Plant host shift: The viability and persistence of a polyphagous, non-native insect

Isabelle Bueno Silva[1], Blake McGrane-Corrigan[2], Oliver Mason[2], Rafael de Andrade Moral[2] and Wesley Augusto Conde Godoy[1*]

[1] Entomology and Acarology Department- ESALQ, Piracicaba, SP, Brazil

[2] Department of Mathematics and Statistics, Maynooth University, Maynooth, Co. Kildare, Ireland

[*] Corresponding author. Email: wacgodoy@usp.br; Phone: +55 (19) 3429-4199

ABSTRACT: *Drosophila suzukii* (Diptera: Drosophilidae) has become a pervasive pest in several countries around the world. Many studies have investigated the preference and attractiveness of potential hosts on this invasive, polyphagous drosophilid. Thus far, no studies have investigated whether a shift of fruit host could affect its ecological viability or spatiotemporal persistence. In this study, we analysed the fecundity and oviposition period jointly with the survival time of *D. suzukii* subject to a shift in host fruit, using a joint modelling method for longitudinal outcomes and time-until-event outcomes. The number of eggs laid by females was higher in raspberry than in strawberry and when setting adults of F1 generation underwent a first host shift. The joint modelling also suggested that insects reared on raspberry survived longer. We then combined experimental results with a two-patch dispersal model to investigate how host shift in a species, that exhibits both passive and density-dependent dispersal, may affect its asymptotic dynamics. In line with empirical evidence, we found that a shift in host choice can significantly affect the growth potential and fecundity of a species such as *D. suzukii*, which ultimately could aid such invasive populations in their ability to persist within a changing environment.

Key words: Spotted-wing *Drosophila*, host shift, nutrition, matrix population model, mathematical model, discrete time, ecological modelling, stability, persistence, dispersal, joint modelling of longitudinal and time-until-event data

Introduction

The movement of species into different areas is important for the functioning of ecological systems since they contribute to increasing the genetic variability of populations and biocomplexity, which in turn affects a species' ecological performance and evolution (Garnas et al. 2016). The adaptation of non-native species to new environments is essential for biological invasion processes, which involve colonization, establishment, and local or regional dispersal events (Hengeveld, 1989). *Drosophila suzukii* (Matsumura, 1931) is an example of such an invader species. It originated in Asia and was first observed outside its native range in 1980 in Hawai'i (Kaneshiro, 1983), and then later in Europe (Calabria et al., 2012), the United States (Bolda et al., 2010) and Mexico (Senasica 2013). *D. suzukii* was first recorded in Brazil in 2013 (Deprá et al., 2014), and then in Argentina, Uruguay, and Chile (Cichón et al., 2015; González et al., 2015; Medina-Muñoz et al., 2015). Compared to other fruit flies, such as *Zaprionus indianus* (Gupta, 1970), *D. suzukii* has a serrated ovipositor (Atallah et al. 2014), which allows the larvae to develop inside its host fruit. This allows the entry of pathogens that can seriously damage the fruit, resulting in significant losses in crop production (Lee, J.C. et al., 2011a; Walsh et al., 2011; Knapp et al, 2020). The morphology and polyphagous behaviour of *D. suzukii* makes it a harmful and pervasive pest of many fruit and berry crops (Lee, J.C. et al., 2011b). Several studies have focused on fruit traits associated with the oviposition choice of *D. suzukii* (Burrack et al., 2013; Kinjo et al., 2013; Poyet et al., 2015; Olazcuaga et al., 2019) and the physiology of the fruit that attracts this drosphilid (Abraham et al., 2015; Wong et al., 2018). For no-choice assays, Diepenbrock et al (2016) found significant differences in the effects of cultivated host- versus non-cultivated host-shift on the biological characteristics of *D. suzukii*. However, there is no study that has analysed the impacts of host shift and dispersal on the recently invasive Brazilian population.

Previous experiments designed to investigate host shift in polyphagous pests have proved important when studying the demographic responses of insects facing new hosts (Kennedy and Storer 2000). Within laboratory experiments can be combined with theoretical models of population growth to allow the population dynamics of such organisms to be simulated over many successive generations based on empirical parameter estimates, longer than what is feasible in vitro (Heaps et al., 2016; Dey and Joshi, 2018).

In recent years, additional structure has been implicitly and explicitly incorporated into mathematical and computational models, as an attempt to account for the movement of insects at different spatiotemporal scales and life stages (Coutinho et al., 2012; Malaquias et al., 2017). The introduction of spatial structure offers a new perspective when investigating the movement of insects between patches (Okubo and Levin 2001; Moretti et al., 2013), a mechanism that may have significant consequences for integrated pest management and conservation strategies (Nestel, 2004). Structural models that have been proposed in the past have tried to model the dynamics of *D. suzukii* by incorporating, for example, probability of occurrence (Ørsted & Ørsted, 2018) and the influence of abiotic factors (Langille et al., 2016; Reyes& Lira-Noriega, 2020; Wikler et al., 2020), however to our knowledge no model has tried to assess the effects of a host-shift on the species' persistence dynamics.

In the present study, we combined laboratory experiments with mathematical modelling to investigate how host shift may affect the local establishment, equilibrium dynamics, and persistence of *D. suzukii.* This multidisciplinary approach is useful to understand how insects may respond to variations in host availability, which ultimately may promote or hinder the ability of *D. suzukii* to persist in new multi-crop landscapes. Our null hypotheses were:

1. host shift (the change of fruit) does not affect *D. suzukii* survival and the fecundity viability of immature individuals,
2. the macronutrient composition does not change due to host shift, and

3. host shift does not affect the equilibrium dynamics and persistence of *D. suzukii* populations.

Methods

Insect rearing and host-shift assay

We reared a population of *D. suzukii* from colonies maintained in the Entomology Laboratory of the Federal University of Pelotas, Rio Grande do Sul State, Brazil. The flies used for the assays were kept in cages (30 × 21 × 17 cm) in climate chambers (Fitotron®) at 25 ± 1°C, relative humidity 70 ± 5% and 14–10 h photoperiod. *D. suzukii* was chosen as a model insect in the present work because it is a continental invasive species of high relevance for fruit growing worldwide and especially in Brazil. The flies received fresh raspberries cultivated without insecticides, obtained from farms in southeastern Brazil, to obtain the first experimental generation. Fruits with eggs were removed and incubated under the same conditions until emergence. Raspberries were chosen as hosts because they are subject to high fruit-fly infestations in Brazil (Klesener et al., 2018).

Flies that emerged in raspberry (generation F1) were placed on either raspberry or strawberry, with five replicates, in a completely randomised design (Figure 1). Each replicate consisted of one test tube (7.8 cm height × 3.8 cm diameter) with one strawberry or two raspberries and ten couples of *D. suzukii*. After the adults of the next (F2) generation emerged, they were placed in another test tube containing raspberries or a strawberry. This step was repeated, in a completely randomised design, but now with three replicates, each consisting of a test tube with five females and three males of *D. suzukii* from the F2 generation (Figure 1). Then, we repeated the entire assay using the same protocols, with the only difference being the number of replicates for the F2 generation, which was five for the second assay (Figure 1). The fruits were replaced daily, and the number of eggs and daily mortality of adults were recorded

over the F1 and F2 generations. We observed the total number of eggs laid in each replicate, egg-adult viability, total oviposition period (in days), and survival time of the adults (in days).

Analysis of Macronutrient Concentrations

Three randomly selected adults from each generation (F1, F2 and F3, Figure 1) were placed individually in Eppendorf tubes containing 100% ethanol. Four macronutrients: protein, lipid, carbohydrate and glycogen were extracted from each fly, following Lorenz's (2003) protocol, and prepared separately for quantification in a spectrophotometer (Epoch Microplate Spectrophotometer, BioTek).

Protein was quantified using 300 µL of Coomassie reagent (Coomassie Plus Protein, Pierce Biotechnology, Inc., Rockford, IL, USA), and 10 µL of each sample, in triplicate. Five standard curves were prepared, based on concentrations from 0 µg/mL to 2000 µg/mL, following the manufacturer's protocol. The absorbance used was 595 nm. For lipid quantification, we used vanillin as the reagent in a sulfuric acid solution, and 10 µL of each sample, in triplicate. We used commercial vegetable oil to obtain the five standard curves (concentrations of 0 mg/dL to 2500 mg/dL), at an absorbance of 525 nm (Van Handel, 1985). Carbohydrates and glycogen were quantified using anthrone reagent (Roe, 1955). For the carbohydrate aliquots, we prepared a 50 µL solution of each sample individually, containing 100 µL of sulfuric acid and 200 µL of anthrone. The glycogen aliquots were prepared with a solution containing 25 µL of the sample, 50 µL of sulfuric acid and 100 µL of anthrone. The five standard curves were constructed, with glucose used as default (concentrations of 0 mg/dL to 100 mg/L) and an absorbance of 620 nm.

Statistical Analyses

Quasi-Poisson models (Demétrio et al., 2014) were fitted to the data for total number of eggs, including the effects of assay (to reflect the experimental design), generation, host, and the interaction between generation and host in the linear predictor, and the natural logarithm of the number of females as an offset term. F tests were performed to assess the significance of the effects, and multiple comparisons were performed by obtaining the 95% confidence intervals for the linear predictors. Goodness-of-fit was assessed using half-normal plots with simulation envelopes (Moral et al., 2017).

To study the association between oviposition behaviour over time and survival times of the insects, a joint model for longitudinal outcomes (oviposition) and time-until-event outcomes (survival times) was fitted to the data (Rizopoulos, 2010). For the longitudinal part of the model, we log-transformed the count data and included the effects of the assay (to reflect the experimental design), generation, host, time, all two-way interactions between generation, host, and time, and the three-way interaction amongst these factors in the linear predictor as fixed effects. We also included a random intercept per female, given that the number of eggs laid by the same female is correlated over time. For the survival part of the model, we used a Cox proportional-hazards model and included the effects of the assay, generation, and host, and the interaction between generation and host in the linear predictor. This modelling strategy allows for the estimation of an association parameter, which in this study measures the effect of fecundity on the mortality risk (Rizopoulos, 2010). We performed likelihood-ratio (LR) tests to assess the significance of the fixed effects for both parts of the model and a Wald test to assess the significance of the association parameter.

The quantitative data for metabolised macronutrients were analysed by fitting linear models including the effect of treatment (F1 raspberry, F2 raspberry, F3 raspberry, and F3

strawberry) in the linear predictor. The significance of the treatment effect was assessed using F tests.

The Model

It has been observed that dispersal is in general an asymmetric process and may have significant consequences for population persistence (Rinnan, 2018), especially when assessing the impacts of a changing climate or monitoring species range shifts (Zhou and Kot, 2011). When introducing explicit spatiality into population models a phenomenon known as Turing instability may arise, where the extinction equilibrium in the absence of dispersal is asymptotically stable, but by allowing dispersal it becomes unstable (Neubert et al., 2002). Adding more spatial structure, such as asymmetric dispersal, into models can provide more qualitative insight into the dynamics of populations.

The experimental results described above illustrate the impacts of nutritional value on local growth as well as the possible effect of shifting between the two hosts on overall population levels. We now describe and analyse two simple mathematical models that exhibit qualitatively similar behaviour over a longer timescale.

Consider a polyphagous, single-species population that inhabits two nonidentical patches and denote the patch population densities, in generation t, by $x_1(t)$ and $x_2(t)$ respectively. Following reproduction on a patch each population then disperses to the other patch with probability $0 \leq d_1, d_2 < 1$. In the context of *D. suzukii* one can consider subscripts 1 and 2 as representing dispersal from strawberry to raspberry and raspberry to strawberry, respectively. We also assume that the population is spatially closed, i.e., individuals reproduce and disperse only on the two specified patches. This may not be ecologically realistic, but our aim is to understand potential effects of dispersal between two differing patches on the overall

population dynamics. A general form for such a model is given by the system of difference equations

$$\begin{aligned} x_1(t+1) &= (1-d_1)g_1\big(x_1(t)\big) + d_2 g_2\big(x_2(t)\big) \\ x_2(t+1) &= (1-d_2)g_2\big(x_2(t)\big) + d_1 g_1\big(x_1(t)\big) \end{aligned} \tag{1}$$

We will consider two formulations of this, corresponding to different choices for the local growth functions, g_i and dispersal terms, d_i. Both models we consider are nonlinear matrix models. Recall that such a model takes the general form

$$x(t+1) = A\big(x(t)\big)x(t),\ x(0) = x_0 \tag{2}$$

where the state vector $x(t) \in \mathbb{R}_+^n$ (the cone of n-dimensional real vectors with all components nonnegative) and $A: \mathbb{R}_+^n \to \mathbb{R}_+^{nxn}$ is a matrix-valued function.

