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Species competition: uncertainty on a double invariant loop

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On the occasion of the 62nd Birthday of Jim Cushing.

The *Tribolium* (flour beetle) competition experiments conducted by Park have been highly influential in ecology. We have previously shown that the dynamics of single-species *Tribolium* populations can be well-described by the discrete-time, 3-dimensional larva–pupa–adult (LPA) model. Motivated by Park's experiments, we explore the dynamics of a 6-dimensional "competition LPA model" consisting of two LPA models coupled through cannibalism. The model predicts a double-loop coexistence attractor, as well as an unstable exclusion equilibrium with a 5-dimensional stable manifold that plays an important role in causing one of the species to go extinct in the presence of stochastic perturbations. We also present a stochastic version of the model, using binomial and Poisson distributions to describe the aggregation of demographic events within life stages. A novel "stochastic outcome diagram," the stochastic counterpart to a bifurcation diagram, summarizes the model-predicted dynamics of uncertainty on the double-loop. We hypothesize that the model predictions provide an explanation for Park's data. This "stochastic double-loop hypothesis" is accessible to experimental verification.

Keywords: Species competition; Invariant loop; Stochasticity; *Tribolium*

1. Introduction

Ecologists have long pondered the problem of species competition. Conventional ecological wisdom says that if two species occupy the same habitat and use the same resources, then one species will outcompete the other. This "competitive exclusion principle" [8,10] is a prediction of the simple mathematical models of Lotka [14] and Volterra [22]. The need to test these predictions experimentally led to a number of laboratory studies, the most influential of which are the experiments of Gause [8] on yeast and protozoa and a long series of studies by Thomas Park and his students at the University of Chicago using two species of flour beetles belonging to the genus *Tribolium* [15,9].

The *Tribolium* competition experiment of Park [18] is a treasure of data. There were a total of 24 treatments involving 8 genetic strains, 16 two-species competitive treatments and 8 single species treatments, each with 10 replicates for a total of 240 individual flour beetle

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cultures. Many cultures were maintained for several years. The research report is based on 2,638,446 census observations. Although these data have been available for 40 years, we are still confronted with the challenge of explaining Park's results.

In previous studies, we have shown that the 3-dimensional discrete-time larva–pupa–adult (LPA) model describes and predicts the dynamics of single-species *Tribolium* populations (for example, see [5]). Recently, we reviewed the history of Park's *Tribolium* competition experiments, discussed the mathematical models that were historically applied to these experiments, and introduced a new two-species model of competition [7]. The new model is 6-dimensional and consists of two LPA models coupled through cannibalism. The data of Thomas Park and colleagues provide an opportunity to further study this "competition LPA model". The data challenge the model. What insights about the experimental observations can be obtained from the two-species model?

In this paper, we study the dynamics of the competition LPA model at biologically reasonable parameter values. The model predicts a double-loop coexistence attractor, as well as an unstable exclusion equilibrium with a 5-dimensional stable manifold. We propose a stochastic double-loop hypothesis as an explanation of an observed time series in the experiment of Park [18].

2. Deterministic competition model

The competition LPA model is:

$$\begin{aligned}
L_{1,t+1} &= b_1 A_{1,t} e^{-c_{el,11}L_{1,t} - c_{ea,11}A_{1,t} - c_{el,12}L_{2,t} - c_{ea,12}A_{2,t}} \\
P_{1,t+1} &= L_{1,t}(1-\mu_{l,1}) \\
A_{1,t+1} &= P_{1,t} e^{-c_{pa,11}A_{1,t} - c_{pa,12}A_{2,t}} + A_{1,t}(1-\mu_{a,1}) \\
L_{2,t+1} &= b_2 A_{2,t} e^{-c_{el,21}L_{1,t} - c_{ea,21}A_{1,t} - c_{el,22}L_{2,t} - c_{ea,22}A_{2,t}} \\
P_{2,t+1} &= L_{2,t}(1-\mu_{l,2}) \\
A_{2,t+1} &= P_{2,t} e^{-c_{pa,21}A_{1,t} - c_{pa,22}A_{2,t}} + A_{2,t}(1-\mu_{a,2})
\end{aligned} \tag{1}$$

The model time step is two weeks, which corresponds to the durations of the L-stage (feeding larva) and P-stage (non-feeding larva, pupa and callow adult) animals. The structure of the single-species LPA model is explained in detail in previous work (see, for example, [4]). In the competition LPA model, each species has its own larval recruitment rates $b_1 > 0$ and $b_2 > 0$, where b_i is the number of larval recruits per adult for species i during one model time step (in the absence of cannibalism). The larval mortality rates $\mu_{l,1}$ and $\mu_{l,2}$ and adult mortality rates $\mu_{a,1}$ and $\mu_{a,2}$, satisfy $0 \le \mu \le 1$, and represent the probability that an animal will die during one model time step. The exponentials represent the fractional reductions due to cannibalism of eggs by larvae and adults ($c_{el,ij}$ and $c_{ea,ij}$, respectively) and of pupae by adults ($c_{pa,ij}$). There are six intra-specific per capita cannibalism coefficients $c_{el,11}$, $c_{el,22}$, $c_{ea,11}$, $c_{ea,22}$, $c_{pa,11}$, $c_{pa,22} > 0$, and six inter-specific per capita cannibalism coefficients $c_{el,12}$, $c_{el,21}$, $c_{ea,12}$, $c_{ea,21}$, $c_{pa,12}$, $c_{pa,21} > 0$. The precise biological interpretation of the c coefficients and the derivation of the exponential nonlinearities are found in [4].

