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10 **STABILIZING INTRANSITIVE LOOPS: SELF-ORGANIZED SPATIAL STRUCTURE**

11 **AND DISJOINT TIME FRAMES IN THE COFFEE AGROECOSYSTEM**

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17   John Vandermeer[1,†] and Doug Jackson[2]

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19 [1]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor,

20   Michigan 48109 USA

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22 [2]Eastern Research Group, 110 Hartwell Ave, Lexington, Massachusetts 02421 USA

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25 † E-mail: jvander@umich.edu

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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, 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: intransitive loops, cellular automata, predator/prey, spatial pattern, Turing effects, spatial ecology

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

61   on our qualitative understanding of a particular subcomponent of an ecosystem, the traditional

62   shaded coffee agroecosystem. Our framing differs from previous literature in its qualitative

63   nature based on observations and experiments in this real system over the past 25 years (Perfecto

64   and Vandermeer 2015), combining other well-known theoretical issues into a coherent

65   framework that corresponds to the long-term observable dynamics in this system. The theory is

66   formed from previous literature on (1) intransitive coupled oscillations, (2) spatial dynamics, (3)

67   self-organization of spatial pattern.

68   The coffee agroecosystem is regarded by some as important both for its tractability in

69   ecological study (Perfecto et al. 2008, 2014, Perfecto and Vandermeer 2008) and its socio-

70   economic importance, reported to be one of the most traded commodities in the world

71   (Lashermes et al. 2008), and the base of economic support for 25 million small scale farming

72   families and many national economies (Utting-Chamorro 2005, Talbot 2004). The pest system

73   in coffee is large and highly variable. However, at any one point in space and time it is usually

74   well-defined and less imposing than the 250 potential pests reported for the species (Le Pelley

75   1968). In particular we focus on one distinct pest, the green coffee scale insect *(Coccus viridis).*

76   A coffee bush may be free of the scale insect pest, or it may have populations of that pest on it,

77   or the pest population may be in a state of undergoing attack from the hymenopteran parasitoid,

78   *Coccophagus* sp. The attack of the parasitoid is vigorous locally (i.e., on a single coffee bush)

79   such that all of the scale insects on a given plant are killed rapidly and the parasitoids then

80   emerge and disappear from the plant. In other words, the system moves from empty plant to pest

81   attacking the plant to pest being attacked by parasitoid to empty plant, evidently an intransitive

82   oscillation, as explained below. Clearly such an oscillation can only occur in a spatially extended

83   system since migration of both predator and prey are essential parameters. The qualitative

84   behavior of such a system when extended in space, closely mimics the classical results of

85   standard predator prey theory.

86   The parasitoid *Coccophagus* sp. is thought to be an effective biological control agent of

87   the scale insect. However, an additional control agent, a coccinelid beetle, *Azya orbigera*, is also

88   effective (Vandermeer et al. 2010, Liere and Perfecto 2008). The combination of two control

89   agents (a parasitoid and a predator) acting directly on a prey item in the same space presents us

90   with a classic case of two species occupying the same niche, suggesting Gause's principle may

91   operate. Yet in 25 years of observations at the same site, both parasitoid and predator have

92   remained common in the system. Part of the theory developed here is aimed at proposing how

93   the complexity of spatial structure can explain this fact.

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

95   coffee's origin as an understory plant in the first place. As has been demonstrated (Vandermeer

96   et al. 2008) the shade-tree nesting ant, *Azteca sericeasur*, moves its nest from shade-tree to

97   shade-tree, presumably in response to a fly parasite in the family Phoridae (*Pseudacteon* sp). The

98   ants forage in the nearby coffee bushes (a single nest in a shade tree typically forages on 5–10

99   surrounding coffee plants). Thus, with respect to this ant species, at the level of a given coffee

100   bush there is an expected cycle of coffee bush without ants, which becomes occupied by *Azteca*

101   ants, which get attacked by Phorid flies, which render the bush free of *Azteca* ants—another

102   intransitive loop. This loop actually creates pattern in the background habitat, which, we argue,

103   could form the background pattern necessary for coexistence of the two biological control

104   agents.

105   It is notable that in this particular real-world system there is a mutualistic ant/hemipteran

106   system, the *Azteca* ant and the scale insect, in which the ant forages on the honeydew produced

107   by the scale insect and while doing so attacks the natural enemies of the scale insect, to the

108   mutual benefit of both scale and ant (Jha et al. 2012, Vandermeer and Perfecto 2006). It is thus

109   most natural that farmers view the ant as a pest also. Yet, as we show in this model exercise, it is

110   the spatial extension of the system that allows the two biological control elements to persist in

111   the long run, effecting autonomous biological control over the scale insect over the entire farm,

112   thus sacrificing a small percentage of the farm (from 3 to 7 percent) as effective spatial

113   repositories of the pest, which keeps the biological control agents alive over the entire region.

114   The spatial dynamics of this system can be understood through a three part theoretical

115   framing: (1) the basic nature of spatial predator/prey systems forming intransitive loops, (2)

116   heterogeneity of spatial structure stabilizing a coupled system of predator prey loops, and (3) the

117   self-organization of that spatial structure, through a pilot pattern formation from a distinct

118   species group.

119

120   **The theoretical framing**

121   The existence of intransitive oscillations in competitive communities was noted

122   theoretically in 1975 (May and Leonard 1975) and claimed to be widespread in plant

123   communities in 2015 (Soliveres et al. 2015), although much earlier Gary Polis noted the general

124   existence of what he called "loops," in his Coajilla Desert food web (Polis 1991), clearly

125   referring to their intransitive nature (species 1 beats species 2 which beats species 3 which beats

126   species 1, a structure similar to the children's game of rock, scissors, paper). Although the

127   original analysis of intransitive competition was based on the classical Lotka-Volterra

128   phenomenological competition equations, it is also the case that intransitivity emerges easily

129   when competition is framed mechanistically (i.e., a consumer/resource or predator/prey

130   dynamic), (Durrett and Levin 1994) and the rather large literature on intransitive competition

131   theory (Kerr et al. 2002, Frean and Abraham 2001, Allesina and Levine 2011, Laird and Schamp

132   2006) is not compromised. However, spatially distributed predation may have an intransitive

133   structure in and of itself, if the scale of interaction is sufficiently small such that predator and

134   prey cannot coexist in perpetuity at an individual isolated site. That is, if an empty space is

135   occupied by a prey item which in turn is occupied by a predator of that prey, and if the predator

136   overexploits the prey (which inevitably happens if the local space in which dynamics occur is

137   small), there is a basic intransitive structure—empty, prey, prey/predator, empty. This structure,

138   which undoubtedly is common in nature, we refer to as an intransitive oscillator.

139   For example, the famed Huffaker experiment (Huffaker 1958) is most often cited as an

140   example of how spatial extension can induce stability in a predator-prey system. Oranges

141   provided the substrate for a predator prey pair. Following an individual orange through time, the

142   pattern was consistently one of an empty orange receiving migrating prey individuals, giving rise

143   to an orange containing a population of prey individuals. Subsequently individuals from the

144   predator population arrived, giving rise to an orange containing populations of both prey and

145   predators. The predators quickly eliminated the prey, giving rise to an empty orange again.

146   Thus, on a single orange the pattern through time is (1) empty orange gives rise to (2) orange

147   with a prey population, gives rise to (3) orange with both predator and prey populations, gives

148   rise to (4) an empty orange. As long as there are both prey and predators migrating, this cycle

149   repeats itself as an evident intransitive oscillation. The key result of the experiment is that when

150   a group of oranges is arranged in a spatial pattern, the basic intransitive oscillation creates a

151   sustained oscillation of predator and prey when averaged over the whole array of oranges, even

152   though each individual orange is unstable.

153 Since both classical predator prey theory and this spatial formulation are oscillatory,

154 when two distinct oscillations occur in the same space, they are likely to interact with one

155 another, which is to say be coupled. The vast literature on coupled oscillators thus becomes

156 relevant (Vandermeer 1993, 2004, 2006, Strogatz and Stewart 1993), and questions of

157 coexistence emerge, depending on the nature of the coupling. Specifically, when two predators

158 are coupled through a single prey (two consumers through a single resource), the expectation is

159 that Gause's principle will come into play.

