

# Stabilizing intransitive loops: self-organized spatial structure and disjoint time frames in the coffee agroecosystem

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**Abstract.** It is familiar knowledge that population dynamics occur in both time and space. In this work, we incorporate three distinct but related theoretical schemata to qualitatively interrogate the complicated structure of part of a real agroecosystem. The three schemata are first, local dynamics translated into intransitive oscillators through spatial movement, second, stabilizing the system through spatial pattern, and third, formation of a self-organized spatial pattern. The real system is the well-studied autonomous pest control in the coffee agroecosystem, in which five insect species (one of which is a pest) are involved in creating a complex community structure that keeps the pest under control (the five species are an ant, *Azteca sericeasur*, a phorid fly parasitoid, *Pseudacteon* sp., a hymenopteran parasitoid, *Coccophagus* sp., a beetle predator, *Azya orbigera*, and the pest itself, the green coffee scale, *Coccus viridis*). We use the qualitative framing of the three theoretical schemata to develop a cellular automata model that casts the basic predator/prey (natural enemy/pest) system as an intransitive oscillator, and then explore the interaction of the two basic predator/prey systems as coupled oscillators within this model framework. We note that Gause's principle of competitive exclusion is not violated with this basic framing (i.e., the two control agents cannot coexist theoretically), but that with a change in the spatial structure of the background habitat, coexistence can be maintained through the tradeoff between regional dispersal and local consumption. Finally, we explore how the other oscillator in the system (the ant and its phorid parasitoid) can act as a pilot system, creating the spatial structure in which the other two oscillators operate, but only in the context of disjoint time frames (between the two control agents and the pilot subsystem).

**Key words:** cellular automata; intransitive loops; predator/prey; spatial ecology; spatial pattern; Turing effects.

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## INTRODUCTION

Ecological dynamics in space has been a major theme in ecology for some time (Tilman and Kareiva 1997, Cronin and Reeve 2005), employing a variety of theoretical approaches (Pacala and Levin 1997, Massol et al. 2011). Here, we propose a unique theoretical framing based on our qualitative understanding of a particular subcomponent of an ecosystem, the traditional shaded coffee

agroecosystem. Our framing differs from previous literature in its qualitative nature based on observations and experiments in this real system over the past 25 yr (Perfecto and Vandermeer 2015), combining other well-known theoretical issues into a coherent framework that corresponds to the long-term observable dynamics in this system. The theory is formed from previous literature on (1) intransitive coupled oscillations, (2) spatial dynamics, and (3) self-organization of spatial pattern.

The coffee agroecosystem is regarded by some as important both for its tractability in ecological study (Greenberg et al. 2008, 2014, Perfecto and Vandermeer 2008) and for its socio-economic importance, reported to be one of the most traded commodities in the world (Lashermes et al. 2008), and the base of economic support for 25 million small-scale farming families and many national economies (Talbot 2004, Utting-Chamorro 2005). The pest system in coffee is large and highly variable. However, at any one point in space and time, it is usually well defined and less imposing than the 250 potential pests reported for the species (Le Pelley 1968). In particular, we focus on one distinct pest, the green coffee scale insect (*Coccus viridis*). A coffee bush may be free of the scale insect pest, or it may have populations of that pest on it, or the pest population may be in a state of undergoing attack from the hymenopteran parasitoid, *Coccophagus* sp. The attack of the parasitoid is vigorous locally (i.e., on a single coffee bush) such that all of the scale insects on a given plant are killed rapidly and the parasitoids then emerge and disappear from the plant. In other words, the system moves from empty plant to pest attacking the plant to pest being attacked by parasitoid to empty plant, evidently an intransitive oscillation, as explained below. Clearly, such an oscillation can only occur in a spatially extended system since migration of both predator and prey are essential parameters. The qualitative behavior of such a system when extended in space closely mimics the classical results of standard predator–prey theory.

The parasitoid *Coccophagus* sp. is thought to be an effective biological control agent of the scale insect. However, an additional control agent, a coccinellid beetle, *Azya orbiger*, is also effective (Liere and Perfecto 2008, Vandermeer et al. 2010). The combination of two control agents (a parasitoid and a predator) acting directly on a prey item in the same space presents us with a classic case of two species occupying the same niche, suggesting Gause's principle may operate. Yet in 25 yr of observations at the same site, both parasitoid and predator have remained common in the system. Part of the theory developed here is aimed at proposing how the complexity of spatial structure can explain this fact.

Coffee is traditionally planted under the canopy of shade-trees, a natural procedure given

coffee's origin as an understory plant in the first place. As has been demonstrated (Vandermeer et al. 2008), the shade-tree nesting ant, *Azteca sericeasur*, moves its nest from shade-tree to shade-tree, presumably in response to a fly parasite in the family Phoridae (*Pseudacteon* sp.). The ants forage in the nearby coffee bushes (a single nest in a shade-tree typically forages on 5–10 surrounding coffee plants). Thus, with respect to this ant species, at the level of a given coffee bush there is an expected cycle of coffee bush without ants, which becomes occupied by *Azteca* ants, which get attacked by Phorid flies, which render the bush free of *Azteca* ants—another intransitive loop. This loop actually creates pattern in the background habitat, which, we argue, could form the background pattern necessary for coexistence of the two biological control agents.

It is notable that in this particular real-world system there is a mutualistic ant/hemipteran system, the *Azteca* ant and the scale insect, in which the ant forages on the honeydew produced by the scale insect and while doing so attacks the natural enemies of the scale insect, to the mutual benefit of both scale and ant (Vandermeer and Perfecto 2006, Jha et al. 2012). It is thus most natural that farmers view the ant as a pest also. Yet, as we show in this model exercise, it is the spatial extension of the system that allows the two biological control elements to persist in the long run, effecting autonomous biological control over the scale insect over the entire farm, thus sacrificing a small percentage of the farm (from 3% to 7%) as effective spatial repositories of the pest, which keeps the biological control agents alive over the entire region.

The spatial dynamics of this system can be understood through a three-part theoretical framing: (1) the basic nature of spatial predator/prey systems forming intransitive loops, (2) heterogeneity of spatial structure stabilizing a coupled system of predator–prey loops, and (3) the self-organization of that spatial structure, through a pilot pattern formation from a distinct species group.

## THE THEORETICAL FRAMING

The existence of intransitive oscillations in competitive communities was noted theoretically in 1975 (May and Leonard 1975) and claimed to

be widespread in plant communities in 2015 (Soliveres et al. 2015), although much earlier Gary Polis noted the general existence of what he called “loops,” in his Coachella Desert food web (Polis 1991), clearly referring to their intransitive nature (species 1 beats species 2 which beats species 3 which beats species 1, a structure similar to the children’s game of rock, scissors, paper). Although the original analysis of intransitive competition was based on the classical Lotka-Volterra phenomenological competition equations, it is also the case that intransitivity emerges easily when competition is framed mechanistically (i.e., a consumer/resource or predator/prey dynamic), (Durrett and Levin 1994*a, b*) and the rather large literature on intransitive competition theory (Freaan and Abraham 2001, Kerr et al. 2002, Laird and Schamp 2006, Allesina and Levine 2011) is not compromised. However, spatially distributed predation may have an intransitive structure in and of itself, if the scale of interaction is sufficiently small such that predator and prey cannot coexist in perpetuity at an individual isolated site. That is, if an empty space is occupied by a prey item which in turn is occupied by a predator of that prey, and if the predator overexploits the prey (which inevitably happens if the local space in which dynamics occur is small), there is a basic intransitive structure—empty, prey, prey/predator, empty. This structure, which undoubtedly, is common in nature, we refer to as an intransitive oscillator.