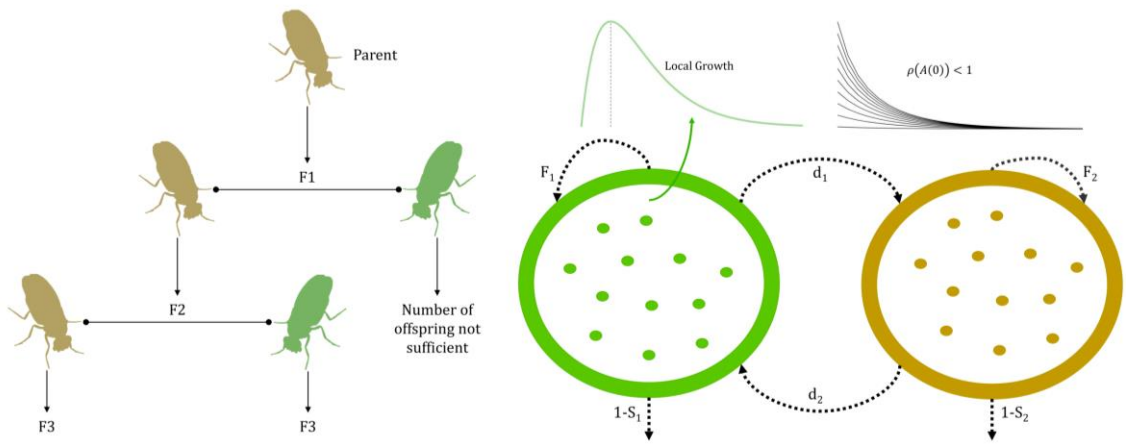

Figure 1 (a) *H*ost-shift assay showing the experimental design performed. Raspberry (grey) was the parent*al* generation and subsequent filial generations where reared on raspberry and strawberry (green). For the raspberry filial generation reared on strawberry there were insufficient population numbers to produce a second strawberry filial generation. **(b)** Population dynamics within and between hosts, governed by both demographic and dispersal parameters. When dispersal is not permitted the local dynamics of each patch is given by the unimodal map g_i.

Experimental Results

Total Fecundity, Oviposition Period and Proportion of Viable Eggs

The daily oviposition rates per female over time are shown in Figure 2. The interaction between generation and host significantly affected the total number of eggs ($F_{1,31}$ = 11.05, p = 0.0023). The number of eggs laid by females was higher in raspberry than in strawberry, for F1 and F2 generations; and the number of eggs laid in strawberry was higher in generation F2 than in F1 (Table 1). When setting adults of F1 generation in first host shift (Figure 1), available eggs were insufficient to have adults and to set up the second host-shift, as performed with raspberry.

The interaction between host and generation did not significantly affect the total oviposition period (LR = 0.54, p = 0.4606). The global test for risk proportionality suggested that the model well fitted the data (X^2 test statistic = 3.16, d.f. = 4, p = 0.5316). Thus, analysing the marginal means indicated that the mean period of oviposition did not differ between generations (LR = 0.10, d.f. = 1, p = 0.7473), but did differ between hosts (LR = 31.77, d.f. = 1, p < 0.0001). Hence, females spent more time ovipositing in raspberry than in strawberry (Table S2).

Table 1 Mean fecundity ± standard error (number of eggs laid per female), for each host and generation. Different upper-case letters denote significant differences in the rows; different lower-case letters denote significant differences in the columns.

Generation	Host	
	Raspberry	*Strawberry*
F1	67.95 ± 7.70 aA	0.20 ± 0.15 bB
F2	50.40 ± 6.44 aA	12.98 ± 11.03 aB

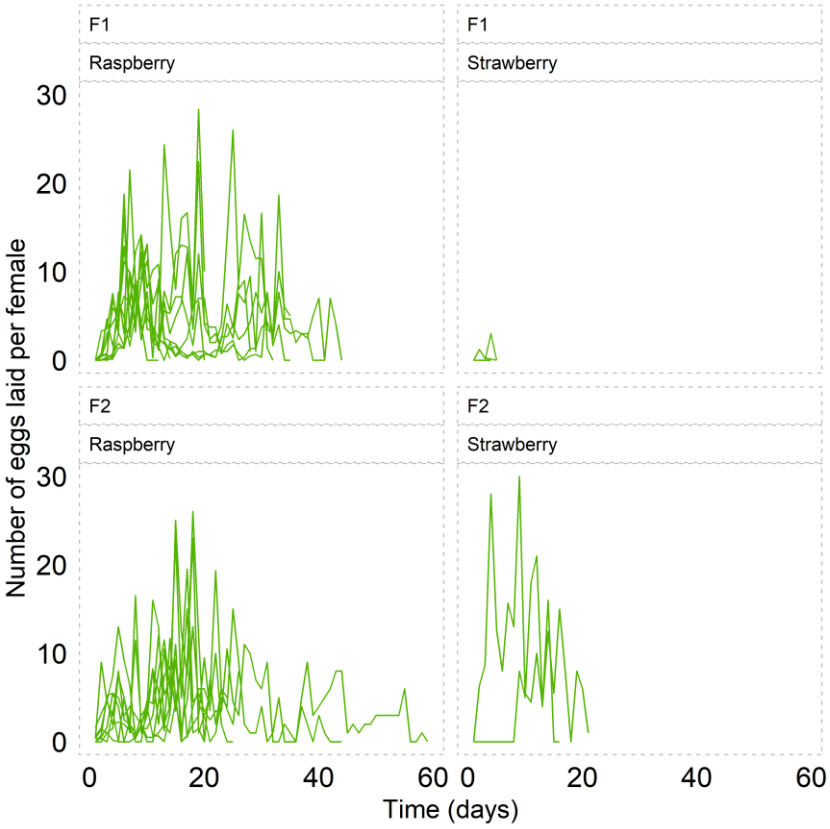

Figure 2 Number of eggs laid per female, in the F1 (A and B) and F2 (C and D) generations. Each line represents one replicate, which included ten and five females for generations F1 and F2, respectively.

The interaction between generation and host did not significantly affect the proportion of offspring that reached the adult stage ($F_{1,18} = 0.07$, $p = 0.8004$). However, there were significant main effects of host ($F_{1,19} = 6.88$, $p = 0.0172$) and generation ($F_{1,20} = 25.77$, $p < 0.0001$). Even though more eggs were laid in raspberry than in strawberry (see Table 1), the offspring were significantly more viable in strawberry (Table S3).

Relationship Between Fecundity and Survival Time

The results from the joint modelling of longitudinal oviposition and survival time indicated no significant effect of the three-way interaction between time, generation, and host (LR = 0.81, d.f. = 1, $p = 0.3678$), nor of the two-way interactions between generation and time (LR = 1.54,

d.f. = 1, p = 0.2145) or host and time (LR = 2.4, d.f. = 1, p = 0.1210). However, the interaction between generation and host was significant (LR = 6.53, d.f. = 1, p = 0.0106), as was the main effect of time (Wald test p < 0.0001). Since the time estimate was negative (–0.0197 with a standard error of 0.0043), we concluded that the oviposition rate decreased over time. For the survival part of the model, the interaction between generation and host was not significant (LR = 0.17, d.f. = 1, p = 0.6777), nor was the main effect of generation (LR = 1.04, d.f. = 1, p = 0.3073). However, the main effect of host was significant (LR = 6.82, d.f. = 1, p = 0.0090), which suggests that insects reared on raspberry survived longer. We conclude that high fecundity is associated with a lower mortality risk, i.e., a longer survival time on the fruit, given the negative estimate of the association parameter (–0.5608 with a standard error of 0.1476, Wald test p < 0.0001). The analysis of macronutrients shows us concentrations of lipid ($F_{3,8}$ = 1.11, p = 0.4010), protein ($F_{3,8}$ = 2.32, p = 0.1520), carbohydrate ($F_{3,8}$ = 0.19, p = 0.8950), and glycogen ($F_{3,8}$ = 0.51, p = 0.6880) did not differ significantly amongst individuals of the F1, F2, and F3 generations (Table S4).

Stability and Persistence Results

We will first recall some key mathematical definitions needed for the results described later in this section. For more detail on these and related results on nonlinear dynamical systems, matrix theory and persistence theory, the reader should consult Appendix 1 and the references therein.

An equilibrium or fixed point $x^\star$ of (2) is a solution of $x = A(x)x$. The equilibrium $x^\star$ is said to be stable if for any $\epsilon > 0$ there exists a $\delta > 0$ such that $|x_0 - x^\star| < \delta \implies |x(\mathrm{t}) - x^\star| < \epsilon$ for all t, where x_0 denotes the initial condition $x(0)$. If, in addition, there is some $R > 0$, such that $x(t) \to x^\star$ as $t \to \infty$ for any solution with $|x^0| < R$, the equilibrium is

locally asymptotically stable. If this holds for any $R > 0$, t is said to be globally asymptotically stable. If the equilibrium at the origin is (locally or globally) asymptotically stable, then $\lim_{t\to\infty} x(t) = 0$ the population asymptotically tends to extinction. The mathematical definitions of persistence, which we will now recall, characterize the opposite situation, where populations are maintained at some positive level asymptotically.

Given a nonlinear matrix model of form (2) with state space $\mathbb{R}_+^n$ we say that the system is uniformly weakly persistent with respect to a persistence function $\eta: \mathbb{R}_+^n \to [0, \infty)$ if, for each solution $x(t) = \left(x_1(t)\ x_2(t)\ \cdots\ x_n(t)\right)$, with initial condition $x(0) = x_0 \in \mathbb{R}_+^n$, such that $\eta(x_0) > 0$, there exists some $\epsilon > 0$, such that

$$\limsup_{t\to\infty} \eta\big(x(t)\big) > \epsilon.$$

The persistence function is typically some quantitative measure of population abundance, such as total size or the size on one patch for example. Intuitively, weak uniform persistence means that for any time $T > 0$, there is some $t > T$ for which the persistence measure exceeds ϵ. A stronger concept of persistence is that of uniform strong persistence, which is identical to the above definition apart from replacing the *limsup* with the *liminf*. Strong uniform persistence means that there is some $T > 0$ such that the persistence function exceeds ϵ for all later times $t > T$.

Model 1: Passive Dispersal

First, we consider the model (1) with local dynamics be given by the function

$$g_i(x_i) = R_i F_i S_i e^{-\alpha x_i} x_i \tag{3}$$

for $i = 1,2$. This function is commonly known in the theoretical ecology literature as the growth, recruitment, or fitness function (Chesson, 2012; Eager at al., 2012). Parameters R_i, S_i, $F_i > 0$ can be interpreted as respectively being the sex ratio, survival probability and fertility

on patch i, and $\alpha > 0$ the influence of density dependence (assumed to be equal for both patches). For this model, we assume both subpopulations move between patches by passive dispersal, that is the asymmetric dispersal parameters d_i are constants in $[0,1)$.

Local patch dynamics were inspired by Prout and McChesney (1985), who used a difference equation to describe intraspecific competition among an immature *D. melanogaster* population and ultimately how this affected adult fertility and survival. They assumed egg survival and fertility were decreasing functions of adult density. They also included a sex ratio of a half to represent the ratio of female to male eggs. We used a similar parametrization, but with constant survival and fecundity parameters. We then introduced a density dependent term $e^{-\alpha x_i}$ which describes the negative effect of density on the local growth rate for patch i.

We may write model (1) in standard nonlinear matrix form (2) with

$$A(x) = \begin{pmatrix} (1-d_1)R_1F_1S_1e^{-\alpha x_1} & d_2R_2F_2S_2e^{-\alpha x_2} \\ d_1R_1F_1S_1e^{-\alpha x_1} & (1-d_2)R_2F_2S_2e^{-\alpha x_2} \end{pmatrix} \quad . \tag{4}$$

The state space is given by $\mathbb{R}_+^2 = \{x \in \mathbb{R}^2 : x \geq 0\}$, consisting of all vectors $x = (x_1\ x_2)^T$ with nonnegative components and $A(x) \in \mathbb{R}^{2\times 2}$ is the (nonnegative) projection matrix (Cushing, 1998). Usually, matrix projection models are often considered when populations show a clear stage or age structure, like for example in models using Leslie matrices (Leslie, 1945), but we will use them to partition our population into two patch subpopulations, each with its own vital rates.

In the absence of dispersal the local dynamics on each isolated patch is given by (3). This is somewhat similar in form to a Ricker map (Ricker, 1954). The local recruitment function is unimodal and has a global maximum at $x_i = \frac{1}{\alpha}$. This implies that the maximum possible population size is $g_i\left(\frac{1}{\alpha}\right) = \frac{R_iF_iS_i}{e\alpha}$, and the population is bounded from reaching arbitrarily large values. Note that the unique nontrivial equilibrium $\hat{x}_i = \frac{\ln R_iF_iS_i}{\alpha} > 0$ if, and

only if, $R_iF_iS_i > 1$. It can also be seen from (3) that if $R_iF_iS_i < 1$, for $i = 1,2,$ then $x(t) \to 0$ as $t \to \infty$, so the population tends to extinction (on both patches) in this case.

