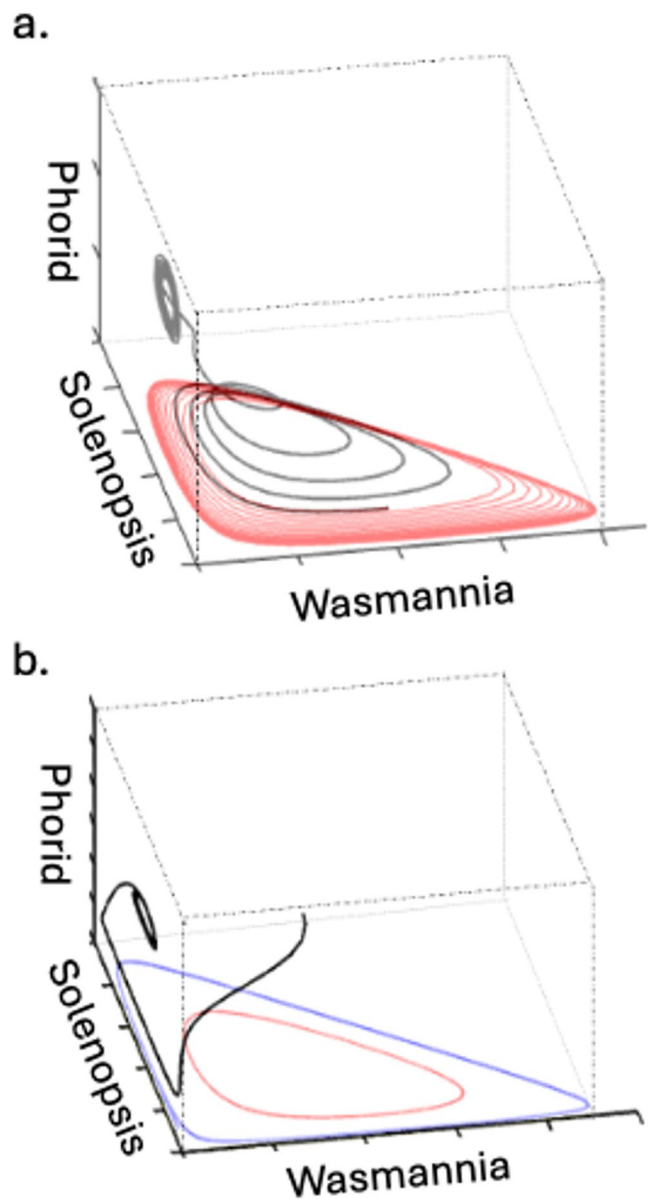


Fig. 3 Alternative trajectories of the 4D system (Eqs. 1a, 1b, 1c, 1d) pictured in PSW space. **(a)** two alternative trajectories. Red orbit is with $\theta = 0$, grey orbit is with $\theta = 2.0$. Parameters are $\alpha_o = \alpha_{ws} = 2$, $m = 0.172$, $f = 2.4$, the symmetrical/neutral system with maximum mortality of the predator. **(b)** Three alternative attractors with $m = 0.124$ and $f = 5.6$. The red and blue attractors are limit cycles persisting on the carrying simplex of the SMW subsystem as P approaches zero, while the black attractor is the single predator prey cycle that exists as M approaches zero

W experiences from S and thus W is able to competitively exclude M from the system. It is also evident that increasing θ does not change this basic pattern, indeed further strengthens the tendency of M moving towards extinction.

The relatively high level of predator mortality (0.172) and low level of functional response (2.4) represent an extreme, with m at its maximum possible value (Fig. 2b). Reducing the value of m , but retaining the assumption of

neutrality (with the equilibrium value of S set at the Hopf critical point – Fig. 2a), we set $m=0.124$ and $f=5.6$. There is a persistence of alternative attractors -- multiple limit cycles in cases where P approaches zero, and a single oscillatory attractor when M approaches zero. Exemplary trajectories pictured in Fig. 3b.

The simultaneous existence of apparently an unlimited number of limit cycles in the SMW subspace (as P approaches zero) plus a stable limit cycle in the PS space (as M approaches zero), sets the stage for what might be expected to be an attractor that moves between these two qualitatively distinct modes, a chaotic attractor. However, extensive searches failed to find such a situation. It seems the case that the extreme symmetry built into the particular point in parameter space mitigates against chaos.