For example, the famed Huffaker experiment (Huffaker 1958) is most often cited as an example of how spatial extension can induce stability in a predator–prey system. Oranges provided the substrate for a predator–prey pair. Following an individual orange through time, the pattern was consistently one of an empty orange receiving migrating prey individuals, giving rise to an orange containing a population of prey individuals. Subsequently, individuals from the predator population arrived, giving rise to an orange containing populations of both prey and predators. The predators quickly eliminated the prey, giving rise to an empty orange again. Thus, on a single orange the pattern through time is (1) empty orange gives rise to (2) orange with a prey population, gives rise to (3) orange with both predator and prey populations, gives rise to (4) an empty orange. As long as there are both prey and

predators migrating, this cycle repeats itself as an evident intransitive oscillation. The key result of the experiment is that when a group of oranges is arranged in a spatial pattern, the basic intransitive oscillation creates a sustained oscillation of predator and prey when averaged over the whole array of oranges, even though each individual orange is unstable.

Since both classical predator–prey theory and this spatial formulation are oscillatory, when two distinct oscillations occur in the same space, they are likely to interact with one another, which is to say be coupled. The vast literature on coupled oscillators thus becomes relevant (Strogatz and Stewart 1993, Vandermeer 1993, 2004, 2006), and questions of coexistence emerge, depending on the nature of the coupling. Specifically, when two predators are coupled through a single prey (two consumers through a single resource), the expectation is that Gause’s principle will come into play.

An additional feature of the Huffaker study is that the predator–prey system induced a spatial structure, wherein distinct patches of prey and predators meander over the space, suggesting that there was something about the pattern or patchiness that is related to the fact that the instability at a small scale became stable at a large scale. Subsequently, a related theoretical literature has evolved, commonly associated with the insights of Alan Turing (1952), in which the prey acts as if it were an activator and the predator a repressor, a metaphorical framing that places the spatial predator–prey system in the general category of reaction–diffusion. Initial theoretical explorations (Segel and Jackson 1972, Levin and Segel 1976, 1985, Levin 1979) have given rise to what seems like a major generalization in ecology (Alonso et al. 2002, McGehee and Peacock-López 2005, Vandermeer et al. 2008, Bendahmane et al. 2016, Peng and Zhang 2016), that predator–prey systems in physical space will tend to form clusters that are Turing-like. This generalization seemingly holds well when the system is cast as a simple intransitive loop, with the additional provision that the spatial structure can form a background pattern that is essential for the persistence of other systems living therein, as described below.

Finally, much of the literature on both intransitive cycles and coupled oscillators in space is framed in terms of a regular background, effectively a regular lattice forming the environmental

network upon which the population dynamics unfolds. We note first that fundamental questions of coexistence require a patterned background rather than a regular lattice (Horn and MacArthur 1972, Levin 2000) and finally note that a patterned background itself may emerge from independent intransitive oscillators.

The rest of this paper is organized as follows: First, we explore the basic dynamics of placing the intransitive cycles in space and coupling them together (in this case the scale insect attacked by the parasitoid and the predator). Second, we explore the nature of the underlying spatial structure and the spatial scale of dispersion scale, casting the problem as a network-transforming issue. Third, we examine the nature of the self-organized pilot pattern formation, in which an additional intransitive oscillator (in this case the ant/phorid predator-prey system) creates the spatial structure on which the original two oscillators can coexist.

### THE DYNAMICS OF COUPLED SPATIAL INTRANSITIVE OSCILLATORS

The green coffee scale insect, *Coccus viridis*, a pest of coffee throughout the world (Coleman and Kannan 1918, Le Pelley 1968), is one of the key components of this system (Vandermeer and Perfecto 2006, Vandermeer et al. 2010, Perfecto and Vandermeer 2015). It attaches mainly to the midrib of the leaves of coffee trees, penetrating the leaf tissue with a sharp proboscis and sucking material out of the leaf. It is basically sessile as an adult but produces crawlers as juveniles. The crawlers are dispersed by wind and must disperse from leaf to leaf on a tree and from plant to plant on a larger scale, plausibly on a regular lattice pattern, but more often than not in a non-random clustered pattern, depending on the spatial nature of the coffee plantings. A well-known parasitoid on the scale is a wasp, *Coccophagus* sp. (Mani et al. 2008). The idealized version of the system is, at the level of an individual plant (1) an individual plant without scales is (2) infested by the crawler stage of the *C. viridis* and rapidly forms local populations on the plant, which (3) attracts the parasitoid *Coccophagus* sp. which eliminates it from the plant, rendering the plant free of scales once again. More generally, an empty site is colonized by a prey item which is

subsequently colonized by a predator item which eliminates it, thus returning the site to an empty state (as outlined in Fig. 1).

We model this basic system as a cellular automaton. Consider a  $n \times n$  lattice with three variables: S (for empty space), P (for predator and prey together), and V (for prey or victim alone), all of which are binary, and  $k_i(x,y)$  is a binary number indicating presence or absence of the  $i$ th variable at the point  $\{x,y\}$ . The number of each of the variables in the Moore neighborhood (the surrounding eight cells) is given as

$$N_i(x,y) = \sum_M k_i(x,y)$$

where  $i = S, P,$  or  $V$  and  $M$  indicates summation in the Moore neighborhood around the point  $\{x,y\}$ . Thus, for example,  $N_S(x,y)$  is the number of empty cells in the Moore neighborhood around point  $x,y$ . The transformation rules for each lattice cell are as follows:

- S changes to V with probability  $mN_V/8$
- V changes to P with probability  $aN_P/8$
- P changes to S with probability  $d$

The parameters  $m, a,$  and  $d$  have clear biological meanings:  $m$  = migration rate of the prey,  $a$  = migration rate of the predator, and  $d$  = feeding rate of the predator (visualized in Fig. 1).

Over the whole lattice, we expect qualitative results that are likely to result from simple quasi-quantitative reasoning (and correspond to classical results): (1) If the predator's death rate is extremely low but its attack rate is extremely

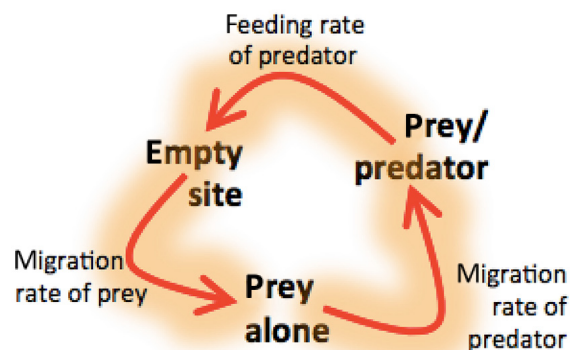


Fig. 1. The basic framework of the model system (note its intransitive nature).



high, we expect that the predator will eliminate all prey and then itself go extinct from a lack of food, thus the elimination of the entire system (the takeover by empty spaces); (2) if the predator death rate is extremely high and the attack rate extremely low, the predator will be eliminated from the system and the prey increase to take over the entire lattice (approach its carrying capacity); (3) with intermediate values of predator attack and death rates, the system will be maintained, as an intransitive loop in space. The detailed nature of these three outcomes will depend on parameter values, but it is worth emphasizing that the overall average behavior of the system is expected to mirror the classical results of predator-prey theory. Results from simple simulations on a  $100 \times 100$  lattice are presented in Fig. 2.