Remark 1: A similar model form to (1) was considered by Vortkamp et al. (2020), who considered a single symmetric dispersal rate and local Ricker recruitment, subject to an Allee effect with threshold A. They found that on a local (per patch) scale, populations exhibited either eventual extinction or nontrivial bistability (existence of two positive stable equilibria). When dispersal was permitted, they found that within certain parameter ranges, dispersal gave rise to persistence of the population and stabilized the dynamics through the appearance and disappearance of what they call asymmetric attractors, where on one patch the population approaches periodic orbits above A and on the other patch, they approach periodic orbits below A. In the context of pest management, we are primarily interested in how the presence/absence of dispersal influences persistence over time and what drives the population on either patch to extinction (eradication). We are also interested in knowing if on either patch, both assumed to differ in nutritional quality, the subpopulations can persist even at low densities. This is a major concern in agricultural management, namely small numbers of individuals persisting on ephemeral low-quality habitat and then exhibiting rapid growth when favourable conditions arise (Reigada et al., 2018).

We first present a simple result on the asymptotic stability of the extinction equilibrium of system (2) with projection matrix given by (4). In the rest of the paper, $\rho(B)$ denotes the spectral radius of a square matrix B (see Appendix 1 for a formal definition). We refer the reader to Appendix 2 for proofs of the results presented below.

Proposition 1. Consider system (2) with $A(x)$ given by (4), $0 \leq d_1, d_2 < 1$ *and* α, $R_i, F_i, S_i > 0$ for $i = 1,2$. If $\rho\big(A(0)\big) < 1$, then $x(t) \to 0$ as $t \to \infty$ for any initial population $x(0)$ in $\mathbb{R}_+^2$.

It is well known that for any induced matrix norm, the spectral radius of B satisfies $\rho(B) \leq |B|$. As the l_1 induced matrix norm is given by the maximum of the column sums of a matrix, it follows that $\rho\big(\mathrm{A}(0)\big) < 1$ if all column sums of $\mathrm{A}(0)$ are less than 1. This implies that a sufficient condition for $\rho\big(\mathrm{A}(0)\big) < 1$ is

$$\mathrm{R_i F_i S_i} < 1, i = 1,2.$$

When this condition holds, Proposition 1 implies eventual extinction on both patches. The above condition could be interpreted as the patch populations having either low survival probabilities and fertility, high fertility but low survival probability or vice versa, which intuitively will lead to the eventual decline of the population.

In the next section, we consider a more realistic modification of this model that takes resource limitations into account and allows for density-dependent dispersal terms. We will study stability of the extinction equilibrium and present several results on persistence for the modified model.

Model 2: Density-Dependent Dispersal

We now modify our first model to allow for intraspecific competition for limited resources on each patch and to model dispersal as a density-dependent process. By assuming random asymmetric dispersal, we let the probability of remaining on patch i be given by $e^{-\mu_i x_i}$.

Using the general model form (1) we now let

$$g_i(x_i) = R_i F_i S_i e^{1-\frac{x_i}{K_i}} x_i \tag{5}$$

and

$$d_i = 1 - e^{-\mu_i x_i} \tag{6}$$

where K_i is the ith patch's carrying capacity. The full model then reads as

$$x_1(t+1) = x_1(t)e^{1-x_1(t)\left(\frac{1}{K_1}+\mu_1\right)}R_1F_1S_1 + x_2(t)e^{1-\frac{x_2(t)}{K_2}}\left(1-e^{-\mu_2 x_2(t)}\right)R_2F_2S_2$$
$$x_2(t+1) = x_2(t)e^{1-x_2(t)\left(\frac{1}{K_2}+\mu_2\right)}R_2F_2S_2 + x_1(t)e^{1-\frac{x_1(t)}{K_1}}\left(1-e^{-\mu_1 x_1(t)}\right)R_1F_1S_1.$$

In compact matrix form the model can be written as $x(t+1) = A\big(x(t)\big)x(t)$ with

$$A(x) = \begin{pmatrix} e^{1-x_1\left(\frac{1}{K_1}+\mu_1\right)}R_1F_1S_1 & e^{1-\frac{x_2}{K_2}}(1-e^{-\mu_2 x_2})R_2F_2S_2 \\ e^{1-\frac{x_1}{K_1}}(1-e^{-\mu_1 x_1})R_1F_1S_1 & e^{1-x_2\left(\frac{1}{K_2}+\mu_2\right)}R_2F_2S_2 \end{pmatrix} \tag{7}$$

As with our first model, the local dynamics of the decoupled system, with $\mu_i = 0$, is given by a modified Ricker equation

$$x_i(t+1) = g_i\big(x_i(t)\big) = x_i(t)p_i e^{r_i\left(1-\frac{x_i(t)}{K_i}\right)}$$

with $r_i = 1$ and $p_i = R_iF_iS_i$. Similar conclusions about local growth for the constant dispersal model also hold for this model, but the maximum now occurs at $K_iR_iF_iS_i$. We have a unique nontrivial equilibrium $\hat{x}_i = K_i(\ln(R_iF_iS_i)+1)) > 0$ if, and only if, $R_iF_iS_i > \frac{1}{e}$. Also note that, in the absence of dispersal, the condition $eR_iF_iS_i < 1$ implies extinction for the population on patch i for this model.

Remark 2: When $\rho\big(A(0)\big) = \max\{eR_1S_1F_1, \mathrm{e}R_2F_2S_2\} < 1$ the extinction equilibrium is locally asymptotically stable. This follows from Proposition 3.12 in (Smith and Thieme, 2011) (it can also be seen by linearization). For our first model formulation, with $A(x)$ given by (4), it can be readily seen that $A(x) \leq A(0)$ for all $x \geq 0$. This allowed us to conclude global asymptotic stability of the equilibrium at

the origin in Proposition 1. However, the condition $A(x) \leq A(0)$ does not hold for $A(x)$ given by (7) so we cannot immediately conclude global asymptotic stability for our second model.

For the remainder of this section, we consider what happens when $\rho\big(A(0)\big) > 1$, so local asymptotic stability of the extinction equilibrium is not guaranteed. It is worth noting at this point that $\rho\big(A(0)\big)$ (for $A(x)$ given by (7)) is greater than unity if $eR_iF_iS_i < 1$ and $eR_jF_jS_j > 1$, for $i \neq j$. A similar remark applies to the case where $A(x)$ is given by (4). This simple observation, combined with the results presented below, will show that dispersal can lead to patch persistence when its absence would result in extinction on a patch. This is akin to dispersal driven growth or what is known as Turing instability (Neubert at al., 2022; Guiver et al., 2017), whereby allowing dispersal prevents a previously declining and isolated population from going extinction, a somewhat similar concept to the so-called rescue effect in metapopulation theory (Hanski, 2008).

In our next result, we note that when the spectral radius of $A(0)$ is greater than 1 there exists a positive patch-coexistence equilibrium of (2), satisfying $F(x) = \mathrm{A}(x)x = x$. Here, the notation $x \gg 0$ means that all components of the vector x are positive.

Proposition 2. *Let* $A(x)$ be given by (7) where $\mu_i \geq 0$, $R_i, F_i, S_i > 0$ *for* $i = 1,2$. Let $F(x) = A(x)x$. Suppose that $\rho\big(A(0)\big) > 1$. Then there exists some $x \gg 0$ with $F(x) = x$.

In the following lemma, we show that for $A(x)$ given by (7), the system (2) is point dissipative (see the Appendix 1 for a formal definition). This simple fact is needed for the results on persistence that follow.

Lemma 1. Let $A(x)$ be given by (7) where $\mu_i \geq 0$, $R_i, F_i, S_i > 0$ for $i = 1,2$. Then there exists some $M > 0$ such that for any $x(0) \in \mathbb{R}_+^2$, $|x(t)|_1 \leq M$ for all $t \geq 1$.

The previous lemma is needed to establish the first of our main results.

Theorem 1. Let $A(x)$ be given by (7) where $\mu_i \geq 0$, $R_i, F_i, S_i > 0$ for $i = 1,2$. Suppose that $\rho\big(A(0)\big) > 1$. Then, there exists some $\epsilon > 0$ such that for a solution of (2),

$$|x(t)|_1 > 0 \Longrightarrow \liminf_{t\to\infty} |x(t)|_1 \geq \epsilon.$$

So, when $\rho\big(A(0)\big) > 1$ system (2), with projection matrix given by (7), is uniformly strongly persistent with respect to the total population size across the two patches, as measured by the l_1 norm of x. We will next show that a stronger result than Theorem 1 is possible, as the system (2) with $A(x)$ given by (7) is also strongly positive (see Appendix 1 for a definition).

Lemma 2. Let $A(x)$ be given by (7) where $\mu_i \geq 0$,, $R_i, F_i, S_i > 0$ for $i = 1,2$. Then for any $x \in \mathbb{R}_+^2 \backslash \{0\}$, $A(x)x \gg 0$.

Lemma 2 implies that $F(x) = A(x)x$ is strongly positive and that $\mathbb{R}_+^2 \backslash \{0\}$ is forward invariant under F, i.e., trajectories that begin inside the positive orthant remain there for all time. With these observations, we can now establish the following result.

Theorem 2. Let $A(x)$ be given by (7) where $\mu_i \geq 0$, $R_i, F_i, S_i > 0$ for $i = 1,2$. Let $\tilde{\eta}(x) = \min\{x_1, x_2\}$. Suppose that $\rho\big(A(0)\big) > 1$. Then, there exists some $\epsilon > 0$ such that

$$\liminf_{t\to\infty} \tilde{\eta}(x(t)) \geq \epsilon$$

for any solution with $x(0) \in \mathbb{R}_+^2 \backslash \{0\}$.

Remark 2: Theorems 1 and 2 guarantee strong persistence for both patches. Locally a sink population may become extinct in the absence of immigration or source patches, but dispersal can allow the overall population the opportunity to persist. For fast-growing species with short life cycles and for those that exhibit irruptive dynamics, like for example insect species, populations can reach (and exceed) their carrying capacity very quickly, likely leading to high intraspecific competition and density dependent dispersal (Powell and Bentz, 2014; Goodsman et al., 2017).

Remark 3: Low quality habitat (sinks) that are distributed among higher quality habitat (sources) can limit the movement of organisms in space, so identifying the mechanisms that limit growth can vary between habitat types (Heinrichs et al., 2016). Our simple modelling approach suggests that dispersal and demographic effects are potential drivers of population persistence of *D. suzukii*. It is for this reason that modelling population dynamics within a spatial framework can provide new qualitative insights into the mechanisms that drive source-sink dynamics.

Numerical Simulations and Bifurcation Diagrams

We simulated our carrying capacity model for t = 40 generations, using the parameter estimates obtained from the experimental procedure (see Figure 3). These estimates are given in Table 2 below. Survival and fertility parameters were empirically estimated from experiments and dispersal parameters obtained from the literature. We assumed a sex ratio of a half as this accurately reflects the ratio in the models of Prout and McChesney (1985). An estimate for α for the first model was obtained from Prout and McChesney (1985), who used a density dependent term of 0.0064 (the sum of f and s, the sensitivity parameters for fertility and survival respectively). To reflect asymmetric dispersal, we used two different density-dependent

dispersal terms. As we have no empirical estimates for density-dependant dispersal for each patch we set $\mu_i \in \left\{\alpha, 2\alpha, \frac{\alpha}{2}\right\}$ with $\alpha = 0.0064$ and $\mu_i \neq \mu_j$, for $i = 1,2$.

By varying the levels of μ_i we saw no qualitative difference in model dynamics, although the rate of oscillations seems to depend on the rate of dispersal. It can be seen in Figure 3 that populations gradually approach a positive steady state, but this is non-monotonic. The demographic parameters considered (Table 2) determine the conditions for the existence of a patch coexistence equilibrium, independent of $\mu_i \in \left\{\alpha, 2\alpha, \frac{\alpha}{2}\right\}$. It can be observed that $\rho\big(A(0)\big) = e(R_1S_1F_1 + R_2F_2S_2) \approx 10.662 > 1$ and so by Proposition 2 we have existence of a positive equilibrium. We have not explored the stability and uniqueness of this fixed point but instead have derived conditions for our population projection matrix that ensures we have both weak and strong persistence. Different methods have been proposed to analyze the sensitivity of parameters in population growth models. Among the approaches used for sensitivity analysis, bifurcation analysis stands out. Bifurcation analysis aims to evaluate the stability properties of steady states under parameter variation. This is particularly useful for investigating the association of ecological patterns of oscillation in populations with changing values of demographic parameters. This approach allows one to quantify the contribution from changes in parameter values to changes in model outputs (Van Voorn and Kooi, 2017).