There are two general structures that are herein referred to as symmetric: (1) the assumption that the predator zero growth isocline (Eq. 3) is coincident with the Hopf point of the predator/prey system (Eq. 4); (2) the assumption that competition coefficients are all =2.0, meaning that the intransitive subsystem has the special behavior that is constrained to the simplex, $S+W+M=1.0$. We relax these two assumptions in turn.

Relaxing the first assumption, we set $m=0.09$ and $f=5.6$, locating the predator prey system well below the Hopf critical line (Fig. 3). With this assumption relaxed, there are, again multiple attractors, but seemingly no dynamic interconnection among them possible. Changing the competition symmetry by allowing $\alpha_o = 1.2$ and $\alpha_{WS} = 3.6$ (thus retaining the average value of competition at 2.0), connects what had been separate alternative attractors (one class with P approaching zero, the other a single focal point attractor with M approaching zero), into one chaotic attractor, as displayed in Fig. 4. Note that a periodic window (Fig. 4a) is easily interpreted as a repeated switch between the intransitive competition behavior and the predator/prey behavior. The nearby chaotic version (Fig. 4b) repeats that repetitive pattern, although never in a precisely periodic fashion (since it is chaotic).

The nature of the chaotic trajectory in Fig. 4b is “hetero” chaotic (Saïke et al. 2024) in that the two components of the dynamical structure have distinct dimensionality of their unstable parts. The local instability of the intransitive competition is one-dimensional (Fig. 4a) while the local instability of the predator/prey system is two-dimensional (Fig. 4a), the definition of hetero-chaos (Saïke et al. 2024), as reflected in the chaos (Fig. 4b).

Returning to the source of symmetry in the original system, we now examine how changing the symmetry involved in the assumption that $2\alpha_o = \alpha_{WS} = 1$, the assumption made so that the underlying intransitive structure is neither stable nor heteroclinic (unstable). Keeping with the

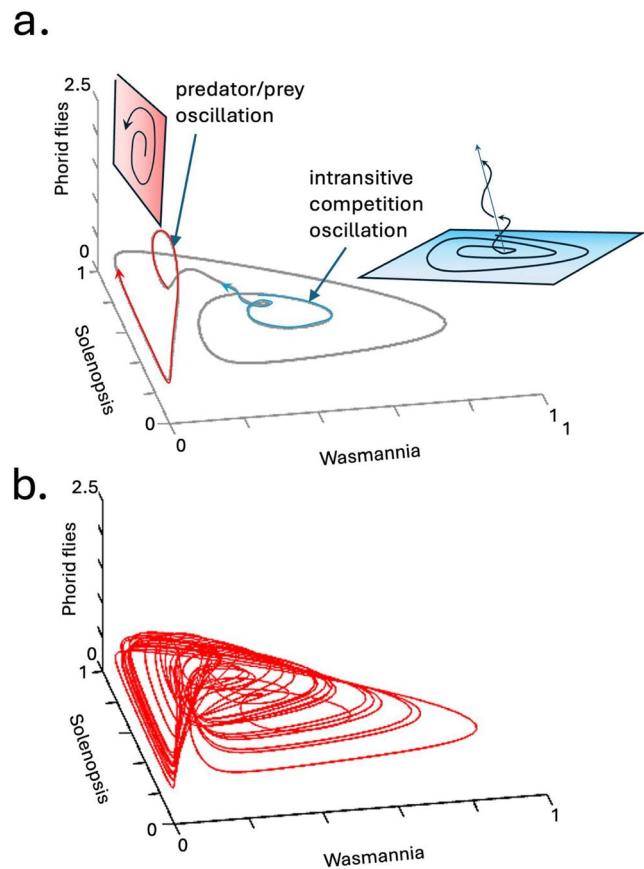


Fig. 4 A periodic attractor with two biologically distinct behaviors and a closely related chaotic attractor. (a) The periodic window at parameter states $\alpha_o = 1.2$, $\alpha_{WS} = 3.6$; $f = 5.6$; $m = 0.1$; $\theta = 2.5$. (b) The related chaotic attractor at the same parameter values, except $m = 0.09$

original parameterization set to its symmetric/neutral form, we assume the parameters are $m = 0.172$, $f = 2.4$, $\theta = 0$. Setting the intransitive system to its heteroclinic form $2\alpha_o + \alpha_{WS} > 6$, regardless of the initiation point, the predator declines to extinction and the intransitive part of the system goes heteroclinic (provided the difference between α_o and α_{WS} is not too large). Allowing the trait-mediated indirect effect, θ , to increase, at the value of 0.83, the system switches from intransitive heteroclinic, to the extinction of M and the dominance of the predator prey system (setting $\alpha_{WS} = 2.5$). The critical value of θ changes as α_{WS} changes but the qualitative result remains the same.

