

Optimized timing of parasitoid release: a mathematical model for biological control of *Drosophila suzukii*

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Received: date / Accepted: date

Abstract

We present a model for the population dynamics of the invasive fruit fly *Drosophila suzukii* and its pupal parasitoid *Trichopria drosophilae*. Seasonality of the environment is captured through a system of delay differential equations with variable delays. The model is used to explore optimal timing for releasing parasitoids in biological control programs. According to the results, releasing parasitoids is most effective between late spring and early summer when the host population begins to increase. A single parasitoid release event can be more efficient than multiple releases over a prolonged period, but multiple releases are more robust to suboptimal timing choices. The findings can be useful for optimizing parasitoid release and should be

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transferable for similar systems. More generally, the model is an example for stage-structured resource-consumer dynamics in a varying environment.

Keywords: parasitoid release timing • optimizing biological control • parasitoid-host dynamics • integrated pest management • spotted wing drosophila • *Drosophila suzukii* • *Trichopria drosophilae*

1 Introduction

The fruit fly *Drosophila suzukii* Matsumura arrived in 2008 to both, Europe and mainland America from its region of origin in East Asia [Hauser, 2011, Calabria et al, 2012, Cini et al, 2012, 2014, Deprá et al, 2014, Asplen et al, 2015, Fraimout et al, 2017]. *D. suzukii* larvae develop in ripe fruit, but unlike most of its relatives it is able to oviposit in undamaged soft-skinned fruit. Host plants include cherry, blueberry, raspberry, strawberry and various non-crop plants [Lee et al, 2011a, Atallah et al, 2014, Asplen et al, 2015, Kenis et al, 2016, Karageorgi et al, 2017, Elsensohn and Loeb, 2018]. The ability to infest undamaged fruit makes it a serious problem in some agricultural areas [Bolda et al, 2010, Lee et al, 2011b, De Ros et al, 2013, Asplen et al, 2015]. Conventional control programs are heavily reliant on pesticides, which are applied multiple times per season [Van Timmeren and Isaacs, 2013]. This control strategy is believed to be effective but is associated with many problems. Some of these problems include ineffectiveness of the pesticides against larvae inside the fruits, adverse effects on natural enemies [Roubos et al, 2014], secondary pest resurgence [Klick et al, 2016], development of insecticide resistance, continuous immigration from population reservoirs [Klick et al, 2016], and unacceptably high pesticide residues [Asplen et al, 2015]. Interestingly *D. suzukii* seems not to be a major problem in its region of origin, where it presumably does not reach extremely high population densities [Asplen et al, 2015]. One reason might be the presence of adapted natural enemies, including most prominently diverse parasitoid wasps which develop inside the juvenile stages of *D. suzukii* [Mitsui et al, 2007].

Given the potential of parasitoid species to reduce their host population, they are considered for biological control programs of *D. suzukii* [Haye et al, 2016]. Classical biological control by introducing the parasitoid species from the region of origin is considered in Europe and America [Daane et al, 2016, Haye et al, 2016], even though their release has yet to be authorized. Moreover, several indigenous parasitoids of *D. suzukii* in the invaded areas are considered for augmentative biological control programs [Chabert et al, 2012, Rossi Stacconi et al, 2013, Gabarra et al, 2015, Miller et al, 2015, Mazzetto et al, 2016, Wang et al, 2016, Knoll et al, 2017]. Among larval parasitoids, *Leptopilina heterotoma* Thomson has been observed to successfully develop on *D. suzukii*, even if its efficacy is strongly limited by the host immunoreaction [Rossi Stacconi et al, 2015]. Among pupal parasitoids, *Pachycrepoideus vindemiae* Rondani and *Trichopria drosophilae* Perkins are the most common species attacking the pest. At the moment, the cosmopolitan *T. drosophilae* appears to be the most suitable species for implementing biocontrol programs [Zhu et al, 2017, Rossi Stacconi

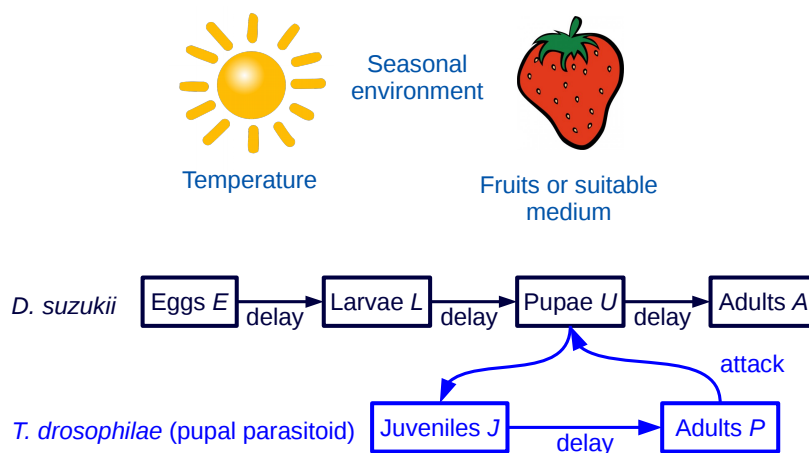


Fig. 1: Flow chart for the stage structured model

et al, 2017]. Augmentative release of this species has been recently tested under field conditions [Rossi Stacconi et al, 2018]. The release significantly increased the proportion of *D. suzukii* juveniles being parasitized, but it is still to be determined whether such releases can be an effective measure against *D. suzukii* infestation. Different aspects concerning the release might need to be optimized for a successful intervention. Besides choosing the right parasitoid species, it is important to target the most appropriate ecological time frame and habitat [Crowder, 2007]. Mathematical models for population dynamics allow us to help determine most optimal timing for inundative releases of parasitoids [Shea and Possingham, 2000, Crowder, 2007, Garay et al, 2015, Hamby et al, 2016]. In this work, we present such a model for augmentative release of the parasitoid *T. drosophilae* against *D. suzukii*. With this model we attempt to answer two questions: (a) when should the parasitoids be released to suppress most efficiently the *D. suzukii* infestation and (b) whether it is more effective to release them at a single event or at several events distributed over time. Note that we investigate how to carry out such a parasitoid most efficiently, but we do not answer the question whether such releases will be generally doable and cost-effective - this question seems to be answerable only by field experiments, which however can be supported by our analysis.

