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REVIEW ARTICLE

A review on temperature and humidity effects on *Drosophila suzukii* population dynamics

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Abstract

1 *Drosophila suzukii* is an invasive polyphagous pest of wild and cultivated soft-skinned fruits, which can cause widespread economic damage in orchards and vineyards.
2 The simulation and prediction of *D. suzukii's* population dynamics would be helpful for guiding pest management. Therefore, we reviewed and summarized the current knowledge on effects of air temperature and relative humidity on different life cycle parameters of *D. suzukii*.
3 The literature summary presented shows that high oviposition rates can occur between 18 and 30 °C. Temperatures between 16 and 25 °C resulted in fast and high egg-to-adult development success of more than 80%. Oviposition and adult life span were positively affected by high relative humidity; however, the factor humidity is so far rarely investigated.
4 We assume that this is one reason why relative humidity usually is not considered in modelling approaches, which are summarized herein. The high number of recently published research articles on *D. suzukii*'s life cycle suggests that there is already a lot of knowledge available on its biology. However, there are still considerable research gaps mentioned in the literature, which are also summarized herein.
5 Nevertheless, we conclude that sufficient temperature data in the literature are suitable to understand and predict population dynamics of *D. suzukii*, in order to assist pest management in the field.

Keywords Spotted wing drosophila, insect, biology, life cycle, orchards, climate, weather, forecasting.

Introduction

The spotted wing drosophila *Drosophila suzukii* (Diptera: Drosophilidae) was first described by Matsumura in Japan in 1931 (Kanzawa, 1939). It is a polyphagous pest of soft-skinned fruits of many different wild and cultivated plants such as cherries and plums (*Prunus* species), strawberries (*Fragaria* species), raspberries and blackberries (*Rubus* species), grapevine (*Vitis* species), and elder (*Sambucus* species). It was introduced to the USA and southern Europe in 2008 (Grassi *et al.*, 2009; Hauser, 2011; Calabria *et al.*, 2012; Cini *et al.*, 2012) and to South America in 2012 (Deprá *et al.*, 2014). In 2011, the pest invaded Germany (Vogt *et al.*, 2012) and has caused increasing widespread economic damage. In worst case, total yield loss is possible (Vogt *et al.*, 2012).

In contrast to other drosophilids, the adult female is able to oviposit in healthy fruits due to its serrated ovipositor (Walsh *et al.*, 2011; Lee *et al.*, 2011b). At optimum environmental conditions, *D. suzukii* can develop up to 13 generations per year (Kanzawa, 1939). Infested fruits collapse quickly and become unmarketable (Lee *et al.*, 2011b; Walsh *et al.*, 2011). The wide host range and preference for ripe fruits combined with its high reproduction potential makes this species extremely harmful and difficult to control (van Timmeren & Isaacs, 2013). Strongly restricted insecticide registration and limited number of applications, as for example in Germany (Köppler *et al.*, 2019), together with low efficacy of insecticides and other control methods

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(Bruck *et al.*, 2011; Pavlova *et al.*, 2017; Schetelig *et al.*, 2018) make plant protection against this pest even more difficult. Therefore, and due to potential harmful side effects of pesticide applications on human health and the environment, integrated pest management (IPM) should be implemented to control *D. suzukii* in crops (Xue *et al.*, 2019).

Drosophila suzukii is usually monitored by vinegar traps but previous studies showed that trap captures did not correlate well with fruit infestation levels and therefore are not sufficient for estimating population size and infestation risk when fruits are ripening (Kirkpatrick *et al.*, 2017). Therefore, in addition to traps a population dynamics model should be developed and used for monitoring and IPM. A population dynamics model usually includes relevant development parameters of the pest such as reproduction linked to the most important driving factors. Especially, the driving factor air temperature has a strong influence on activity and development of *D. suzukii* (Vayssières *et al.*, 2009; Hamby *et al.*, 2013; Tochen *et al.*, 2014, 2016b). Consequently, population dynamics modelling of *D. suzukii* is subjected to a detailed understanding of the development depending on temperature (Racca *et al.*, 2011) in addition to other potential driving factors such as humidity.

A large number of studies focused on the influence of temperature on *D. suzukii's* life cycle (Kaçar *et al.*, 2016; Jakobs *et al.*, 2017; Rendon *et al.*, 2018; Saeed *et al.*, 2018; Shaw *et al.*, 2018; Alford *et al.*, 2019; Chen *et al.*, 2019; Enriquez & Colinet, 2019; Santoiemma *et al.*, 2019; Stockton *et al.*, 2019; Tait *et al.*, 2019; Enriquez *et al.*, 2020; Saeed *et al.*, 2020; Xue & Ma, 2020), whereas relative humidity was rarely investigated (Rogers *et al.*, 2016; Diepenbrock & Burrack, 2017; Eben *et al.*, 2018; Guédot *et al.*, 2018; Wong *et al.*, 2018). In temperate regions, usually only a small initial population of *D. suzukii* can be observed in spring (Zerulla *et al.*, 2015). Nevertheless, the population of summer morph flies can increase greatly during summer and fall (Asplen *et al.*, 2015) when environmental conditions, especially temperature, are favourable. Population increase of *D. suzukii* was found to be highest at 21 °C (Tochen *et al.*, 2014; Ryan *et al.*, 2016), whereas hot summers with temperatures higher than 30 °C (Harris *et al.*, 2014; Kinjo *et al.*, 2014; Tochen *et al.*, 2014; Ryan *et al.*, 2016; Evans *et al.*, 2018) can reduce population size (Gutierrez *et al.*, 2016; Tochen *et al.*, 2016b; Eben *et al.*, 2018) and consequently infestation risk for ripening fruits. Under heat stress female flies, for example, develop smaller ovaries (Green *et al.*, 2019) and males produce less sperm resulting in reduced fertility (Green *et al.*, 2019) and reduced offspring (Eben *et al.*, 2018; Evans *et al.*, 2018; Green *et al.*, 2019). In addition, the life span of adults is shortened by heat stress (Evans *et al.*, 2018; Green *et al.*, 2019). Extremely low relative humidity values can additionally contribute to negative effects on *D. suzukii's* life cycle (Gutierrez *et al.*, 2016; Tochen *et al.*, 2016b; Eben *et al.*, 2018). In temperate regions, when temperatures decline to roughly 10 to 15 °C (Zerulla, 2019), winter morph flies (Clemente *et al.*, 2018; Fraimout *et al.*, 2018) undergo reproductive diapause (Zerulla *et al.*, 2015; Rossi-Stacconi *et al.*, 2016; Shearer *et al.*, 2016). For a very short period of time, winter morph flies are able to survive low temperatures up to −7.5 °C (Stockton *et al.*, 2019). In mild winters, adult flies become occasionally active and can be trapped (Harris *et al.*, 2014). There is evidence that *D. suzukii* is able to reproduce early in the year but further reproduction is usually limited by the low availability of ripe host fruits (Briem *et al.*, 2016; Kenis *et al.*, 2016; Wiman *et al.*, 2016; Grassi *et al.*, 2018; Panel *et al.*, 2018).