Reducing the predator mortality rate to its lowered, but still at the Hopf point, we set $m = 0.127$ and $f = 5.6$. At $\theta = 2.3$, the system switches from a heteroclinic cycle to a predator/prey system with M absent. Further explorations of parameter space suggests that this pattern is common, wherein there are alternative attractors, but no chaotic behavior. It is only when the predator prey system alone is unstable (theoretical equilibrium of S less than the point of the Hopf bifurcation), and the intransitive system alone

is stable but non-symmetric, that chaos emerges. That is, the main controlling forces leading to chaos are an unstable predator-prey component and a non-symmetric competitive system with a non-zero trait-mediated predator effect (i.e., $\alpha_{WS} > \alpha_o$, $T_c \leq 2$, $\theta > 0$).

Discussion

Herein, based on an intensively studied natural system, we present a simplified model of two coupled oscillators, each of which is driven by distinct biological mechanisms, predator/prey oscillations and intransitive competitive oscillations, intended to represent a system of three species of ants and a species complex of a parasitic fly that attacks one of them. A major component, evident from natural history observations of the system, is the behavioral changes in one ant species induced by the aggressive attacks of the parasite, effectively an additional non-linearity in the basic population equations (Vandermeer and Perfecto 2023). Using a “stripped down” version of the classic interaction equations of community ecology (Eqs. 1a, 1b, 1c, 1d), we show that under a wide variety of parameter values the 4D system resolves into either (1) a 3D system involving predator-prey and subdominant competitor, (2) a 3D intransitive system involving all three competitors, or (3) a hetero-chaotic system involving all four species, wherein the “shadow” of each of the two biological formulations can be seen, qualitatively, in the trajectories (similar to that noted in Vandermeer and Perfecto (2024), but absent the situating in “hetero”-chaos). If restricted to a perfectly symmetrical version of the model the first two alternative modes are generally embedded in the system (the two 3D modes) -- which one emerges depends on initial conditions. Relaxing the symmetry by allowing either the predator/prey system or the intransitive system to become unstable, it is possible for a chaotic attractor to emerge.

Subsequent to our original report on this system (Vandermeer and Perfecto 2023), changes in the field, as yet unreported in the literature, suggest to us that changes in the spatial pattern of this four dimensional system and, especially, changes in the spatial pattern of the phorid parasitoids, including sections of the study site seemingly representing more of a predator/prey dynamics while other sections retain the signature of intransitivity, are qualitatively suggestive of a heterochaotic pattern. Yet, by its very nature, such qualitative suggestiveness is unlikely to be resolvable into anything more precise, which is not the intent of the qualitative modeling presented herein. Furthermore, as in all studies of chaos, the entanglement with stochastic processes can make interpretation difficult, although in at least one example (King et al. 2004) it is precisely the

stochasticity that makes the chaos understandable in a laboratory population.

The general structure of the natural system that motivates this theoretical exercise is likely to be common, perhaps a common generalized module in larger networks. The old assumption that competition is usually transitive has broken (Soliveres et al. 2015), and the indirect effects of predators is now understood to be common (Peacor et al. 2022). Combining these two effects may, as reported herein, result in hetero-chaos. In plant competition, for instance, shoot competition is undoubtedly transitive – by virtue of stature alone species A beats B beats C, but A also necessarily beats C (the taller plant shades the shorter). In contrast, root competition (nutrient competition) is generally three dimensional such that although A shades C, C may utilize a soil nutrient more efficiently than A, such that its sum competitive effect on A overwhelms the reciprocal shading effect (Kiær et al. 2013), and an intransitive competitive structure emerges. Add an herbivore and the basic structure for hetero-chaos emerges. The lack of reports of these two structures occurring simultaneously in nature may be an artifact of failure to search for them.