160 An additional feature of the Huffaker study is that the predator prey system induced a spatial

161 structure, wherein distinct patches of prey and predators meander over the space, suggesting that

162 there was something about the pattern or patchyness that is related to the fact that the instability

163 at a small scale became stable at a large scale. Subsequently, a related theoretical literature has

164 evolved, commonly associated with the insights of Alan Turing (1952), in which the prey acts as

165 if it were an activator and the predator a repressor, a metaphorical framing that places the spatial

166 predator prey system in the general category of reaction-diffusion. Initial theoretical

167 explorations (Segel and Jackson 1972, Levin and Segel 1976, Levin 1979) have given rise to

168 what seems like a major generalization in ecology (Vandermeer et al. 2008, Alonso et al. 2002,

169 McGehee and Peacock-Lopez 2005, Bendahmane et al. 2016, Peng and Zhang 2016), that

170 predator prey systems in physical space will tend to form clusters that are Turing-like. This

171 generalization seemingly holds well when the system is cast as a simple intransitive loop, with

172 the additional provision that the spatial structure can form a background pattern that is essential

173 for the persistence of other systems living therein, as described below.

174 Finally, much of the literature on both intransitive cycles and coupled oscillators in space

175 is framed in terms of a regular background, effectively a regular lattice forming the

176 environmental network upon which the population dynamics unfolds. We note first that

177 fundamental questions of coexistence require a patterned background rather than a regular lattice

178 (Horn and MacArthur 1972, Levin 2000), and finally note that a patterned background itself may

179 emerge from independent intransitive oscillators.

180 The rest of this paper is organized as follows: First, we explore the basic dynamics of

181 placing the intransitive cycles in space and coupling them together (in this case the scale insect

182 attacked by the parasitoid and the predator). Second, we explore the nature of the underlying

183 spatial structure and the spatial scale of dispersion scale, casting the problem as a network-

184 transforming issue. Third, we examine the nature of the self-organized pilot pattern formation,

185 in which an additional intransitive oscillator (in this case the ant/phorid predator–prey system)

186 creates the spatial structure on which the original two oscillators can coexist.

187

188 **The dynamics of coupled spatial intransitive oscillators**

189   The green coffee scale insect, *Coccus viridis*, a pest of coffee throughout the world

190 (Coleman and Kannan 1918, LePelley 1968), is one of the key components of this system

191 (Vandermeer et al. 2010, Vandermeer and Perfecto 2006, Perfecto and Vandermeer 2015). It

192 attaches mainly to the midrib of the leaves of coffee trees, penetrating the leaf tissue with a sharp

193 proboscis and sucking material out of the leaf. It is basically sessile as an adult but produces

194 crawlers as juveniles. The crawlers are dispersed by wind and must disperse from leaf to leaf on

195 a tree and from plant to plant on a larger scale, plausibly on a regular lattice pattern, but more

196 often than not in a non-random clustered pattern, depending on the spatial nature of the coffee

197 plantings. A well-known parasitoid on the scale is a wasp, *Coccophagus* sp. (Mani et al. 2008).

198 The idealized version of the system is, at the level of an individual plant (1) an individual plant

199 without scales is (2) infested by the crawler stage of the *Coccus viridis* and rapidly forms local

200 populations on the plant, which (3) attracts the parasitoid *Coccophagus* sp. which eliminates it

201 from the plant, rendering the plant free of scales once again. More generally, an empty site is

202 colonized by a prey item which is subsequently colonized by a predator item which eliminates it,

203 thus returning the site to an empty state (as outlined in figure 1).
204

205   We model this basic system as a cellular automaton. Consider a nxn lattice with three

206 variables, S (for empty space), P (for predator and prey together) and V (for prey or victim

207 alone), all of which are binary, and $k_i(x,y)$ is a binary number indicating presence or absence of

208 the ith variable at the point $\{x,y\}$. The number of each of the variables in the Moore

209 neighborhood (the surrounding eight cells) is given as,

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

210   where i = S, P, or V and M indicates summation in the Moore neighborhood around the point

211    $\{x,y\}$. Thus, for example, $N_S(x,y)$ is the number of empty cells in the Moore neighborhood

212   around point x,y. The transformation rules for each lattice cell are as follows:

213

214   S changes to V with probability $mN_V/8$

215   V changes to P with probability $aN_P/8$

216   P changes to S with probability d

217

218   The parameters m, a and d have clear biological meanings: m = migration rate of the prey, a =

219   migration rate of the predator, and d = feeding rate of the predator (visualized in Figure 1).

220   Over the whole lattice we expect qualitative results that are likely to result from simple

221   quasi-quantitative reasoning (and correspond to classical results): (1) if the predator's death rate

222   is extremely low but its attack rate is extremely high, we expect that the predator will eliminate

223   all prey and then itself go extinct from a lack of food, thus the elimination of the entire system

224   (the takeover by empty spaces); (2) if the predator death rate is extremely high and the attack rate

225   extremely low, the predator will be eliminated from the system and the prey increase to take over

226   the entire lattice (approach its carrying capacity); (3) with intermediate values of predator attack

227   and death rates, the system will be maintained, as an intransitive loop in space. The detailed

228   nature of these three outcomes will depend on parameter values, but it is worth emphasizing that

229   the overall average behavior of the system is expected to mirror the classical results of predator

230   prey theory. Results from simple simulations on a 100×100 lattice are presented in Figure 2.

231   The nature of the coexistence parameter space is complicated but intuitive and simple

232   simulations reveal a host of potentially interesting temporal behaviors and spatial patterns on the

233   lattice. However, there is an interesting generalization that can be gleaned from Figure 2. Taking

234   prey migration rate as a tuning parameter, whence the overall behavior of the system is complete

235   extinction of the whole system when the prey migration is too low (that which would happen if

236   the parameter were to the left of the left hand panel of Figure 2) ranging to complete coexistence

237   of both predator and prey (that which would happen if the parameter were to the right of the right

238   hand panel of Figure 2). Between these two predictable circumstances, the system will be more

239   unpredictable, yet with a clear statistical pattern, as illustrated in Figure 2. If either of the other

240   two parameters are taken as tuning parameters, the qualitative results are equally intuitively

241   obvious. And if we construct a parameter that simultaneously increases predator attack rate while

242   decreasing predator death rate, the system will go from complete elimination of the predator and

243   persistence of the prey over the whole lattice to a state of emptiness (neither predator nor prey

244   survive and the whole lattice is empty). In all of these qualitative observations it is important to

245   note that the three-element persistent solution is always an intransitive loop.

246   Corresponding to the framework we seek to study (coupled intransitive oscillators) the

247   green scale insect has another important predator, a lady beetle, *Azya orbigera*. It is qualitatively

248   clear, if difficult to measure quantitatively, that the lady beetle and the parasitoid have different

249   dispersal qualities and different attack rate properties (Liere et al. 2012, Jha et al. 2012), yet the

250   basic idea of the two together corresponds to the theoretical structure of coupled oscillators

251   (Figure 3), a framework that has given rise to a substantial literature (Vandermeer 1993, 2004,

252   2006, Strogatz and Stewart 1993). In accord with this recent literature it is of interest to query the

253   current framework with respect to a second predator in the system, effectively a situation of

254   competition with the two predators seeking sustenance from the same food source, and

255   conceptually fitting into the category of a system of coupled oscillators. The two predators are,

256   structurally, in competition with one another.

257

258   Thus, expanding the original model, we have,

259

260   S changes to V with probability $m\mathrm{N_V}/8$

261   V changes to P_1 with probability $a_1\mathrm{N_{P_1}}/8$

262   V changes to P_2 with probability $a_2\mathrm{N_{P_2}}/8$

263   P_1 changes to S with probability d_1

264   P_2 changes to S with probability d_2

265

266   as the fundamental model (illustrated in Figure 3). However, in running the model there is

267   another emergent state, P_1P_2. So as to avoid an unnecessary additional time step, we transform

268   P_1P_2 to S during the same time step (i.e., the rule $P_1P_2 \rightarrow P_1$ with probability $\square$ and $P_1P_2 \rightarrow P_2$

269   with probability $1 - \square\square$ generates what is effectively a new nonlinear element into the model

270   which mitigates against the simplicity of the original formulation, adding an additional

271   parameter, p_1).