Our model takes into account the stage structure of the populations, and we collect parameters for both species and the seasonal environment from various sources. A brief introduction to the model and the results of the simulations are given in Section 2 and 3. In Section 4, we finally discuss our results, and implications for general consumer-resource interactions and biological control in different contexts. The details of the model can be found in the supplementary material.

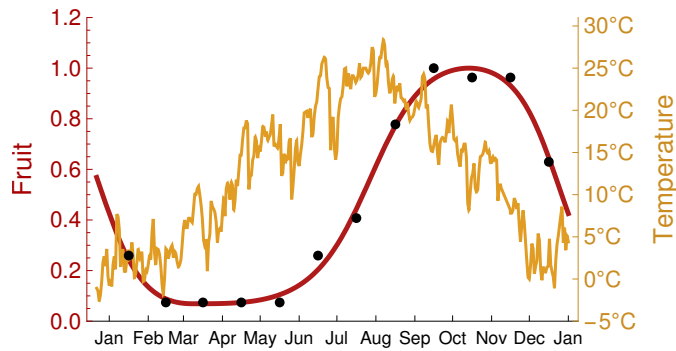


Fig. 2: Number of host species suitable for *D. suzukii* development in northern France and daily mean temperature in S.Michele all'Adige, Italy (2014)

2 Theory and calculations

The population dynamics of *D. suzukii* and *T. drosophilae* are modelled through a system of delay differential equations analogous to similar models [Nisbet and Gurney, 1983, Nelson et al, 2013, McCauley et al, 2008, Ewing et al, 2016]. The equations are written out in the supplementary material.

D. suzukii structure consists of eggs (E), larvae (L), pupae (U) and adults (A), and that of *T. drosophilae* of juveniles (J) and adults (P). Transitions through life stages are presented within a simple biological control system flowchart in Fig. 1.

Fecundities, mortalities and developmental delays are assumed to depend on the environment. Our model accounts for two time-dependent environmental factors: the temperature $C(t)$ and the availability of fruit (or other suitable host medium) $F(t)$.

The temperature data has been measured at an elevation of 228m a.s.l. in S. Michele all'Adige, Province of Trento, North Italy (provided by Fondazione Edmund Mach). From these data we draw a continuous temperature curve $C(t)$ by two different methods to test whether they result in different conclusions. The first method was to obtain a generic expectation for the temperature profile by fitting a sinusoidal curve over the course of one year. The second method was to obtain realistic curves for the different years by fitting piecewise linear functions to the daily mean temperature, see Fig. 2.

The function for the seasonal fruit availability $F(t)$ has been created with the data from Poyet et al [2015], who report for each month the number of plant species carrying fruits suitable for *D. suzukii* in a region of northern France. We assume that the numbers of fruiting species also reflect the total availability of suitable host and create a continuous function by fitting a stretched sinusoidal curve to the data, see Fig. 2. To investigate the impact of different fruit ripening times, we shift this function forward and backward in time.

For both species, the time spent in the juvenile stages depends on the temperature C . Following the approach of Nisbet and Gurney [1983], we model a temperature-

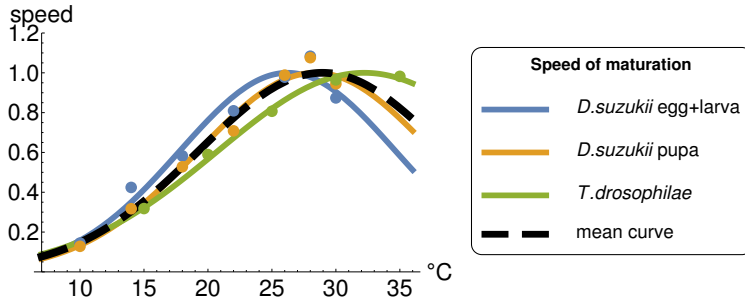


Fig. 3: Maturation speed of different life stages of *D. sukukii* and its pupal parasitoid *T. drosophilae*

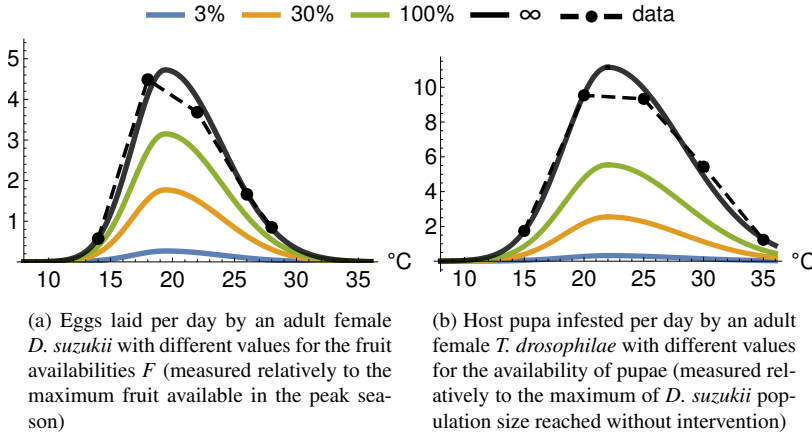


Fig. 4: Daily fecundities

dependent maturation rate, which is for each stage defined as the inverse of the length of the time spent in that stage. It turns out, that the maturation rates of the different stages scale very similarly with the temperature. We therefore use a single (Gaussian) function $g(C)$ for the maturation rate of all stages, and assume that insects in stage i (where $i = E, L, U$ or J) progress to the next stage when their maturation level reaches the value Ω_i . We normalize the maturation rate $g(C)$ so that it has a maximum value of 1, and thus Ω_i represent the minimum stage durations (at optimal temperature). Fig. 3 shows the fit of this model to delays measured in the laboratory [Tochen et al, 2014, Amiresmaeili, 2017].