The literature survey for this review article started in March 2017 and ended in February 2020. During this time period, the literature database Google scholar was frequently used, whereby the following phrase was entered: '*Drosophila suzukii* and temperature' or '*Drosophila suzukii* and humidity'. The records retrieved were screened for their relevance, and more references that were of interest could often be found within the relevant articles. In addition, the rubric 'cited by' of frequently cited articles was screened for appropriate records. Only articles published in English were considered, mainly focusing on horticulture including agriculture.

We considered studies conducted worldwide which address *D. suzukii's* life cycle depending on temperature and relative humidity. Life cycle parameters include oviposition, development success and duration, adult life span, and survival in heat and cold. We analysed published results and summarized optimum values and thresholds for *D. suzukii's* development. Finally, we present a synthesis of whether or not data in the literature are suitable and sufficient to understand *D. suzukii* biology and population dynamics. Similar review articles were published by Asplen *et al.* (2015) and Hamby *et al.* (2016), however, since then a lot of additional original articles on *D. suzukii* population dynamics, especially related to temperature effects, were published, which are considered herein. Therefore, the presented summary of results is up-to-date, timely, and not published yet. In addition, four summary tables (summary of materials and methods used, summary of modelling studies and summary of research gaps) are presented, also not published yet.

Temperature effects on *D. suzukii* population dynamics

A detailed knowledge of *D. suzukii's* thermal tolerance and thresholds is crucial for understanding its biology in order to develop and fine-tune pest management methods. The following sections summarize the current knowledge related to thermal biology of *D. suzukii* including oviposition, development success, development duration, and survival.

Temperature-dependent oviposition

In order to predict damage risk of fruits, temperature-dependent oviposition of *D. suzukii* is crucial because it strongly affects the adult flies' reproduction success (Tochen *et al.*, 2014; Zerulla *et al.*, 2017; Evans *et al.*, 2018; Zerulla, 2019). For example, maturity of females' ovaries (Zerulla *et al.*, 2015; Evans *et al.*, 2018; Grassi *et al.*, 2018; Green *et al.*, 2019; Zerulla, 2019) and males' sperm production (David *et al.*, 2005; Evans *et al.*, 2018; Grassi *et al.*, 2018; Green *et al.*, 2019), are both known to be negatively impacted by extreme temperatures, finally leading to reduced oviposition success.

The optimum temperature for oviposition of summer morph female *D. suzukii* varied roughly between 22 and 28 °C across experiments (Fig. 1). In average, the number of laid eggs per

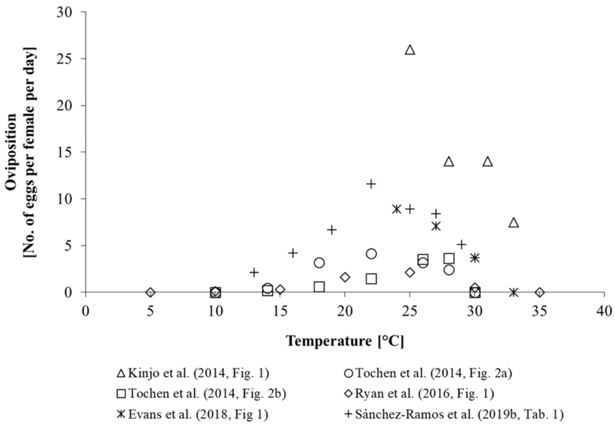

Figure 1 Oviposition of summer morph *Drosophila suzukii* depending on temperature. Results of different laboratory studies, gained under constant temperatures. *Note*: Tochen *et al.* (2014), Fig. 2a,b therein, presented their oviposition data using eggs per female per life span as a unit. Therefore, we converted these data into eggs per female per day.

female per day at optimum temperatures varied from about 4 to 26 (Fig. 1). The lower threshold for oviposition was determined between 5 and 10 °C, given that no eggs were laid at these temperatures (Fig. 1). The upper threshold for oviposition of *D. suzukii* was defined between 30 and 35 °C across studies (Fig. 1).

Interestingly, the number of eggs presented by Kinjo *et al.* (2014) is much higher compared to the other studies. A possible reason is that different materials and methods were used across studies including oviposition medium (Kinjo *et al.*, 2014), relative humidity (Tochen *et al.*, 2016b), age of females (Tochen *et al.*, 2014), and genetic background of flies (Gutierrez *et al.*, 2016), see also Tables 1 and 2.

Oviposition data (Fig. 1) reported by Ryan *et al.* (2016) and Tochen *et al.* (2014) are in agreement with Grumiaux *et al.* (2019) and Wallingford *et al.* (2016) who tested oviposition of *D. suzukii* in the field under fluctuating temperatures. Therefore, laboratory values of roughly about 2 to 4 eggs per female per day (Fig. 1) can be assumed to be plausible for wild *D. suzukii* flies.

Temperature-dependent egg-to-adult development

Drosophila suzukii's life cycle consists of the following stages: egg, larva (1st, 2nd, 3rd instar), pupa and adult fly. The percentage of eggs developing successfully into an adult fly strongly depends on temperature (Lee *et al.*, 2011a). Under optimum temperature conditions (Lee *et al.*, 2011a), *D. suzukii* has a high reproduction rate with up to 13 generations per year (Kanzawa, 1939). Consequently, the pest can become a phytosanitary problem within a very short time period.

Approximately 19 to 25 °C is the optimum temperature range for the egg-to-adult development success (Fig. 2). The lower and upper threshold was defined at 8 °C and between 30 and 33 °C, respectively, given that no complete egg-to-adult development took place at these temperatures (Fig. 2). The percentage of successfully developed adult *D. suzukii* at the optimum temperatures varied between 59 and 100% across studies (Fig. 2), probably depending on the different experimental materials and methods used (Tables 1 and 2). For example, larval nutrition substrate varied across experiments and may have influenced the development success (Bellamy *et al.*, 2013; Burrack *et al.*, 2013; Hardin *et al.*, 2015; Jaramillo *et al.*, 2015; Lee *et al.*, 2015; Schlesener *et al.*, 2018).

The egg-to-adult development duration was consistently shortest at about 28 °C (Fig. 3) across studies with minimum development durations from 9.5 to 11 days (Fig. 3). Similar fast development occurred from 24 to 31 °C (Fig. 3), whereby the development success was poor at temperatures above 30 °C (Fig. 2).

In summary, 13 to 30 °C resulted in relatively high development success of about 60 to 100% (Fig. 2); however, different durations of roughly about 10 to 30 days for egg-to-adult development were recorded in this temperature range (Fig. 3).