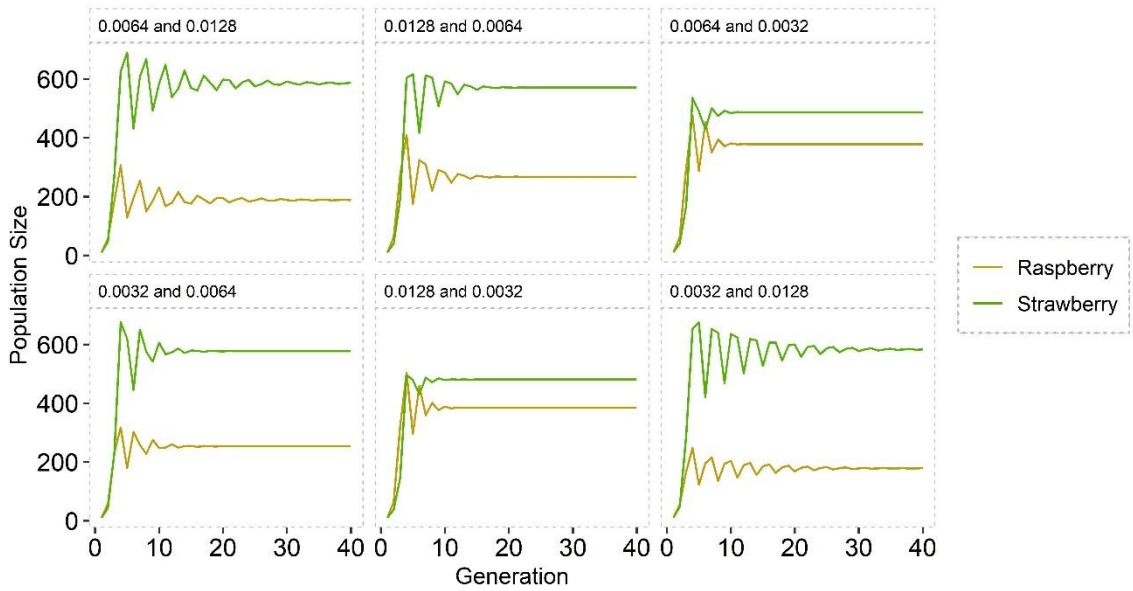

Figure 3 Simulations of carrying capacity model over 40 generations, using six different combinations of $\mu_i \in \left\{\alpha, 2\alpha, \frac{\alpha}{2}\right\}$, for i = 1,2 and $\alpha = 0.0064$, where both patches have different parameter values. Each simulation resulted in both patch populations approaching a positive fixed point/equilibrium after initial transient oscillations. Other model parameters are given in Table 2.

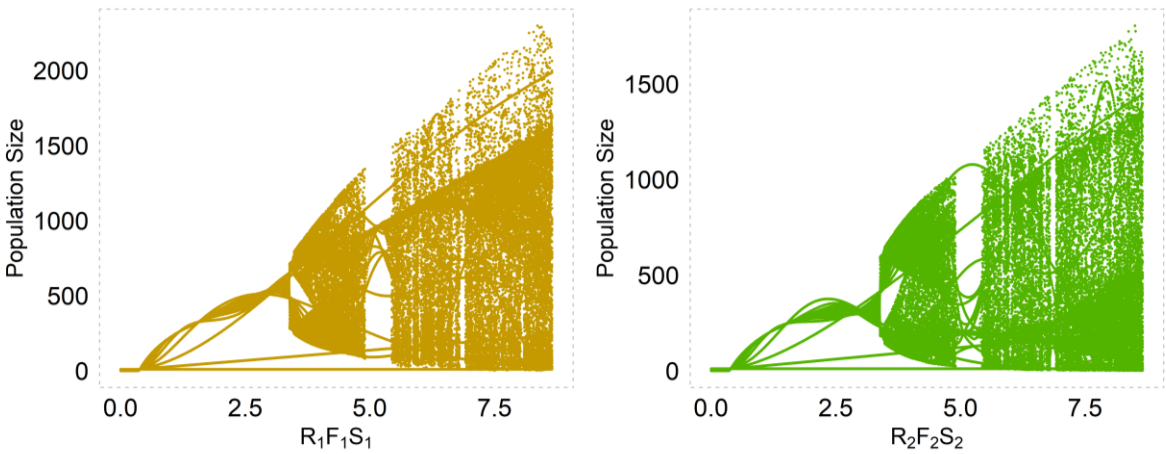

Figure 4 Bifurcations diagrams with $R_iF_iS_i$ (i = 1,2) for x_1 (left) and x_2 (right) using local Ricker recruitment, with parameters specified in Table 1, $\mu_1 = 0.0064$ and $\mu_2 = 0.0128$.

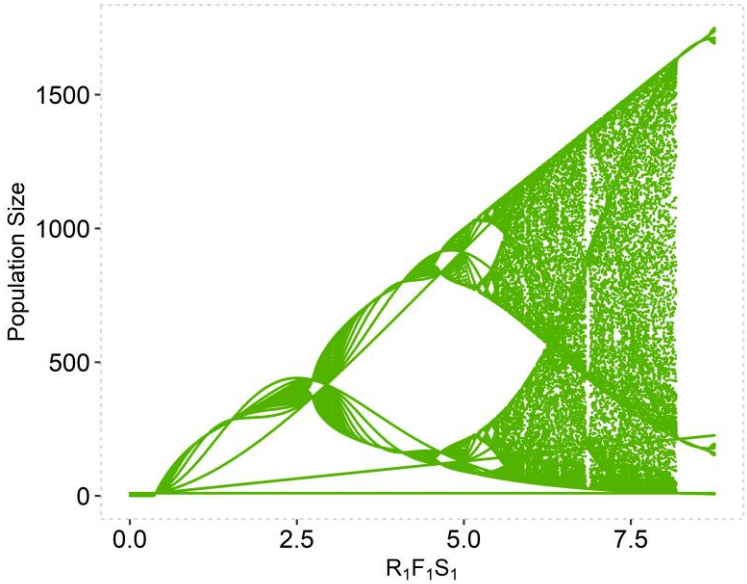

Figure 5 Bifurcations diagram with $R_1F_1S_1$ for x_1 using local Ricker recruitment, with parameters specified in Table 1.

The first period doubling bifurcation in Figure 4 seems to occur at similar values for both patch populations and before this we see a general increase in population sizes, which suggests that some regulatory processes must occur after initial increases in density limiting the subpopulations intrinsic growth. In the bifurcation diagram for the coupled model (Figure 5) we observe various changes in the stability of equilibria, which suggests that the coupled dynamics have more emergent complex behaviours than the isolated Ricker type dynamics.

Mathematical models of ecological systems are usually expressed with differential and/or difference equations with variables describing population sizes and parameters, which can be influenced by environmental conditions or demographic effects. Bifurcation diagrams emerge from relationships between parameter values and population sizes (Dercole & Rinaldi, 2012).

Table 2 Parameter estimates for carrying capacity model. Demographic parameters were estimated from experimental procedure and dispersal parameters obtained from the literature.

Parameter	R_1	S_1	F_1	R_2	S_2	F_2	K_1	K_2	α
Estimate	0.5	0.335	9.43	0.5	0.216	21.7	200	300	0.005

Usually, the parametric space on the one axis determines significant changes on the other axis, expressing long-term population behaviour. As a result of this relationship, it is possible to observe stable trajectories, limit cycles with fixed maximum and minimum limiting values and chaos, a regime characterized by total unpredictability, that is, by the absolute absence of fixed cycles (Luque et al., 2011). For our extended model we obtained bifurcation diagrams for varying $R_iS_iF_i$ and μ_i for i = 1,2 (see Figure 4). We chose the product of the demographic parameters as they play an important role in determining conditions for persistence and the presence of a positive equilibrium. The narrow range within the parameter space of the (μ_1, μ_2) shows how sensitive density-dependent dispersal is. We can see a large convex area (dark green) where limit cycles have period greater than 32. As we increase both μ_1 and μ_2 we approach stable trajectories, which correspond to more density dependent effects on individuals who remain on each patch. This may be because $R_iF_iS_i \gg 0$ (for i =1,2) and so $\rho\big(A(0)\big) > 1$, meaning subpopulations may have higher survival probabilities or increased fertility on their respective patches. Each patch also has a nonzero influx/outflow of individuals to/from it and this may permit sufficient genetic mixing, with dispersal being one of the main drivers of genetic variation in insect species (Raymond et al., 2013).

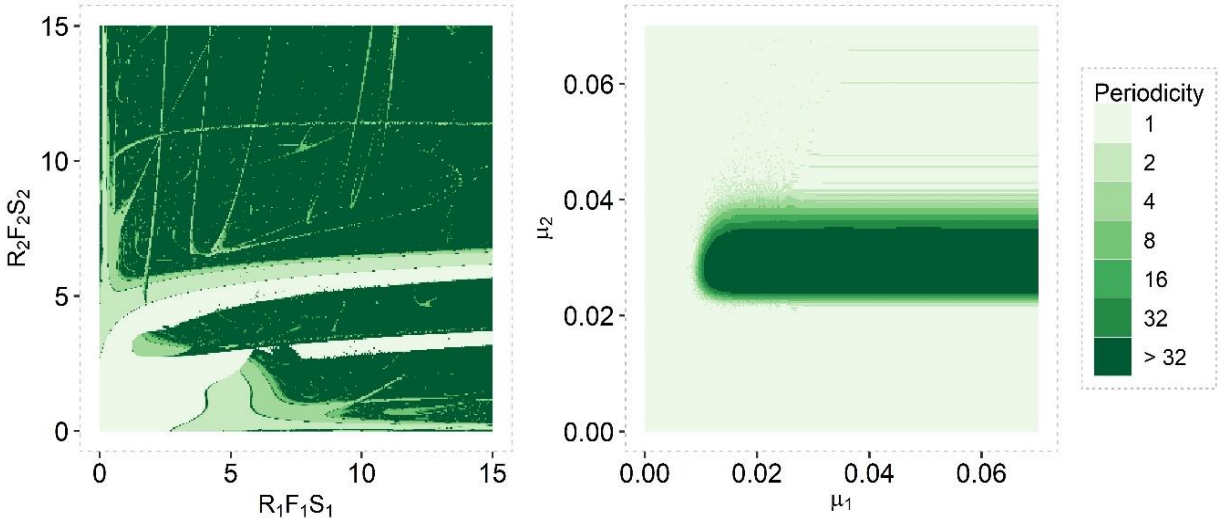

Figure 6 Bifurcation diagrams for the parameter product $R_iS_iF_i$ (left) and μ_i $(right)$ for $i = 1,2$, showing the number of unique population sizes according to the colour gradient (stability for values of 1 and limit cycles for higher values than 1). We considered the last 100 observations after iterating our carrying capacity model for 1000 generations**.** Initial conditions where (10, 10) for both. Note that we only show bifurcation diagrams for patch 1 as the diagrams are identical for patch 2.

In Figure 6 as we increase both parameter values, more complex dynamic behaviour occurs. Using the bifurcation diagram in Figure 6 (left) we simulated trajectories for 4 different points that correspond to varying limit cycle periodicity (see Figure 7). Within a narrow range of the parameter space trajectories seem to approach a stable fixed point, the uniqueness of which is undetermined. But as we allow demographic parameters to reach values above 5, trajectories are quite unpredictable, in that the period of these limit cycles begin to get larger than 32. Many models exhibit complex changing behaviour like that seen in Figure 6, as for some parameter values the dynamics can be quite smooth but changing them can lead to indefinite oscillations and sometimes even deterministic chaos (May, 1995).