Fecundity of adult *D. sukukii* depends on temperature C and fruit availability F through a multiplicative formula. The dependence of the maximal fecundity on temperature $\eta_A(C)$ is fitted to available data [Tochen et al, 2014], and the dependence on fruit availability is through a Holling-type 2 function. The resulting formula for

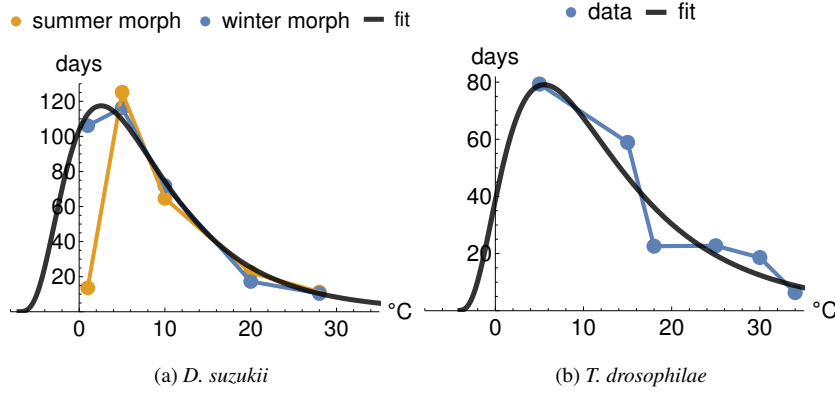


Fig. 5: Average adult life length of *D. suzukii* and *T. drosophilae*

the realized fecundity is

$$\beta_A = \lambda_A \frac{\eta_A(C) \alpha_A F}{1 + \alpha_A F} \quad (1)$$

where $\lambda_A = 0.5$ is the sex-ratio [Emiljanowicz et al, 2014] and α_A is a parameter (the 'attack rate' of *D. suzukii* towards available fruit) to be adjusted. Fig. 4a shows the dependence of fecundity on temperature for different levels of fruit availability together with laboratory data considered as estimates valid for unlimited resource availability.

In the same way, maximal parasitoid fecundity $\eta_P(C)$ is fitted to data available at different temperatures [Rossi Stacconi et al, 2017], and the realized fecundity β_P is assumed to depend additionally on the host density U , yielding

$$\beta_P = \lambda_P \frac{\eta_P(C) \alpha_P U}{1 + \alpha_P U} \quad (2)$$

where α_P needs to be adjusted (the 'attack rate' of *T. drosophilae* towards available *T. drosophilae* pupae), and the sex ratio is $\lambda_P = 0.53$. The resulting curves are shown in Fig. 4b together with the laboratory data.

Mortality of both species depends on temperature, and for *D. suzukii* larva it depends additionally on fruit availability and the number of competing larvae. For both species, average adult survival can be modeled with a skewed Gaussian function. The fits to data from [Shearer et al, 2016] and [Amiresmaeili, 2017] are shown in Fig. 5. For *D. suzukii*, the phenotypic plasticity between summer and winter morph is accounted for by assuming that at all temperatures the flies exhibit the better adapted phenotype.

Further details on that and on other model assumptions can be found in the supplementary material. The model is implemented with *Wolfram Mathematica* [Wolfram Research, 2016] and the code is freely available on request.

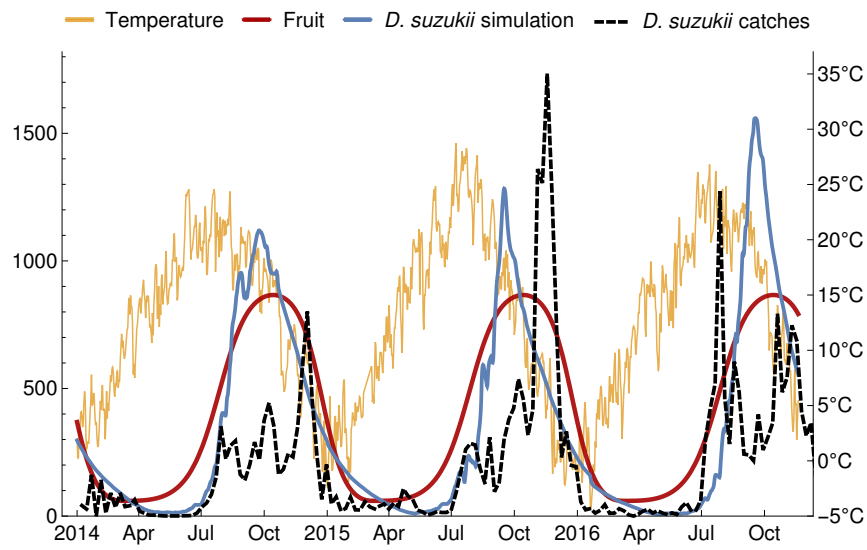


Fig. 6: Simulated *D. suzukii* adult population size, mean *D. suzukii* trap catches and mean daily temperature from S.Michele all'Adige, Province of Trento, Italy during 2014-2016

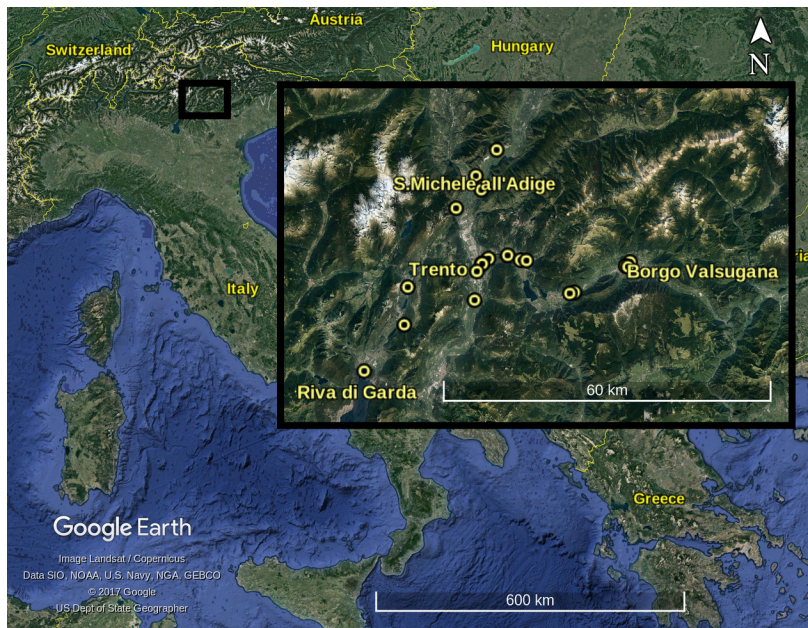


Fig. 7: *D. suzukii* trap placement in the Province of Trento during 2014 to 2016