Chaotic systems are now appreciated as more diverse than the early simple examples, such as the logistic map. The many forms they take in models and, apparently, in nature make it difficult to even define, some suggesting that it “cannot” now be satisfactorily defined mathematically with a simple conceptual framing (Sanders and Yorke 2015). Saïke and colleagues (Saïke et al. 2018) conjecture that almost all high dimensional systems are chaotic in one form or another, suggesting a challenging future for empiricists studying complicated systems. Sanders and Yorke (2015) further expand on some evident complexities emerging in the general field of chaos science, one of which is hetero-chaos. Among the various and sometimes almost monstrous issues of complexity in chaotic systems, hetero-chaos suggests a particular structure wherein there exist various loci of instabilities each of which has a distinct dimensionality, “unstable dimension variability.” We argue that the present study system is an example of hetero-chaos. Two distinct loci of dynamics can be seen, predator/prey and intransitive competition, corresponding to the two alternative dynamics inherent in the natural system. These two dynamical structures contain distinct dimensionalities of instability, the definition of hetero-chaos (Saïke et al. 2024).

More general and larger ecological systems are likely to be far more complicated, perhaps just as complicated as the infamous complexity of global weather models (Patil et al. 2001), and the well-known cascading non-linearities frequently involved suggest that they are more likely than not to be generally chaotic (Rogers et al. 2022; Munch et al. 2022), perhaps in the sort of complicated ways suggested

for other systems (e.g., Sanders and Yorke 2015). Appreciation of the range of behaviors commonly referred to as chaotic (Sanders and Yorke 2015), such as hetero-chaos, is contributive to the resolution the disturbing and confusing patterns in time and space that those of us who work in the field on natural systems have come to appreciate (or have become frustrated with).

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Author contributions All work was done by John Vandermeer.

Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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References