Temperature-dependent adult life span

The life span of adult *D. suzukii* flies directly affects population size and reproduction. Since insects are poikilothermal, their metabolic rate and life span are greatly influenced by the environmental temperature. Usually, the higher the temperature, the higher the metabolism rate, the lower the life span of insects (Rockstein, 1974).

In general, life span (adult emergence to mortality) of summer morph flies decreased with increasing temperature within a range from 10 to 33 °C (Fig. 4), although absolute life span values differed greatly across studies. Life span was longest at 10 or 16 °C, respectively, with maximum ages of 33 and 60 days (Fig. 4), whereby even higher life spans of *D. suzukii* up to 160 days were found under specific laboratory conditions (Emiljanowicz *et al.*, 2014; Toxopeus *et al.*, 2016; Grumiaux *et al.*, 2019). At 33 °C, adult *D. suzukii* survived a few days only (Fig. 4). Differences in experimental methods used across studies such as quality of nutrition source, *D. suzukii* strain origin, and relative humidity might be responsible for the variation of absolute life span values across studies (Chabert *et al.*, 2013; Emiljanowicz *et al.*, 2014; Lin *et al.*, 2014; Hamby *et al.*, 2016; Toxopeus *et al.*, 2016; Tochen *et al.*, 2016b), see also Tables 1 and 2.

Kanzawa (1939) measured similar life spans of adult *D. suzukii* flies, in Japan from May to August under field conditions (fluctuating temperatures), like Kim *et al.* (2015) in the laboratory. Therefore, the laboratory data of Kim *et al.* (2015) appear to be relevant and can be assumed as plausible for wild flies during the growing season.

Heat survival

Survival of *D. suzukii* at low temperatures is widely studied (Kimura, 2004; Zerulla *et al.*, 2015; Plantamp *et al.*, 2016; Rossi-Stacconi *et al.*, 2016; Toxopeus *et al.*, 2016; Jakobs *et al.*, 2017; Zerulla *et al.*, 2017; Everman *et al.*, 2018; Fraimout *et al.*, 2018; Panel *et al.*, 2018; Stockton *et al.*, 2018; Wallingford *et al.*, 2018), whereas survival at high temperatures during summer is rarely studied (Kimura, 2004; Enriquez & Colinet, 2017; Eben *et al.*, 2018; Evans *et al.*, 2018; Green

Table 1 Materials and methods used in the experimental studies considered in Figs 1 to 4, and 8 related to the effect of temperature on different investigated life cycle parameters of *Drosophila suzukii*

		Experimental conditions					
Reference	Investigated parameters	Temperatures tested	Relative humidity	Photoperiod	Diet/fruit	Rearing conditions	*D. suzukii* strain
Kinjo *et al.* (2014)	Oviposition, egg-to-adult development success, egg-to-adult development duration	25, 28, 31, 33 °C	60%	Not given	Grape juice agar	Cornmeal-yeast diet, 60% RH, 16L : 8D	Yamagata Prefecture, Japan
Tochen *et al.* (2014)	Oviposition, egg-to-adult development duration, adult life span	10, 14, 18, 22, 26, 28, 30 °C	65%	16L : 8D	Cherries, blueberries	Cornmeal-malt diet, 22 °C, 65% RH, 16L : 8D	Willamette Valley, Oregon, USA
Kim *et al.* (2015)	Egg-to-adult development success, egg-to-adult development duration, adult life span	16, 19, 22, 25, 28 °C	60%	16L : 8D	Cornmeal-malt diet	Cornmeal-malt diet, 22 °C, 70 to 80% RH, 16L : 8D	Not given
Ryan *et al.* (2016)	Oviposition, egg-to-adult development duration, egg-to-adult development success	5, 6, 7, 8, 9, 10, 15, 20, 25, 30, 31, 32, 33, 34, 35 °C	47%	16L : 8D	Standard lab diet	Cornmeal-malt diet, 22 °C, 25% RH, 15L : 9D	Ontario, Canada
Tochen *et al.* (2016b)	Oviposition, egg-to-adult development duration, adult life span	21 °C	20, 33, 71, 82, 94% (tested)	Not given	Blueberries	Cornmeal-malt diet, 22 °C, 65% RH, 16L : 8D	Corvallis, Oregon, USA
Evans *et al.* (2018)	Oviposition, egg-to-adult development success, adult life span	24, 27, 30, 33 °C	70%	14L : 10D	Cornmeal-molasses-yeast diet	Cornmeal-molasses-yeast diet, 24 °C, 70% RH, 14L : 10D	Clarke County, Georgia, USA
Sánchez-Ramos *et al.* (2019a)	Egg-to-adult development success, egg-to-adult development duration	10, 13, 16, 19, 22, 25, 27, 28, 29, 30, 31 °C	80 to 85%	16L : 8D	Cornmeal diet with sugar beet juice	Cornmeal diet with sugar beet juice, 19 °C, 70% RH, 16L : 8D	San Pol de Mar, Barcelona, Spain
Sánchez-Ramos *et al.* (2019b)	Oviposition, adult life span	13, 16, 19, 22, 25, 27, 29, 30 °C	80 to 85%	16L : 8D	Cornmeal diet with sugar beet juice	Cornmeal diet with sugar beet juice, 19 °C, 70% RH, 16L : 8D	San Pol de Mar, Barcelona, Spain

Tochen *et al.* (2016b) tested different humidity conditions rather than different temperatures. Only experiments with constant laboratory conditions are considered herein. Experiments with fluctuating temperatures or field conditions such as in Wallingford *et al.* (2016) and Chen *et al.* (2019) are not mentioned in this table.

Table 2 Materials and methods used in the experimental studies considered in Figs 5 to 7, and 9 related to the effect of temperature on the survival of *Drosophila suzukii*