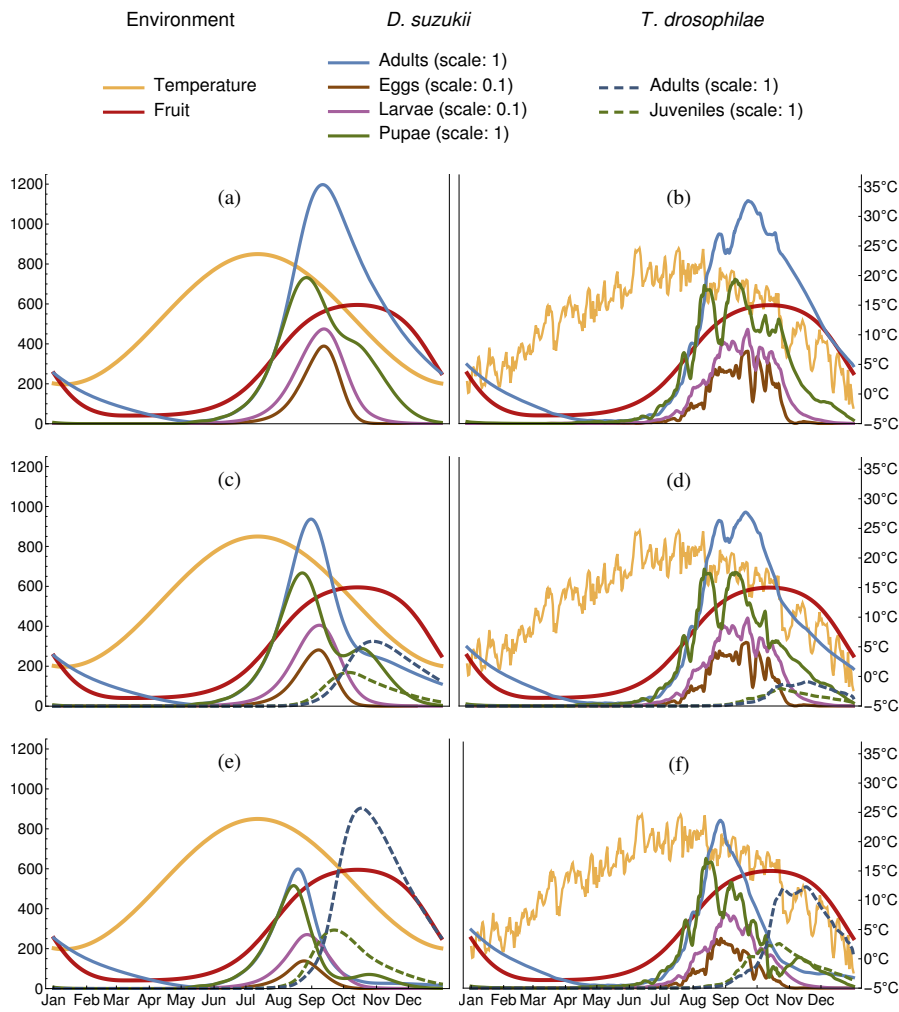


Fig. 8: Simulated *D. suzukii* population size without (a, b) and with parasitoids introduced on 1 April (c, d) and 1 June (e, f). Figures a, c, and e (left) were created using the sinusoidal temperature curve and b, d, and f (right) interpolating the daily mean temperatures. Curves were created using weather data originally collected during 2014 in S. Michele all'Adige at 228m a.s.l., Province of Trento, Italy. The number of parasitoids released corresponds to 0.1% of the maximal *D. suzukii* adult population size reached in the simulations without intervention

3 Results

Fig. 6 shows a simulation of *D. suzukii* adult population dynamics for the years 2014-2016, superimposed with weekly average catches of *D. suzukii* adults from 22 traps

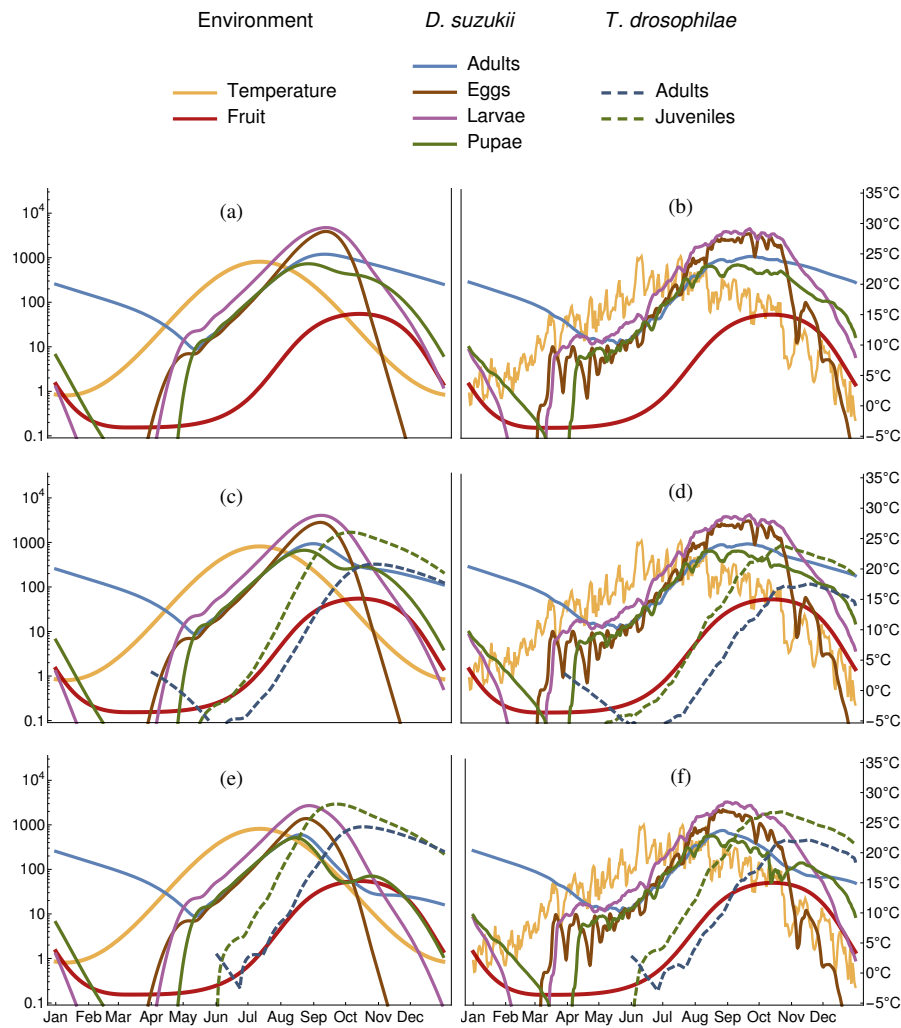


Fig. 9: Simulations of different parasitoid release scenarios. The plots are the same as in Fig. 8, but the population densities are shown in logarithmic scale