- Blanchard F (2008) Topological chaos: what may this mean?. hal-00276838
- Caswell H (1978) Predator-mediated coexistence: a nonequilibrium model. *Am Nat* 112(983):127–154
- Crutchfield JP (2012) Between order and chaos. *Nat Phys* 8(1):17–24
- Dawson S, Grebogi C, Sauer T, Yorke JA (1994) Obstructions to shadowing when a Lyapunov exponent fluctuates about zero. *Phys Rev Lett* 73(14):1927
- Desharnais RA, Henson SM, Costantino RF, Dennis B (2024) Capturing chaos: a multidisciplinary approach to nonlinear population dynamics. *J Difference Equations Appl* 30(8):1002–1039
- Feener DH Jr, Brown BV (1992) Reduced foraging of solenopsis geminata (Hymenoptera: Formicidae) in the presence of parasitic pseudacteon spp. (Diptera: Phoridae). *Ann Entomol Soc Am* 85(1):80–84
- Gause GF (1932) Experimental studies on the struggle for existence. *J Exp Biol* 9:389–402
- Ghys É (2013) October. The Lorenz attractor, a paradigm for chaos. *Chaos: Poincaré seminar 2010*. Springer Basel, Basel, pp 1–54
- Golubski AJ, Westlund EE, Vandermeer J, Pascual M (2016) Ecological networks over the edge: hypergraph trait-mediated indirect interaction (TMII) structure. *Trends Ecol Evol* 31(5):344–354
- Kiær LP, Weisbach AN, Weiner J (2013) Root and shoot competition: a meta-analysis. *J Ecol* 101(5):1298–1312
- King AA, Costantino RF, Cushing JM, Henson SM, Desharnais RA, Dennis B (2004) Anatomy of a chaotic attractor: subtle model-predicted patterns revealed in population data. *Proc Natl Acad Sci* 101(1):408–413
- Lorenz EN (1963) Deterministic nonperiodic flow. *Journal of the Atmospheric Sciences* 20, 130–41.1. *Prog Phys Geog* 32(4):475–480
- Lorenz E (1993) Our Chaotic Weather. Chapter 3 in Lorenz, E. 1993. *The essence of chaos* Univ. of Wash Press
- Lotka AJ (1925) *Elements of physical biology*. Williams & Wilkins
- MacArthur R (1955) Fluctuations of animal populations and a measure of community stability. *Ecology* 36(3):533–536
- May RM (1971) Stability in multispecies community models. *Math Biosci* 12(1–2):59–79
- May RM (1972) Will a large complex system be stable? *Nature* 238(5364):413–414
- May RM (1973) *Stability and complexity in model ecosystems*, vol 6. Princeton University Press
- May RM, Leonard WJ (1975) Nonlinear aspects of competition between three species. *SIAM J Appl Math* 29(2):243–253
- Morrison LW, Gilbert LE (1999) Host specificity in two additional Pseudacteon spp. (Diptera: Phoridae), parasitoids of Solenopsis fire ants (Hymenoptera: Formicidae). *Florida Entomologist*, pp.404–409
- Morrison LW, Dall'Aglio-Holvorcem CG, Gilbert LE (1997) Oviposition behavior and development of pseudacteon flies (Diptera: Phoridae), parasitoids of solenopsis fire ants (Hymenoptera: Formicidae). *Environ Entomol* 26(3):716–724
- Munch SB, Rogers TL, Johnson BJ, Bhat U, Tsai CH (2022) Rethinking the prevalence and relevance of chaos in ecology. *Annu Rev Ecol Evol Syst* 53(1):227–249
- Patil DJ, Hunt BR, Kalnay E, Yorke JA, Ott E (2001) Local low dimensionality of atmospheric dynamics. *Phys Rev Lett* 86(26):5878
- Peacor SD, Dorn NJ, Smith JA, Peckham NE, Cherry MJ, Sheriff MJ, Kimbro DL (2022) A skewed literature: few studies evaluate the contribution of predation-risk effects to natural field patterns. *Ecol Lett* 25(9):2048–2061
- Rogers TL, Johnson BJ, Munch SB (2022) Chaos is not rare in natural ecosystems. *Nat Ecol Evol* 6(8):1105–1111
- Saiki Y, Sanjuán MA, Yorke JA (2018) Low-dimensional paradigms for high-dimensional hetero-chaos. *Chaos: Interdisciplinary J Nonlinear Sci*, 28(10)
- Saiki Y, Takahasi H, Yorke JA (2021) Piecewise linear maps with heterogeneous chaos. *Nonlinearity* 34(8):5744
- Saiki Y, Takahasi H, Yamamoto K, Yorke KJA, J. A (2024) The dynamics of the heterochaos Baker maps. arXiv preprint arXiv:2401.00836, 2024
- Sander E, Yorke JA (2015) The many facets of chaos. *Int J Bifurcat Chaos* 25(04):1530011
- Soliveres S, Maestre FT, Ulrich W, Manning P, Boch S, Bowker MA, Prati D, Delgado-Baquerizo M, Quero JL, Schöning I, Gallardo A (2015) Intransitive competition is widespread in plant communities and maintains their species richness. *Ecol Lett* 18(8):790–798
- Strogatz SH (2024) *Nonlinear dynamics and chaos: with applications to physics, biology, chemistry, and engineering*. Chapman and Hall/CRC
- Vandermeer J, Perfecto I (2020) Endogenous Spatial pattern formation from two intersecting ecological mechanisms: the dynamic coexistence of two noxious invasive ant species in Puerto Rico. *Proc Royal Soc B* 287(1936):20202214
- Vandermeer J, Perfecto I (2023) Intransitivity as a dynamic assembly engine of competitive communities. *Proc Natl Acad Sci* 120(15):e2217372120. <https://doi.org/10.1073/pnas.2217372120>
- Vandermeer J, Perfecto I (2024) Combining intransitive and higher order effects in a coupled oscillator framework: a case study of an ant community. *Ecology* 105(2):e4218

- Vandermeer J, Perfecto I (2025) Keystone predator and keystone intransitivity and the rescue of a competitively subdominant species. *Proc Natl Acad Sci* 122(33):e2421005122
- Vandermeer J, Flores J, Lindemeyer J, Perfecto I (2022) Spatiotemporal foraging dynamics of *Solenopsis invicta* (Hymenoptera: Formicidae) and its potential effects on the Spatial structure of interspecific competition. *Environ Entomol* nvac058. <https://doi.org/10.1093/ee/nvac058>
- Volterra V (1927) Fluctuations in the abundance of a species considered mathematically. *Nature* 119(2983):12–13
- Zeeman EC, Zeeman ML (2002) An n-dimensional competitive Lotka–Volterra system is generically determined by the edges of its carrying simplex. *Nonlinearity* 15(6):2019

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