272   Extensive simulations support what we believe is intuitive, that P_1 and P_2 should form a

273   kind of stochastic extinction in this system. That is, the long-term coexistence of P_1 and P_2 is not

274   possible, regardless the values of the tuning parameters (if □is added as an additional parameter

275   (see discussion in previous paragraph), there are knife-edge sections of the parameter space that

276   allow for coexistence—we ignore those situations as probably uninteresting). Similar

277   formulations in the literature generate identical results (e.g., Frean and Abraham 2001), which

278   reflect the classic notion of Gause's principle.

279   Strict cellular automata rules are quite restrictive when a second predator is added,

280   especially in the light of the much-discussed competition/migration tradeoff. That is, the need for

281   only local interactions (any given cell receives migrants only from its immediate neighbor cells),

282   mitigates against a framework in which either predator or prey can engage in long distance

283   migration, even though local parameters are tunable. This restriction can be seen as an obvious

284   mechanism of why the two predators are unable to coexist, sort of a spatial form of Gause's

285   exclusion principle. And it is also the case that creating a situation where one predator is a poor

286   feeder but migrates rapidly, while the other predator is a poor migrator but feeds rapidly (in

287   search for the ecologically proverbial tradeoff), does not dampen the apparent result that the two

288   predators will not coexist except at knife edge sections of parameter space, (structurally similar

289   to the famous survival of the weakest , in which a genotype of a weaker competitor will exclude

290   the genotype of a stronger competitor due to spatial constraints; Frean and Abraham 2001).

291   However, this result depends on what we argue is an overly restrictive constraint on the

292   background habitat—that it is a regular network (Newman 2010).

293

294   **The structure of the background habitat**

295   A convenient tool for examination of underlying geometry, without imposing strict point-to-

296   point dynamics, is found in the burgeoning field of network theory. Indeed, if the probability of

297   migration as a function of distance is strongly convex (in the sense that probability is close to 1.0

298   for close distances and falls rapidly towards zero at some critical distance), we can think of the

299   geometric space as a network. The coffee plants are nodes and any pair of plants closer than the

300   critical distance is connected by an edge. The background on which the dynamic process

301   operates is thus a formal network with nodes and edges. In the real system, although plants may

302   be concentrated in rows, or on hillside contours, in more traditional systems they frequently seem

303   more like a natural plant population. That is, the distribution of plants on the ground is far from a

304   regular lattice, even though such a planting pattern may have been the original intent of the

305   farmer. In Figure 4 we show the distribution of coffee bushes in a small (20×20 m) plot, in

306   southwestern Chiapas, Mexico, illustrating the combination of regularity (from the original

307   intention of the farmer in planting the bushes) plus irregularity (from random deaths and

308   subsequent replanting). Thus, we have a network that could be ideally considered a regular

309   lattice, although its deviation from regularity suggests other idealizations could be possible, as

310   discussed later. The dynamics of the scale insect population and its predators operates on a

311   network like this.

312   It is reasonable to suggest that the background habitat is viewed differently by the three

313   players in our real world system. For example, the parasitoids are likely to disperse locally and

314   build up high population densities locally (Comption, 2002). The beetles, however, fly actively

315   and are known to disperse widely (Liere et al. 2012). It might then be reasonable to suggest that

316   the parasitoids are local dispersers and view the habitat as a lattice (perhaps with some of the

317   nodes clustered), while the beetles, flying widely searching for scale insects, view the habitat

318   differently. While many spatial models in ecology presume a regular Euclidean space as the

319   underlying spatial geometry, the geometry faced by most systems in nature does not conform to

320   this idealization. The migration distance and/or the geometric position of occupation sites may

321   alter the dynamic rules. For example, if one of the predators is a long-distance migrator, that

322   effectively changes the regular lattice network to what is effectively a small world network.

323   Similarly, if nodes are clustered in space, or the rules of migration effectively make them so, the

324   background habitat is a clustered distribution (which may or may not be scale-free, i.e., the

325   distribution of number of connections per node may or may not be a power function). Although

326   other framings are possible, we find it convenient to begin with a regular lattice and consider

327   modifications in (1) physical positions of the nodes (habitat spaces), and (2) local versus long

328   distance connections (small world structure). We summarize our categorization scheme in Figure

329   5.

330   With this framing we note that the failure of the dispersal/competition tradeoff paradigm

331   to stabilize the system (make it persistent) takes on a slightly more complicated form. As noted

332   above, with a simple modification of the rates of migration and attack rates of the two predators

333   in the simple CA model it is not possible to maintain both predators in the system. In the context

334   of our actual system, we examine the consequences of assuming one predator operates on a strict

335   lattice structure (as we expect of the parasitoid in the running example) while the other exists on

336   a small world network, resulting from its long distance dispersal (as we expect of the beetle

337   predator in our running example). Thus, our framework generates a system structured such that a

338   clustered lattice underlays the dynamics of one species (i.e., Figure 5c), while a clustered small

339   world pattern underlays the dynamics of the other species (i.e., Figure 5d). With proper

340   parameter settings it is evident that both intransitive loops could coexist in perpetuity, an

341   expectation that is revealed in simple simulations (e.g., Figure 6).

342

343   **Self-organized structure of the background habitat**

344

345   Extensive simulations repeat the pattern shown in Figure 6, namely, on a regular lattice

346   with or without small-world connections the two species are unable to persist together, but on a

347   clustered lattice with small world connections there are extensive areas of parameter space that

348   permit coexistence, apparently in perpetuity. The coexistence arrives through the standard

349   mechanism of a tradeoff between dispersal and competition (Levins and Culver 1971, Cadotte et

350   al. 2006), with the strong competitor (low predator dispersal rate and high attack rate)

351   dominating the larger clusters of available sites while the strong disperser (low predator attack

352   rate and high dispersal rate) dominates the smaller isolated available sites. Thus we see the

353   coupled intransitive loops reflect the underlying structure assumed to exist regularly in both

354   theory and in real systems.

355   There is another intransitive loop in the system. Most farms are managed with shade trees

356   above the coffee bushes. As noted above, the arboreal *Azteca* ant locates its nesting sites in those

357   shade trees, and forages on the nearby coffee trees. As its colony grows, it buds, forming new

358   colonies in nearby shade trees, thus forming clusters of nests (Vandermeer et al. 2010, Jackson et

359   al. 2014). But the ant is attacked by a parasitic fly (*Pseudacteon* spp.) that effectively causes the

360   clusters of nests to disappear (either all nests in the cluster are moved far away or they die).

361   Thus, we have the intransitive loop of (1) empty coffee bush is found by (2) an *Azteca* colony

362   (nesting in a nearby shade tree), which ultimately is (3) attacked by the fly parasitoid, eventually

363   abandoning its nesting site (or dying). As argued elsewhere (Vandermeer et al. 2008), this

364   system is similar to the classic Turing mechanism in that the phorid acts as a repressor and the

365 ant, by moving its nests and occupying other trees, is the activator, with the whole system

366 operating on the background network of shade trees that are potential sites for the ant nests. This

367 Turing-like mechanism creates clusters of nests in an otherwise relatively uniform environment

368 (Figure 7). Most importantly, as noted elsewhere (Jackson et al. 2014), any other organisms that

369 use the ant nests as background habitat will respond to particular critical distances according to

370 their own biological properties.

371   Thus, the basic intransitive spatial structure of the *Azteca* ant, the phorid fly and the

372 empty trees gives rise to clustering in space, and each cluster of ant nests represents a connected

373 component in the context of network theory. The dependence of the scale/parasitoid complex on

374 this structure represents a spatial structure created by one system (the *Azteca*/Phorid system) in

375 which the other system (the scale/parasitoid/beetle system) is forced to exist. Yet in another

376 sense, the system is composed of three coupled intransitive loops as illustrated in figure 8 -- the

377 empty site may be (1) occupied by the scale insect (the prey), and then attacked by the wasp

378 (predator 1), or (2) occupied by the scale insect (the prey), and then attacked by the beetle

379 (predator 2), or (3) occupied by the Azteca ants (alternative prey) and then attacked by the phorid

380 parasitoid (alternative predator).