We will use the term "within the axis" when referring to scenarios involving only one of the two species. Thus we will refer to equilibria of the form $(L_1^*, P_1^*, A_1^*, 0, 0, 0)$ with $L_1^*, P_1^*, A_1^* > 0$ as "horizontal-axis equilibria," and equilibria of the form $(0, 0, 0, L_2^*, P_2^*, A_2^*)$ with $L_2^*, P_2^*, A_2^* > 0$ as "vertical-axis equilibria." The competition LPA map has a unique horizontal-axis equilibrium [4] provided

$$b_1 \frac{1 - \mu_{l,1}}{\mu_{a,1}} > 1, \tag{2}$$

and a unique vertical-axis equilibrium provided

$$b_2 \frac{1 - \mu_{l,2}}{\mu_{a,2}} > 1. \tag{3}$$

To study the stability of an axis equilibrium with respect to invasion by the second species, we consider the Jacobian matrix of the competition LPA map. The Jacobian evaluated at $(L_1^*, P_1^*, A_1^*, 0, 0, 0)$ is a 6×6 matrix with a 3×3 block of zeros in the lower left corner. This means that the eigenvalues of the 6×6 matrix are the eigenvalues of the 3×3 block in the upper left corner and the eigenvalues of the 3×3 block in the lower right corner. We assume that the equilibrium is stable in the absence of a second species, and thus that the three eigenvalues of the upper left block are all within the unit circle. The three eigenvalues of the lower right block will then determine if an equilibrium that is stable within the axis will remain stable in the presence of small numbers of a second species. The lower right block is

$$\begin{pmatrix} 0 & 0 & b_2 e^{-c_{el,21}L_1^* - c_{ea,21}A_1^*} \\ 1 - \mu_{l,2} & 0 & 0 \\ 0 & e^{-c_{pa,21}A_1^*} & 1 - \mu_{a,2} \end{pmatrix}$$

with characteristic polynomial

$$\lambda^3 - (1 - \mu_{a,2})\lambda^2 - b_2(1 - \mu_{l,2})e^{-c_{el,21}L_1^* - (c_{ea,21} + c_{pa,21})A_1^*}. \tag{4}$$

Satisfaction of the *Jury conditions* [12] provides a necessary and sufficient condition that all three eigenvalues lie within the unit circle in the complex plane, and thus provides a sufficient condition for the stability of the axis equilibrium.

THEOREM 1 *A horizontal-axis equilibrium* $(L_1^*, P_1^*, A_1^*, 0, 0, 0)$ *is stable whenever*

$$b_2 \frac{1 - \mu_{l,2}}{\mu_{a,2}} e^{-c_{el,21}L_1^* - (c_{ea,21} + c_{pa,21})A_1^*} < 1. \tag{5}$$

Proof Define

$$\alpha = b_2(1 - \mu_{l,2})e^{-c_{el,21}L_1^* - (c_{ea,21} + c_{pa,21})A_1^*}.$$

Then the Jury conditions are equivalent to:

(i) $\mu_{a,2} > \alpha$
(ii) $2 - \mu_{a,2} > -\alpha$
(iii) $\alpha < 1$
(iv) $|1 - \alpha^2| > |(1 - \mu_{a,2})\alpha|$

Assume that (i) is true, so that $0 < \alpha < \mu_{a,2}$. Since $\mu_{a,2} \leq 1$, (ii) is trivial and (iii) follows from (i). Since $0 < \alpha < 1$ implies $\alpha^2 < 1$, the absolute values on the both sides of (iv) can be removed. This reduces (iv) to a quadratic inequality in α:

$$\alpha^2 + (1 - \mu_{a,2})\alpha - 1 < 0.$$

Since by assumption $0 < \alpha < \mu_{a,2}$, the above inequality holds if

$$\mu_{a,2}^2 + (1 - \mu_{a,2})\mu_{a,2} - 1 \leq 0$$

which reduces to $\mu_{a,2} \leq 1$; thus (iv) follows from (i). Thus, all of the Jury conditions are satisfied if (and only if) $\mu_{a,2} > \alpha$, that is, if and only if

$$b_2 \frac{1 - \mu_{l,2}}{\mu_{a,2}} e^{-c_{el,21}L_1^* - (c_{ea,21} + c_{pa,21})A_1^*} < 1.$$

□

A similar argument shows that the vertical-axis equilibrium $(0, 0, 0, L_2^*, P_2^*, A_2^*$ is stable whenever

$$b_1 \frac{1 - \mu_{l,1}}{\mu_{a,1}} e^{-c_{el,12}L_2^* - (c_{ea,12} + c_{pa,12})A_2^*} < 1. \tag{6}$$

As expected, raising inter-specific competition leads to stable extinction states which implies competitive exclusion.

3. Population time series

The time series records that we examine were obtained from the experiment conducted by Park [18]. In the experiment, single- and mixed-species cultures of four genetic strains of *Tribolium confusum* Duval (labeled bI, bII, bIII, bIV) and four genetic strains of *Tribolium castaneum* Herbst (labeled cI, cII cIII, cIV) were cultured in shell vials with 8 g of standard medium (95% whole wheat flour and 5% dried brewer's yeast by weight) and maintained in an incubator at 29°C, 70% relative humidity. Single-species populations were initiated with 8 adults (4 males and 4 females) while the mixed-species populations were initiated with 4 adults (2 males and 2 females) of each species. At 30-day intervals the number of adults were counted. Following the adult census all life stages (eggs, larvae, pupae and adults) were returned to fresh medium. The single-species cultures were maintained for 870 days. The mixed-species cultures were maintained until one or the other species went extinct. The longest culture was continued for 1740 days or 4.8 years.

Our objective was to establish a version of the two-species LPA competition model that would serve as a hypothesis to interpret the observed population time series. We focused, in particular, on the mixed-species culture involving genetic strain bII of *T. confusum* and genetic strain cIV of *T. castaneum*. The unusual time series pattern (see the top panel of figure 5) was called "recalcitrant" by Park [18]. We used information from several sources to obtain parameter values: first, the statistical analyses of time series data on *T. castaneum* [6], second, assay experiments on fecundity, fertility, rate of development and adult longevity of the two species [17] and, third, assay experiments on the cannibalistic interactions of adults eating eggs, adults eating pupae and larvae eating eggs of the two species [19]. The parameter values are given in table I.

Table 1. Parameter values.