The nature of the coexistence parameter space is complicated but intuitive and simple simulations reveal a host of potentially interesting temporal behaviors and spatial patterns on the lattice. However, there is an interesting generalization that can be gleaned from Fig. 2. Taking prey migration rate as a tuning parameter, whence the overall behavior of the system is complete extinction of the whole system when the prey migration is too low (that which would happen if the parameter were to the left of the left-hand panel of Fig. 2) ranging to complete coexistence of both predator and prey (that which would happen if the parameter were to the right of the right-hand panel of Fig. 2). Between these two predictable circumstances, the system will be more unpredictable, yet with a

clear statistical pattern, as illustrated in Fig. 2. If either of the other two parameters are taken as tuning parameters, the qualitative results are equally intuitively obvious. And if we construct a parameter that simultaneously increases predator attack rate while decreasing predator death rate, the system will go from complete elimination of the predator and persistence of the prey over the whole lattice to a state of emptiness (neither predator nor prey survive and the whole lattice is empty). In all of these qualitative observations, it is important to note that the three-element persistent solution is always an intransitive loop.

Corresponding to the framework we seek to study (coupled intransitive oscillators) the green scale insect has another important predator, a lady beetle, *Azya orbigera*. It is qualitatively clear, if difficult to measure quantitatively, that the lady beetle and the parasitoid have different dispersal qualities and different attack rate properties (Jha et al. 2012, Liere et al. 2012), yet the basic idea of the two together corresponds to the theoretical structure of coupled oscillators (Fig. 3), a framework that has given rise to a substantial literature (Strogatz and Stewart 1993, Vandermeer 1993, 2004, 2006). In accord with this recent literature, it is of interest to query the current framework with respect to a second predator in the system, effectively a situation of competition with the two predators seeking sustenance from the same food source, and conceptually fitting into the category of a system of coupled oscillators. The two predators are, structurally, in competition with one another.

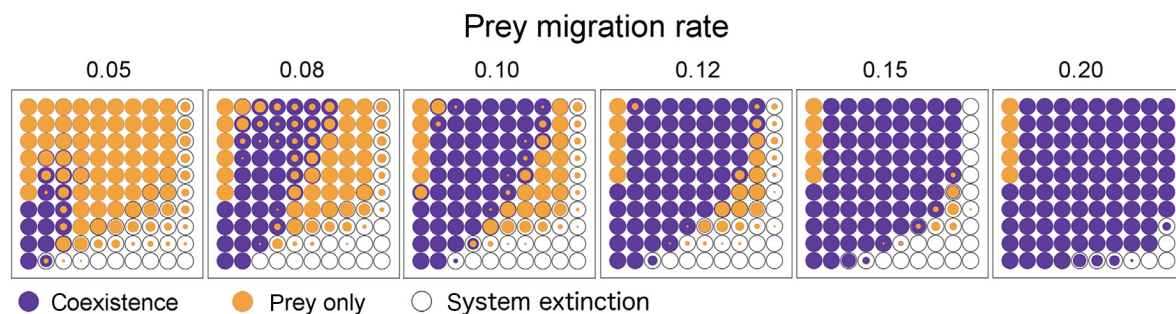


Fig. 2. Parameter space study of long-term outcome of cellular automata model, plotting predator attack rate (abscissa) vs. predator death rate (ordinate), with proportional bubbles representing coexistence (prey/pred), or predator extinction and prey survival (prey = K) or extinction of the whole system (empty). Axes on each graph range from 0 to 1.

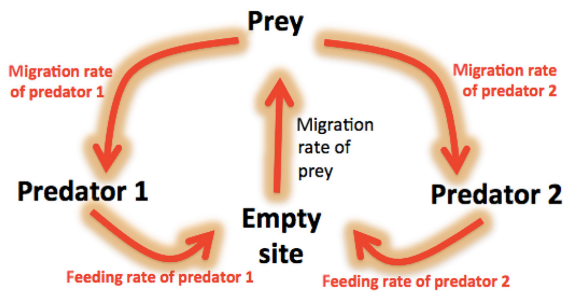


Fig. 3. Coupling two intransitive loops.

Thus, expanding the original model, we have,

$S$  changes to  $V$  with probability  $mN_V/8$   
 $V$  changes to  $P_1$  with probability  $a_1N_{P_1}/8$   
 $V$  changes to  $P_2$  with probability  $a_2N_{P_2}/8$   
 $P_1$  changes to  $S$  with probability  $d_1$   
 $P_2$  changes to  $S$  with probability  $d_2$

as the fundamental model (illustrated in Fig. 3). However, in running the model there is another emergent state,  $P_1P_2$ . So as to avoid an unnecessary additional time step, we transform  $P_1P_2$  to  $S$  during the same time step (i.e., the rule  $P_1P_2 \rightarrow P_1$  with probability  $\alpha$  and  $P_1P_2 \rightarrow P_2$  with probability  $1-\alpha$ , generates what is effectively a new nonlinear element into the model which mitigates against the simplicity of the original formulation, adding an additional parameter,  $\alpha$ ).

Extensive simulations support what we believe is intuitive, that  $P_1$  and  $P_2$  should form a kind of stochastic extinction in this system. That is, the long-term coexistence of  $P_1$  and  $P_2$  is not possible, regardless the values of the tuning parameters (if  $\alpha$  is added as an additional parameter (see discussion in previous paragraph), there are knife-edge sections of the parameter space that allow for coexistence—we ignore those situations as probably uninteresting). Similar formulations in the literature generate identical results (e.g., Freaan and Abraham 2001), which reflect the classic notion of Gause's principle.

Strict cellular automata rules are quite restrictive when a second predator is added, especially in the light of the much-discussed competition/migration tradeoff. That is, the need for only local interactions (any given cell receives migrants only from its immediate neighbor cells) mitigates against a framework in which either predator or prey can engage in long-distance migration, even

though local parameters are tunable. This restriction can be seen as an obvious mechanism of why the two predators are unable to coexist, sort of a spatial form of Gause's exclusion principle. And it is also the case that creating a situation where one predator is a poor feeder but migrates rapidly, while the other predator is a poor migrator but feeds rapidly (in search for the ecologically proverbial tradeoff), does not dampen the apparent result that the two predators will not coexist except at knife-edge sections of parameter space (structurally similar to the famous survival of the weakest, in which a genotype of a weaker competitor will exclude the genotype of a stronger competitor due to spatial constraints; Freaan and Abraham 2001). However, this result depends on what we argue is an overly restrictive constraint on the background habitat—that it is a regular network (Newman 2010).