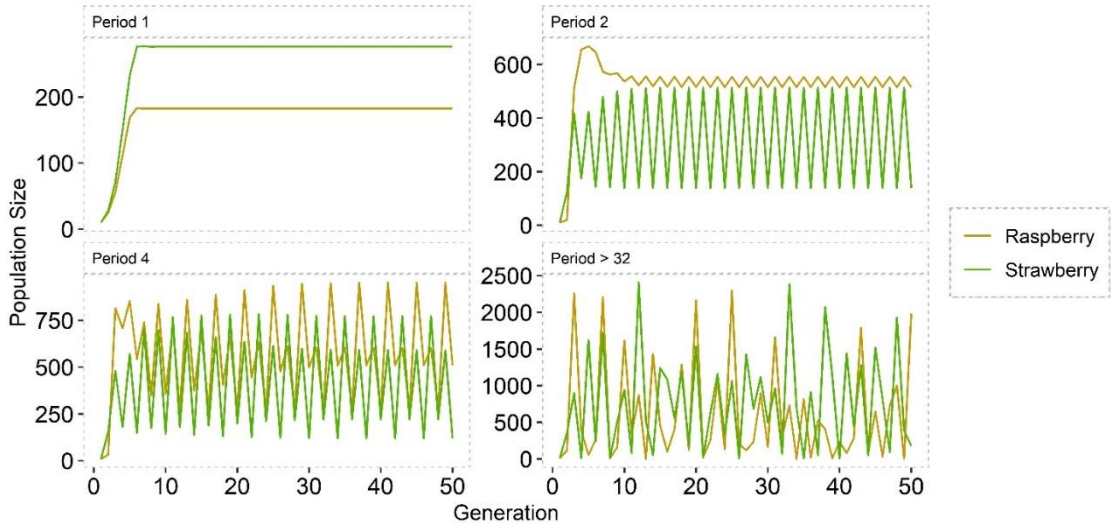

Figure 7 Patch dynamics of flies on strawberry (grey) and raspberry (green) patches with initial conditions (10, 10), showing the influence of the $R_iS_iF_i$ parameter space with $\mu_1 = 0.0064$ and $\mu_2 = 0.0128$. Periods refer to the period of the limit cycle simulations. The top left graph shows trajectories tending to a positive fixed-point/equilibrium for both *D. suzukii* populations ($R_1S_1F_1$ = 1, $R_2S_2F_2$ = 1). The top right graph indicates a two-point limit cycle ($R_1S_1F_1$ = 5, $R_2S_2F_2$ = 0.5) and the bottom graphs show a 4-point limit cycle ($R_1S_1F_1$ = 6.25, $R_2S_2F_2$ = 1) and > 32 point limit cycle ($R_1S_1F_1$ = 14, $R_2S_2F_2$ = 4). Increasing both values of $R_iS_iF_i$ seems to show loss of stability for longer than 30 generations (bottom right graph) but then after transient oscillations the population approaches a nontrivial equilibrium.

Discussion

No-choice and choice tests are frequently used to evaluate the host and/or prey range of insects (Faria et al., 1999; Van Driesche & Murray 2004; Diepenbrock et al., 2016). Studies comparing choice with no-choice conditions have found that insects undergo important changes in behaviour, mainly in new areas they occupy. In our experiments, the results of the no-choice change of fruits showed that the quality of the food source impacted fecundity, period of oviposition and proportion of viable populations for *D. suzukii*, thus rejecting hypotheses 1 and 2. When exploiting resources in crop edges with different host plants, insects in extensive monocultures have little resource choice. In these circumstances, knowledge of the

performance and adaptive potential of invading species is desirable, because successful invaders can become major pests at high densities.

The response of the biological parameters to this host shift showed that disturbances mainly affect the proportion of nutrients necessary to allow immature individuals to develop, as already shown for other *Drosophila* species (Lee, K.P. et al., 2008; Matavelli et al., 2015; Rodrigues et al., 2015). The change in this nutrient proportion, even evaluated indirectly as in the present study, helps to understand the changes in ecological viability of a species.

In the present study, the high number of eggs of *D. suzukii* found in the second generation, for insects reared on strawberry, may reflect their parental nutritional conditions, as insects of one generation that feed on good-quality host plants are likely to successfully produce subsequent filial generations (Matzkin et al., 2013). Even though the control group, i.e., (raspberry), produced a high number of eggs, the egg-adult proportion was high in the group fed on strawberry. This could be explained by both the high number of eggs in food with good nutritional quality, which can increase competition for resources for example (Hardin et al., 2015) and, in the group impacted by a change in food quality, the high viability seems to indicate maximum resource use of the offspring, i.e., a trade-off. In adverse environmental conditions, the reproductive cost to individuals may change to compensate for impaired fitness, resulting in trade-offs between reproduction investment and adult survival (Stearns, 1989). For *D. suzukii*, strategies involving offspring number and viability in conditions of host shift have not been previously described.

The negative impact of biological parameters could not be explained by the intake of macronutrients, not rejecting hypothesis 3. A possible explanation is the diversity of the microbiota associated with these insects, since symbiotic bacteria can help their insect host to assimilate nutrients (Shin et al., 2011; Sommer & Newell, 2018; Su et al., 2013). The diversity of symbionts can drastically affect assimilation of nutrients, which changes with environmental

conditions and with corresponding changes to the host food source (Obadia et al., 2018; Yun et al., 2014; Guidolin & Cônsoli, 2017), even at optimal nutrient ingestion. Therefore, the development of polyphagous insects may be effected by different factors acting together, including endosymbiosis, as shown for *D. melanogaster* (Shin et al., 2011) and *D. suzukii* (Bing et al., 2018).

The results for the joint modelling for *D. suzukii*, considering the association parameter, indicate that fecundity can be related to the risk of mortality. Interest in joint models has recently increased, especially for studying the association between longitudinal and time-to-event processes (Alsefri et al., 2020). This approach makes it possible to analyse the risks involved in an interacting/feedback system, particularly the relationship between fecundity and population mortality, as in the current study.

The present study was conducted on an ecological temporal scale, and the data on the influence of host-shift were evaluated over two generations. The dispersal model employed in this study arose from a classical metapopulation perspective, proposed to analyse the dispersal of insects between finitely many patches (Hanski & Gaggiotti 2004, Moretti et al., 2013, Dey & Joshi, 2018). Mathematical models of population growth coupled by migration or dispersal have often been used to analyse population stability by employing the use of bifurcation diagrams (Ruxton, 1996; Moretti et al, 2013; Pal et al., 2018). Values of demographic parameters and dispersal rates generally have a strong association with the stability of population equilibria (Moretti et al., 2013; Pal et al., 2018; Cheng et al., 2019).

Dispersal has been suggested as a possible stabilising mechanism for populations that inhabit local sinks, through what has been termed dispersal driven growth (DDG) (Guiver et al. 2017). Our model results further support this hypothesis for spatially structured populations, by showing that dispersal may rescue a species from extinction, even when fertility and survival probabilities are low on one of the patches, i.e., patch populations have low local fitness. In

model simulations (see Figure 3) we found that, including density dependent dispersal and intraspecific competition, trajectories approach a (seemingly) stable nontrivial equilibrium. It must be kept in mind that these simulations excluded demographic or environmental stochasticity and so although our final deterministic model ‘skeleton’ seems to approach a positive fixed point after some time, these somewhat smooth dynamics might oscillate significantly, and may even get arbitrarily close to the basin of attraction of the extinction equilibrium (Hastings et al., 2021).

In the context of pest control the opposite of DDG is usually desired (Mazzi and Dorn, 2012), and so our results show that the disruption of common dispersal events could be a mechanism to prevent long term population persistence. DDG is an important means for preventing extinction, especially for populations that are dispersing in the absence of external immigration, from matrix habitat or marginal source patches, like for example in agricultural landscapes (Duelli and Obrist, 2003). Ephemeral patch dynamics, whereby patches are sequentially restored and destroyed, play a significant role in allowing pest populations that undergo pulsed dispersal to persist (Reigada et al., 2015). Even in the presence of control strategies, such as the use of pesticides or the introduction of natural enemies, pests may exhibit what is referred to as the hydra effect, whereby increasing their mortality rate results in a positive contribution to population growth (McIntire and Juliano, 2018; Costa and dos Anjos, 2018).

Knowing the potential consequences that host shift and biocontrol have on the persistence of crop pests is then vital for food security and for understanding mechanisms of controlling invasions (Bernal and Medina, 2018). By including spatial structure in models of herbivore pest dynamics, managers may have the opportunity to determine what series of patches contribute to overall decline/growth of a population (James et al., 2015). Not only does this afford one to know the direct effects of dispersal on a focal host plant, but it also could

help one understand the indirect role that pest control could have on adjacent natural matrix habitats (Rand, Tylianakis and Tscharntke, 2006). Our models demonstrate that in the absence of dispersal, and under certain constraints on parameter values, subpopulations on both patches will go extinct. But when dispersal is allowed between patches, we have shown that both uniform strong persistence and patch-persistence can arise, given that the spectral radius of the population projection matrix is greater than unity. When this occurs, we have also found the existence of a positive steady state. The stability properties of this fixed point is not known but simulations suggest that populations asymptotically approach this (seemingly unique) fixed point, following transient oscillations around it. For brevity we have excluded analysis to determine equilibria stability, as persistence is known as a more robust condition that is commonly used to understand a model's qualitative properties (Jansen and Sigmund, 1998). Ultimately our models suggest that dispersal is a vital mechanism by which populations can persevere in a spatial context and inhibiting dispersal, even between two patches (the simplest spatial case), could have significant consequences for the longevity of patchy populations.

The bifurcation analysis performed in this study showed regions of stability and instability in the parametric spaces of the product of fecundity, survival and sex ratio. The limit of the values investigated in the bifurcation diagrams are compatible with real values obtained in our experiments. The instability of both populations of *D. suzukii* in general can tend to occur with higher values of the parameters, with exceptions. Among the factors capable of changing the population stability in drosophilids, density, competition, food quality, fecundity and migration stand out (Tung et al., 2018).

Studies that emphasise the relationship of demographic parameters with the stability of equilibria has long been discussed (Ruxton, 1996; Moretti et al, 2013; Pal et al., 2018; Cheng et al., 2019). There are compensatory mechanisms that can explain the relationship between life history and the demographic parameters involved in the growth rate and carrying capacity,

which suggests possible compensations for populations in low and high densities, as already investigated in *D. melanogaster* (Mueller & Ayala, 1981).

The availability of food resources can determine the formation of high densities per unit of food substrate in insects and consequently trigger intraspecific competition for food (Hardin et al., 2015), which negatively influences the magnitude of demographic parameters associated with population growth and equilibrium (Klomp, 1964; Johst; Berryman & Lima, 2008). High survival and fecundity values are generally associated with limit cycles and can even produce deterministic chaos (Johst; Berryman & Lima, 2008). Polyphagous insects such as *D. suzukii* can resort to fruit exchange because of the fly density on the fruit that has been initially exploited (Hardin et al., 2015; Olazcuaga et al, 2019) and the changing conditions of a food source can thus enhance competition between flies on a per-patch level.

As revised in Dey & Joshi (2018), migration associated with food source can also interfere with the stability of a population. They tested different quantities of adults migrating between patches and concluded that the effect on persistence and constancy of the population can be altered by quality of food and immigration rate between patches. Considered in an applied scenario, the movement of pests between different patches can result in damaging economic losses. In pest control programs the aim is to present actions that maintain the density of pests in an equilibrium level below damaging economic thresholds (Zhang et al, 2018; Wieser et al, 2019; Bryant et al, 2020), so the analysis of parameter values that lead to the loss of stability, resulting in unpredictable population outbreaks, has an unquestionable utility for integrated pest management strategies (Costa & Faria, 2010). The ecological interactions between different species of drosophilids and their varied food sources have been systematically studied in the past (Buruga & Olembo 1971), due to the importance of these species in attacking ripening fruit. Considering the modified structure of the ovipositor of *D. suzukii* females (Atallah et al. 2014) and the expression of genes associated with

chemoreceptors (Crava et al. 2016), the strong response to the food source (fruit host in particular) becomes apparent. The ability of *D. suzukii* to pierce the integument of still-healthy fruits makes it a harmful pest, and therefore, plant host-shift is highly important in commercial fruit growing. Future extensions to the models proposed in this paper could include stage structure, like that of the infamous LPA model (Dennis et al., 2001), in order to deduce what stages of development may affect host shift and population growth. The empirical and theoretical results obtained in this study furthers the understanding of host-shift, it's possible ecological mechanism and biological consequences for *D. suzukii*, in particular when different host fruits are available.

Appendix 1

Definitions and Notation

$\mathbb{R}^{n\times n}$ denotes the space of all real positive square matrices of dimension n and $\mathbb{R}^n$ the usual n-dimensional real Euclidean space.

Given an $n \times n$ matrix $A \in \mathbb{R}^{n\times n}$, the **spectrum** $\sigma(A)$ of A is the set of all eigenvalues of A. The **spectral radius** of A is

$$\rho(A) \triangleq \max\{|\lambda|: \lambda \in \sigma(A)\}$$

For $x \in \mathbb{R}^n$ we define the l_p vector norm as

$$|x|_p \triangleq \left(\sum_1^n |x_i{}^p|\right)^{\frac{1}{p}}$$

and the matrix norm induced by the l_p norm as

$$|A|_p \triangleq \sup_{|x|_p=1}\{|Ax|_p\}.$$

We mainly work with the $l_1$norm here. We use the same notation $|\cdot|$ for both the vector and matrix norms. This should not cause confusion as we use lowercase letters for vectors and uppercase letters for matrices.

A system of the form (2) is said to be **point-dissipative or ultimately bounded** if there is some $M > 0$ such that for all $x(0) \in \mathbb{R}_+^n$, there exists some $T > 0$ such that $|x(t)| \leq M$ for all $t \geq T$.