$b_1 = 10$	$b_2 = 10$	$\mu_{l,1} = 0.2$	$\mu_{l,2} = 0.2$	$\mu_{a,1} = 0.14$	$\mu_{a,2} = 0.14$
$c_{el,11} = 0.012$	$c_{el,22} = 0.003$	$c_{ea,11} = 0.006$	$c_{ea,22} = 0.015$	$c_{pa,11} = 0.064$	$c_{pa,22} = 0.01$
$c_{al,12} = 0.01$	$c_{el,21} = 0.062$	$c_{ea,12} = 0.011$	$c_{ea,21} = 0.007$	$c_{pa,12} = 0.017$	$c_{pa,21} = 0.03$

The two-species competition model has 18 parameters, any one of which could serve as a bifurcation parameter. We chose to examine the biological consequences of the changing the magnitude of the interspecific coefficient of egg eating by the larvae of species one on species two, namely, $c_{el,21}$. A bifurcation diagram is given in the top two panels of figure 1.

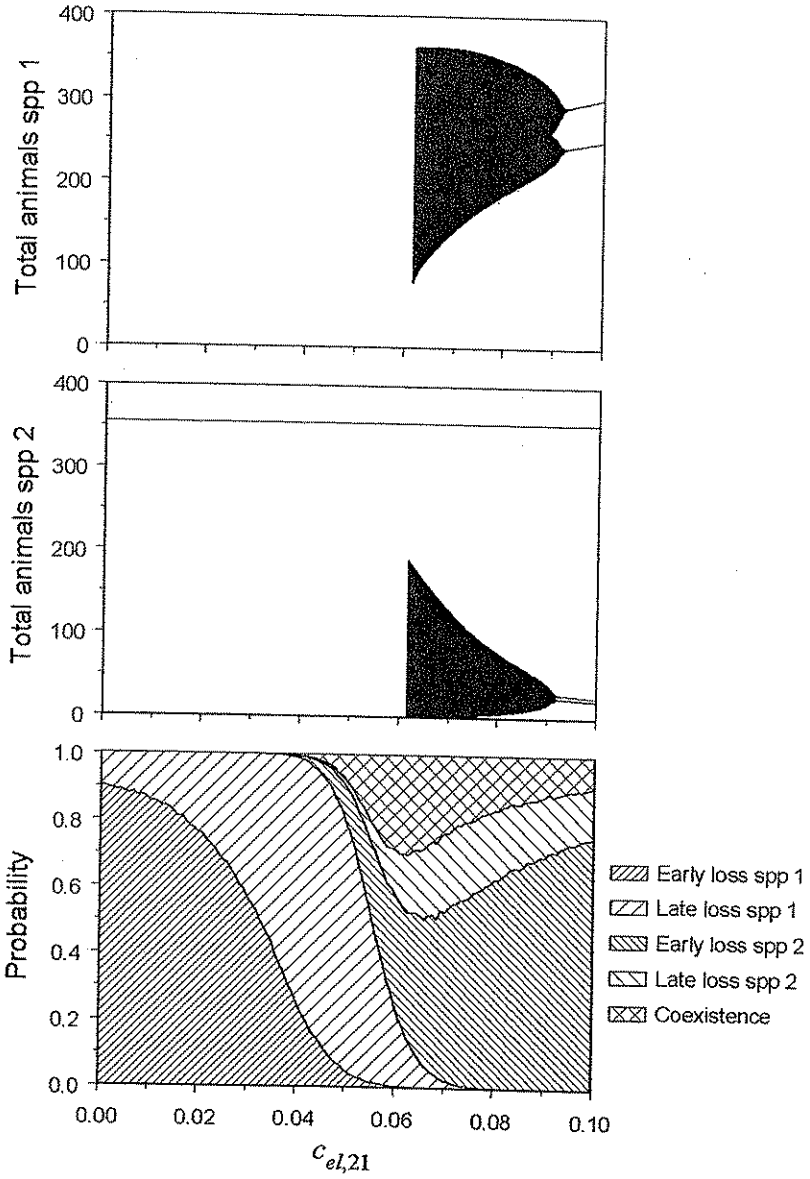

Figure 1. Top two panels. Bifurcation diagram. Bottom panel. Stochastic outcome diagram.

A stochastic counterpart to the bifurcation diagram, which is discussed fully in a later section, is displayed in the bottom panel of the figure.

3.1 Coexistence double-loop

The two top panels of figure 1 show bifurcation diagrams (for the parameters in table I) for the total population of species one and species two as $c_{el,21}$ varies from 0 to 0.10. There is a vertical-axis equilibrium at

$$(0, 0, 0, 114.04, 91.23, 148.14),$$

with

$$b_1 \frac{1 - \mu_{l,1}}{\mu_{a,1}} e^{-c_{el,12}L_2^* - (c_{ea,12} + c_{pa,12})A_2^*} = 0.29 < 1$$

implying asymptotic stability. Note that the parameter $c_{el,21}$ has no effect on the asymptotic stability of this equilibrium, so this extinction state will act as an attractor regardless of what happens as we vary $c_{el,21}$.

The stable axis equilibrium (0,0,0,114.04,91.23,148.14) will exist in the presence of a second attractor. The nature of the second attractor depends on the value of the bifurcation parameter $c_{el,21}$. Reading from right to left in figure 1, we can identify the following sequence of changes in the second attractor. A coexistence two-cycle is the second attractor if $0.092 < c_{el,21} < 0.17$. The second attractor is a coexistence double-loop for $0.061 < c_{el,21} < 0.092$. As $c_{el,21}$ drops through 0.061, the double-loop vanishes, leaving the vertical axis equilibrium as the only attractor.

Figure 2 shows the double-loop coexistence attractor for $c_{el,21} = 0.062$, and figure 3 displays the corresponding time series for adults (top panel) and larvae (bottom panel) of both species.