## THE STRUCTURE OF THE BACKGROUND HABITAT

A convenient tool for examination of underlying geometry, without imposing strict point-to-point dynamics, is found in the burgeoning field of network theory. Indeed, if the probability of migration as a function of distance is strongly convex (in the sense that probability is close to 1.0 for close distances and falls rapidly toward zero at some critical distance), we can think of the geometric space as a network. The coffee plants are nodes, and any pair of plants closer than the critical distance is connected by an edge. The background on which the dynamic process operates is thus a formal network with nodes and edges. In the real system, although plants may be concentrated in rows, or on hillside contours, in more traditional systems they frequently seem more like a natural plant population. That is, the distribution of plants on the ground is far from a regular lattice, even though such a planting pattern may have been the original intent of the farmer. In Fig. 4, we show the distribution of coffee bushes in a small ( $20 \times 20$  m) plot, in southwestern Chiapas, Mexico, illustrating the combination of regularity (from the original intention of the farmer in planting the bushes) plus irregularity (from random deaths and subsequent replanting). Thus, we have a network that could be ideally considered a regular lattice, although its

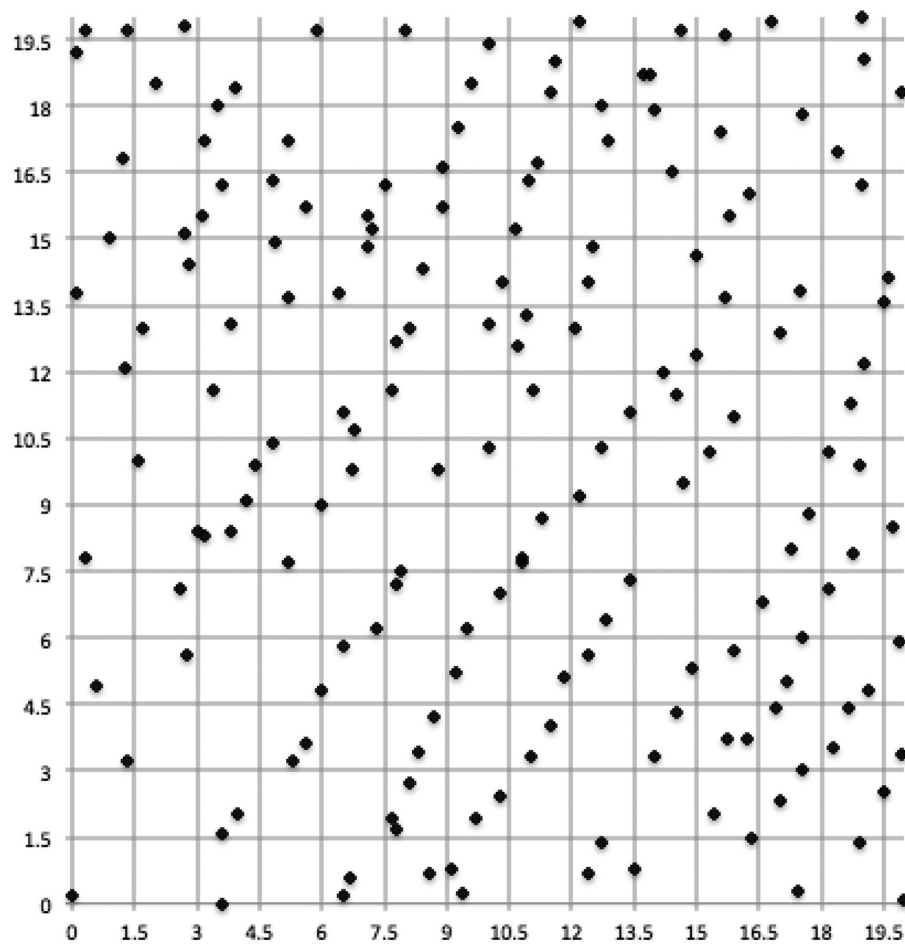


Fig. 4. Distribution of coffee trees on a  $20 \times 20$  m plot in Mexico, illustrating both the original intention of planting trees in rows, but, because of deaths and replanting, also the non-regular nature of the distribution.

deviation from regularity suggests other idealizations could be possible, as discussed later. The dynamics of the scale insect population and its predators operates on a network like this.

It is reasonable to suggest that the background habitat is viewed differently by the three players in our real-world system. For example, the parasitoids are likely to disperse locally and build up high population densities locally (Compton 2002). The beetles, however, fly actively and are known to disperse widely (Liere et al. 2012). It might then be reasonable to suggest that the parasitoids are local dispersers and view the habitat as a lattice (perhaps with some of the nodes clustered), while the beetles, flying widely searching for scale insects, view the habitat differently. While many spatial models in ecology presume a

regular Euclidean space as the underlying spatial geometry, the geometry faced by most systems in nature does not conform to this idealization. The migration distance and/or the geometric position of occupation sites may alter the dynamic rules. For example, if one of the predators is a long-distance migrator, that effectively changes the regular lattice network to what is effectively a small-world network. Similarly, if nodes are clustered in space, or the rules of migration effectively make them so, the background habitat is a clustered distribution (which may or may not be scale-free, i.e., the distribution of number of connections per node may or may not be a power function). Although other framings are possible, we find it convenient to begin with a regular lattice and consider modifications in (1) physical

positions of the nodes (habitat spaces) and (2) local vs. long-distance connections (small-world structure). We summarize our categorization scheme in Fig. 5.

With this framing, we note that the failure of the dispersal/competition tradeoff paradigm to stabilize the system (make it persistent) takes on a slightly more complicated form. As noted above, with a simple modification of the rates of migration and attack rates of the two predators in the simple CA model, it is not possible to maintain both predators in the system. In the context of our actual system, we examine the consequences of assuming one predator operates on a strict lattice structure (as we expect of the parasitoid in the running example) while the other exists on a small-world network, resulting from its long-distance dispersal (as we expect of the beetle predator in our running example). Thus, our framework generates a system structured such that a clustered lattice underlays the

dynamics of one species (i.e., Fig. 5c), while a clustered small-world pattern underlays the dynamics of the other species (i.e., Fig. 5d). With proper parameter settings, it is evident that both intransitive loops could coexist in perpetuity, an expectation that is revealed in simple simulations (e.g., Fig. 6).

### SELF-ORGANIZED STRUCTURE OF THE BACKGROUND HABITAT

Extensive simulations repeat the pattern shown in Fig. 6, namely, on a regular lattice with or without small-world connections, the two species are unable to persist together, but on a clustered lattice with small-world connections, there are extensive areas of parameter space that permit coexistence, apparently in perpetuity. The coexistence arrives through the standard mechanism of a tradeoff between dispersal and competition (Levins and Culver 1971, Cadotte et al. 2006), with the strong competitor (low predator dispersal rate and high attack rate) dominating the larger clusters of available sites while the strong disperser (low predator attack rate and high dispersal rate) dominates the smaller isolated available sites. Thus, we see the coupled intransitive loops reflect the underlying structure assumed to exist regularly in both theory and in real systems.

There is another intransitive loop in the system. Most farms are managed with shade-trees above the coffee bushes. As noted above, the arboreal *Azteca* ant locates its nesting sites in those shade-trees and forages on the nearby coffee trees. As its colony grows, it buds, forming new colonies in nearby shade-trees, thus forming clusters of nests (Vandermeer et al. 2010, Jackson et al. 2014). But the ant is attacked by a parasitoid fly (*Pseudacteon* spp.) that effectively causes the clusters of nests to disappear (either all nests in the cluster are moved far away or they die). Thus, we have the intransitive loop of (1) empty coffee bush is found by (2) an *Azteca* colony (nesting in a nearby shade-tree), which ultimately is (3) attacked by the fly parasitoid, eventually abandoning its nesting site (or dying). As argued elsewhere (Vandermeer et al. 2008), this system is similar to the classic Turing mechanism in that the phorid acts as a repressor and the ant, by moving its nests and occupying other trees, is

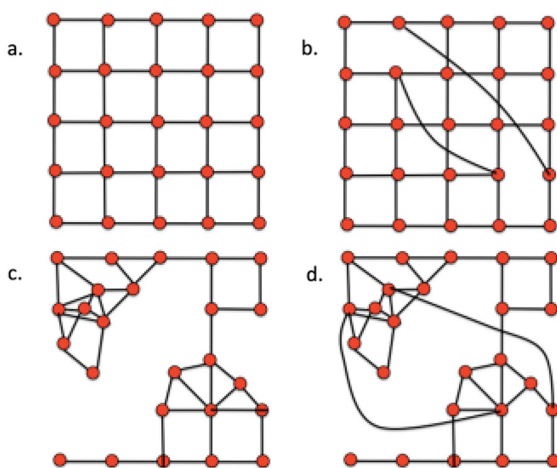


Fig. 5. The four qualitatively distinct network structures considered. (a) A regular lattice where the small circles are the habitats which the predators and prey may occupy (coffee bushes in the present context), and the connections represent the possible migration pathways. (b) The regular lattice in (a) with two connections randomly broken and randomly reattached, creating a small-world structure. (c) A clustered pattern of habitats. (d) The same clustered pattern in (c) but with a random two connections broken and randomly reattached to create a clustered small-world spatial pattern. In all cases, there are 25 nodes (coffee bushes) and 40 connections (dispersal pathways).



