Global analysis of the seasonal abundance of the invasive pest *Drosophila suzukii* reveal temperature extremes determine population activity potential

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1. Abstract

Background: The global pest spotted winged drosophila (*Drosophila suzukii*) continues to cause significant economic impact to fruit production in areas where it is established, in addition to newly invaded ranges. Management activities spanning national biosecurity responses to farm-scale pest control are limited by the inability to predict the timing and severity of seasonal outbreaks of *D. suzukii* and its climatic drivers.

Results: Here, we compiled and analysed data on international seasonal abundances for *D. suzukii* under different climates, crop types, and management contexts to improve the predictability of seasonal population dynamics. In relating seasonal abundances to environmental predictors, specifically temperature, we found strong negative effects of exposure to high and low temperatures during the preceding month. Unlike most regional studies on *D. suzukii* phenology that focus on temperature in the physiological development range, we show that thermal extremes better explain seasonal population fluctuations.

Conclusion: While trap catches remain an indirect measure of infestations and must be interpreted carefully in terms of crop risk, our results should support monitoring programs through enhanced knowledge of the climatic factors affecting *D. suzukii* population activity. The negative impact of high temperatures suggests that late-season management strategies focusing on manipulating crop microclimates to temperatures above 25 °C can reduce *D. suzukii* abundance. We show that early season abundance is modulated by climate, particularly the depth of cold extremes experienced in the preceding time period. These associations may be further developed into early-season crop risk forecasts to support monitoring programs.

2. Introduction

The highly invasive spotted wing drosophila (SWD; *Drosophila suzukii*) has emerged as a serious pest of international significance to global fruit production, laying eggs in ripening fruits of more than 145 plant species [1], including economically important stone fruits and berries. It was first detected in Europe and North America in 2008 [2,3], and since 2012 it has also been found to be widespread in South America [4]. Most recently, *D. suzukii* has been detected on the African continent [5,6]. Estimated yearly losses due to *D. suzukii* exceeded 500 million US dollars in just three states of the US [7], and in Europe *D. suzukii* has been shown to infest up to 80 % of fruits in some fields [8].

An important tool in integrated pest management (IPM) strategies is the use of models that predict the spatial and temporal distribution of pests. Recently, species distribution models have shed light on the potential geographic distribution of *D. suzukii*, and have pinpointed likely invasion points and areas of high suitability requiring extra surveillance efforts [9–12]. However, when a pest is already well established attention should instead shift to focus on trying to understand temporal patterns in population dynamics in order to improve pest management. To address management priorities relating to *D. suzukii*, which is now widespread in many parts of the globe, regionally-specific research has accumulated on the population biology of *D. suzukii* [13–22]. Such studies often relate trap catches throughout the year to environmental conditions, mostly temperature, to reflect how local climate affect fluctuations in seasonal abundance.

Seasonal fluctuations in trap catches vary widely across geographic regions and climates, crop management strategies (e.g. trapping and pesticide applications), proximity to non-crop host plants, (e.g. bordering wild and cultivated host plants). Despite the growing number of local studies on the population ecology of *D. suzukii*, there has so far been no attempt to synthesise this regional data to understand broader patterns across the diverse climates, commodities, and management contexts where *D. suzukii* is currently found. This presents an opportunity for a macro-ecological study on the general processes underpinning seasonal population dynamics of *D. suzukii* across local contexts. Improved predictability of these dynamics can enhance ongoing management in production areas currently affected by *D. suzukii* through targeted monitoring efforts and the application of proactive pest management strategies. For locations preparing for possible incursions, such as Australia and New Zealand, improved predictability will provide insights into the likely seasonal behaviour of pest populations under different production contexts (e.g. crop type and management practices), which will enhance pest management capabilities, biosecurity preparedness, and incursion responses.

Here, we compile data on international seasonal abundances of *D. suzukii* for different climates, crops, and management contexts covering the major geographic areas of both native and invasive occurrence. This allowed us to investigate how climatic variation and management factors explain variation in seasonal abundance of *D. suzukii* through time. Of particular interest is how potentially stressful temperatures outside the species optimum affect both the start of emergence and peak abundance of *D. suzukii*. Locally, it has been suggested, for instance, that cold winter conditions causes high mortality leading to a decreased or absent spring population, and subsequently a slower build-up of individuals during the proceeding growing season [13,23]. Similarly, trap catches have been found to decline at high temperatures during summer or prolonged warm periods, such as heat waves [17,22,24]. We do not know, however, the generality of these patterns, and whether climatic factors, or management factors, can explain seasonal abundances across broad scales.

3. Methods

3.1 Seasonal abundance data and geographic distribution

Abundance data was compiled from a review of field studies of *D. suzukii* in which seasonal abundances were measured through trap catches, covering the major geographic areas of both native and invasive occurrences. Data was compiled from source tables or, where unavailable, extracted from digitised figures. From each study, we recorded the trap count of *D. suzukii*, trapping method, date of inspection, trapping period, trap location, year of first regional detection, and main crop plant monitored. To place these studies in the context of the current global extent of *D. suzukii*, we mapped the approximate range of *D. suzukii* using previously published data sets of *D. suzukii* occurrences [12,25] and recent records.