in the Province of Trento (obtained from the Fondazione Edmund Mach, S. Michele all'Adige, Italy). Precisely, the traps are those maintained over all three years that are at an elevation below 500m a.s.l. (their elevations vary between 77m and 489m a.s.l.). One of the locations is S. Michele all'Adige, where also the temperature data we use was measured. A map of the different trap locations is shown in Fig. 7. Simulations and catch data have some differences, especially for lower catches during summer and large peaks in autumn, at a time when simulated densities are declining; possible reasons for such discrepancies are examined in the discussion. However, the over-

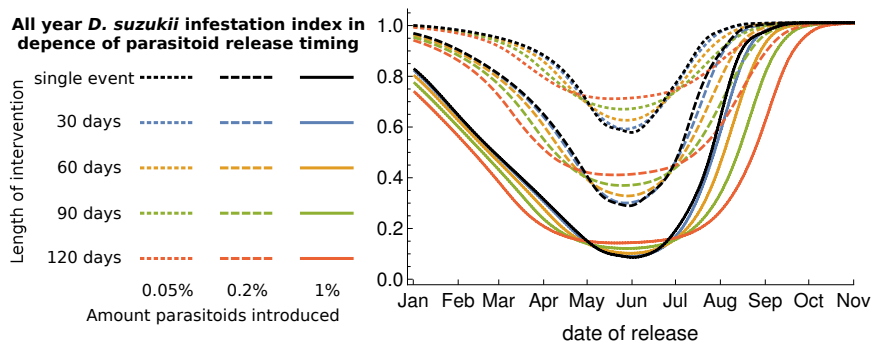


Fig. 10: Effect of time of parasitoid introduction and amount of parasitoids introduced on all year *D. suzukii* infestation index (which is proportional to the total amount of *D. suzukii* eggs laid over the year). The dotted, dashed and straight lines correspond to an overall introduction of 0.05%, 0.2% and 1% of parasitoids compared to the yearly maximum of *D. suzukii* adults reached without parasitoid intervention. The black lines correspond to a scenario where all parasitoids are released at a single event at the date given on the x-axis. The other lines correspond to an equally distributed parasitoid release around the date on the x-axis for 30, 60, 90 and 120 days. The underlying temperature curve is the generic sinusoidal fit used before

all multi-year patterns of simulations and catch data roughly agree; thus, we deem the model reasonable enough to be used as a baseline for investigating the potential impact of parasitoid introductions.

Fig. 8 shows different scenarios for a one-year simulation, with and without parasitoid introduction. The temperature curve corresponds to the weather in S. Michele all' Adige in 2014, approximated by a sinusoid curve (left panels) or interpolated from daily mean temperatures (right panels). The upper plots show the densities of the different stages of *D. suzukii* in simulations without parasitoid introduction. In the other plots adult parasitoids are released on 1 April (central row) or on 1 June (bottom row).

Corresponding simulations on left and right panels differ somewhat: with the actually observed temperature (right side), *T. drosophilae* reaches lower densities and has a smaller effect on the *D. suzukii* population. Still, the patterns moving from top to bottom are extremely similar between the two columns: parasitoid release on 1 April has a smaller effect on the host population than parasitoid release on 1 June, with the latter reducing the peak adult *D. suzukii* density by around 30-50% and shortening the time *D. suzukii* is at high densities. Parasitoid juvenile densities peak in all release scenarios between August and September.

The same plots are repeated in Fig. 9 in logarithmic scale to show the population dynamics during the early part of the year. In this figure, *D. suzukii* juveniles appear in April, and *T. drosophilae* juveniles appear between May and June, with a relatively small difference between the early and late release scenarios. The figure offers an explanation why the earlier parasitoid releases were less effective than the later releases: at the time of the early releases in April, there were no *D. suzukii* pupae present in the simulated population; thus, the populations of adult parasitoids