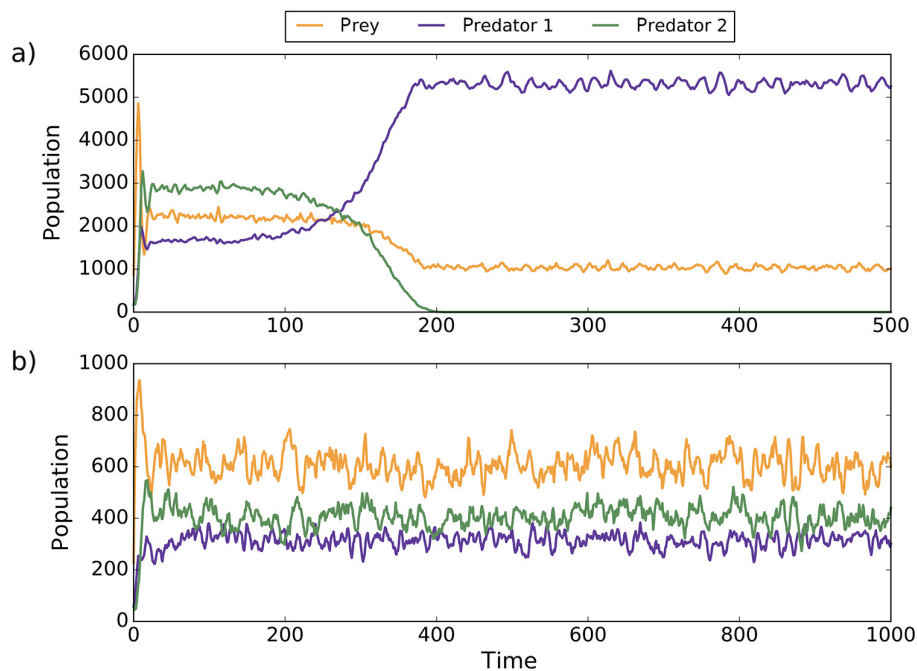


Fig. 6. Exemplary simulation results on a regular  $100 \times 100$  lattice with one predator a long-distance migrator (predator 2) and the other a strong competitor (predator 1). (a) On a regular lattice, one of the predators always goes extinct (which one depends on parameters), regardless of the parameter tradeoff of dispersion vs. competition. (b) With a fixed non-random background habitat representing a clustered small-world habitat (as in Fig. 5d), a variety of parameter combinations allows for such coexistence.

the activator, with the whole system operating on the background network of shade-trees that are potential sites for the ant nests. This Turing-like mechanism creates clusters of nests in an otherwise relatively uniform environment (Fig. 7). Most importantly, as noted elsewhere (Jackson et al. 2014), any other organisms that use the ant nests as background habitat will respond to particular critical distances according to their own biological properties.

Thus, the basic intransitive spatial structure of the *Azteca* ant, the phorid fly, and the empty trees gives rise to clustering in space, and each cluster of ant nests represents a connected component in the context of network theory. The dependence of the scale/parasitoid complex on this structure represents a spatial structure created by one system (the *Azteca*/Phorid system) in which the other system (the scale/parasitoid/beetle system) is forced to exist. Yet in another sense, the system is composed of three coupled intransitive loops as illustrated in Fig. 8—the empty site may be (1) occupied by the scale insect (the prey) and then

attacked by the wasp (predator 1), or (2) occupied by the scale insect (the prey), and then attacked by the beetle (predator 2), or (3) occupied by the *Azteca* ants (alternative prey) and then attacked by the phorid parasitoid (alternative predator).

The scale insect is strongly influenced by the *Azteca* ant (the alternative prey of Fig. 8), a major element in this system, extensively studied earlier (Vandermeer et al. 2010). The ant makes its nests in the shade-trees in coffee farms and tends scales on the nearby coffee bushes, which is to say prevents the two predators from attacking the scale insects. Thus, there are alternative effective habitats in which the scale insect may occur: (1) coffee trees associated with a nest of the ant, *Azteca sericeasur*, and (2) coffee trees not associated with the ant—either of the predators have complete access to the scale insects in those areas in which the ants are absent, but greatly reduced access when the ants are present. Consequently, the ants occupying shade-trees effectively create a network on which the two natural enemy

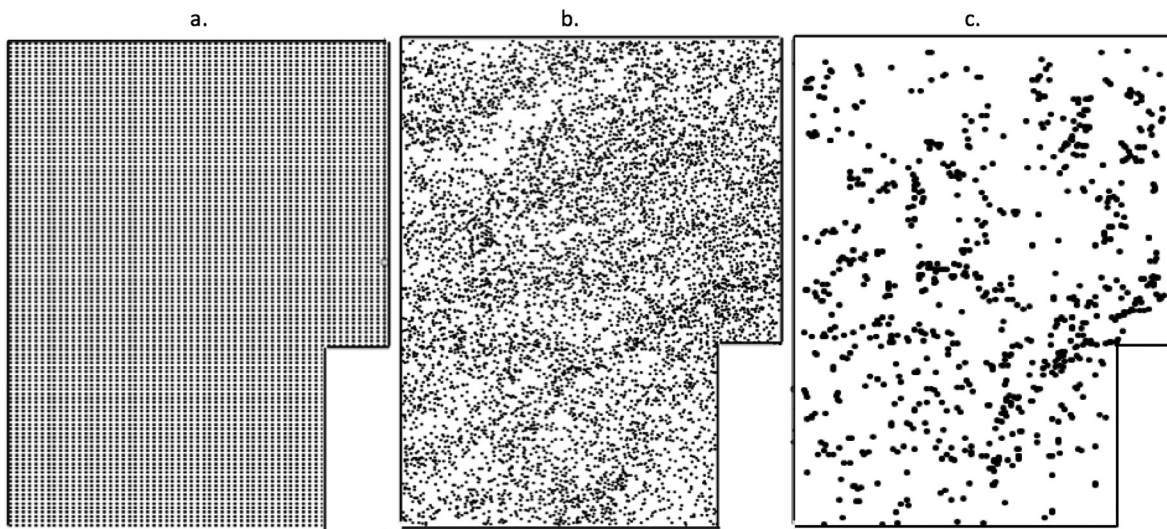


Fig. 7. Three snapshots of a 45-hectare plot in a Mexican coffee farm. (a) Theoretical distribution of 6700 trees arranged in a regular lattice, as would be (and was) the underlying assumption from a simple cellular automata model of the system. (b) The actual distribution of shade-trees (about 6700) on the farm in 2014, showing the obvious deviation from the regular lattice. (c) The distribution of shade-trees that contained Azteca nests in 2014, illustrating the clustered nature of the nest distribution.