381   The scale insect is strongly influenced by the *Azteca* ant (the alternative prey of figure 8),

382 a major element in this system, extensively studied earlier (Vandermeer et al. 2010). The ant

383 makes its nests in the shade trees in coffee farms and tends scales on the nearby coffee bushes,

384 which is to say prevents the two predators from attacking the scale insects. Thus, there are

385 alternative effective habitats in which the scale insect may occur: (1) coffee trees associated with

386 a nest of the ant, *A. sericeasur*, and (2) coffee trees not associated with the ant—either of the

387 predators have complete access to the scale insects in those areas in which the ants are absent,

388 but greatly reduced access when the ants are present. Consequently, the ants occupying shade

389 trees effectively create a network on which the two natural enemy systems must operate, that is,

390 all the area in the coffee farm that is without ant nests. For this reason we add a third intransitive

391 loop to the system (Figure 8), the ant/phorid system. Note that one of the intransitive loops (the

392 alternative prey/alternative predator loop of Figure 8), through the Turing mechanism

393 (Vandermeer et al. 2008) forms the clustered spatial pattern in which the other two predators

394 must exist, thus creating a basic self-organizing process whereby the system as a whole may

395 persist.

396   Expanding the basic CA model to include this third loop, we have two new variables, A =

397   occupied by Azteca ants, and P3, occupied by Azteca ants and their parasitic phorid flies, and the

398   CA model becomes,

399   S changes to V with probability $m_1 N_V/8$

400   V changes to P_1 with probability $a_1 N_{P1}/8$

401   V changes to P_2 with probability $a_2 N_{P2}/8$

402   P_1 changes to S with probability d_1

403   P_2 changes to S with probability d_2

404   S changes to A with probability $m_2 N_A/8$

405   A changes to P_3 with probability $a_3 P_3/8$

406   P3 changes to S with probability d_3

407

408   There is an inherent conflict in the structure of the system regarding the switch from S to V

409   versus the switch from S to A. In this model we first consider the S to A switch, which, if it

410   happens, makes the cell unavailable for the S to V switch.

411   The subcomponent of this model that includes only the loop, S to A to P_3, is similar to

412   the model we studied earlier, and results in spatial clusters of ant nests on the grid. Thus this

413   third loop is expected to create a spatial pattern within which the first two loops (S, V, P_1 and

414   S,V,P_2) exist, what we call a "pilot pattern" (taking a very approximate metaphorical clue from

415   so-called pilot wave theory of particle physics, e.g., Valentini 2010) that will permit the

416   coexistence of the other two predators and their intransitive loops, much like the fixed clusters

417   did, as, for example, Figure 6b. However, it is evident that the pilot pattern created by this third

418   loop can take a variety of forms, three examples of which are illustrated in Figure 9. Note that

419   the clusters where the other two loops must exist are the open spaces.

420   If the spatial pattern formed by the pattern-forming intransitive loop (the pilot

421   intransitivity) were to remain constant, clearly that would be no different than fixing an arbitrary

422   background as we did in the case of Figure 6b. With a completely connected network (e.g.,

423   Figure 9a), as already mentioned, the background is essentially a single background habitat and

424   the results reported above are repeated (i.e., extinction of one of the original predators). With an

425   unconnected patchy network (e.g., Figure 9b), the big patches favor the non-dispersing predator

426   and the small patches favor the dispersing predator, and for many parameter combinations we

427 should expect the two predators will coexist (as happened above with the fixed spatial pattern).

428 However, extensive simulations with this situation show that coexistence of the original two

429 predators is impossible. When the generated pilot pattern is continually changing, the system

430 effectively merges all the patches stochastically, and the average over time essentially becomes a

431 single patch.

432   Thus, we see that as long as the constructed spatial system of permitted sites is not a

433 completely connected network (e.g., if it is as in Figure 9b), and as long as the pattern is fixed,

434 coexistence is possible (e.g., Figure 6b). But with a dynamic system, even though seemingly

435 favorable patchiness is created by the third (pilot pattern) loop, coexistence is impossible (data

436 not shown). Thus, at one extreme, if the system that generates the pattern (the alternative

437 prey/alternative predator; Figure 8) operates at the same temporal scale as the original coupled

438 system (prey/predator 1/predator 2), coexistence is impossible, but at the other extreme, if the

439 temporal scale is very long (i.e., the constructed pattern is constant), coexistence is common. The

440 question thus arises as to what happens at intermediate temporal scales.

441   Let the temporal scale of the constructing system be $\Box$. If $\tau \to \infty$ the constructed space is

442 fixed for the original coupled system, whereas if $\Box = 1$, the constructing system has the same

443 time scale as the original coupled system. So, with $\tau \to \infty$ the background system is constant and

444 the two predators coexist (with proper parameter values, e.g., Figure 6b). If $\Box = 1$, the

445 background system changes at the same rate as the original coupled system changes and

446 effectively creates a single average environment, leading to the inevitable extinction of one or

447 the other predators (data not shown). Clearly a value of $\Box > 1$ but $< \infty$ can result in either result

448 and we can imagine a critical value, $\Box_{crit}$, above which the original coupled two predator system

449 will persist in perpetuity and below which competitive exclusion will result. Several relevant

450 time series are illustrated in Figure 10 and snapshots of one of the spatial patterns that emerges

451 when $\Box > \Box_{crit}$ is illustrated in Figure 11.

452

453   Thus, a clustered spatial structure created by an independent intransitive loop can create

454 persistence of a distinct set of coupled intransitive loops, but only if the former has a disjointed

455 time frame, that is, only if the pilot pattern-forming loop operates in a longer time frame than the

456 coupled system living in that spatial structure. There are parameter combinations where the

457 relationship between the time frame difference ($\Box$) seems to form a proportional relationship to

458   the time to extinction (T) estimate (Figure 12), but other combinations where there is an

459   accelerating relationship between □and T (Figure 12). Most importantly, there seems to be some

460   parameter combinations for which the function that relates T to □□ diverges at some critical

461   □□ (□$_{\text{crit}}$), as illustrated in Figure 12. It is also the case that the time to extinction scales as the

462   inverse of the critical point, which is to say, the equation,

463

464    $$T = \frac{f}{\left(1 - \frac{K(a-b)}{m}\right)^{z}}$$ 1

465

466   describes well the time to extinction (T) relative to the scaling parameter (*f*) and the critical

467   exponent (*z*), according to the dynamic scaling hypothesis (Djurberg et al. 1997).

468

469   **Conclusion**

470   Herein we argue that a spatially explicit intransitive system consisting of empty cell

471   giving rise to cell with prey giving rise to cell with prey/predator giving rise to empty cell is a

472   good model for at least the system we model here, the pest system of a Mexican coffee

473   agroecosystem. For the actual system being modelled, the prey is a pest species, the green coffee

474   scale insect. There are two predators, a wasp parasitoid and a beetle, and coupling them together

475   creates a situation in which, theoretically, coexistence is impossible. We note that the general

476   qualitative framing here is hard to ignore as basically identical to the operation of the system in

477   nature (individual coffee trees that get attacked by scale insects, but then the scale insects are

478   attacked by both of these biological control agents). Yet our generalization that such a coupled

479   intransitive system cannot persist is inconsistent with the clear observations in nature over the

480   past 20 years that both of these biological control agents persist in the system, indeed are

481   responsible for maintaining this pest below significant damage thresholds (Vandermeer et al.

482   2010). Adding the underlying non-regular pattern of the cells in the system (the coffee bushes on

483   the farm), enables the co-persistence of the two biological control agents. But that underlying

484   spatial pattern is itself a consequence of a distinct intransitive oscillator, what we call the pilot

485   system. As noted by Barabás (personal communication), this metaphor is perhaps stretched, in

486   that the system forming the pattern is doing nothing more than that. To liken it to the dynamic

487   process in the De Broglie-Bohm theory is certainly very approximate, yet the underlying

488   consequences of both the original pilot wave and our pilot pattern are similar and we argue that

489   this approximate metaphor is potentially useful.