We next recall the notion of *strong positivity* for the function $F(x) = A(x)x$ from Smith and Thieme (2011). $F^m = F \circ F \circ \cdots \circ F$ (m times) is the m-fold composition of the function F with itself, for m a positive integer.

A function $F: \mathbb{R}_+^n \to \mathbb{R}_+^n$ is said to be **strongly positive** if for all $c > 0$ there exists some positive integer $t > 0$ such that $F^t(x) \gg 0$ for all $x \in \mathbb{R}_+^n$ with $0 < |x(t)| \leq c$.

A matrix $B \in \mathbb{R}^{n\times n}$ is said to be **irreducible** if there is no proper subset $I \subset \{1, .. n\}$ for which $b_{ij} = 0$ for all $i \in I, j \in \{1, \dots, n\} \backslash I$.

Perron-Frobenius Theorem (Horn and Johnson, 1989): If a nonnegative matrix A is irreducible, then $\rho(A) > 0$ and there exists unique positive right and left eigenvectors corresponding to $\rho(A)$.

It follows from the above theorem that for A $\in$ $\mathbb{R}^{n\times n}$ nonnegative, n $\geq$ 2, $\rho(A) < 1 \Leftrightarrow \exists$ some vector v $\gg 0$ in $\mathbb{R}^n$ such that $Av \ll v$.

Relevant Results From Smith and Thieme (2011)

We recall here the most relevant facts from the reference (Smith and Thieme (2011)) in this section. Throughout, unless stated otherwise, $F(x) = A(x)x$ is a nonlinear matrix function such as appears in the system definition (2).

Theorem A1 (Theorem 7.5 in (Smith and Thieme (2011)): Let $F: \mathbb{R}_+^n \to \mathbb{R}_+^n$ be continuous and assume that there exists $R > 0$, $y \in \mathbb{R}_+^n$ and some nonnegative matrix D such that $\rho(D) < 1$ and

$$F(x) \leq y + Dx$$

for $x \in \mathbb{R}_+^n$ and $|x| \geq R$. Also let F be differentiable at 0, $F'(0)$ be nonnegative, and $\rho\big(F'(0)\big) > 1$. Then for $F(x) = A(x)x$ there exists some nonzero $x \in \mathbb{R}_+^n$ such that $F(x) = x$.

Theorem A2 (Theorem 7.9 in (Smith and Thieme (2011)): Let $F: \mathbb{R}_+^n \to \mathbb{R}_+^n$ be a differentiable mapping. Suppose that:

1. $\mathbb{R}_+^n \backslash \{0\}$ is forward invariant under F.

2. There exists $r_0 > 1$ and $v \gg 0$ such that $A_0^* v \geq r_0 v$, where $A_0 = F'(0)$ and A_0^* denotes its transpose.

3. The system (2) defined by F is point-dissipative.

Then system (2) is uniformly η-persistent for $\eta(x) = |x|$ where $|\cdot|$ is any norm on $\mathbb{R}_+^n$.

In the following result, we use the notation $x(t, x_0)$ to denote the solution of the system (2) at time t corresponding to the initial condition x_0.

Theorem A3 (Theorem 7.15 in (Smith and Thieme (2011)): Suppose 1-3 from Theorem A2 hold, and F is strongly positive. Let $\hat{\eta}(x) = \min_i x_i$. Define

$$X_0 \triangleq \left\{x_0 \in \mathbb{R}_+^n : \hat{\eta}\big(x(t, x_0)\big) = 0, t = 0,1,2, \cdots\right\}.$$

Then there exists some $\epsilon > 0$ such that

$$\liminf_{t \to \infty} \hat{\eta}\big(x(t)\big) \geq \epsilon$$

for any solution of (2) with $x(0) \in \mathbb{R}_+^n \backslash X_0$.

Appendix 2

Proofs

Proof of Proposition 1: As $e^{-\alpha x_i} \leq 1$ for $x_i \geq 0$, $i = 1,2$, $A(x) \leq A(0)$ for all $x \geq 0$ in $\mathbb{R}^2$. It now follows that for any $x(0) \in \mathbb{R}_+^n$,

$$x(t) = A\big(x(t-1)\big)A\big(x(t-2)\big)\cdots A\big(x(1)\big)A\big(x(0)\big)x(0) \leq A(0)^t x(0).$$

As $\rho\big(A(0)\big) < 1$, $A(0)^t \to 0$ as $t \to \infty$ and the result follows.

Proof of Proposition 2: First note that for $x \geq 0$

$$F(x) = \begin{pmatrix} e^{1-x_1\left(\frac{1}{K_1}+\mu_1\right)} R_1F_1S_1x_1 + e^{1-\frac{x_2}{K_2}}(1-e^{-\mu_2 x_2})R_2F_2S_2x_2 \\ e^{1-\frac{x_1}{K_1}}(1-e^{-\mu_1 x_1})R_1F_1S_1x_1 + e^{1-x_2\left(\frac{1}{K_2}+\mu_2\right)} R_2F_2S_2x_2 \end{pmatrix}.$$

It can be seen that $e^{1-\frac{x_i}{K_i}}(1-e^{-\mu_i x_i})x_i \leq K_i \; and \; e^{1-x_j\left(\frac{1}{K_j}+\mu_j\right)}x_j \leq K_j$ for $x_i \geq 0$, $i \neq j$ and $i, j = 1,2$. And so, it is easy to see that there exists $y \gg 0$ with $F(x) \leq y$ for all $x \in \mathbb{R}_+^n$. As F is continuous and $F'(0) = A(0)$ is irreducible, it follows from Theorem A1 that there exists some $x \in \mathbb{R}_+^n \backslash \{0\}$ with $F(x) = x$. Now note that $A(x)$ is strictly positive which immediately implies that $x \gg 0$.

Proof of Lemma 1: First note that for $x(0) \in \mathbb{R}_+^n$ this implies $x(t) \in \mathbb{R}_+^n$ for all $t \geq 0$. Thus the l_1 norm of $x(t)$ is given by $\mathbf{1}^T x(t)$. Moreover, for any $t \geq 1$, $x(t) = A\big(x(t-1)\big)x(t-1)$ for some $x(t-1) \in \mathbb{R}_+^n$. From the form of $A(x)$, we can see that for $x = (x_1 \quad x_2)^T$,

$$\mathbf{1}^T A(x) = \left(R_1F_1S_1e^{1-\frac{x_1}{K_1}} \quad R_2F_2S_2e^{1-\frac{x_2}{K_2}}\right).$$

Hence

$$|A(x)x|_1 = x_1R_1F_1S_1e^{1-\frac{x_1}{K_1}} + x_2R_2F_2S_2e^{1-\frac{x_2}{K_2}}.$$

As $x_i e^{-bx_i} \leq (be)^{-1}$, if we let $b = \frac{1}{K_i}$ we have

$$x_i e^{-\frac{x_i}{K_i}} \leq K_i (e)^{-1} \Leftrightarrow x_i e^{1-\frac{x_i}{K_i}} \leq K_i \ \forall \ x \geq 0.$$

Therefore

$$|A(x)x|_1 = x_1 R_1 F_1 S_1 e^{1-\frac{x_1}{K_1}} + x_2 R_2 F_2 S_2 e^{1-\frac{x_2}{K_2}}$$
$$\leq \ R_1 F_1 S_1 K_1 + \ R_1 F_1 S_1 K_2$$

As our solution $x(t)$ is of the form $A(x)x$ for any $t \geq 1$, this proves the lemma with $M = R_1 F_1 S_1 K_1 + R_2 F_2 S_2 K_2$.

Proof of Theorem 1: First note that it follows from the form of $A(x)$ that $x > 0$ implies $A(x)x \gg 0$ so it is certainly true that $\mathbb{R}_+^n \backslash \{0\}$ is forward invariant. Also $\rho\big(A(0)\big) > 1$ implies that $\rho(A(0)^T) > 1$ so there exists some $v \gg 0$ with $A(0)^T v \gg v$. This implies that we can choose $r_0 > 1$ with $A(0)^T v \geq r_0 v$. Finally, Lemma 1 implies that the system defined by $F(x) = A(x)x$ is point dissipative. The result now follows immediately from Theorem A2.

Proof of Theorem 2: $F(x) = A(x)x$ is strongly positive and $\mathbb{R}_+^n \backslash \{0\}$ is invariant under F. It follows from Lemma 1 that the system (2) is point-dissipative. Note that $F'(0) = A(0)$ and if $\rho\big(A(0)\big) > 1$, then $\rho(A(0)^T) > 1$ so there exists some $v \gg 0$, $r_0 \geq 1$ with $A(0)^T v \geq r_0 v$. This follows from Perron-Frobenius Theorem (Horn and Johnson, 1989). The result now follows immediately from Theorem A3. This implies patch-persistence when $\rho\big(A(0)\big) > 1$.

Appendix 3

Tables

Table S2 Mean oviposition period ± standard error (s.e.) in days, for each generation and host. Means followed by the same letter do not differ statistically.

Generation	Mean ± s.e.	Host	Mean ± s.e.
F1	15.20 ± 2.86 a	*Raspberry*	27.56 ± 2.69 a
F2	17.90 ± 3.94 a	*Strawberry*	5.17 ± 1.20 b

Table S3 Means ± standard errors (s.e.) of the percentage of viable eggs for generations and hosts. Means followed by the same letter do not differ statistically.

Generation	Mean ± s.e.	Host	Mean ± s.e.
F1	16.91 ± 5.14 b	*Raspberry*	21.60 ± 3.49 b
F2	32.10 ± 5.88 a	*Strawberry*	33.47 ± 14.69 a

Table S4 Mean macronutrient concentrations (µg/µL) ± standard errors for each generation.

Generation	Macronutrient			
	Lipid	Protein	Carbohydrate	Glycogen
F1 – raspberry	10.43 ± 0.1075 a	0.13 ± 0.0064 a	0.02 ± 0.0066 a	0.03 ± 0.0148 a
F2 – raspberry	10.37 ± 0.0756 a	0.13 ± 0.0061 a	0.02 ± 0.0003 a	0.04 ± 0.0074 a
F3 – raspberry	10.27 ± 0.0563 a	0.12 ± 0.0049 a	0.02 ± 0.0014 a	0.05 ± 0.0123 a
F3 – strawberry	10.43 ± 0.0399 a	0.14 ± 0.0074 a	0.02 ± 0.0020 a	0.03 ± 0.0117 a

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The authors declare that they have no conflict of interest.