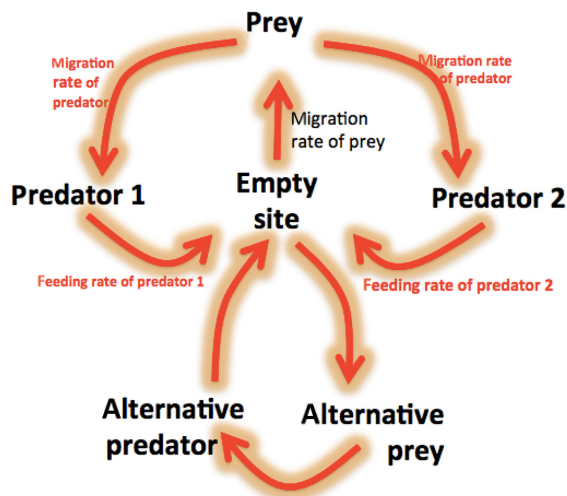


Fig. 8. The three connected intransitive loops with alternative prey.

systems must operate, that is, all the area in the coffee farm that is without ant nests. For this reason, we add a third intransitive loop to the system (Fig. 8), the ant/phorid system. Note that one of the intransitive loops (the alternative prey/alternative predator loop of Fig. 8), through the Turing mechanism (Vandermeer et al. 2008)

forms the clustered spatial pattern in which the other two predators must exist, thus creating a basic self-organizing process whereby the system as a whole may persist.

Expanding the basic CA model to include this third loop, we have two new variables, A = occupied by Azteca ants, and P<sub>3</sub>, occupied by Azteca ants and their parasitic phorid flies, and the CA model becomes,

- S changes to V with probability  $m_1 N_V / 8$
- V changes to P<sub>1</sub> with probability  $a_1 N_{P1} / 8$
- V changes to P<sub>2</sub> with probability  $a_2 N_{P2} / 8$
- P<sub>1</sub> changes to S with probability  $d_1$
- P<sub>2</sub> changes to S with probability  $d_2$
- S changes to A with probability  $m_2 N_A / 8$
- A changes to P<sub>3</sub> with probability  $a_3 P_3 / 8$
- P<sub>3</sub> changes to S with probability  $d_3$

There is an inherent conflict in the structure of the system regarding the switch from S to V vs. the switch from S to A. In this model, we first consider the S to A switch, which, if it happens, makes the cell unavailable for the S to V switch.

The subcomponent of this model that includes only the loop, S to A to P<sub>3</sub>, is similar to the model

we studied earlier, and results in spatial clusters of ant nests on the grid. Thus, this third loop is expected to create a spatial pattern within which the first two loops ( $S, V, P_1$ , and  $S, V, P_2$ ) exist, what we call a “pilot pattern” (taking a very approximate metaphorical clue from so-called pilot wave theory of particle physics, e.g., Valentini 2010) that will permit the coexistence of the other two predators and their intransitive loops, much like the fixed clusters did, as, for example, Fig. 6b. However, it is evident that the pilot pattern created by this third loop can take a variety of forms, three examples of which are illustrated in Fig. 9. Note that the clusters where the other two loops must exist are the open spaces.

If the spatial pattern formed by the pattern-forming intransitive loop (the pilot intransitivity) were to remain constant, clearly that would be no different than fixing an arbitrary background as we did in the case of Fig. 6b. With a completely connected network (e.g., Fig. 9a), as already mentioned, the background is essentially a single background habitat and the results reported above are repeated (i.e., extinction of one of the original predators). With an unconnected patchy network (e.g., Fig. 9b), the big patches favor the non-dispersing predator and

the small patches favor the dispersing predator, and for many parameter combinations, we should expect the two predators will coexist (as happened above with the fixed spatial pattern). However, extensive simulations with this situation show that coexistence of the original two predators is impossible. When the generated pilot pattern is continually changing, the system effectively merges all the patches stochastically, and the average over time essentially becomes a single patch.

Thus, we see that as long as the constructed spatial system of permitted sites is not a completely connected network (e.g., if it is as in Fig. 9b), and as long as the pattern is fixed, coexistence is possible (e.g., Fig. 6b). But with a dynamic system, even though seemingly favorable patchiness is created by the third (pilot pattern) loop, coexistence is impossible (data not shown). Thus, at one extreme, if the system that generates the pattern (the alternative prey/alternative predator; Fig. 8) operates at the same temporal scale as the original coupled system (prey/predator 1/predator 2), coexistence is impossible, but at the other extreme, if the temporal scale is very long (i.e., the constructed pattern is constant), coexistence is common. The question thus

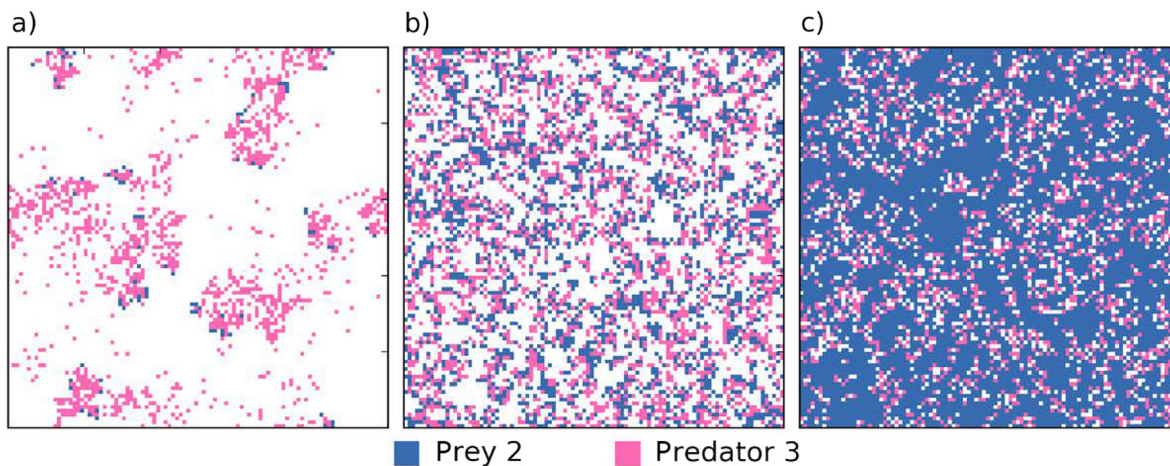


Fig. 9. Examples of the structure generated by the empty space/prey/predator intransitive loop, where the empty patches are the constructed habitat created for the original coupled intransitive loop system. (a) Large patches at a parameter setting with a spanning cluster (of white) and a completely connected network (of white), effectively creating a single patch and the effective structure of a simple lattice. (b) More constrained patches where both large and small patches exist, creating the background for a sustained coexistence of both original intransitive loops, where one predator is a good competitor and the other a good disperser, just on the border of a spanning cluster. (c) Highly isolated patches.



arises as to what happens at intermediate temporal scales.

Let the temporal scale of the constructing system be  $\tau$ . If  $\tau \rightarrow \infty$  the constructed space is fixed for the original coupled system, whereas if  $\tau = 1$ , the constructing system has the same time scale as the original coupled system. So, with  $\tau \rightarrow \infty$ , the background system is constant and the two predators coexist (with proper parameter values, e.g., Fig. 6b). If  $\tau = 1$ , the background system changes at the same rate as the original coupled system changes and effectively creates a single average environment, leading to the inevitable extinction of one or the other predators (data not shown).