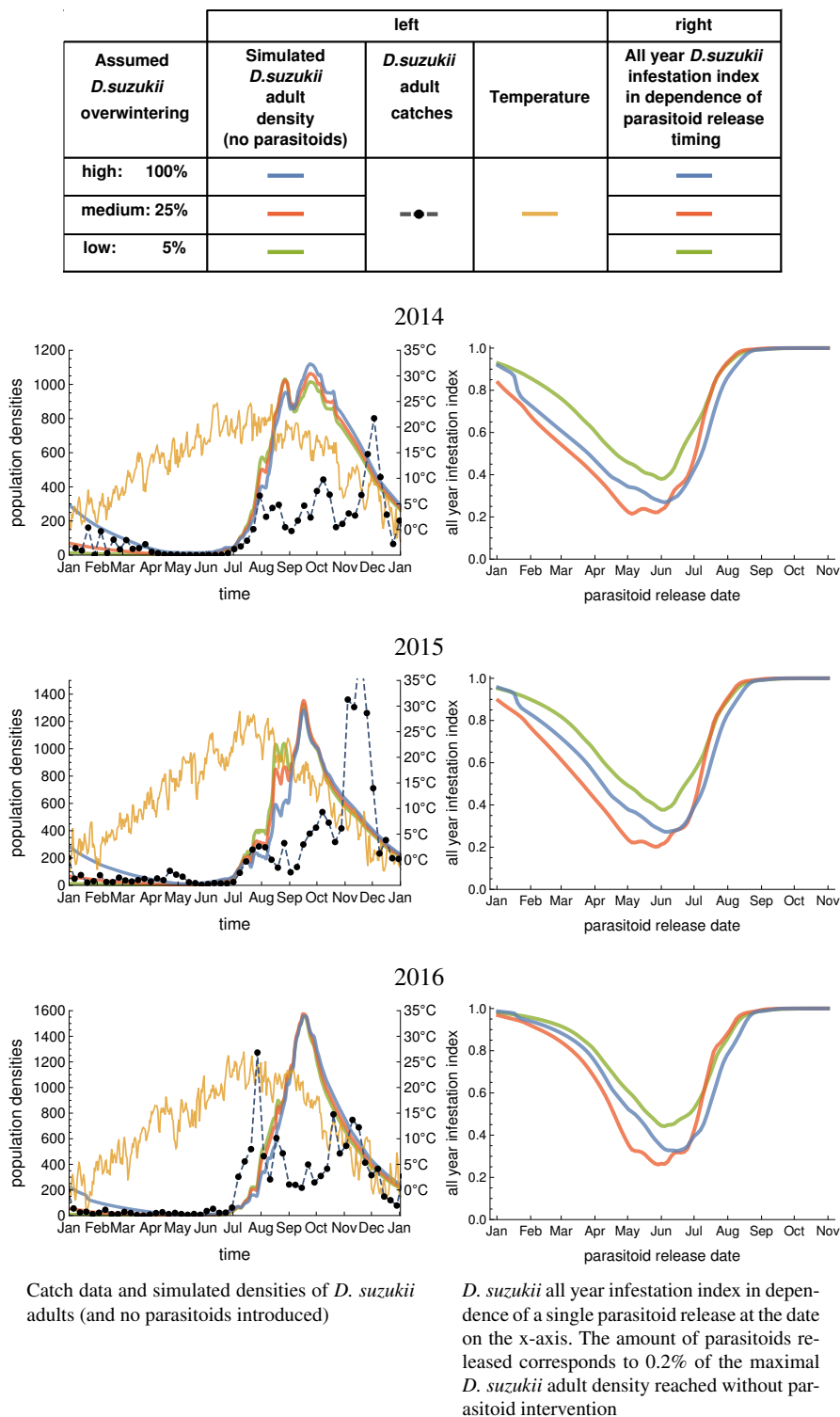


Fig. 11: Simulations with daily mean temperature data of the years 2014-2016. Left: simulated *D. suzukii* adult densities and catch data. Right: success of a parasitoid intervention in dependence of its timing. Three scenarios for the winter survival are simulated: high, medium and low survival corresponds to starting the year with 100%, 25% and 5% of the *D. suzukii* adults at the end of the previous year (without parasitoid intervention). For each survival scenario, the *D. suzukii* attack rate α_A is adjusted so that the simulations fit roughly the onset of the catch data

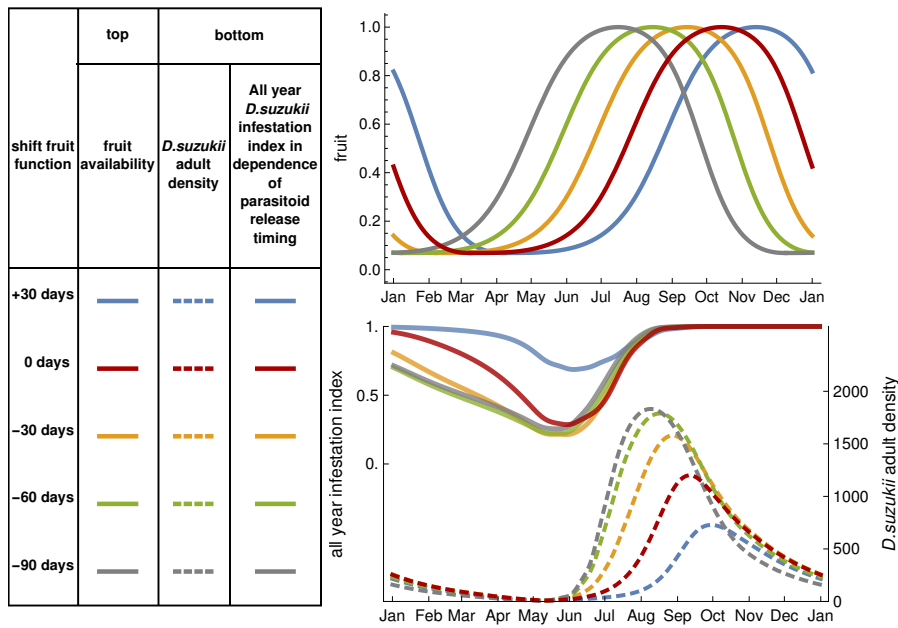


Fig. 12: Simulations with different fruit ripening times (obtained by shifting the fruit function forward and backward in time). Upper plot: fruit availability. Lower plot: adult *D. suzukii* population density without intervention, and all year *D. suzukii* infestation index in dependence of the timing of a single parasitoid release (on the x-axis). The amount of parasitoids released corresponds to 0.2% of the maximal *D. suzukii* adult density reached without parasitoid intervention and the non-shifted fruit function. The underlying temperature curve is the generic sinusoidal fit used before

declined without reproducing as they had no hosts. By the time of the late releases in June, host pupae were present and thus adults could successfully initiate a growing parasitoid population.

In order to compare different parasitoid release scenarios, we measure the success of an intervention through the “all year *D. suzukii* infestation index”, which is proportional to the *D. suzukii* eggs laid during the year. A low infestation index is assumed to indicate a successful intervention. We also experimented an alternative measure of infestation, aiming at assessing the damage caused to ripening fruit, and the results obtained with either measure are very similar.

Fig. 10 shows the effects of different scenarios of parasitoid release in terms of the “all year *D. suzukii* infestation index” compared to the no-intervention scenario. The scenarios differ in the amount of parasitoids released and in the time span over which the release is carried out. The total amount of parasitoids released corresponds to 0.05%, 0.2% and 1% of the peak density *D. suzukii* adults reach without parasitoid intervention. The time span of the introduction ranges from a single event up to 120

days. In order to obtain more general results, we consider the case of a sinusoidal temperature curve.