	Experimental conditions							*D. suzukii* characteristics			
Reference	Investigated parameters	Temperatures tested	Exposure durations	Relative humidity	Photoperiod	Diet/fruit	Rearing conditions	Stage	Phenotype	Sex	Strain
Kimura (2004)	LLT, ULT	−3 to 36 °C	24 hours	88 to 95%	Not given	Not given	Corn-malt diet, 23 °C, 15L : 9D	Adults	Summer morph	♂ ♀	Sapporo, Tokyo
Dalton *et al.* (2011)	LD	1, 3, 5, 7, 10 °C	12 weeks	80%	16L : 8D / 12L : 12D	Cornmeal-yeast diet	Cornmeal-yeast diet, 25 °C	Adults	Not given	♂ ♀	Oregon, USA
Jakobs *et al.* (2015)	LLT	−13 to 0 °C	1 hour	Not given	Not given	None	Banana diet, 21.5 °C, 60% RH, 13L : 11D	Adults	Summer morph	♂ ♀	Halton Hills, Ontario, Canada
	LD	0 °C	12 hours to 10 days	Not given	Not given	None					
Plantamp *et al.* (2016)	LD	−4, −2, 0, 2 °C	8 to 144 hours	42 to 45%	Not given	Cornmeal-yeast diet	Cornmeal-yeast diet, 21 °C, 60% RH, 12L : 12D	Adults	Summer morph	♂ ♀	Sainte-Foy-lès-Lyon, France
Ryan *et al.* (2016)	LD	−5, −3, −1, 1, 3, 5 °C	42 hours	Not given	Not given	Banana diet	Cornmeal-malt diet, 22 °C, 25% RH, 15L : 9D	Adults	Summer morph	♂ ♀	Ontario, Canada
Toxopeus *et al.* (2016)	LLT	−13 to 0 °C	1 hour	Not given	Not given	Banana diet	Banana diet, 21.5 °C/11 °C, 60% RH, 13L : 11D/10L : 14D	Adults	Summer and winter morph	♂ ♀	Halton Hills, Ontario, Canada
	LD	0 °C	A few days	Not given	Not given	Banana diet					
Enriquez and Colinet (2017)	LLT, ULT	−5, −2.5, 0, 2.5, 5, 7.5 °C and 30, 31, 32, 33, 34, 35, 37 °C	Up to 4 weeks	Not given	Not given	Not given	Cornmeal-yeast diet, 25 °C, 65 to 70% RH, 12L : 12D	Adults, pupae	Summer morph	♂ ♀	Sugana Valley, Trentino, Italy
Enriquez and Colinet (2017)	LLT, ULT	0, 2.5, 5, 7.5°C and 32, 33, 34, 35, 37 °C	Up to 13 days	5 to 10% and 80 to 100% (tested)	Not given	Not given	Cornmeal-yeast diet, 25 °C, 65 to 70% RH, 12L : 12D	Pupae	—	—	Sugana Valley, Trentino, Italy
Stockton *et al.* (2018)	LLT	−9.4, −6.7, −3.9, −1.1, 1.7, 4.4 °C	Up to 4 weeks	25%	10L : 14D	Cornmeal diet	Cornmeal diet, 25 °C, 65% RH, 14L : 10D	Adults	Summer and winter morph	♂ ♀	Geneva, New York, USA

Enriquez and Colinet (2017) tested both different temperature and humidity conditions. Only experiments with constant laboratory conditions are considered herein. Experiments with fluctuating temperatures or down cooling such as in Stephens *et al.* (2015) are not mentioned in this table.

LLT = Lower lethal threshold, ULT =Upper lethal threshold, LD = Lethal duration.

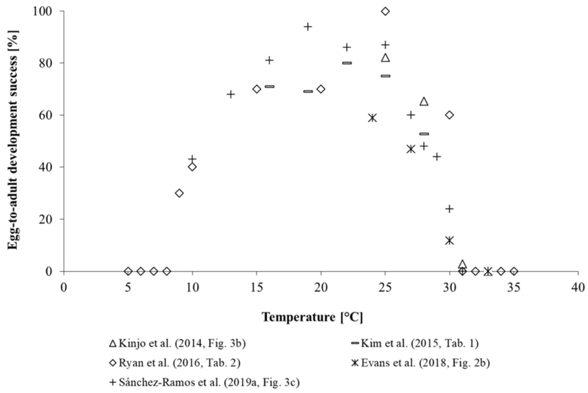

Figure 2 Egg-to-adult development success (%) of *Drosophila suzukii* depending on temperature. Results of different laboratory studies, gained under constant temperatures.

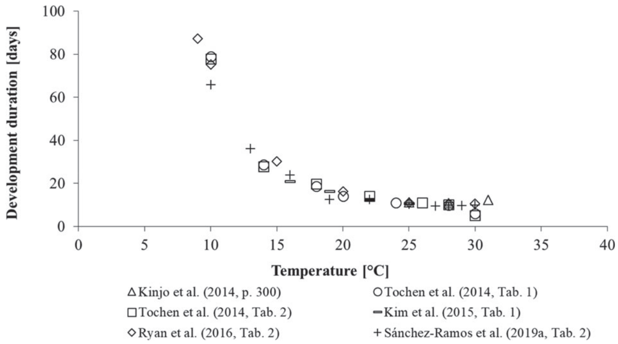

Figure 3 Egg-to-adult development duration (days) of *Drosophila suzukii* depending on temperature. Results of different laboratory studies, gained under constant temperatures. *Note:* At 31 °C development was fast, however, almost no adults developed successfully (Fig. 2, see Kinjo *et al.* (2014)).

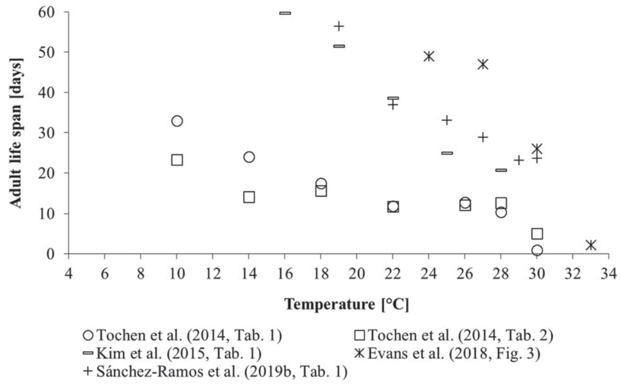

Figure 4 Life span of summer morph adult *Drosophila suzukii* flies depending on temperature. Results of different laboratory studies, gained under constant temperatures. *Note*: Tochen *et al.* (2014) only investigated females, whereas the values of the other authors represent the mean life spans of males and females.

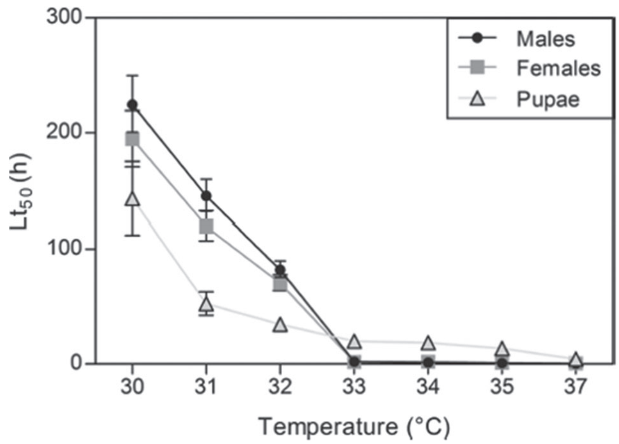

Figure 5 Survival (50%) of summer morph adult *Drosophila suzukii* flies and pupae at heat according to Enriquez and Colinet (2017), Fig. 4. Results gained in the laboratory under constant temperatures and different exposure durations (hours) (reproduced with permission).