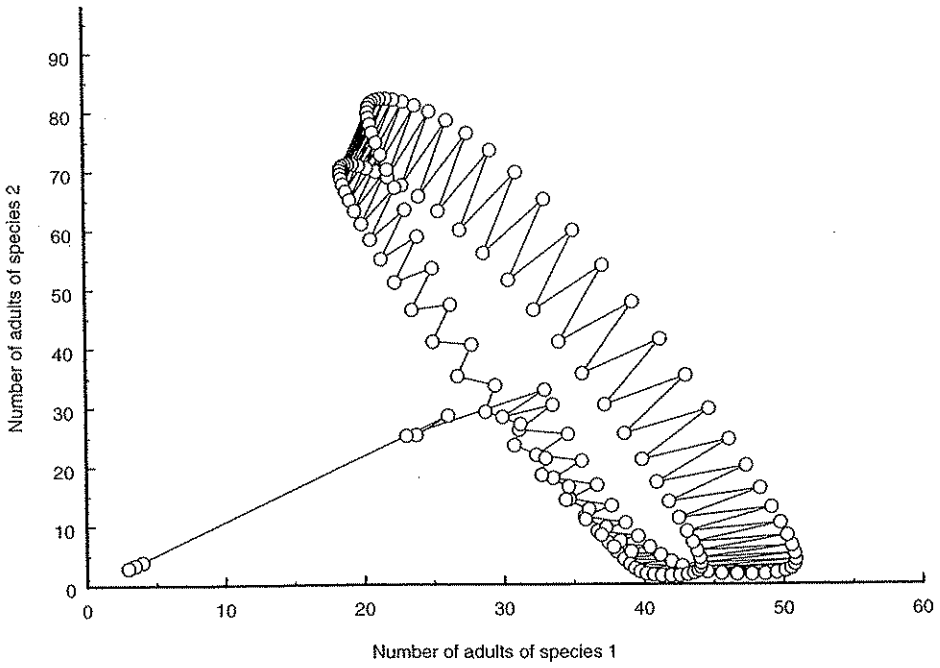

Figure 2. Deterministic double-loop using the parameter values in table I. Initial condition is the same as that in the Park experiment, namely, (0,0,4,0,0,4). After roughly ten time steps the orbit moves onto the attractor.

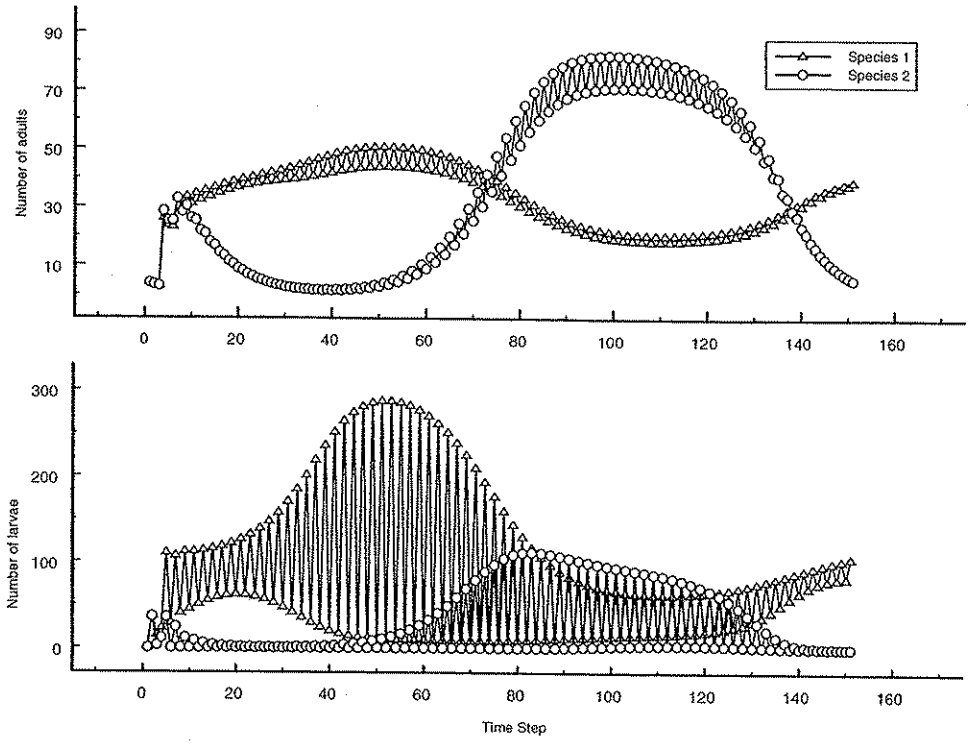

Figure 3. Top panel. Adult numbers of species one and species two associated with the double-loop in figure 2. Bottom panel. Larval time series of species one and species two associated with the coexistence double-loop in figure 2. Notice that the two-cycle oscillations in larval numbers are synchronous.

Our working hypothesis is that this is the underlying deterministic skeleton for the recalcitrant mixed species culture of *T. confusum* strain bII and *T. castaneum* strain cIV [18].

The situation on the horizontal axis is somewhat complex. A two-cycle with coordinates

$$(9.36, 247.55, 45.48, 0, 0, 0), \quad (309.43, 7.49, 52.59, 0, 0, 0)$$

acts as an attractor in the absence of species two. A horizontal-axis equilibrium (98.36,78.69,40.93,0,0,0) is *unstable* within the axis. The Jacobian evaluated at this unstable equilibrium has five eigenvalues inside the unit circle

$$\lambda_{1,2} = -0.0026 \pm 0.06754i$$
$$\lambda_3 = -0.1586$$
$$\lambda_4 = 0.86528$$
$$\lambda_5 = 0.59352$$

and one eigenvalue

$$\lambda_6 = -1.1219$$

outside the unit circle. The equilibrium is therefore a saddle with a 5-dimensional stable manifold and 1-dimensional unstable manifold. The eigenvector associated with λ_6 is (0.814, -0.58, 0.026, 0,0,0); hence the 1-dimensional unstable manifold lies *within* the horizontal axis. As a result, this equilibrium, though unstable, exerts a strong pull on orbits, even those with initial conditions far from the horizontal axis.