490   The so-called pilot system in this case has been elaborated extensively elsewhere (Li et

491   al. 2016, Philpott et al. 2009, Vandermeer et al. 2008, Perfecto and Vandermeer 2015), whereby

492   the *Azteca* ants that form a spatial patchwork in the system (Figure 7c) actually restrict the

493   operation of the two predators locally (within a patch of *Azteca*), but also, through their

494   mutualistic effect on the scale insects, supply the source of scale insects that migrate into the

495   empty cells (the coffee plants unaffected by the *Azteca* ants). It is thus ironic that the protectors

496   of a pest (the *Azteca* ants protect the scale insects) are actually the keepers of the source of that

497   pest, but also responsible for the underlying spatial pattern, both of which are necessary to

498   maintain the pest's natural enemies over the whole farm. Only a small percentage of shade trees

499   contain *Azteca* nests, but those are sources of the scales that help maintain the predators over the

500   rest of the farm. Furthermore, the time frame of the systems corresponds qualitatively with the

501   idea of dynamic scaling (Eq. 1). The *Azteca* ants operate on a time scale of from months to

502   years, while the parasitoid and beetle are on a week to month time schedule.

503   Thus, it is (1) the demographic parameters of the coupled predator/prey systems, (2) the

504   structure of the background habitat, (3) the construction of that structure by a distinct

505   predator/prey system (the pilot system), and (4) the disjoint time frame between the pilot system

506   and the biological control systems, which collectively generate the ultimate result of persistence

507   of the system. This ultimately intuitive structure seems to be responsible for maintaining the

508   control of the potentially important pest, the green coffee scale, in perpetuity. It is ironic that

509   some farmers view the *Azteca* ants as themselves pests since they are mutualistically associated

510   with the scale insects. Yet it is clear from the basic intransitive structures embedded in the

511   system that the *Azteca* ants are crucial for maintaining control over this pest over a large area—a

512   complex web of ecological interactions is thus responsible for control of a pest in one of the most

513   important crops in the world.

514   There may be a generalization here. That dynamic interactions among organisms can

515   create the habitats in which other organisms exist, a pilot pattern, is certainly not new. For

516   example, in 1926 Tansley and Chipp noted:

517   ". . . it is really the whole of the living organisms together, plus the inorganic factors

518   working upon them, which make up, . . . a 'system' . . . But such a 'system' considered

519   fundamentally . . . must include the 'inorganic' factors of the habitat and these obviously

520   cannot be considered as 'members' of the community; and if we take the inorganic factors

521   as external, why not biotic factors such as grazing animals?"

522 and even earlier Darwin's humblebees found refuge in old mouse nests. More recent literature

523 repeats, in one form or another, a similar idea (e.g., Wu and Loucks 1995, Holt and Keitt 2000),

524 in one case even referring to the cells of the environment being caused by other organisms

525 (Caswell 1978).

526   While such work treats the issue generally, the notion of a pilot pattern as guiding spatial

527 structure fits in with these basic insights. If grazing animals avoid the edge of a forest for fear of

528 predators lurking there, the grasses they feed on receive a spatial respite. The grasses care not

529 whether the herbivore-free patch is caused by an underlying edaphic factor (inorganic) or by the

530 threat of predators. Thus, the pilot pattern for the grass is caused by the grazing animals and their

531 predators. Our results suggest that, while this framework seems to make sense, at its simplest

532 level there must be some disjunction in the time frame of the pilot system versus the time frame

533 of the responsive system. If the pattern shifts in the same time scale as the responsive system, it

534 cannot operate as a pilot, at least in our simple model. We propose that this is a general rule.

535

536 **Acknowledgments**

540

541

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674   **Figure legends**

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

676   Figure 2. Parameter space study of long term outcome of cellular automata model, plotting

677   predator attack rate (abscissa) versus predator death rate (ordinate), with proportional bubbles

678   representing coexistence (prey/pred), or predator extinction and prey survival (prey=K) or

679   extinction of the whole system (empty). Axes on each graph range from 0 to 1.

680   Figure 3. Coupling two intransitive loops.

681   Figure 4. Distribution of coffee trees on a 20×20 m plot in Mexico, illustrating both the original

682   intention of planting trees in rows, but, because of deaths and replanting, also the non-regular

683   nature of the distribution.

684   Figure 5. The four qualitatively distinct network structures considered. (a) A regular lattice

685   where the small circles are the habitats which the predators and prey may occupy (coffee bushes

686   in the present context), and the connections represent the possible migration pathways. (b) The

687 regular lattice in (a) with two connections randomly broken and randomly reattached, creating a

688 small world structure. (c) A clustered pattern of habitats. (d) The same clustered pattern in (c) but

689 with a random two connections broken and randomly reattached to create a clustered small world

690 spatial pattern. In all cases there are 25 nodes (coffee bushes) and 40 connections (dispersal

691 pathways).

692 Figure 6. Exemplary simulation results on a regular 100×100 lattice with one predator a long

693 distance migrator (Predator 2) and the other a strong competitor (Predator 1). (a) On a regular

694 lattice, one of the predators always goes extinct (which one depends on parameters), regardless

695 of the parameter tradeoff of dispersion versus competition. (b) With a fixed non-random

696 background habitat representing a clustered small world habitat (as in Figure 5d), a variety of

697 parameter combinations allows for such coexistence.

698 Figure 7. Three snapshots of a 45 hectare plot in a Mexican coffee farm. (a) theoretical

699 distribution of 6,700 trees arranged in a regular lattice, as would be (and was) the underlying

700 assumption from a simple cellular automata model of the system. (b) the actual distribution of

701 shade trees (about 6,700) on the farm in 2014, showing the obvious deviation from the regular

702 lattice. (c) the distribution of shade trees that contained Azteca nests in 2014, illustrating the

703 clustered nature of the nest distribution.

704 Figure 8. The three connected intransitive loops with alternative prey.

705 Figure 9. Examples of the structure generated by the empty space/prey/predator intransitive loop,

706 where the empty patches are the constructed habitat created for the original coupled intransitive

707 loop system. (a) Large patches at a parameter setting with a spanning cluster (of white) and a

708 completely connected network (of white), effectively creating a single patch and the effective

709 structure of a simple lattice. (b) More constrained patches where both large and small patches

710 exist, creating the background for a sustained coexistence of both original intransitive loops,

711 where one predator is a good competitor and the other a good disperser, just on the boarder of a

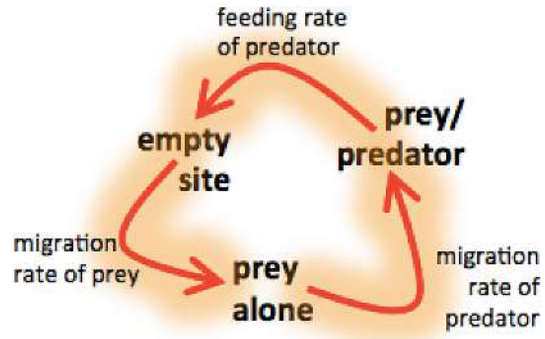712 spanning cluster. (c) Highly isolated patches.

713 Figure 10 . Exemplary time series of predators with the dispersion/consumption tradeoff, with

714 the Azteca/Phorid system creating pattern. (a) illustration of the operation of the Azteca/Phorid

715 system for the first 50 time steps with the resulting spatial structure remaining constant after that

716 point. Note the persistence of both predators in the system. (b) same as a, but the Azteca/Phorid

717 system remaining in the dynamic structure throughout. Note the extinction of predator 1 at time
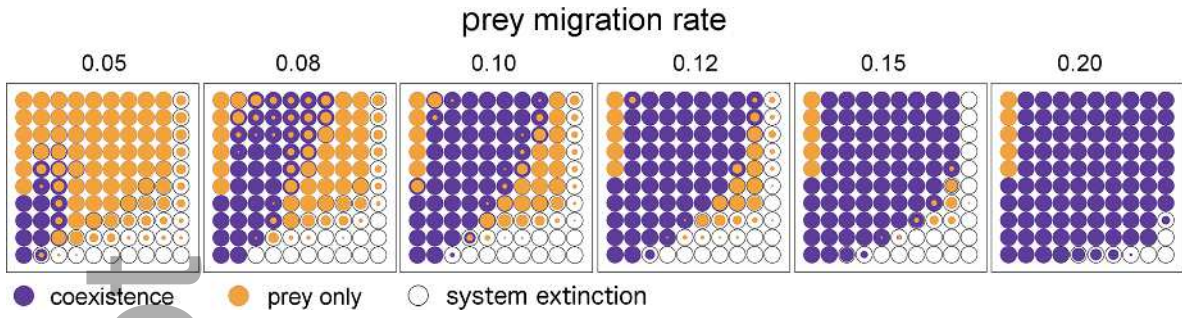
718   step 100. (c) four examples of the parameter □, illustrating the persistence of the system for □=

719   10 and above. Note how the dynamic pattern of both predators reflects the particular value of □.