The lowest infestation index was obtained by releasing the parasitoids at the beginning of June, corresponding to the time when the *D. suzukii* population begins to grow. The optimal timing does not depend on the amount of parasitoids released, which however strongly affects the impact of the intervention. A single parasitoid release at the optimal time is slightly more effective than continuous release of the same amount of parasitoids over an extended period centered around that date; however only a very long release period (several months) decreases the success substantially. On the other hand a continuous release increases the tolerance towards a suboptimal timing.

In Fig.11, we examine optimal parasitoid release timing with realistic temperature curves, which are created by interpolating daily mean temperature in S.Michele all'Adige from 2014 to 2016. Besides testing how much the optimal parasitoid release timing changes between the years, we test if the optimal timing is influenced by our assumptions on the winter survival of *D. suzukii*.

The left side of the figure shows simulations of *D. suzukii* without introducing the parasitoid. The plots correspond to three different scenarios concerning the overwintering: high, medium and low winter survival. For the high winter survival, the population densities at the beginning of the year are those at the end of the previous year. This corresponds to the overwintering assumption in the other figures. However little is known on how many *D. suzukii* adults do survive the winter, and survival might be lower than expected by our model (for details see the Discussion). Thus we try scenarios with medium and low winter survival, where we reduce the *D. suzukii* adult density at the beginning of the year to 25% and 5% of the density of the previous year. To make all simulations fit with the yearly onset of the *D. suzukii* population growth, we adjust the *D. suzukii* attack rate separately for each scenario ($\alpha_A = 2, 4$ and 10 for high, medium and low winter survival respectively).

On the right side of the figure, we investigate how the timing of a single parasitoid release affects the success of the intervention in the different years and scenarios. The number of parasitoid introduced equals to 0.2% of the maximal *D. suzukii* adult density obtained for 2014 with high winter survival. The optimal release date is spread around the beginning of June, and there is little difference between the different years. Also the assumption on winter survival has no clear effect on the optimal release timing; hereby it is important to note that winter survival and *D. suzukii* attack rate were balanced out to match the observed catch data. Without fitting the model, either factor could of course cause different responses.

In Fig.12, we investigate the influence of the ripening time of fruit in our model. For this purpose, the fruit function used for the other simulations is shifted by +30, 0, -30, -60 and -90 days. For the temperature curve, we use the generic sinusoid fit described before. The plot shows adult *D. suzukii* densities without parasitoid release, and the impact of a single parasitoid intervention in dependence of the release date. The amount of parasitoids released corresponds to 0.2% of the maximal *D. suzukii* adult density reached without intervention (and the non-shifted fruit function). The simulations show that earlier fruit availability can trigger earlier *D. suzukii* growth and higher maximal population densities. However, at some point earlier fruit avail-

ability does not additionally anticipate *D. suzukii* growth, suggesting that the low temperature becomes the limiting factor. The optimal parasitoid release date is anticipated only slightly with earlier fruit availability. This suggests, that early during the year, the performance of the parasitoid itself is limited by the low temperature. For the last scenario, the fruit availability is shifted towards the end of the season. As expected, this delays *D. suzukii* growth and the optimal parasitoid release timing. Besides that, maximal *D. suzukii* population levels are lower and the parasitoid is less effective because both species cannot build up high densities this late in the year.

4 Discussion

Our findings suggest that the success of a biological control strategy of *D. suzukii* by means of the pupal parasitoid *T. drosophilae* depends strongly on the time when the parasitoids are released. With our assumptions on the fruit availability and the climate of the Province of Trento (northern Italy), the optimal time of release is estimated to lie between late spring and early summer, when the *D. suzukii* population begins to grow according to the model. Simulations of the population dynamics and the main results on the timing of parasitoid interventions can be seen in Fig. 6 - 12.

Generally, choosing the right time for a parasitoid intervention is about finding a balance between an early and a late release. On one hand, the intervention should be late enough in the season so that *D. suzukii* has started reproducing since only the pupal stage is attacked by the parasitoid. On the other hand, the intervention should be early enough to augment the parasitoid density and decimate the *D. suzukii* population before crops are becoming susceptible. An early intervention could possibly benefit from a “bottleneck” effect by intervening when the pest population has a low density. For other control methods based on pesticides, such an early intervention has been suggested to be effective already in late winter to early spring [Rossi Stacconi et al, 2016]. However our simulations do not confirm that early interventions can be efficient for biological control with parasitoids. The explanation is that parasitoids –in contrast to pesticides– need sufficiently warm conditions and target only a juvenile stage of the pest species, which is present only after the population starts reproducing [Wiman et al, 2016]. Yet early parasitoid release has been tested in the field [Rossi Stacconi et al, 2018] and it did result in an increased proportion of parasitized *D. suzukii* juveniles throughout the season. A later release –as suggested by our model– has to our knowledge not yet been tested in the field. Such an experiment would be essential to validate or reject our expectations, since the model can be only a simplified picture of reality and it is based on a range of assumptions – which also depend on local factors. In the following, we shall discuss some key assumptions and their possible implications.

Our model has been adjusted with *D. suzukii* catch data from northern Italy, where the pest deals serious damage to the local fruit production. Comparing catch data and model simulation in Fig. 6, we see that the overall temporal patterns coincide but catches are lower than simulations in summer and higher in autumn. This could point out to some problems with our model, but we believe that one important reasons for this difference is simply that catch data do not represent population densities

equally over the whole year – i.e. the vinegar baited traps may be less attractive during summer when fruit abundance is high. Indeed, analysis of weekly catches in orchards generally show higher numbers of adults after the harvest [Rossi Stacconi et al, 2016]. We overall deem the model realistic enough, since it reproduces well the begin of the yearly *D. suzukii* outbreak – which seems to be the most important event for timing the parasitoid intervention.

D. suzukii is a strongly seasonal pest due to the seasonality of its environment. Our model accounts for two environmental factors: temperature and availability of suitable fruit. We chose those factors because they are key influences and because they follow clear seasonal patterns. Still other factors might influence the populations, for example wind, rain and humidity [Tochen et al, 2016]. Additional experiments could help to understand their relevance and refine future models.

For most simulations, we estimated the fruit availability by the number of plant species carrying suitable fruit. This might not only misestimate the total number of fruit, but it also represents only one possible scenario. Our additional simulations for crops with different ripening times show, that earlier fruit availability can anticipate the optimal timing for releasing the parasitoid up to mid-May, when the temperatures becomes suitable for the reproduction of *D. suzukii* and *T. drosophilae*, see the tolerance curves in Fig. 4. Similarly late fruit ripening results in a later optimal release timing, but also in decreased maximal population size of both species because the low temperatures in autumn limit their reproduction.