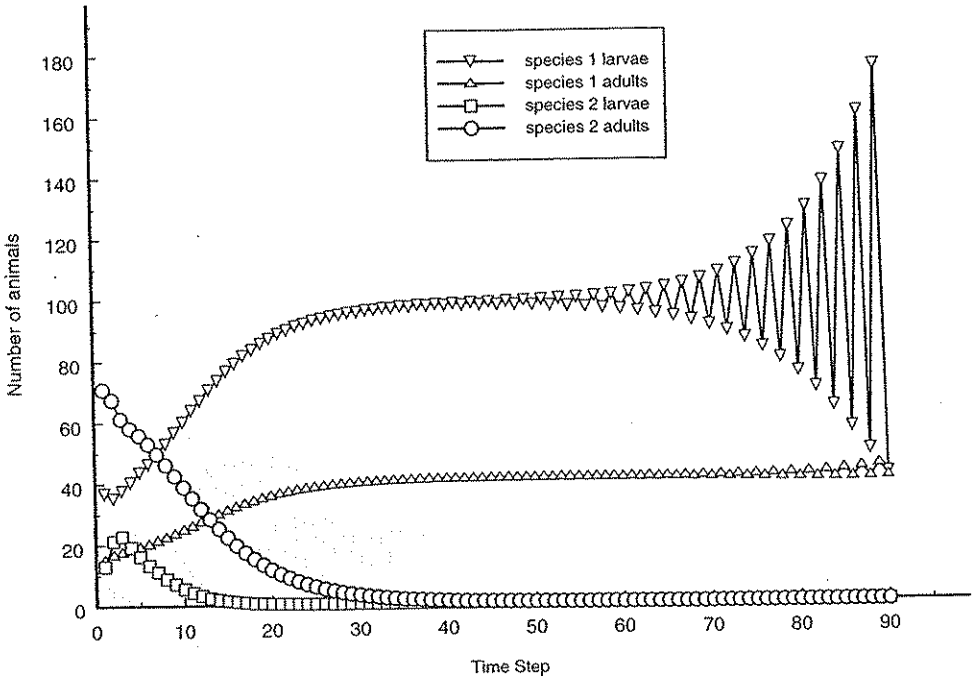

Figure 4. Time series displaying the influence of the 5-dimentional stable manifold associated with the unstable axis equilibrium (98.36,78.69,40.93,0,0,0) of species one. The initial condition is (37,33,15,13,21,71).

Figure 4 shows a time series for larvae and adults of both species with an initial condition of (37,33,15,13,21,71), which is far from the unstable axis equilibrium (98.36,78.69,40.93,0,0,0), but very close to the stable manifold of this horizontal-axis equilibrium. We will see that this unstable equilibrium (with its 5-dimensional stable manifold and 1-dimensional unstable manifold) plays an important role in the extinction of species two in a stochastic version of the competition model.

3.2 *Stochastic double-loop hypothesis*

Probabilistic variation, in such fundamental biological processes as the number of eggs a beetle oviposits and egg survival in the presence of egg-eating larvae and adults, is part of flour beetle dynamics. The aggregation of these demographic events within the life stages was described by the binomial and Poisson distributions in a single species model [6]. That stochastic formulation can be easily extended to the two-species case.

In the stochastic model, the system variables $L_{1,t+1}$, $P_{1,t+1}$, $A_{1,t+1}$, $L_{2,t+1}$, $P_{2,t+1}$, and $A_{2,t+1}$ are random variables whose probability distributions are dependent upon the values of the system variables realized in time t. In what follows, upper case letters are used to denote the random variables and lower case letters the realized values that the random variables are conditioned upon.

The random variable describing the number of L_1-stage animals at time $t+1$ is a compound process: a random number of potential recruits is produced (with conditional mean $b_1 a_{1,t}$), and each potential recruit subsequently undergoes a survival process where the conditional survival probability, $e^{-c_{el,11}l_{1,t}-c_{ea,11}a_{1,t}-c_{el,12}l_{2,t}-c_{ea,12}a_{2,t}}$, depends on the system state variables $l_{1,t}$, $l_{2,t}$, $a_{1,t}$, and $a_{2,t}$. We assumed that the number of potential recruits has a Poisson distribution with a mean

of $b_1 a_{1,t}$, and that the number of subsequent survivors has a binomial distribution. Thus, the conditional distribution of $L_{1,t+1}$ given $L_{1,t} = l_{1,t}$, $L_{2,t} = l_{2,t}$, $A_{1,t} = a_{1,t}$, and $A_{2,t} = a_{2,t}$ becomes a Poisson distribution with mean $b_1 a_{1,t} e^{-c_{el,11} l_{1,t} - c_{ea,11} a_{1,t} - c_{el,12} l_{2,t} - c_{ea,12} a_{2,t}}$.

The number of P_1-stage animals at time $t+1$ is produced by a random survival process. Each of the $l_{1,t}$ larvae are at risk of death with probability $\mu_{l,1}$. Therefore, the distribution of $P_{1,t+1}$ given $L_{1,t} = l_{1,t}$ was taken to have a binomial $(l_{1,t}, (1 - \mu_{l,1}))$, distribution.

The number of A_1-stage animals at time $t+1$ is the sum of two independent survival processes: recruits from the P_1-stage, denoted $R_{1,t+1}$, which survived cannibalism with probability $e^{-c_{pa,11} a_{1,t} - c_{pa,12} a_{2,t}}$ to become adults, and surviving adults, denoted $S_{1,t+1}$, which made the transition from time t to time $t+1$ with probability $1 - \mu_{a,1}$. We assumed a binomial distribution for both these survival processes.

Similar assumptions were made for species two to produce the following Poisson–binomial (PB) model for two competing species:

$$
\begin{aligned}
L_{1,t+1} &\sim \text{Poisson } (b_1 a_{1,t} e^{-c_{el,11} l_{1,t} - c_{ea,11} a_{1,t} - c_{el,12} l_{2,t} - c_{ea,12} a_{2,t}}) \\
P_{1,t+1} &\sim \text{binomial } (l_{1,t}, 1 - \mu_{l,1}) \\
R_{1,t+1} &\sim \text{binomial } (p_{1,t}, e^{-c_{pa,11} a_{1,t} - c_{pa,12} a_{2,t}}) \\
S_{1,t+1} &\sim \text{binomial } (a_{1,t}, 1 - \mu_{a,1}) \\
A_{1,t+1} &= R_{1,t+1} + S_{1,t+1} \\
L_{2,t+1} &\sim \text{Poisson } (b_2 a_{2,t} e^{-c_{el,21} l_{1,t} - c_{ea,21} a_{1,t} - c_{el,22} l_{2,t} - c_{ea,22} a_{2,t}}) \\
P_{2,t+1} &\sim \text{binomial } (l_{2,t}, 1 - \mu_{l,2}) \\
R_{2,t+1} &\sim \text{binomial } (p_{2,t}, e^{-c_{pa,21} a_{1,t} - c_{pa,22} a_{2,t}}) \\
S_{2,t+1} &\sim \text{binomial } (a_{2,t}, 1 - \mu_{a,2}) \\
A_{2,t+1} &= R_{2,t+1} + S_{2,t+1}
\end{aligned}
\tag{7}
$$

here " $\sim$ " means "is distributed as."