Clearly, a value of  $\tau > 1$  but  $< \infty$  can result in either result and we can imagine a critical value,  $\tau_{crit}$ , above which the original coupled two predator system will persist in perpetuity and below which competitive exclusion will result. Several relevant time series are illustrated in Fig. 10 and snapshots of one of the spatial patterns that emerges when  $\tau > \tau_{crit}$  is illustrated in Fig. 11.

Thus, a clustered spatial structure created by an independent intransitive loop can create persistence of a distinct set of coupled intransitive loops, but only if the former has a disjointed time frame, that is, only if the pilot pattern-forming loop operates in a longer time frame than the

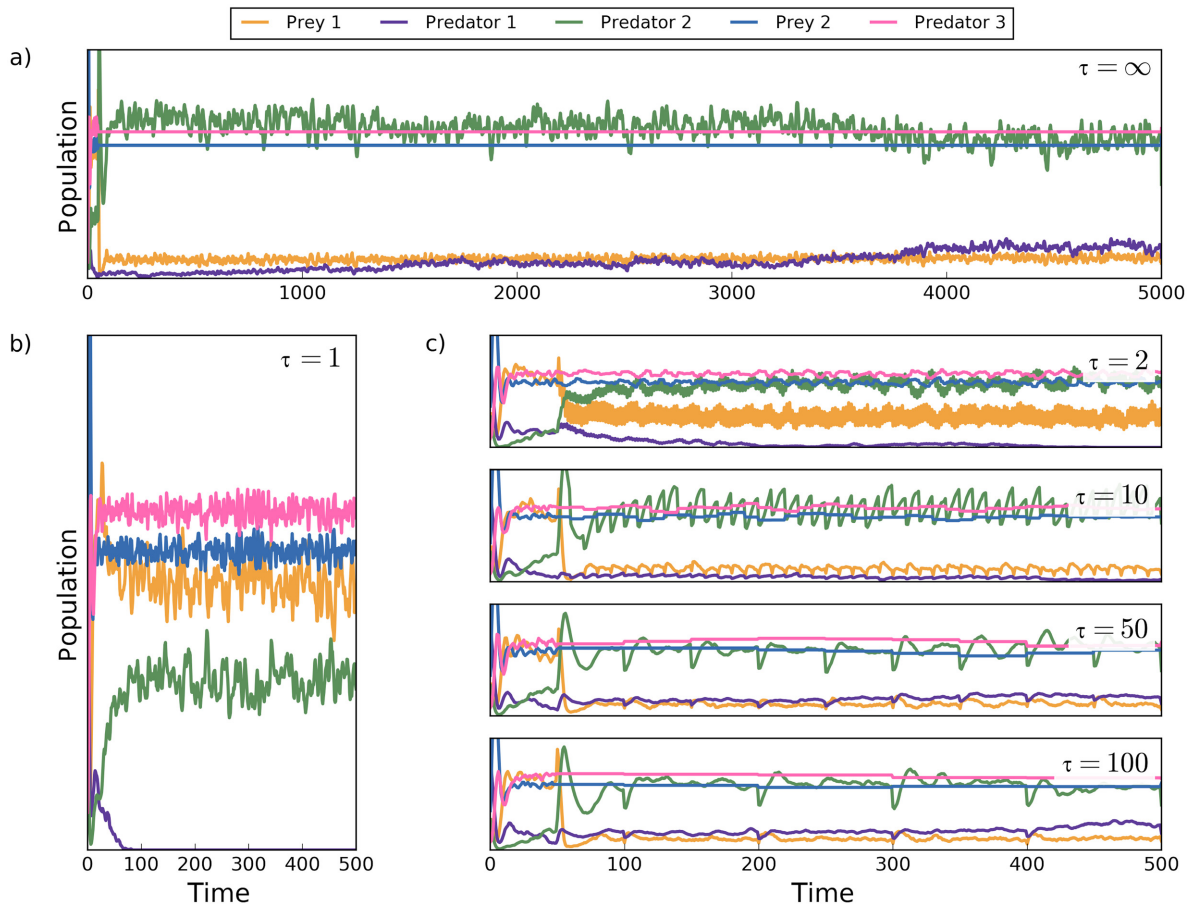


Fig. 10. Exemplary time series of predators with the dispersion/consumption tradeoff, with the Azteca/Phorid system creating pattern. (a) Illustration of the operation of the Azteca/Phorid system for the first 50 time steps with the resulting spatial structure remaining constant after that point. Note the persistence of both predators in the system. (b) Same as a, but the Azteca/Phorid system remaining in the dynamic structure throughout. Note the extinction of predator 1 at time step 100. (c) Four examples of the parameter  $\tau$ , illustrating the persistence of the system for  $\tau = 10$  and above. Note how the dynamic pattern of both predators reflects the particular value of  $\tau$ .



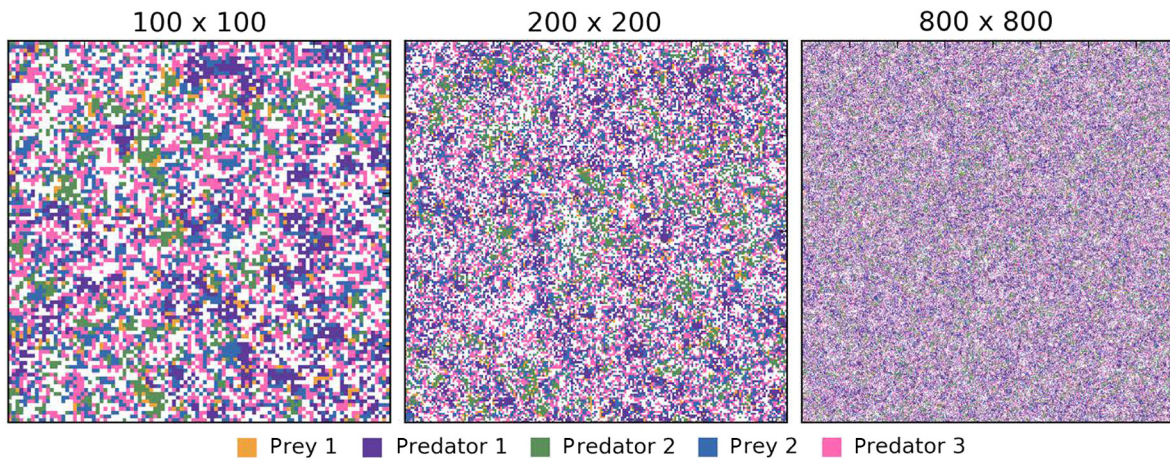


Fig. 11. Spatial structure emerging from three interpenetrating intransitive loops, where prey 2 and predator 3 (coupled with empty sites) are the members of the intransitive loop that provides the pilot pattern in which the other two intransitive loops live. (Parameter set is the same as parameter set b in figure 9, with  $\tau = 25$ ).

coupled system living in that spatial structure. There are parameter combinations where the relationship between the time frame difference ( $\tau$ ) seems to form a proportional relationship to the time to extinction ( $T$ ) estimate (Fig. 12), but other combinations where there is an accelerating relationship between  $\tau$  and  $T$  (Fig. 12). Most importantly, there seem to be some parameter combinations for which the function that relates  $T$  to  $\tau$  diverges at some critical  $\tau$  ( $\tau_{crit}$ ), as illustrated in Fig. 12. It is also the case that the time to extinction scales as the inverse of the critical point, which is to say, the equation,

$$T = \frac{f}{\left(1 - \frac{\tau}{\tau_{crit}}\right)} \quad (1)$$

describes well the time to extinction ( $T$ ) relative to the scaling parameter ( $f$ ) and the critical exponent ( $z$ ), according to the dynamic scaling hypothesis (Djurberg et al. 1997).