720   Figure 11. Spatial structure emerging from three interpenetrating intransitive loops, where prey 2

721   and predator 3 (coupled with empty sites), are the members of the intransitive loop that provides

722   the pilot pattern in which the other two intransitive loops live. (Parameter set is the same as

723   parameter set b in figure 9, with □ = 25).

724   Figure 12. Time to extinction versus □ on a 100×100 lattice□. Open symbols for parameter

725   set A, Closed symbols for parameter set B. Note the open symbols follow a linear relationship

726   with □, (line is best fit linear least squares regression), while the closed circles fit well the

727   equation $T = 146.77/(1-\square\square_{crit})^{4.209}$ where the divergence is $\square_{crit} = 25.15$. For the parameter set

728   B, any value of □ larger than $\square_{crit}$ is expected to be "stable" in the sense that the expected time

729   to extinction approaches infinity. Equation graph is from the dynamic scaling hypothesis (Eq. 1).

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prey migration rate

0.05   0.08   0.10   0.12   0.15   0.20
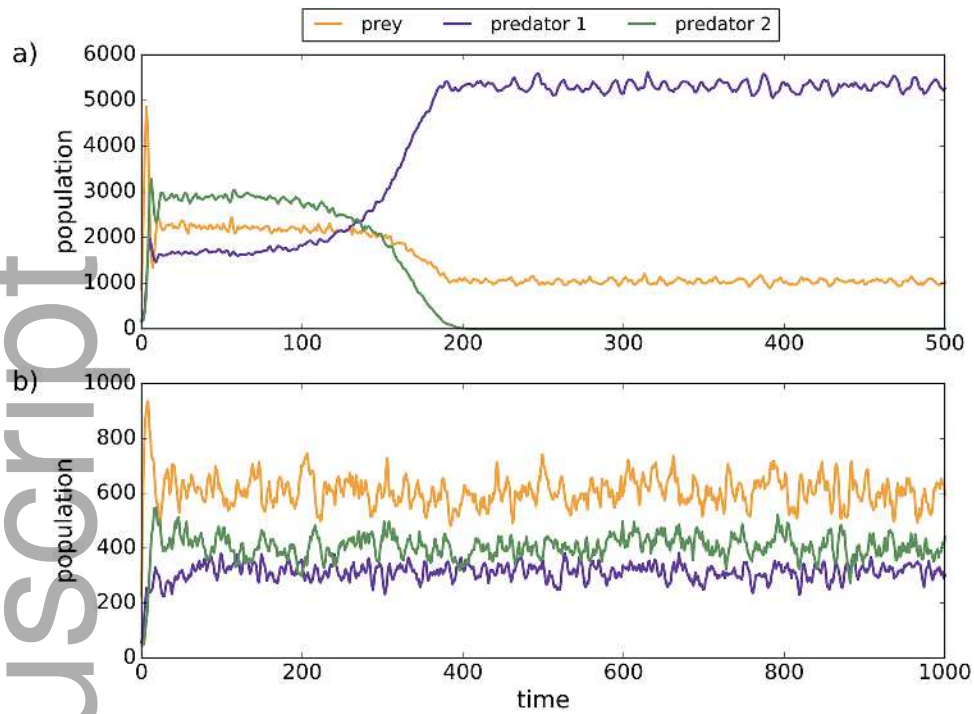
● coexistence   ● prey only   ○ system extinction
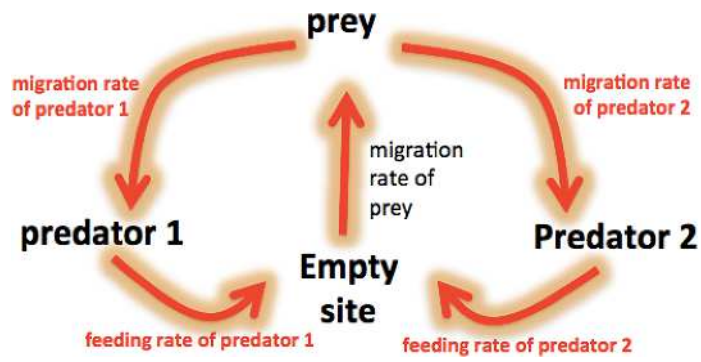
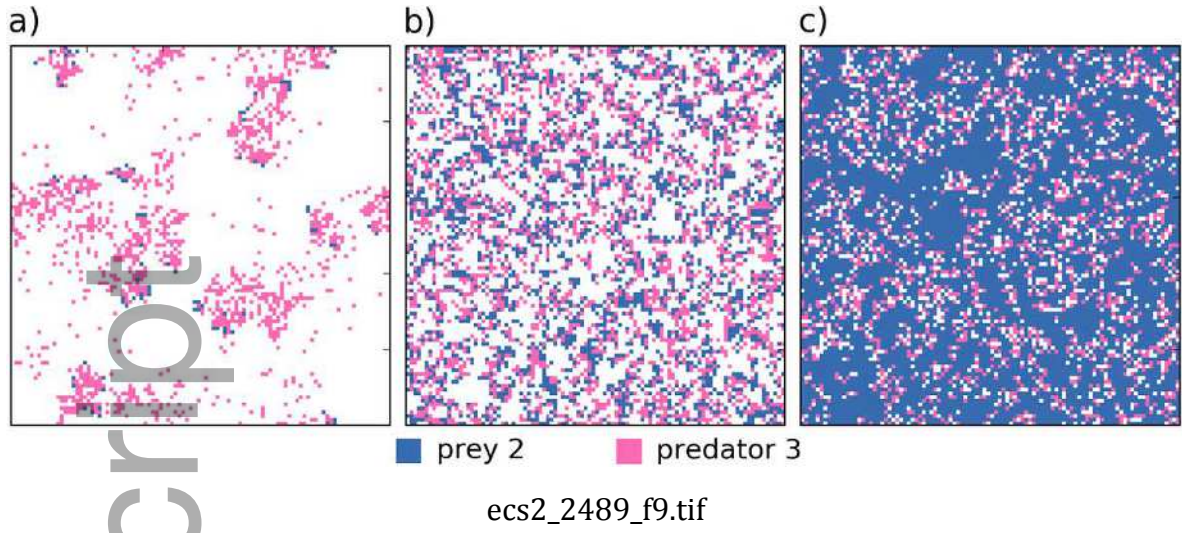ecs2_2489_f2.tif