The expectation of the stochastic process is the same as the deterministic model (1), but the stochastic dynamics are confined to the 6-dimensional lattice of non-negative integers [11]. The latter is an important consideration when dealing with population extinction.

A *stochastic outcome diagram* is a counterpart to a bifurcation diagram that summarizes the model-predicted, long term outcomes of a stochastic model (see the bottom panel of figure 1). The frequency of occurrences of five time series patterns, based on the time a species goes extinct, are identified: the early or late loss of species one, the early or late loss of species two and coexistence. (Extinction of both species is a possibility, but it was never observed in the experiments or in any of our simulations.) Early elimination was defined as the loss of a species in the time interval $0 < t \leq 60$, late loss in the interval $60 < t \leq 150$, and coexistence as the presence of both species at $t > 150$. The frequency of each of these events was computed using the parameters in table I for 10000 PB-model realizations for $c_{el,21}$ from 0.00 to 0.10 every 0.0025. The results are presented as a filled area chart, so the height of the fill is the proportion of a certain outcome. For example, with $c_{el,21} = 0.01$ there is a predicted early loss of species one in approximately 85% of the realizations and a late loss of species one in 15% of the runs; species one is always lost. As $c_{el,21}$ increases, there is a reduction in the frequency of the early loss of species one and a corresponding increase in the late loss of species one. Just beyond the value of

$c_{el,21} = 0.04$ there is a qualitative change in the stochastic model-predicted outcomes. For example, at $c_{el,21} = 0.055$ the model predicts the simultaneous occurrence of all five possible outcomes. That means that in an experiment with many replicates the forecast is that species one is lost in 50% of the replicates, species two is lost in 30% and the species coexist in 20% of the replicates. Deterministically species one is always lost. Stochastically the forecast is the probability of a particular outcome. This region of the stochastic outcome diagram corresponds to what Park called a "zone of indeterminism," a phrase he introduced into ecology in 1956 [16]. Although in Park's case he forecast the loss of either species one or species two; coexistence was not predicted by his model.

The traditional bifurcation diagram together with the stochastic outcome graph give us the opportunity to address a fundamental question of population theory: How do deterministic forces and stochastic events combine to produce population trajectories? For example, when $c_{el,21} = 0.062$ the deterministic orbit with initial condition (0,0,4,0,0,4) leads to species coexistence (figures 2 and 3). However, by time $t = 150$ in the PB model, only 30% of the stochastic realizations lead to coexistence, while 15% result in the of loss of species one and 55% of the stochastic runs to a loss of species two (see figure 1 bottom panel). A clue to understanding the interplay of the deterministic forces and stochastic fluctuations may involve the 5-dimensional stable manifold and the 1-dimensional unstable manifold of the unstable equilibrium of species one. With an initial stage vector of 4 adults of each species (Park's experimental condition) the unstable equilibrium and its stable and unstable manifolds have little influence on the deterministic model orbit. However, demographic variability, as given in the PB model of species competition, allows for the possibility that an orbit will be placed by chance near the stable manifold of the unstable equilibrium and species two will be pulled toward extinction (figures 5 and 6).

The stochastic PB model (7) was used to further investigate the hypothesis that the 5-dimensional stable manifold of the unstable horizontal-axis equilibrium plays a role in the extinction of species two. If this hypothesis is true, then extinction of species two should coincide with a "flyby" of the unstable axis equilibrium by species one. To evaluate this hypothesis, we calculated the Euclidian distance between the realizations of the stochastic model and the unstable axis equilibrium for both species:

$$d_{1,t} = \sqrt{\left(L_{1,t} - L_1^*\right)^2 + \left(P_{1,t} - P_1^*\right)^2 + \left(A_{1,t} - A_1^*\right)^2} \tag{8}$$

$$d_{2,t} = \sqrt{L_{2,t}^2 + P_{2,t}^2 + A_{2,t}^2} \tag{9}$$

where $(L_1^*, P_1^*, A_1^*) = (98.36, 78.69, 40.93)$. We then chose simulations of the PB model with the initial condition (0,0,4,0,0,4) from the Park experiment which met each of the following conditions: (i) $d_{2,t} > 20$ at $t = 50$, (ii) $d_{2,t} < 20$ at $t = 60$, (iii) $d_{2,t} = 0$ for $t \geq 100$. These conditions ensured that stochastic extinction events of species two are more or less aligned in time. We ran the PB stochastic model until 100 realizations had been accumulated that met these criteria. On the left side of figure 7 are plotted $d_{1,t}$ and $d_{2,t}$ for the first five realizations; the mean of all 100 realizations are plotted on the right side of figure 7. Whenever species two goes extinct ($d_{2,t} \to 0$), there is a decrease in $d_{1,t}$, indicating a trajectory that passes near the unstable axis equilibrium. Although the exact timing and "nearness" of the flyby varies from one stochastic realization to the next, it happens in a consistent and predictable manner, lending support to the hypothesis of the 5-dimensional stable manifold as factor in the extinction of species two.