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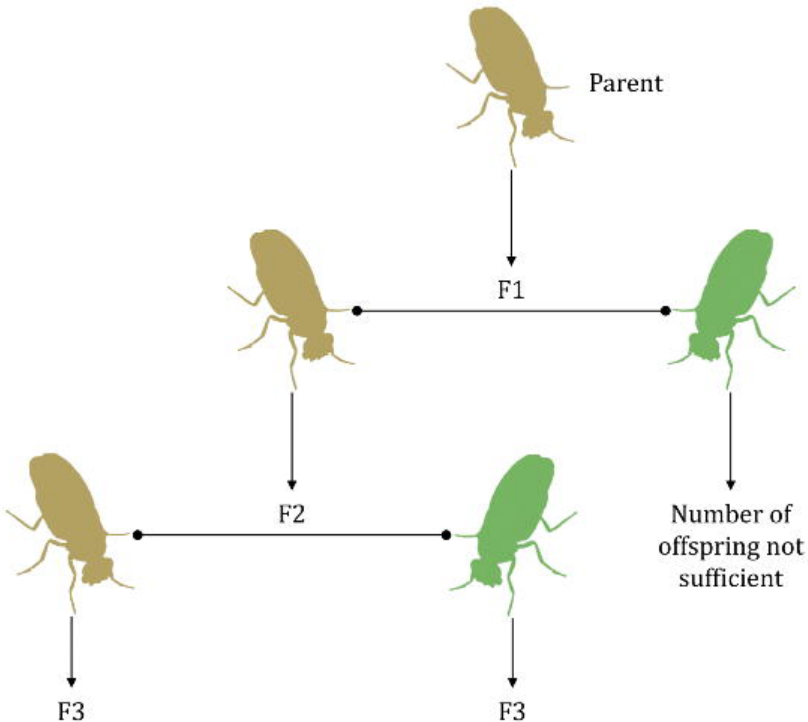
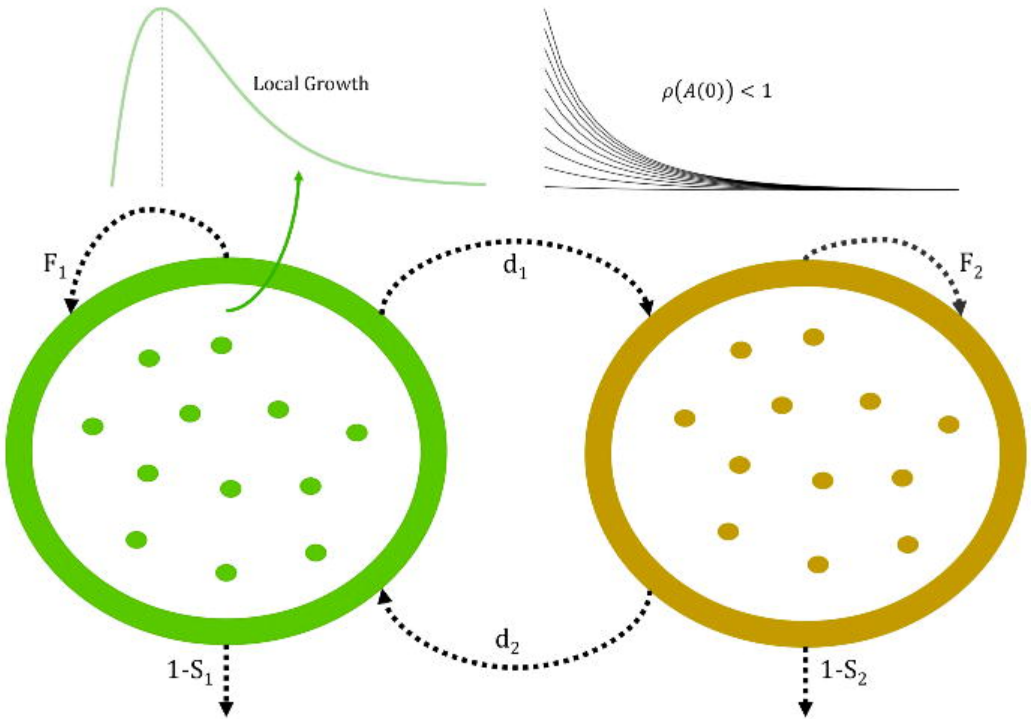
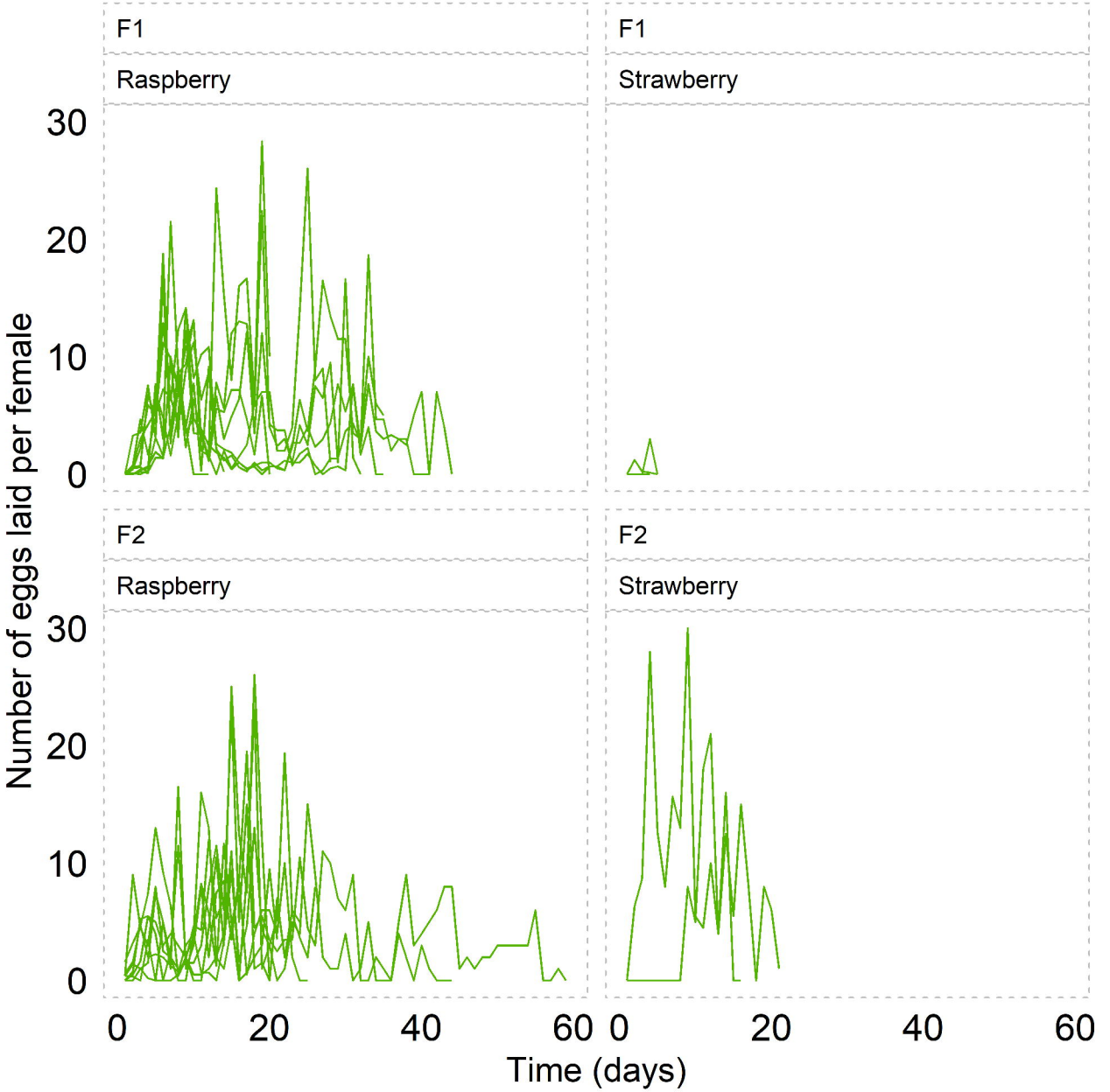
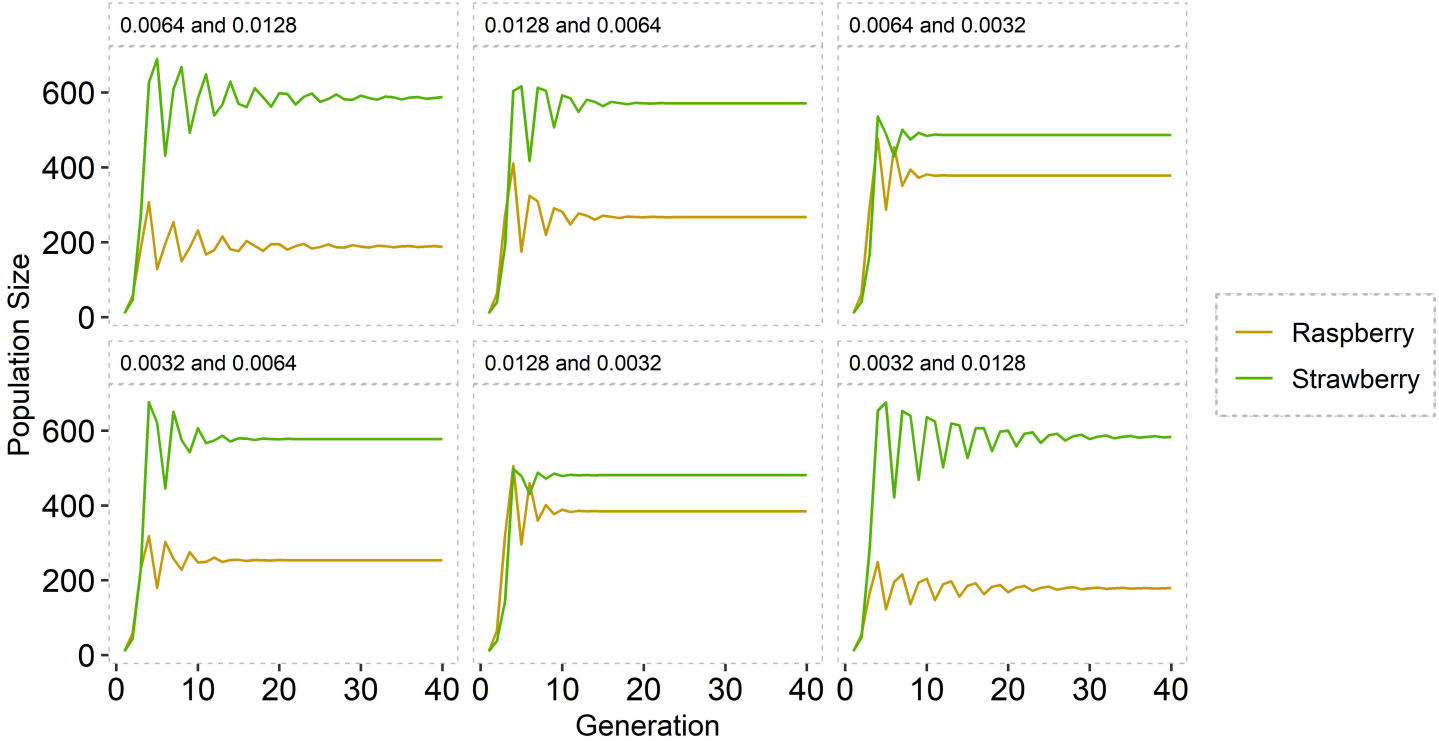
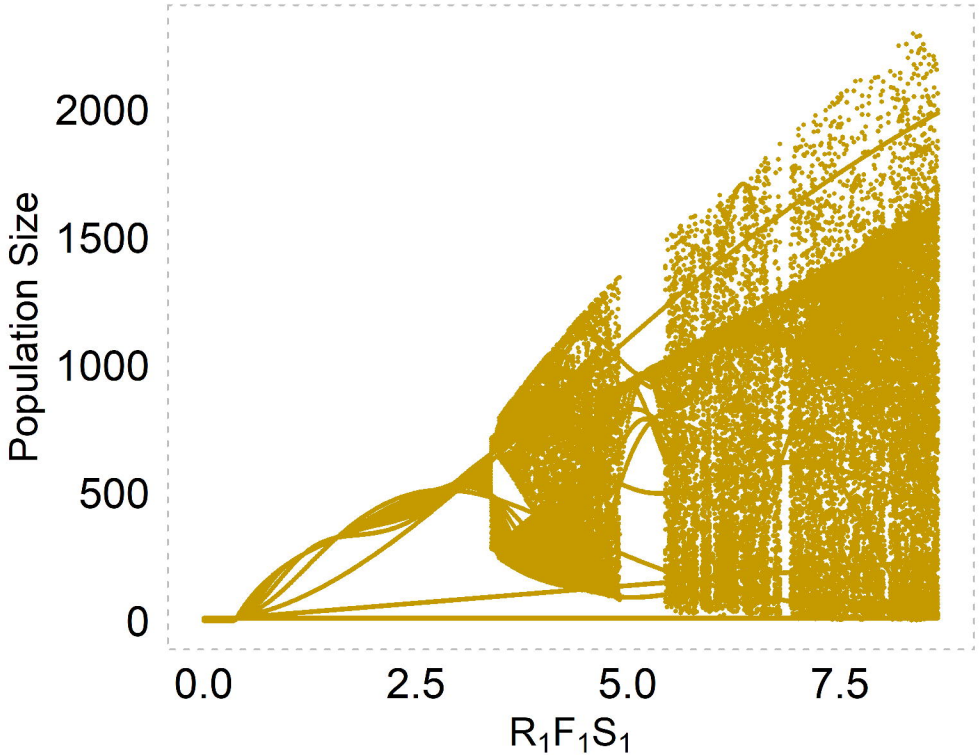
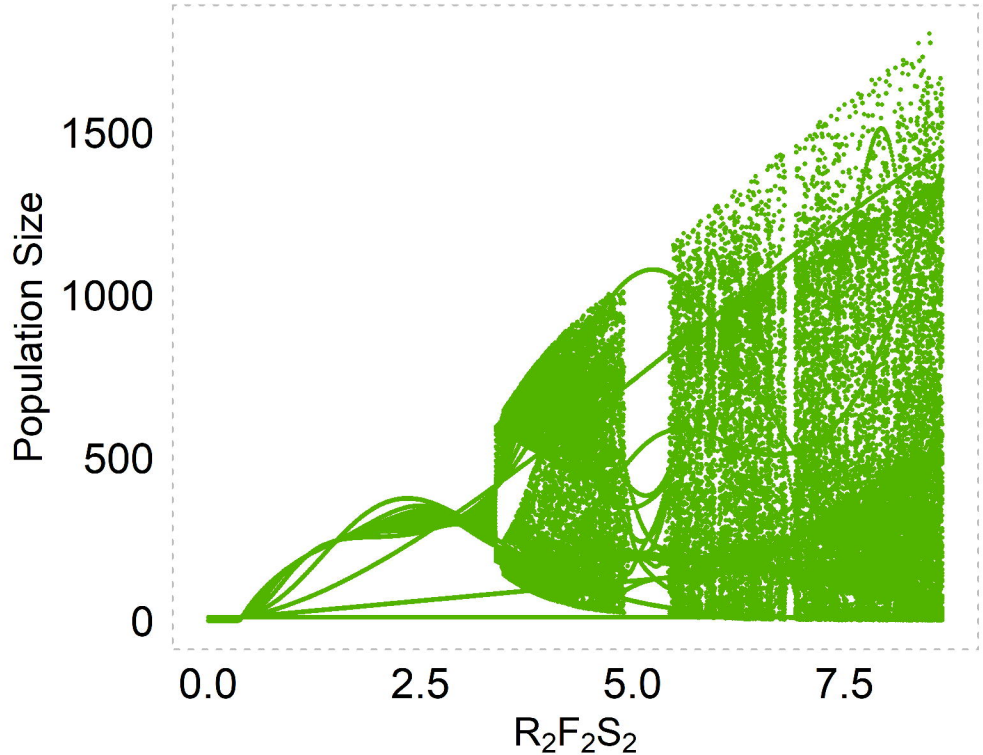