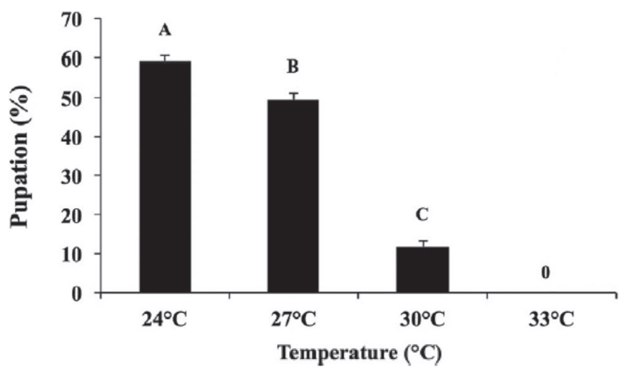

Figure 6 Egg-to-pupa development success (% pupation) of *Drosophila suzukii* at high constant temperatures according to Evans *et al.* (2018), Fig. 2a (reproduced with permission).

et al., 2019). Adult *D. suzukii* flies can avoid heat stress by migration into cooler habitats (Tonina *et al.*, 2016; Green *et al.*, 2019; Xue *et al.*, 2019) and by shifting activity e.g. oviposition to cooler periods of the day (Shaw *et al.*, 2018; Xue *et al.*, 2019). In contrast to adults, immature stages, especially eggs, are confined to the environmental conditions at the oviposition site (Dillon *et al.*, 2009; Green *et al.*, 2019). Larvae are conditionally able to move to thermally more favourable locations and may choose an adequate pupation site (Dillon *et al.*, 2009). In general, pupae are known to be the most heat resistant life stage of *Drosophila* species (Krebs & Loeschcke, 1995; Dillon *et al.*, 2009).

According to Enriquez and Colinet (2017) survival of summer morph adults and pupae decreased with increasing temperatures from 30 to 37 °C (Fig. 5). In addition, adult males were more heat tolerant than females at constant temperatures (Fig. 5) (Enriquez & Colinet, 2017) as well as at fluctuating temperatures (not shown) (Eben *et al.*, 2018). When comparing life stages, pupae appeared to be less heat tolerant below 33 °C but more heat tolerant above 33 °C than adults (Fig. 5). However, mortality due to heat (Fig. 6) already takes place in egg or larvae stage (Evans *et al.*, 2018).

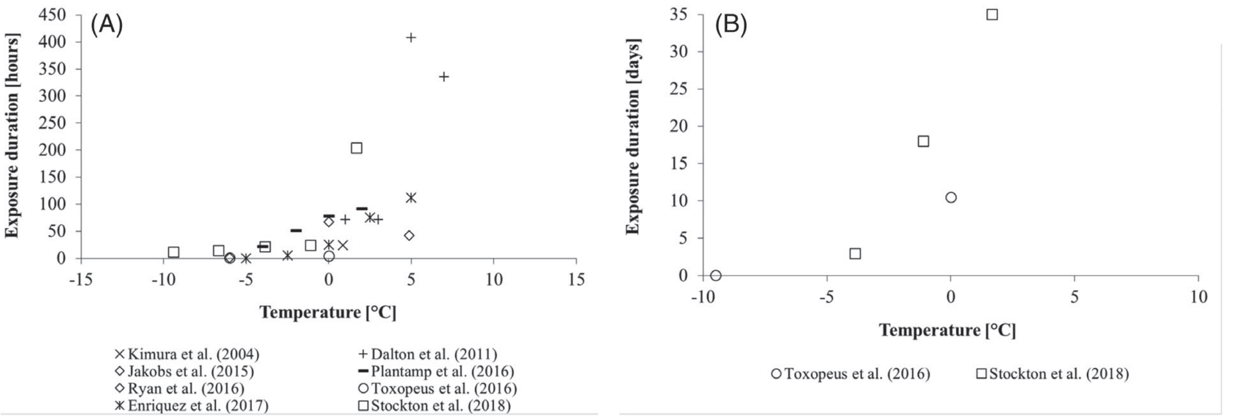

Figure 7 Survival (50%) of summer (A) and winter (B) morph adult *Drosophila suzukii* (mean of males and females). Results of different laboratory studies, gained under constant temperatures and different exposure durations (hours or days) without previous acclimation.

In summary, an upper threshold of about 33 °C can be defined for survival of *D. suzukii* according to Figs 5 and 6.

Adult cold survival

Lethal temperatures are one of the key factors limiting survival of insects (Ratte, 1985), whereby, most adult insects can survive exposure to a much lower temperature than at which they become inactive (Mellanby, 1939).

In general, survival of summer (Fig. 7A) and winter (Fig. 7B) morph flies decreased with declining temperatures within the tested range of 7.5 to −10 °C and exposure durations from 8 hours to 35 days. Winter morph flies survived lower temperatures at longer durations (Fig. 7B) compared to summer morph flies (Fig. 7A).

Results are in agreement with studies investigating the critical thermal minimum (CT_{min}) which represents the chill coma onset temperature. CT_{min80} (80% of flies fall into chill coma) was found between 0.4 to 0.5 °C for summer morph flies and between −5.5 to −2.5 °C for winter morph flies (not shown) (Jakobs *et al.*, 2015; Toxopeus *et al.*, 2016; Stockton *et al.*, 2018). Therefore, winter morph flies are more cold tolerant than summer morph flies regarding chill coma onset temperature as well.

However, the identified supercooling points (SCP) do not support the finding that winter morph flies are more cold tolerant because SCP_{50} (50% of flies freeze) values of summer morph (−17.9 to −20.2 °C) and winter morph flies (−17.3 to −17.7 °C) were similar (Jakobs *et al.*, 2015; Stephens *et al.*, 2015; Toxopeus *et al.*, 2016). This specific parameter suggests cold tolerance of winter and summer morph flies not to be different at extremely low temperatures for short time periods.

In general, it is unclear if females are more cold tolerant than males because there are contradictory results in the literature (Jakobs *et al.*, 2015; Plantamp *et al.*, 2016; Ryan *et al.*, 2016; Enriquez & Colinet, 2017; Stockton *et al.*, 2019). When comparing life stages, pupae appeared to be less cold tolerant than adults (Enriquez & Colinet, 2017; Stockton *et al.*, 2018). In some cases, cold tolerance of both morphotypes can be improved by acclimation (Jakobs *et al.*, 2015; Stockton *et al.*, 2018).

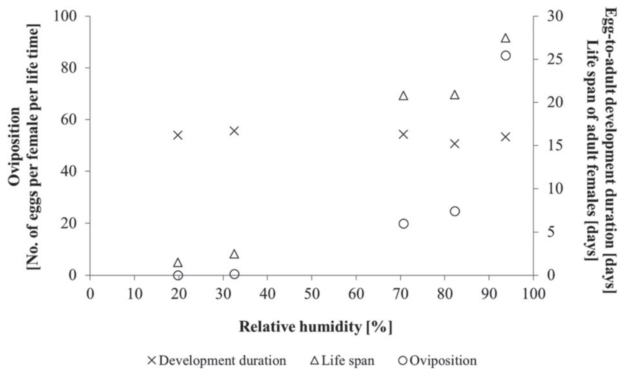

Figure 8 Mean oviposition per female per lifetime, mean egg-to-adult development duration and mean adult female life span of *Drosophila suzukii* depending on relative humidity at 21 °C according to Tochen *et al.* (2016b).