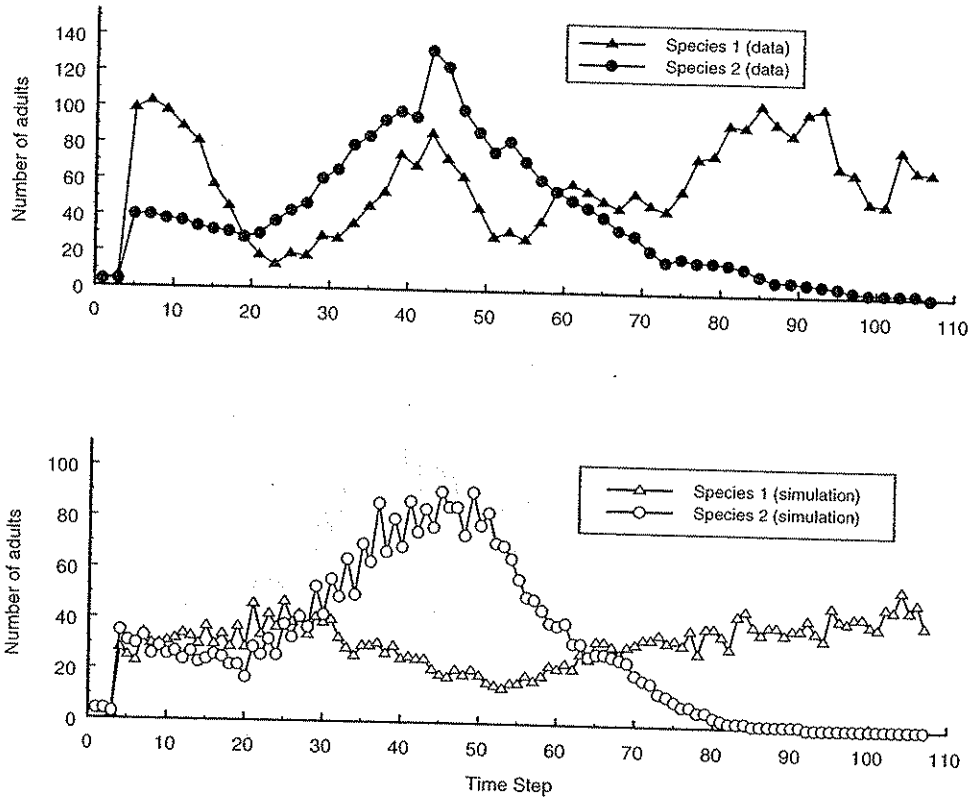

Figure 5. Top panel. Adult data observed in Park *et al.* (1964, Table L, p.160), *T. castaneum* strain cIV and *T. confusum* strain bII. Bottom panel. Stochastic model simulation of adult numbers of species one and species two with the same initial conditions as in the Park experiment, (0,0,4,0,0,4), using the parameter values given in table I. Notice that at time step 48 the two species community, (15,41,19,4,92,74), starts to be drawn toward the unstable axis equilibrium of species one under the influence of the stable manifold. The result is the extinction of species two. See figure 6 for a display of the larval numbers of each species.

4. Discussion

A stochastic double-loop hypothesis is proposed as an explanation for the adult time series pattern observed in the mixed species culture of strain cIV of *T. castaneum* and strain bII of *T. confusum* (figure 5, top panel). A statement of the hypothesis and how it explains the data are summarized as follows:

1. A coexistence double-loop is the attractor of the deterministic model.
2. Associated with the unstable axis equilibrium (98.36, 78.69, 40.93, 0,0,0) of *T. castaneum*, are a 5-dimensional stable manifold and a 1-dimensional unstable manifold.
3. The deterministic model, for the initial conditions used in the Park experiment, predicts that the two species will coexist. Coexistence was not observed; *T. confusum* was lost.
4. Probabilistic variation incorporated into the model gives rise to a stochastic double-loop hypothesis.
5. In the stochastic model 55% of the realizations resulted in the loss of *T. confusum*.
6. The proposed explanation of the loss of *T. confusum* is based on the influence of the stable and unstable manifolds of the unstable axis equilibrium of *T. castaneum*.

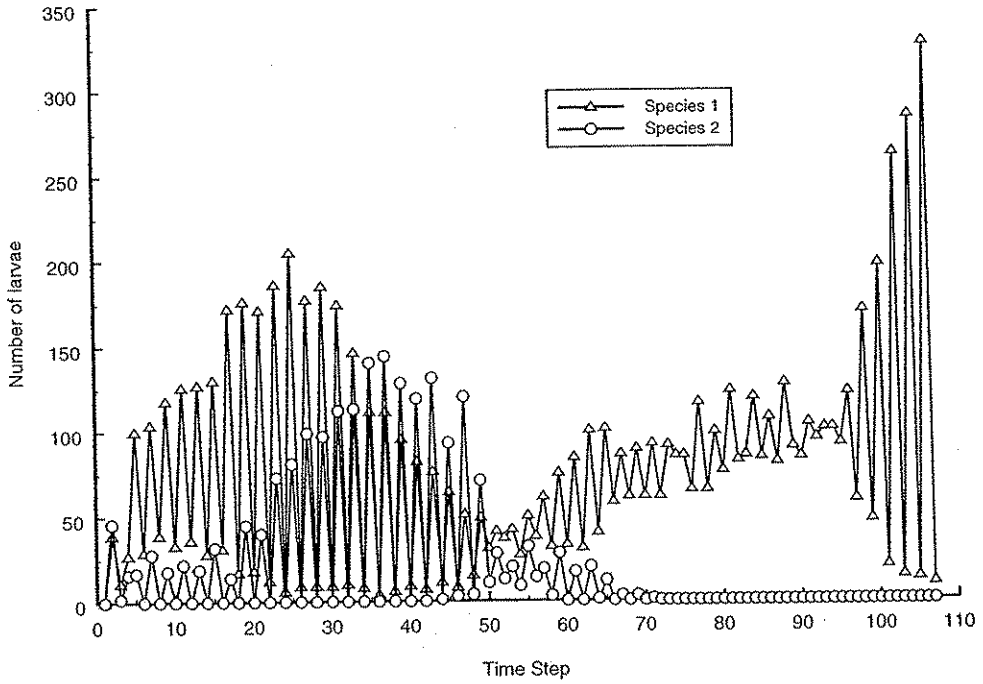

Figure 6. Stochastic model simulation of larval numbers of species one and species two with initial condition (0,0,4,0,0,4) showing the influence of the stable 5-dimentional stable manifold. Notice that at time step 48 the two species community, (15,41,19,4,92,74), starts to be drawn toward the unstable axis equilibrium of species one which results in the extinction of species two.