Parent
F1
F2
F3
F3
Number of offspring not sufficient

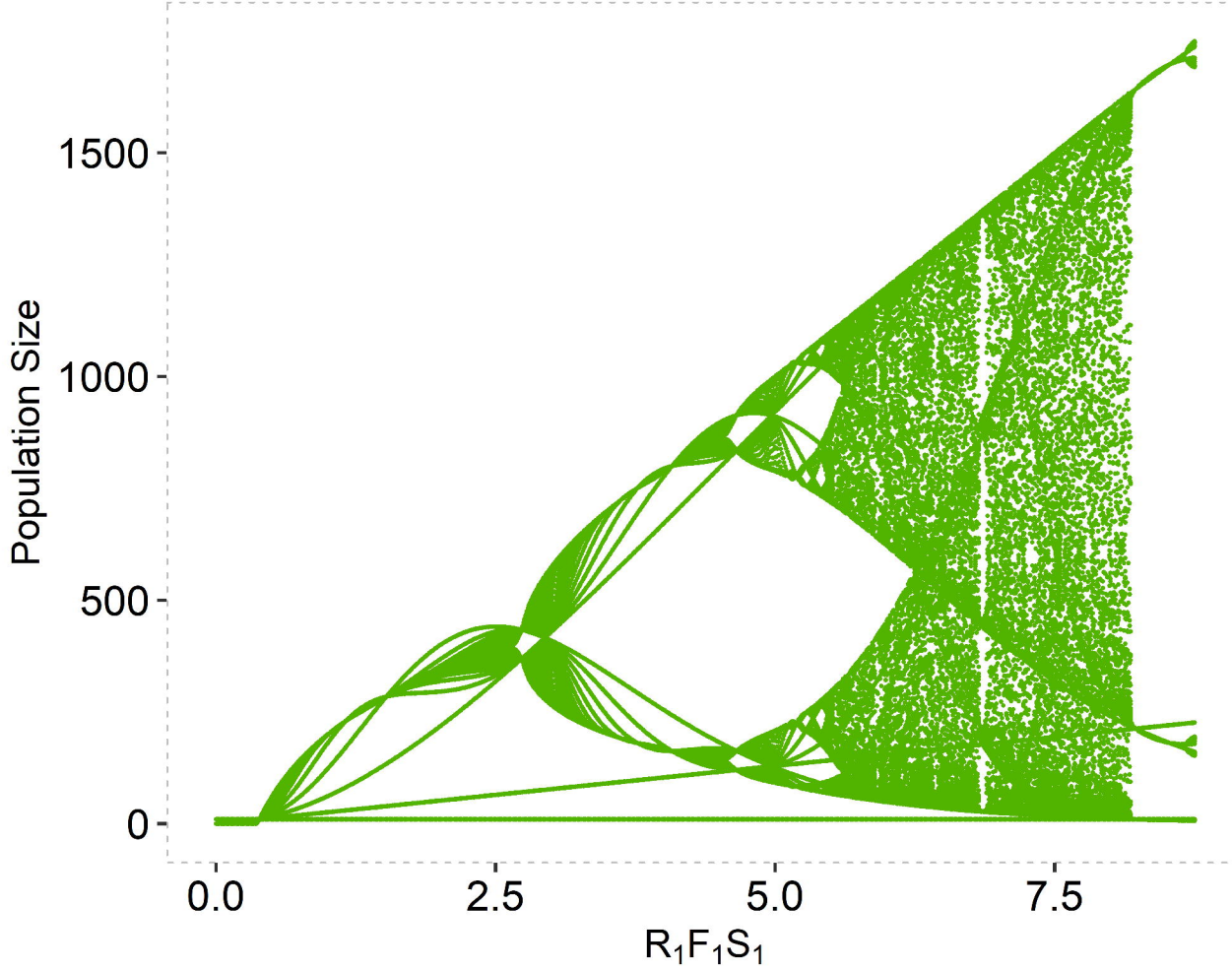

Local Growth
$\rho(A(0)) < 1$
F_1
d_1
F_2
d_2
$1\text{-}S_1$
$1\text{-}S_2$

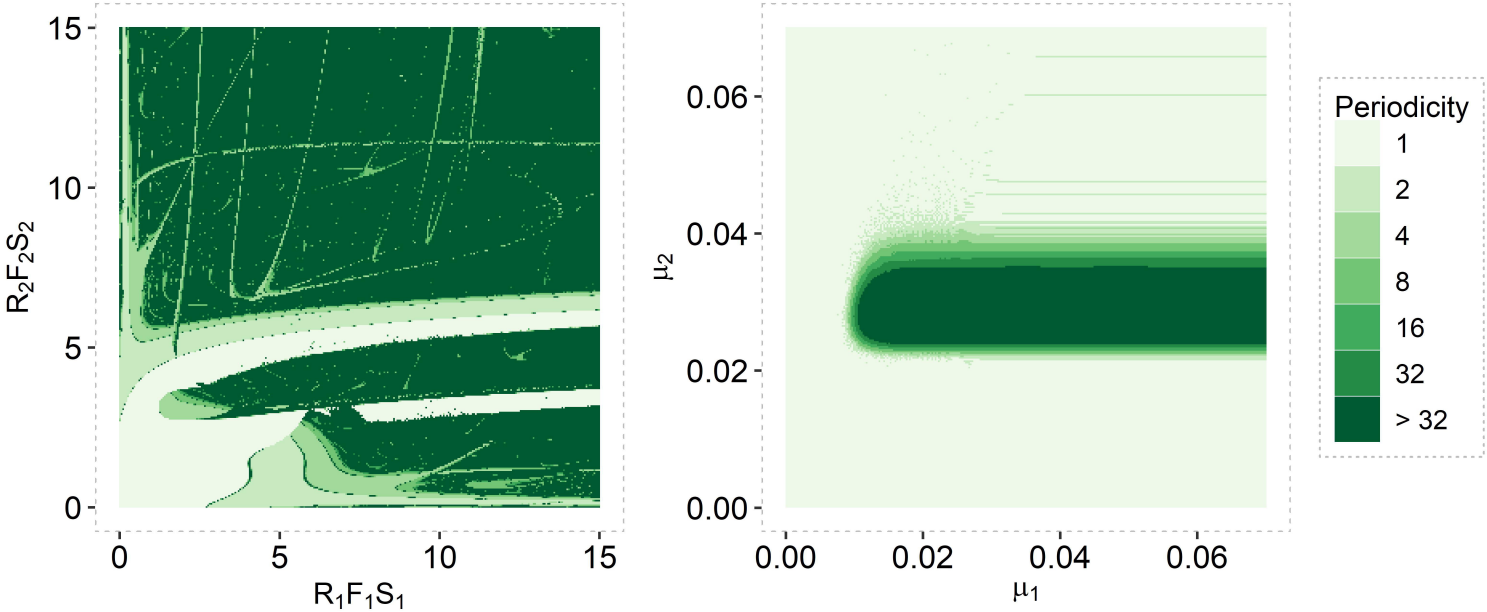

F1
Raspberry
F1
Strawberry
F2
Raspberry
F2
Strawberry
Number of eggs laid per female
0
10
20
30
0
20
40
60
Time (days)

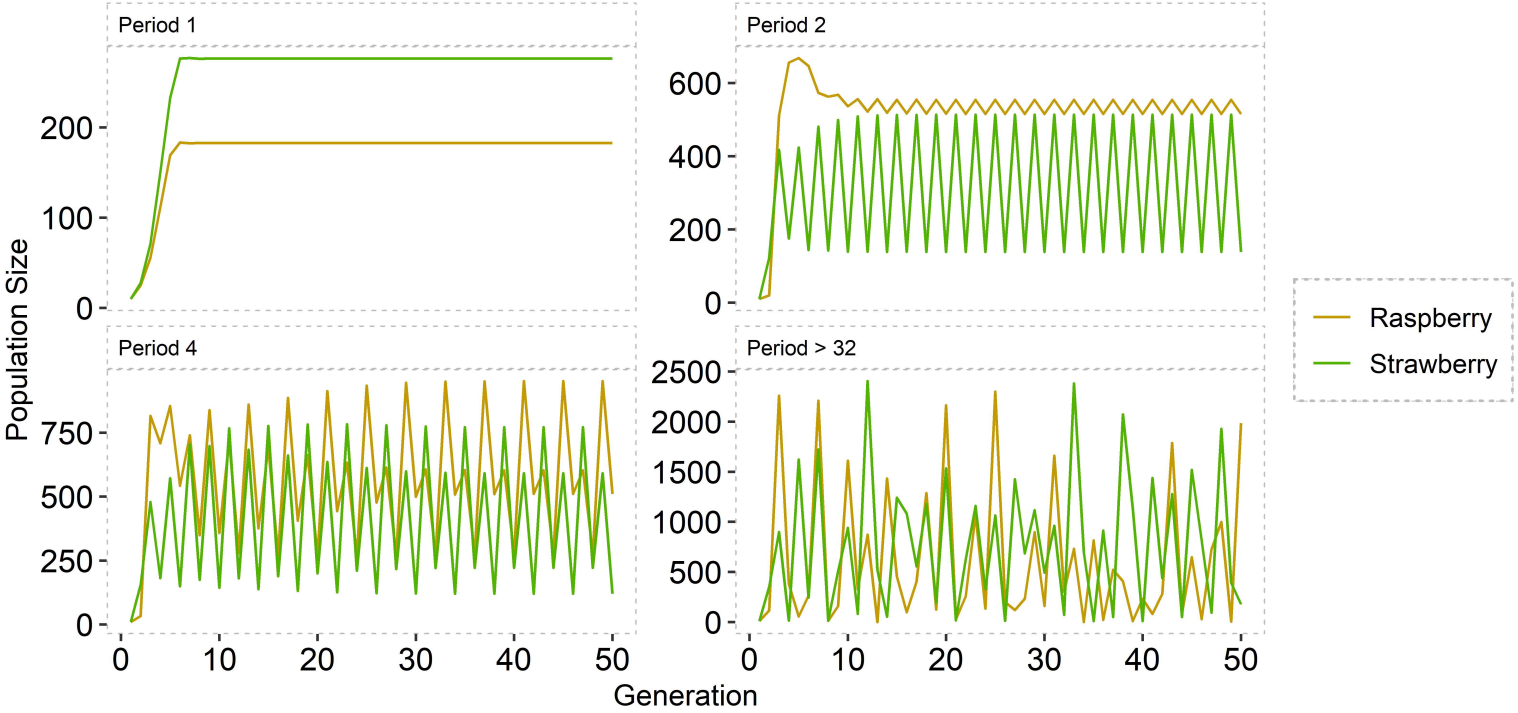

0.0064 and 0.0128
0.0128 and 0.0064
0.0064 and 0.0032
0.0032 and 0.0064
0.0128 and 0.0032
0.0032 and 0.0128
Population Size
0
200
400
600
Generation
0
10
20
30
40
Raspberry
Strawberry


Population Size
2000
1500
1000
500
0
0.0
2.5
5.0
7.5
$R_1F_1S_1$


Population Size
1500
1000
500
0
0.0
2.5
5.0
7.5
$R_2F_2S_2$


1500
1000
500
0
Population Size
0.0
2.5
5.0
7.5
$R_1F_1S_1$


15
10
5
0
$R_2F_2S_2$
0
5
10
15
$R_1F_1S_1$
0.06
0.04
0.02
0.00
μ_2
0.00
0.02
0.04
0.06
μ_1
Periodicity
1
2
4
8
16
32
> 32


Period 1
Period 2
Period 4
Period > 32
Population Size
Generation
Raspberry
Strawberry
0
100
200
250
500
750
1000
1500
2000
2500
10
20
30
40
50