In summary, results suggest that *D. suzukii* is chill-susceptible and freeze-intolerant (Kimura, 2004; Jakobs *et al.*, 2015; Stephens *et al.*, 2015; Toxopeus *et al.*, 2016). However, *D. suzukii* is able to hibernate in sheltered natural environment such as wooded areas, beneath leaf litter, and snow pack as well as in anthropogenic structures such as compost piles or structural debris (Kanzawa, 1939; Jakobs *et al.*, 2015; Stephens *et al.*, 2015; Zerulla *et al.*, 2015; Pelton *et al.*, 2016; Rossi-Stacconi *et al.*, 2016; Wallingford *et al.*, 2016, 2018; Stockton *et al.*, 2018, 2019). These behavioural microhabitat choices make modelling *D. suzukii* overwinter mortality very difficult or even impossible because the actual hibernation conditions cannot be determined (Langille *et al.*, 2016).

Humidity effects on *D. suzukii* population dynamics

Besides temperature, relative humidity can influence insect development. Especially, low humidity combined with heat stress reduces insect survival (Bubliy *et al.*, 2012); thus, hot summer temperatures combined with arid conditions can impact

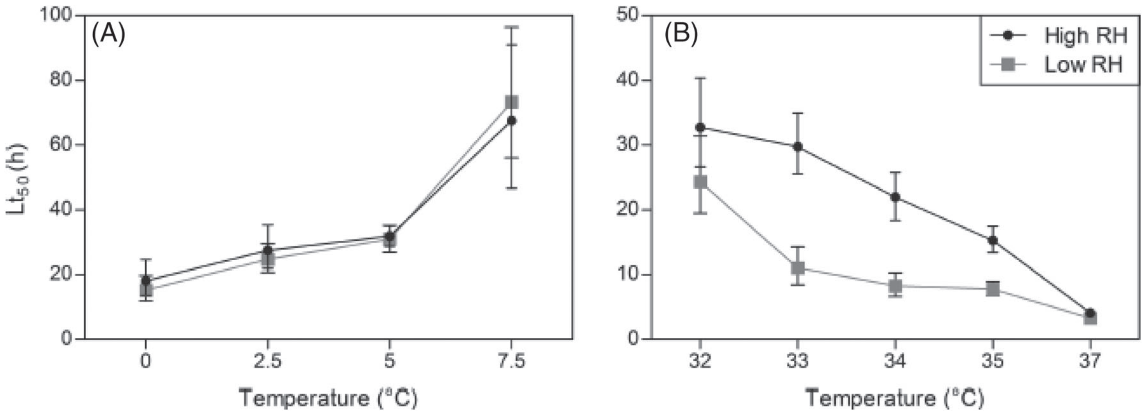

Figure 9 Survival (LT_{50} (h)) of *Drosophila suzukii* pupae depending on exposure duration (h) at low (5 to 10%) and high (80 to 100%) relative humidity and low (A) and high (B) temperatures according to Enriquez and Colinet (2017) Fig. 6 (reproduced with permission).

the aestivation success of *D. suzukii* (Gutierrez *et al.*, 2016; Eben *et al.*, 2018). In contrast, high relative humidity at favourable temperatures is usually beneficial for *D. suzukii*, often resulting in population increase and therefore in a higher infestation risk for fruits (Dos Santos *et al.*, 2017).

In laboratory studies at constant relative humidity levels between 20 and 94% both oviposition and life span of adult *D. suzukii* greatly increased with increasing humidity (Fig. 8) (Tochen *et al.*, 2016b). However, humidity had no effect on egg-to-adult development duration (Fig. 8) and generation time (data not shown) (Tochen *et al.*, 2016b). Nevertheless, Tochen *et al.* (2016b) found a high and appropriate relative humidity to be in general favourable for *D. suzukii* population dynamics.

Further studies revealed relative humidity to affect survival of pupae in heat (32 to 37 °C) (Fig. 9A) but not in cold (0 to 7.5 °C) (Fig. 9B). With increasing high temperatures (Fig. 9B) pupae survived longer at high (80 to 100%) compared to low (5 to 10%) relative humidity (Enriquez & Colinet, 2017). This is in agreement with Eben *et al.* (2018) who investigated survival of adult *D. suzukii* flies under high and low relative humidity.

In summary, besides temperature, relative humidity appears to be a useful factor for understanding and modelling *D. suzukii* population dynamics as suggested by the results of Tochen *et al.* (2016b) and Guédot *et al.* (2018).

Conclusions

There are substantial data on temperature-dependent life cycle parameters available to understand and predict *D. suzukii* population dynamics. Indeed, there are already some modelling studies published (Table 3) which considered these data. Five studies predicted population dynamics, four studies predicted geographic distribution. Oviposition is the most often life cycle parameter used (Table 3) suggesting that it is important for modelling. In addition, egg-to-adult development success and duration as well as adult life span are often considered (Table 3). Less often used are adult heat and cold survival as well as reproductive diapause (Table 3). Literature data which are frequently used include Tochen *et al.* (2014), Dalton *et al.* (2011), Emiljanowicz *et al.* (2014), and Ryan *et al.* (2016), suggesting that data provided by them are suitable for modelling. Meanwhile, additional literature data regarding temperature effects on *D. suzukii's* life cycle are published (Enriquez and Colinet (2017), Evans *et al.* (2018), Jakobs *et al.* (2015), Kim *et al.* (2015), Sánchez-Ramos *et al.* (2019a), Sánchez-Ramos *et al.* (2019b), Stockton *et al.* (2018), Toxopeus *et al.* (2016)) which can be included in future modelling approaches.

Besides temperature, relative humidity appears to be a useful factor for modelling *D. suzukii* population dynamics and geographic distribution as oviposition and life span of adult *D. suzukii* greatly increased with increasing humidity (Tochen *et al.*, 2016b). However, only one modelling study, namely the one by Gutierrez *et al.* (2016), considered relative humidity (data of Tochen *et al.* (2016b) used therein) in order to develop a physically based demographic model of *D. suzukii* (Table 3). All other mechanistic and correlative models published so far considered temperature only to predict population dynamics and geographic distribution of *D. suzukii* (Table 3). This is maybe due to the fact that temperature is much better investigated compared to relative humidity. However, it would be useful to investigate oviposition success and survival (Enriquez & Colinet, 2017) of adult *D. suzukii* at low compared to high relative humidity, particularly, under heat and cold stress. For example, high relative humidity may compensate for sub- and supra-optimal temperature conditions.