ecs2_2489_f3.tif
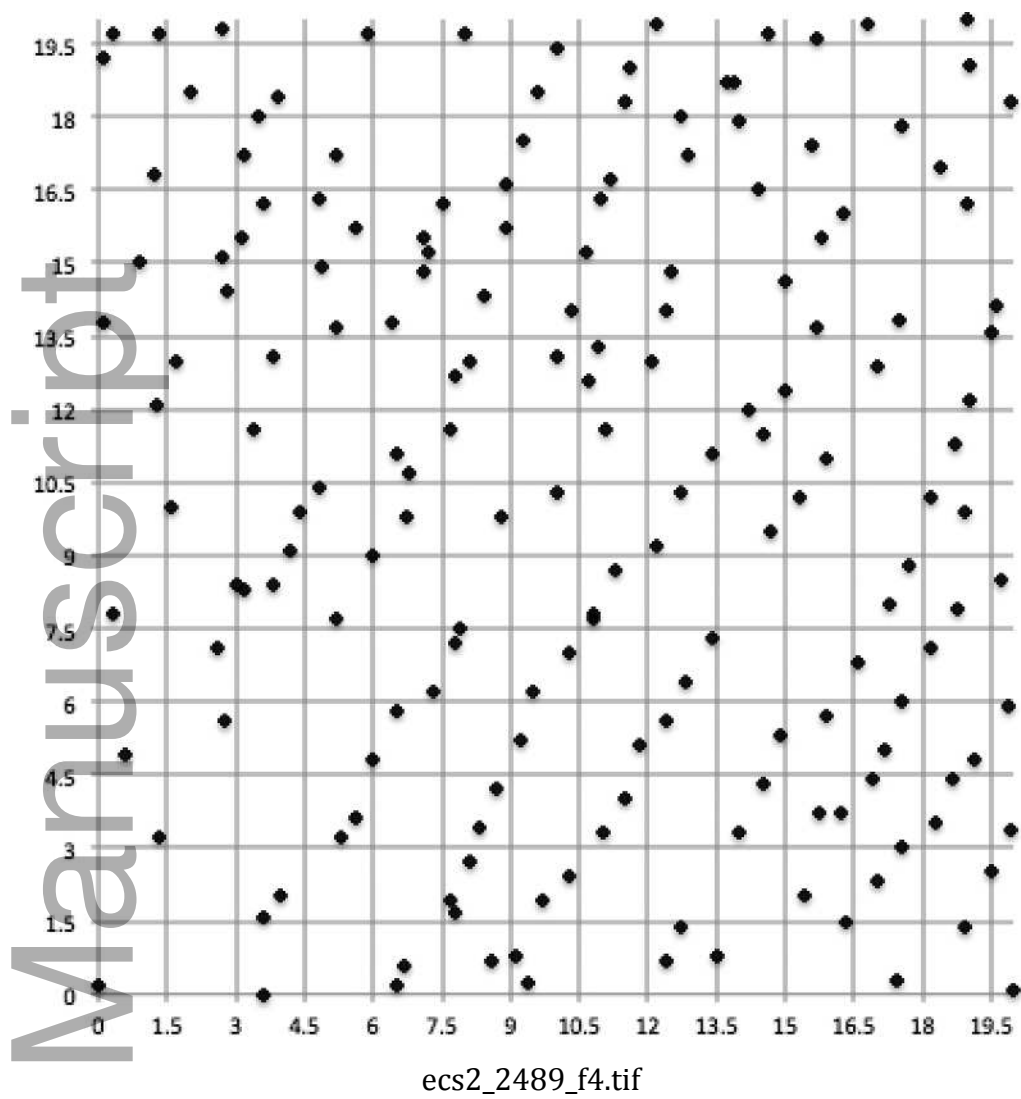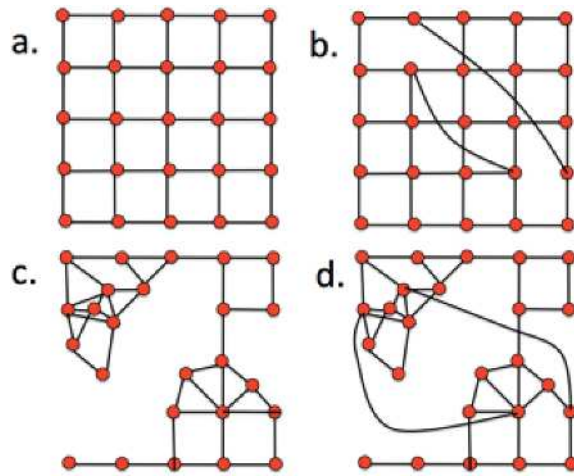
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ecs2_2489_f5.tif

ecs2_2489_f6.tif
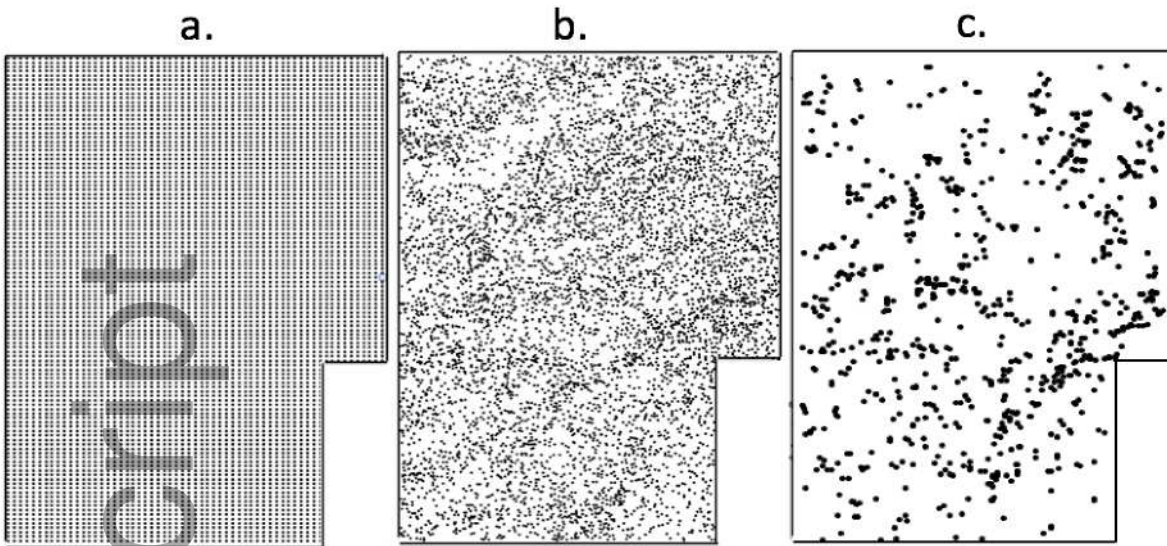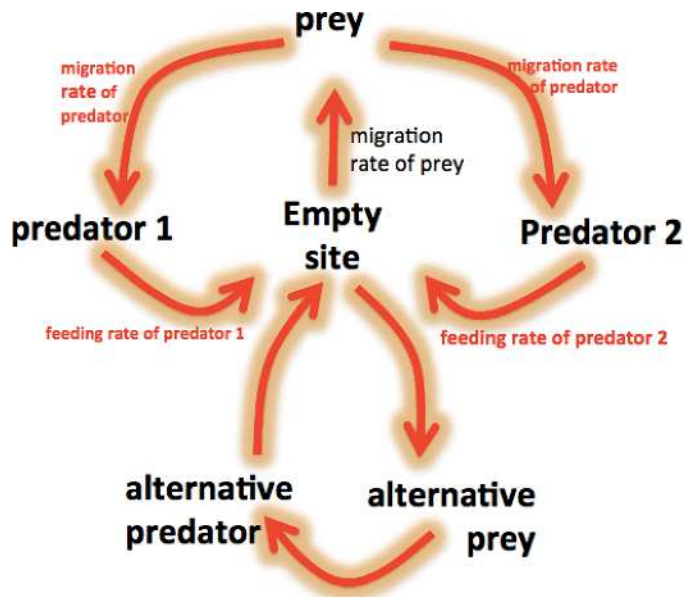
a.   b.   c.