## CONCLUSION

Herein we argue that a spatially explicit intransitive system consisting of empty cell giving rise to cell with prey giving rise to cell with prey/predator giving rise to empty cell is a good model for at least the system we model here, the pest system of a Mexican coffee agroecosystem. For the actual system being modeled, the prey is a

pest species, the green coffee scale insect. There are two predators, a wasp parasitoid and a beetle, and coupling them together creates a situation in which, theoretically, coexistence is impossible. We note that the general qualitative framing here is hard to ignore as basically identical to the operation of the system in nature (individual coffee trees that get attacked by scale insects, but then the scale insects are attacked by both of these biological control agents). Yet our generalization that such a coupled intransitive system cannot persist is inconsistent with the clear observations in nature over the past 20 yr that both of these biological control agents persist in the system, indeed are responsible for maintaining this pest below significant damage thresholds (Vandermeer et al. 2010). Adding the underlying non-regular pattern of the cells in the system (the coffee bushes on the farm) enables the co-persistence of the two biological control agents. But that underlying spatial pattern is itself a consequence of a distinct intransitive oscillator, what we call the pilot system. As noted by Barabás (*personal communication*), this metaphor is perhaps stretched, in that the system forming the pattern is doing nothing more than that. To liken it to the dynamic process in the De Broglie-Bohm theory is certainly very approximate, yet the underlying consequences of both the original pilot wave and our pilot pattern are similar and we argue that this approximate metaphor is potentially useful.

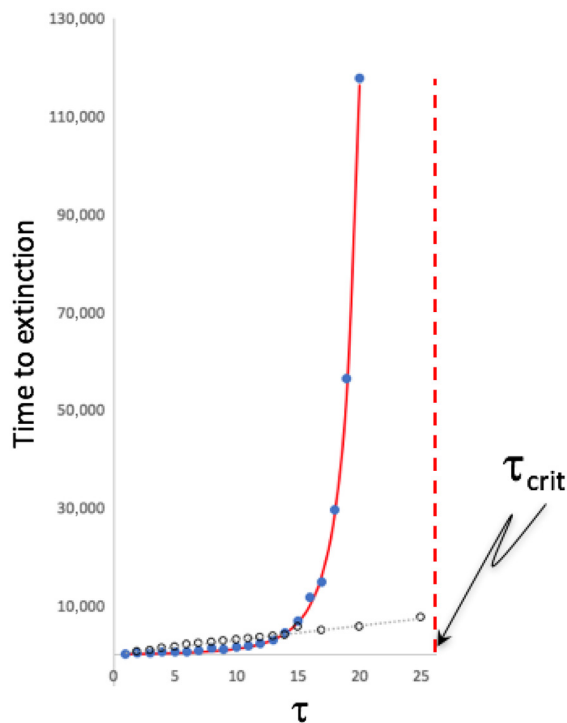


Fig. 12. Time to extinction vs.  $\tau$  on a  $100 \times 100$  lattice. Open symbols for parameter set A and closed symbols for parameter set B. Note the open symbols follow a linear relationship with  $\tau$  (line is best fit linear least-squares regression), while the closed circles fit well the equation  $T = 146.77/(1-\tau/\tau_{\text{crit}})^{4.209}$  where the divergence is  $\tau_{\text{crit}} = 25.15$ . For the parameter set B, any value of  $\tau$  larger than  $\tau_{\text{crit}}$  is expected to be “stable” in the sense that the expected time to extinction approaches infinity. Equation graph is from the dynamic scaling hypothesis (Eq. 1).

The so-called pilot system in this case has been elaborated extensively elsewhere (Vandermeer et al. 2008, Philpott et al. 2009, Perfecto and Vandermeer 2015, Li et al. 2016), whereby the *Azteca* ants that form a spatial patchwork in the system (Fig. 7c) actually restrict the operation of the two predators locally (within a patch of *Azteca*), but also, through their mutualistic effect on the scale insects, supply the source of scale insects that migrate into the empty cells (the coffee plants unaffected by the *Azteca* ants). It is thus ironic that the protectors of a pest (the *Azteca* ants protect the scale insects) are actually the keepers of the source of that pest, but also responsible for the underlying spatial pattern, both of which are necessary to maintain the pest’s natural enemies

over the whole farm. Only a small percentage of shade-trees contain *Azteca* nests, but those are sources of the scales that help maintain the predators over the rest of the farm. Furthermore, the time frame of the systems corresponds qualitatively with the idea of dynamic scaling (Eq. 1). The *Azteca* ants operate on a time scale of from months to years, while the parasitoid and beetle are on a week to month time schedule.

Thus, it is (1) the demographic parameters of the coupled predator/prey systems, (2) the structure of the background habitat, (3) the construction of that structure by a distinct predator/prey system (the pilot system), and (4) the disjoint time frame between the pilot system and the biological control systems, which collectively generate the ultimate result of persistence of the system. This ultimately intuitive structure seems to be responsible for maintaining the control of the potentially important pest, the green coffee scale, in perpetuity. It is ironic that some farmers view the *Azteca* ants as themselves pests since they are mutualistically associated with the scale insects. Yet it is clear from the basic intransitive structures embedded in the system that the *Azteca* ants are crucial for maintaining control over this pest over a large area—a complex web of ecological interactions is thus responsible for control of a pest in one of the most important crops in the world.

There may be a generalization here. That dynamic interactions among organisms can create the habitats in which other organisms exist, a pilot pattern, is certainly not new. For example, in 1926 Tansley and Chipp, noted:

... it is really the whole of the living organisms together, plus the inorganic factors working upon them, which make up... a ‘system’... But such a ‘system’ considered fundamentally... must include the ‘inorganic’ factors of the habitat and these obviously cannot be considered as ‘members’ of the community; and if we take the inorganic factors as external, why not biotic factors such as grazing animals?

and even earlier Darwin’s humblebees found refuge in old mouse nests. More recent literature repeats, in one form or another, a similar idea (e.g., Wu and Loucks 1995, Holt and Keitt 2000), in one case even referring to the cells of the environment being caused by other organisms (Caswell 1978).

While such work treats the issue generally, the notion of a pilot pattern as guiding spatial structure fits in with these basic insights. If grazing animals avoid the edge of a forest for fear of predators lurking there, the grasses they feed on receive a spatial respite. The grasses care not whether the herbivore-free patch is caused by an underlying edaphic factor (inorganic) or by the threat of predators. Thus, the pilot pattern for the grass is caused by the grazing animals and their predators. Our results suggest that, while this framework seems to make sense, at its simplest level there must be some disjunction in the time frame of the pilot system vs. the time frame of the responsive system. If the pattern shifts in the same time scale as the responsive system, it cannot operate as a pilot, at least in our simple model. We propose that this is a general rule.

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Computer code is available here: dougjack. (2018, September 15). dougjack/predPreyInSpace: First release of predPreyInSpace (Version v1.0.0). Zenodo. <https://doi.org/10.5281/zenodo.1419579>.

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