Concerning applied modelling approaches to assist *D. suzukii* control in the field, we suggest using important life cycle parameters only, mainly based on temperature, including reproduction and survival as suggested already by Wiman *et al.* (2014). In addition, an applied model should consider fruit ripening and extreme temperatures in the field (extreme heat > 30 °C, extreme cold < 0 °C) because start of fruit ripening indicates a potential infestation risk for the grower in order to apply control methods timely and extreme temperatures set natural limits for oviposition risk. Any other parameter, which is not well investigated or difficult to simulate due to its complex nature including interactions with diverse biotic and abiotic factors might worsen the estimation precision of population dynamics models. This is in agreement with Wiman *et al.* (2014) who concluded that a model can only be a simplified picture of reality and should not pretend

Table 3 Modelling studies which predict *Drosophila suzukii* population dynamics and/or geographic distribution

Reference	Model type	Model prognosis	*D. suzukii* life cycle parameters used	Data sources used
Coop and Dreves (2013)	Degree day model	Initial emergence and oviposition, total no. of generations per year	Oviposition, egg-to-adult development success, egg-to-adult development duration	Kanzawa (1936), Kanzawa (1939), Dreves (2010/2011), unpublished
Dos Santos *et al.* (2017)	Species distribution model (SDM) (maximum entropy modeling (MaxEnt) algorithm, genetic algorithm for ruleset production (GARP))	Global distribution, probability of occurrence	No concrete information provided by the authors	Dalton *et al.* (2011), Lin *et al.* (2014), Tochen *et al.* (2014)
de la Vega and Corley (2019)	Hybrid model: population dynamics model and SDM (mechanistic range-limit model combined with a correlative distribution model (MaxEnt))	Distribution in America	Lower lethal temperature (LLT) for egg-to-adult development, LLT for 50% survival of adult population, LLT for adult survival, LLT for 25% female survival in 24 hours, LLT for 20% adult survival in 1 hour, super cooling point (SCP), critical thermal minimum (CT_{min})	Kimura (2004), Dalton *et al.* (2011), Jakobs *et al.* (2015), Ryan *et al.* (2016)
Gutierrez *et al.* (2016)	SDM (physically based demographic model, degree-day model)	Distribution in North America, Europe, Mediterranean Basin; relative abundance of pupae	Oviposition, egg-to-adult development duration, adult heat and cold survival, reproductive diapause	Dalton *et al.* (2011), Kinjo *et al.* (2014), Tochen *et al.* (2014), Asplen *et al.* (2015), Zerulla *et al.* (2015), Plantamp *et al.* (2016), Tochen *et al.* (2016b)
Langille *et al.* (2016)	Population dynamics model (time stage structured population dynamics model)	Female population size, initial occurrence	Oviposition, egg-to-adult development success, egg-to-pupa development duration, reproductive quiescence	Emiljanowicz *et al.* (2014), Kinjo *et al.* (2014), Tochen *et al.* (2014), Ryan *et al.* (2016)
Langille *et al.* (2017)	Population dynamics model (global circulation models (CMIP5), population dynamics model)	Distribution in USA and Canada; relative population size	Initial population of fecund females, diapause termination temperature, diapause induction date based on daylight hours	Emiljanowicz *et al.* (2014), Ryan *et al.* (2016)
Pfab *et al.* (2018)	Population dynamics model (stage-structured resource-consumer dynamics model)	Optimal timing for releasing parasitoids	Maturation, oviposition, sex ratio, adult life span	Emiljanowicz *et al.* (2014), Tochen *et al.* (2014), Poyet *et al.* (2015), Shearer *et al.* (2016), Amiresmaeili (2017), Rossi Stacconi *et al.* (2017)
Wiman *et al.* (2014)	Population dynamics model (degree-day model, Leslie matrix population model)	Population increase, stage structure	Oviposition, egg-to-adult development duration, adult life span	Tochen *et al.* (2014)
Wiman *et al.* (2016)	Population dynamics model (degree day cohort-level population model)	Impact of pest management on population size	Oviposition, development success, egg-to-adult development duration, immature and adult life spans	Dalton *et al.* (2011), Emiljanowicz *et al.* (2014), Tochen *et al.* (2014)

Experimental studies which also include modelling approaches (e.g. Ryan *et al.*, 2016) are not considered in this table. Modelling studies which do not include experimental literature data related to temperature and relative humidity, such as Fraimout and Monnet (2018), Tait *et al.* (2018), Ørsted *et al.* (2019), Santoiemma *et al.* (2019) and Kamiyama *et al.* (2020) are also not considered in this table.

an unrealistic high accuracy, particularly not under field conditions.

In addition, for practical application, these population dynamics models should be linked to crop phenology (see above) and weather forecasts to assist advisors and growers to control *D. suzukii* in the field using chemical and nonchemical methods (Wiman *et al.*, 2014). However, to the best of our knowledge, currently these linked models (population dynamics module

Table 4 Selected future research perspectives mentioned in the literature related to population dynamics of *Drosophila suzukii* (more parameters than discussed above)