7. Our interpretation of the data is that demographic chance events pushed the two species culture close to the stable manifold of the unstable axis equilibrium, which then resulted in the two species community being drawn toward the unstable axis equilibrium of *T. castaneum* with the subsequent loss of *T. confusum.*

The observed adult time series pattern (figure 5, top panel) is similar to that predicted by a realization of the stochastic model influenced by the stable manifold (figure 5, bottom panel). The model-predicted larval time series also reveals the influence of the stable manifold (figure 6). Repeated simulations of the stochastic model in which *T. confusum* goes extinct reveal a consistent trend whereby the trajectory of the two species system brings *T. castaneum* near its unstable axis equilibrium as *T. confusum* is lost, lending support to hypothesis that the 5-dimensional stable manifold is a factor in bringing about the extinction of *T. confusum.*

Under ideal circumstances, one could explore the stochastic double-loop hypothesis in more detail with more complete analyses of the experimental data. Following the paradigm of Cushing *et al.* [4], this would include parameter estimation and model validation. Unfortunately, the only source for the *Tribolium* competition data is the original publication by Park and his colleagues [18] which, except for a few replicates, contains only time series data for the mean number of adults. Larvae and pupae of *T. castaneum* and *T. confusum* were not recorded in the Park experiment. More complete tests of the model, including the double-loop hypothesis, await further experimentation.

The bifurcation and stochastic outcome diagrams in figure 1 suggest a tentative explanation of a central feature of the Park experiment [18], namely, "one strain of *T. castaneum* (cI) invariably

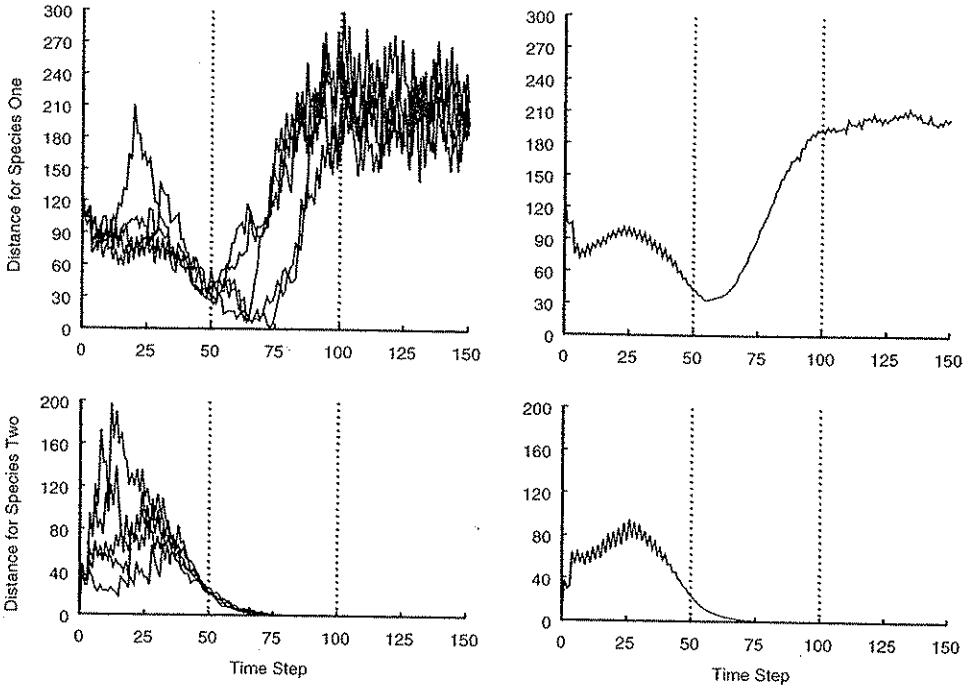

Figure 7. Realizations of the stochastic PB model where species two goes extinct within the interval $50 < t \leq 100$ (dashed lines). The distance of species one from its unstable axis equilibrium (98.36,78.69,40.93) is plotted in the top two graphs and the distance of species two from the extinction point (0,0,0) is plotted in the lower two graphs. In the left panels are five realizations of the stochastic model; on the right are the mean trajectories for 100 stochastic realizations. Associated with the extinction of species two is a flyby of the unstable axis equilibrium by species one. See text for additional details.

wins every encounter with *T. confusum*; another strain (cIV) usually wins its encounters, while the two other strains (cII and cIII) usually lose their encounters." Returning to the stochastic outcome graph, if we associate different values of the bifurcation parameter, $c_{el,21}$, with the genetic strains of *T. castaneum* we obtain an interpretation of the above quotation. With small values of the bifurcation parameter, the *T. castaneum* strains cII and cIII are forecast to lose their encounters with the genetic strains of *T. confusum*; with an intermediate value of $c_{el,21}$ strain cIV is predicted to sometimes win and sometimes lose its encounters; with a slightly larger value of $c_{el,21}$ strain cI is forecast to invariably win every encounter with each genetic strain of *T. confusum*. Interestingly, in egg-eating assay experiments, Park and his colleagues [19] determined the ordering by genetic strain of the rates of *T. castaneum* larvae eating *T. confusum* eggs to be $\text{cII} \approx \text{cIII} \ll \text{cIV} < \text{cI}$, which is consistent with the model predictions. However, we recognize that these genetic strains may differ with respect to other parameters and that more rigorous tests of the model will require additional study.

For the particular set of parameter values that we investigated (table I), the LPA model makes a prediction that is different from the predictions based on classical Lotka-Volterra competition theory, namely, that species coexistence is enhanced when interspecific competition is sufficiently strong, i.e. $c_{el,21} > 0.05$. This result is consistent with the application of the LPA model to the mixed species data of *T. castaneum* strain cIV-a and *T. confusum* strain bI [7]. Increased competition in a consumer/resource model has also been shown to promote species coexistence [21].

Park's "principle of competitive indeterminacy" stimulated mathematical model builders to examine the role of chance events in multi-species communities [1, 13, 20]. Stochastic models are increasingly important in the characterization of ecological dynamics [2–4]. In this paper, we continue the tradition of using flour beetles to explore stochastic population theory by introducing a stochastic outcome diagram which extends the traditional deterministic bifurcation diagram by summarizing the long term stochastic outcomes. These two diagrams placed together as in figure 1 provide a more complete picture of the dynamics than either diagram presented separately.

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