For all simulations, we used the temperature measured in S.Michele all’Adige in northern Italy at 228m a.s.l. This represents a region heavily affected by *D. suzukii*, but the pest is known to thrive on a wide range of climates [Asplen et al, 2015]. Thus our results need to be interpreted carefully when considering another location. Generally a good strategy could be to release the parasitoids when the *D. suzukii* population starts to grow, but custom simulations could help to understand specific scenarios.

We also assume, for the sake of simplicity, that environment is homogeneous and affects all individuals in the same way. In nature however, the environment is heterogeneous on many scales. For example, individuals can avoid extreme temperatures by finding shelter under leaf piles or by seasonal migration between different altitudes, which is another possible explanation for the unexpected low number of catches in summer [Tait et al, 2016, Rossi Stacconi et al, 2016]. Similarly, resources are distributed heterogeneously in time and space (i.e. fruit through different plant communities and their individual ripening times as discussed before). Note that the catch data presented in Fig. 6 corresponds to mean catches from traps at different locations, while single traps would show much stronger variation due to the populations spatial heterogeneity. Obviously, local presence of the pest determines optimal parasitoid release timing. An interesting question is, whether the spread of *D. suzukii* can be limited effectively at the beginning of the season by intervening at a source population, i.e. close to the overwintering habitat [Klick et al, 2016]. In order to answer such questions, a (stochastic) spatially-structured model could be helpful.

Understanding the way *D. suzukii* overwinters is a key for its successful control [Rossi Stacconi et al, 2016]. Besides seasonal migration, current research has revealed a specially adapted winter morph with largely increased tolerance towards

low temperatures at the cost of a reduced fecundity [Kaçar et al, 2015, Shearer et al, 2016, Grassi et al, 2017]. The morph is induced by cold temperatures during juvenile development in autumn [Toxopeus et al, 2016], and flies of this morph might reproduce during spring, giving rise to the first new generation [Rossi Stacconi et al, 2016]. There are data on the temperature tolerance of the two morphs [Shearer et al, 2016], but no quantitative information is available on the fecundity of the winter morph or on the environmental cues for shifting between the two morphs. In order to still capture the broad temperature tolerance of *D. suzukii*, we simply assumed that the whole population is always adapted to the current environment. Although this method allows to simulate multiple year dynamics, it might overestimate winter survival since individuals adapt during their larval stage and maladapted adults are believed to die when the temperatures drop. To test the influence of our assumptions, we simulated alternative scenarios with lower winter survival and stronger reproduction. Those simulations suggest no clear effects on the results, but still more information on survival, fecundity and transition of the different morphs could help to understand population dynamics of *D. suzukii* and the best times for control efforts.

The parameters for both species were taken from various experiments reported in the literature. Such experiments depend on different factors in their setup, and different insect strains can behave differently. One particularly critical parameter is the "parasitoid attack rate", which –in contrast to the maximum daily fecundity– is difficult to estimate experimentally. As we could only guess this parameter roughly, we performed a sensitivity analysis on its impact. According to that analysis, a higher value for this parameter could justify a slightly earlier parasitoid release (see the supplementary material). The effect is limited, but still additional experiments to determine this and other parameters could help to refine our analysis.

In our model, we neglect the complex ecological web in which both species are embedded. These include various predators, parasitoids and other drosophilids which can be infested by *T. drosophilae*. Such third species can have a wide range of effects on the populations and possible control efforts. For example additional hosts for the parasitoid can be disadvantageous when they dilute the parasitoid attacks on other hosts, or beneficial by helping to increase the parasitoid density. If in this example, additional hosts reproduce earlier in the season than *D. suzukii*, those could justify an earlier release in order to augment parasitoid densities in the field. It seems difficult to draw general conclusions on the impact of further species, but specific cases could be analyzed with support of simulations that extend our approach including other species.

In this analysis, we focused on the pupal parasitoid *T. drosophilae*, which however is not the only parasitoid wasp known to attack *D. suzukii*. Other parasitoids include species resident in the area of origin of *D. suzukii* [Mitsui et al, 2007], as well as species resident in the newly invaded areas [Rossi Stacconi et al, 2015]. It was not in the scope of this work to compare efficacy of different parasitoids, and neither to examine whether a single species or multiple species should be introduced. However, we believe that our findings can be transferred widely for other parasitoid wasps, as they have similar needs on the environment. This also includes parasitoids attacking other juvenile stages than pupae, since the different juvenile stages appear in the field virtually at the same time when *D. suzukii* is reproducing.

Our model is an example for consumer-resource dynamics of stage-structured populations. Such systems can lead to a variety of dynamics, as discussed in the monograph of [De Ros et al, 2013]. What makes our system particular, is the seasonality of the environment. Our results underline, that for understanding seasonal patterns of such systems, one needs to be aware of direct effects of the environment (e.g. on fecundity, mortality and development), as well as indirect effects via the stage-structure of the populations (e.g. the prevalence of the vulnerable juvenile stage of *D. suzukii*).

In summary, we believe that the present analysis yields useful insights for designing optimal strategies of parasitoid release. However, only experience can validate our predictions. First field experiences have been obtained by Rossi Stacconi et al [2018] in Italy, and further trials are planned in the USA (VW - personal communication). The tools developed in our work may be useful for understanding the outcome of such experiments. We hope that our study will help to improve integrated pest management of *D. suzukii*.

5 Authors' contributions

FP and AP formalized the mathematical model; MVR, GA, AG and VW provided the biological background; FP ran all the simulations. All authors contributed critically to the drafts and gave final approval for publication.

6 Acknowledgments

This work was funded by the Autonomous Province of Trento (Italy), Research funds for Grandi Progetti, Project LExEM (Laboratory of excellence for epidemiology and modelling, <http://www.lexem.eu>). We thank the editor and two anonymous reviewers who helped to improve this manuscript. We also thank Gabriella Tait for having provided unpublished data that have helped in understanding the dynamics of *Drosophila suzukii* population in the Province of Trento.

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