ecs2_2489_f7.tif

ecs2_2489_f8.tif

a) b) c)

prey 2   predator 3

ecs2_2489_f9.tif

Legend: prey 1, predator 1, predator 2, prey 2, predator 3

a) $\tau = \infty$

b) $\tau = 1$

c) $\tau = 2$

$\tau = 10$
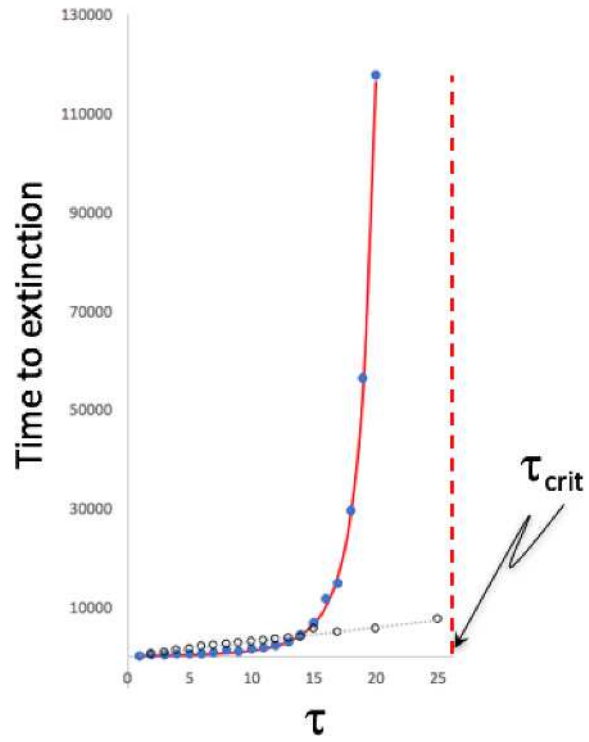
$\tau = 50$

$\tau = 100$

| 100 x 100 | 200 x 200 | 800 x 800 |
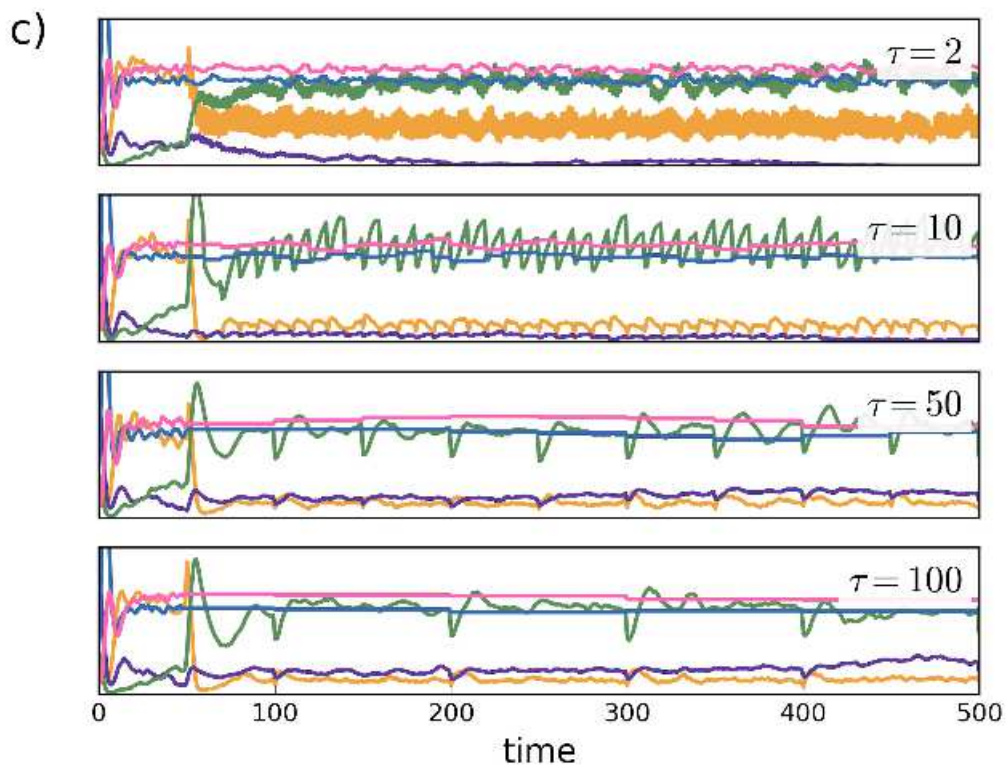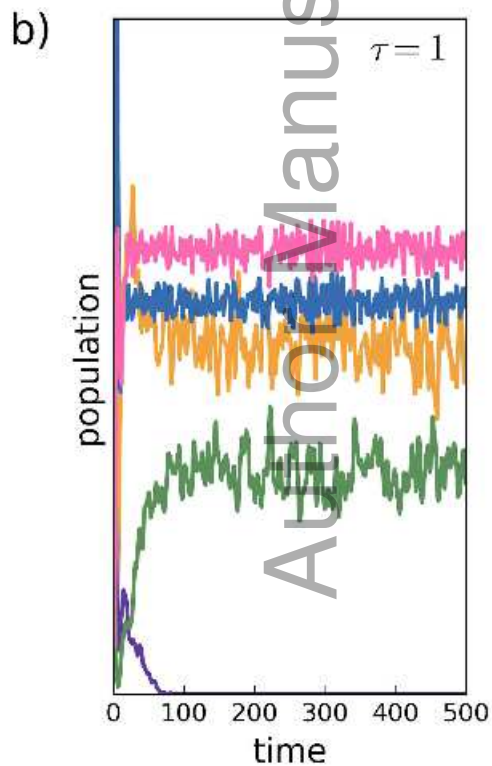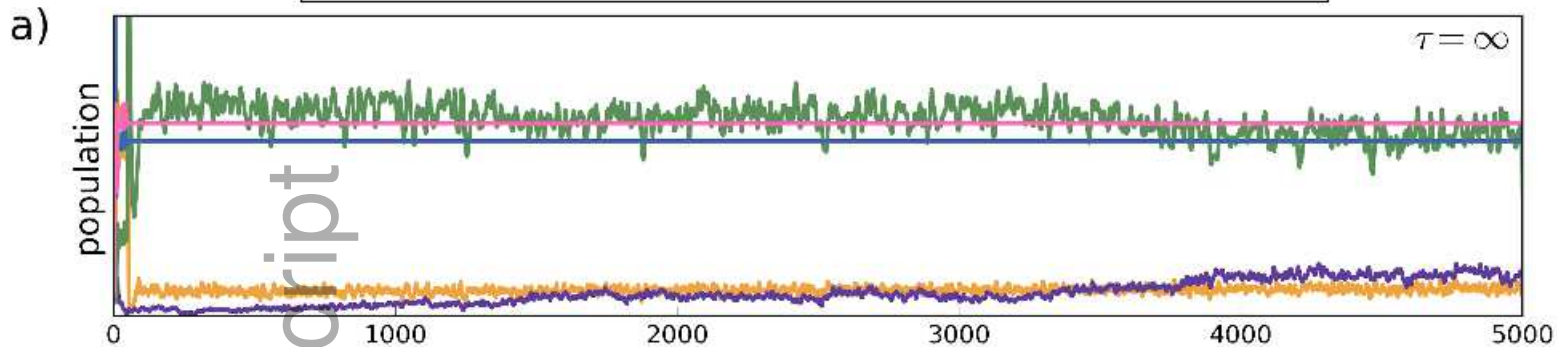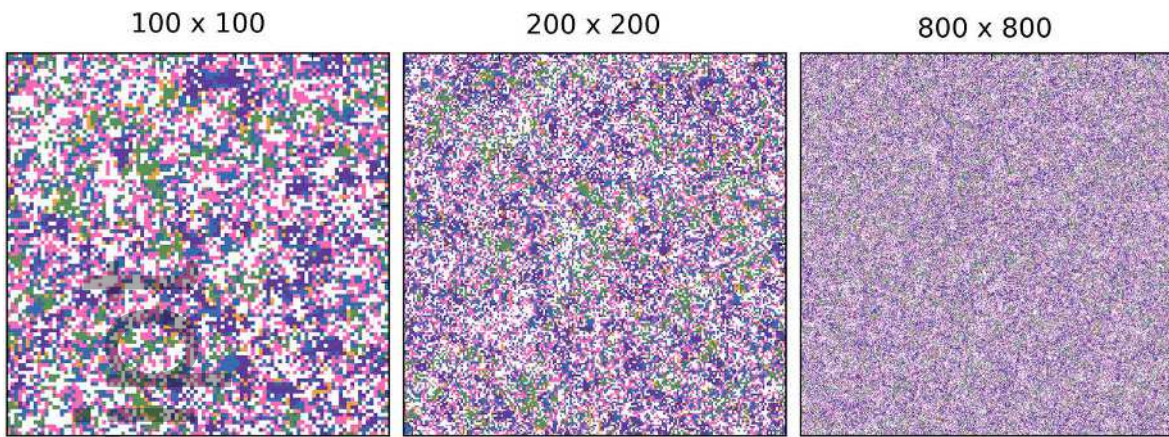
■ prey 1 ■ predator 1 ■ predator 2 ■ prey 2 ■ predator 3

ecs2_2489_f11.tif

ecs2_2489_f12.tif