	Research gap and references (examples) highlighting it	Current research status and references with related work
Temperature	Temperature-related life cycle rates of the individual life stages (Tochen *et al.*, 2014)	Meanwhile often investigated by Kinjo *et al.* (2014), Kim *et al.* (2015), Ryan *et al.* (2016), Enriquez and Colinet (2017), Evans *et al.* (2018), Sánchez-Ramos *et al.* (2019a) and more or less conclusive
	Population dynamics at upper and lower extreme temperatures (Tochen *et al.*, 2014; Wiman *et al.*, 2014; Asplen *et al.*, 2015; Gutierrez *et al.*, 2016; Hamby *et al.*, 2016)	Meanwhile often investigated by Kimura (2004), Dalton *et al.* (2011), Jakobs *et al.* (2015), Stephens *et al.* (2015), Plantamp *et al.* (2016), Ryan *et al.* (2016), Toxopeus *et al.* (2016), Wiman *et al.* (2016), Enriquez and Colinet (2017), Stockton *et al.* (2018) and more or less conclusive
	Seasonal cold hardening/adaptation of winter morphs/developmental acclimation (Stephens *et al.*, 2015; Hamby *et al.*, 2016; Toxopeus *et al.*, 2016; Wallingford *et al.*, 2016; Wallingford & Loeb, 2016; Pfab *et al.*, 2018)	Some progress made by Jakobs *et al.* (2015), Stephens *et al.* (2015)
	Differences in thermal tolerance between sexes (Ryan *et al.*, 2016)	Meanwhile often investigated by Kimura (2004), Jakobs *et al.* (2015), Stephens *et al.* (2015), Plantamp *et al.* (2016), Ryan *et al.* (2016), Shearer *et al.* (2016), Toxopeus *et al.* (2016), Wallingford and Loeb (2016), Wallingford *et al.* (2016), Enriquez and Colinet (2017), Eben *et al.* (2018), Stockton *et al.* (2018) but contradictory results found
	Influence of fluctuating temperatures and field conditions on population dynamics (Dalton *et al.*, 2011; Tochen *et al.*, 2014; Langille *et al.*, 2016; Enriquez & Colinet, 2017; Pfab *et al.*, 2018)	Some progress made by Dalton *et al.* (2011), Wallingford and Loeb (2016), Wallingford *et al.* (2016), Wallingford *et al.* (2018), Grumiaux *et al.* (2019), Enriquez *et al.* (2020)
	Influence of temperature on the reproductive diapause (Dalton *et al.*, 2011; Asplen *et al.*, 2015; Zerulla *et al.*, 2015; Hamby *et al.*, 2016; Langille *et al.*, 2016; Plantamp *et al.*, 2016; Pfab *et al.*, 2018; Wallingford *et al.*, 2018)	Meanwhile often investigated by Zerulla *et al.* (2015), Plantamp *et al.* (2016), Rossi-Stacconi *et al.* (2016), Toxopeus *et al.* (2016), Wallingford and Loeb (2016), Wallingford *et al.* (2016), Zhai *et al.* (2016), Grassi *et al.* (2018), Rendon *et al.* (2018) and more or less conclusive
Humidity	Influence of humidity on population dynamics (Tochen *et al.*, 2014; Wiman *et al.*, 2014; Hamby *et al.*, 2016; Langille *et al.*, 2016; Pfab *et al.*, 2018)	Not yet investigated except for Tochen *et al.* (2016b)
	Influence of humidity on the reproductive diapause (Zerulla *et al.*, 2015; Panel *et al.*, 2018)	Not yet investigated
Modelling	Development of an hibernation risk model (Dalton *et al.*, 2011)	Not yet investigated except for Leach *et al.* (2019)
	Integrating population models into management programmes (Wiman *et al.*, 2016; Sánchez-Ramos *et al.*, 2019a)	Some progress made by Pfab *et al.* (2018), Drummond *et al.* (2019)
	Linking population models to weather forecasts (Wiman *et al.*, 2014; Panel *et al.*, 2018)	Not yet investigated except for Coop and Dreves (2013), http://uspest.org/risk/models?spp=swd
	Model validation in the field (Hamby *et al.*, 2016; Pfab *et al.*, 2018)	Not yet investigated except for Leach *et al.* (2019)
	Sensitivity analyses of the models (Pfab *et al.*, 2018)	Not yet investigated except for Langille *et al.* (2016)
	Integrating phenology models of specific cultivated host plants into population modelling (Wiman *et al.*, 2014; Asplen *et al.*, 2015; Langille *et al.*, 2016; Panel *et al.*, 2018; Pfab *et al.*, 2018; Rendon *et al.*, 2018)	Not yet investigated except for Drummond *et al.* (2019)
Further topics	Influence of photoperiod on the reproductive diapause (Asplen *et al.*, 2015; Hamby *et al.*, 2016; Langille *et al.*, 2016)	Some progress made by Toxopeus *et al.* (2016), Wallingford *et al.* (2016), Zhai *et al.* (2016)
	Influence of morphology on the reproductive diapause (Shearer *et al.*, 2016)	Not yet investigated except for Wallingford and Loeb (2016)
	Influence of temperature, humidity and photoperiod on the transition between the morphs (Asplen *et al.*, 2015; Shearer *et al.*, 2016)	Some progress made by Toxopeus *et al.* (2016), Wallingford *et al.* (2016), Fraimout *et al.* (2018), Guédot *et al.* (2018)
	Influence of wind and rain on population dynamics (Pfab *et al.*, 2018)	Not yet investigated except for Dos Santos *et al.* (2017)
	Influence of desiccation on hibernation success (Jakobs *et al.*, 2015; Enriquez & Colinet, 2017)	Some progress made by Toxopeus *et al.* (2016), Terhzaz *et al.* (2018), Alford *et al.* (2019)
	Influence of starvation on hibernation success (Jakobs *et al.*, 2015)	Not yet investigated except for Tochen *et al.* (2016a)
	Seasonal migration/avoidance of extreme temperature (Wiman *et al.*, 2014; Stephens *et al.*, 2015; Hamby *et al.*, 2016; Langille *et al.*, 2016)	Meanwhile often investigated by Klick *et al.* (2016), Tonina *et al.* (2016), Wang *et al.* (2016), Wong *et al.* (2018), Cahenzli *et al.* (2018), Tait *et al.* (2018) with different objectives but more or less conclusive
	Influence of landscapes/habitats on the seasonal abundance/habitats as wintering grounds (Asplen *et al.*, 2015; Pfab *et al.*, 2018; Stockton *et al.*, 2018)	Some progress made by Klick *et al.* (2016), Pelton *et al.* (2016), Tonina *et al.* (2016), Wang *et al.* (2016), Drummond *et al.* (2019)
	Integrating the impact of natural enemies on survival and fecundity into population modelling (Tochen *et al.*, 2014; Pfab *et al.*, 2018)	Not yet investigated except for Pfab *et al.* (2018), Drummond *et al.* (2019)

+ crop phenology module + weather forecast module) are missing.

The high number of published research articles, during roughly the past 10 years, on *D. suzukii*'s life cycle suggests that there is already a lot of knowledge available on its biology. Nevertheless, there are still considerable future research perspectives mentioned in the literature. A few selected examples of research perspectives (knowledge gaps) are listed in Table 4. Interestingly, many research gaps were mentioned by different authors across years repeatedly and are still not or rarely investigated only: for example, (i) cold hardening related to temperature effects, (ii) almost all life cycle parameters related to humidity effects, (iii) considering host phenology related to modelling, and (iv) the impact of natural enemies on *D. suzukii* population dynamics (Table 4). On the other hand, several knowledge gaps were addressed recently by different scientists such as population dynamics at upper and lower extreme temperatures (Table 4).

Surprisingly, there are more future research perspectives regarding temperature mentioned compared to humidity (Table 2), although temperature is the much better investigated factor (see introduction). This suggests that temperature appears to be the most important driver for *D. suzukii's* life cycle (as suggested by Figs 1 to 9) and consequently most scientists seem to believe that a very deep knowledge is necessary related to temperature compared to humidity effects. An additional explanation is that most scientists investigated temperature rather than humidity; thus, these publications state future research priorities related to temperature (biased pattern) rather than humidity. Furthermore, presumably it is more difficult to include the effects of relative humidity in a predictive model, for example, within climate change projections (Langille *et al.*, 2017) because it is often not as readily available as temperature.

To conclude, there are sufficient temperature data in the literature available to understand and predict *D. suzukii* population dynamics in order to assist pest management in the field, although there are still research gaps prevalent.

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