3.2 Environmental predictors

To build climatic variables at the study locations and time period we utilised Global Surface Summary of the Day (GSOD) weather data from the USA National Centers for Environmental Information (NCEI), which were retrieved using the 'GSODR' R package [26]. We selected weather stations based on their proximity to each study site, which resulted in over 80% of the compiled studies having available data from weather stations within 30 km of the study site.

To better interpret seasonal patterns in abundance across a range of trapping methods, growing conditions and management contexts, trap count data were scaled by the maximum observed number of individuals for each unique study, crop, or trapping method. It has been previously noted that trap data for *D. suzukii* do not necessarily represent pressures in the field [22,23], thus scaling by the maximum observed trap count also serves to minimise inference on absolute counts with more emphasis placed on relative changes through a season.

Environmental covariates for each monitoring point were constructed from the climatic data, including the mean temperature across the preceding 30 days, as well as the accumulated degree days

(DD) below both 5°C and above 25°C [27,28]. These temperature thresholds approximately represent the lower temperature bounds of development and the decreasing phase of population growth rate, respectively [9]. To calculate these covariates, available minimum and maximum daily temperatures were converted to hourly temperatures with an idealized daily temperature curve that uses a sine curve for daytime warming and a logarithmic decay function for night time cooling with the 'chillR' R package [29].

3.3 Statistical analysis

To analyse seasonal trends in *D. suzukii* trap abundance we used generalized additive mixed models (GAMM). A GAMM relaxes the more restrictive assumption of generalized additive models (GAM) that the data are independent, which is unlikely to hold in many ecological contexts when repeated observations have been made on abundances through time [30–32]. A GAMM (family=quasibinomial) was used to examine the scaled seasonal abundance (0 - 1) against covariates for seasonality, climatic conditions, host crop, and trapping method. Specifically, scaled abundance ($\mu_{i[ab]}$) for site i with crop a and trapping method b could be represented as follows:

$$logit(\mu_{i[ab]}) = f_1(j_i) + f_2(T_i) + f_3(D_{i(T<Tmin)}) + f_4(D_{i(T>Tmax)}) + \varepsilon_{i(a)} + \varepsilon_{i(b)}$$

$$\varepsilon_{i(a)} = N(0, \sigma_a^2)$$

$$\varepsilon_{i(b)} = N(0, \sigma_b^2)$$

where $f_1(j_i)$ was a smoothing function (penalized cubic regression spline) of days after January 1 (or July 1 for Northern hemisphere) following the incursion year (j_i) for the ith observation. The terms $f_2(T_{mean})$, $f_3(D_{i(T<Tmin)})$, and $f_4(D_{i(T>Tmax)})$ were smoothing functions of mean temperature, accumulated DDs below 5°C, and the accumulated DDs above 25°C of the preceding 30 days, respectively. The terms $\varepsilon_{i(a)}$, and $\varepsilon_{i(b)}$ corresponded to the random effects term of main crop and trapping method, respectively. To account for auto-correlation we used a moving average correlation structure of order $p = 2$, where the order of observations specified the time covariate for each study [33,34].

4. Results

We reviewed published field studies of *D. suzukii* in which seasonal abundances were measured through trap catches. From 13 studies and 117 unique locations (**Figure 1**) this resulted in observations for 12,494 trapping periods (median trapping period = 12 days; ranging 1 to 48 days) across 20 host species (see **Supplementary Table S1**). We also mapped the approximate current geographic distribution spanning 58 countries from latitudes 41.5 degrees south to 63 degrees north (**Figure 1**), including the first reported occurrences on the African continent [5,6], as well as the northernmost record recently discovered in Finland [35].

As expected, the data on trap catches showed strong seasonal trends (**Figure 2**) across as much as seven years of trap data in some areas (e.g. Briem *et al.* 2018). Of the fixed effect predictors, days after January 1 in the Southern hemisphere (or July 1 in the Northern hemisphere) following the incursion year was significant ($F_{9.98} = 81.7$, $p < 0.001$; **Table 1**). Partial dependency plots showing the marginal response of scaled abundance indicate an increasing effect of day from approximately day 250 until approximately day 150 (**Figure 3A**); that is around early March to the end of November in the Northern hemisphere, and early September to the end of May in the Southern hemisphere. We also observed a trend of mean temperature of the preceding 30 days of increasing trap catches from approximately 15 to 25 °C (**Figure 3B**), although this effect was not significant ($F_1 = 3.07$, $p = 0.0795$; **Table 1**). Interestingly, we observed an approximately linear negative effect of accumulated DDs above 25 °C in the preceding month on scaled abundance (**Figure 3C**), and a similarly linear negative effect of accumulated DDs below 5 °C in the preceding month (**Figure 3D**). Both smoothing terms were significantly negative ($F_{3.59} = 24.46$, $p < 0.001$, and $F_{1.0} = 27.25$, $p < 0.001$, for DD above 25 °C and DD below 5 °C, respectively; **Table 1**). We similarly observed significant effects of both crop type and trapping method on abundance (**Table 1**; **Figure S1**).

To visualise the negative effect of accumulated DD below 5 °C and seasonal abundances, we used the GAMM to predict scaled seasonal abundance through time, while fixing other main effects simulating spring conditions (mean monthly temperature at 10 °C, and accumulated DDs above 25 °C at 10 °C/month). We predicted relative abundance at 0, 5, 10, 50, and 100 accumulated DDs below 5 °C in a field of grapes using apple cider vinegar traps, i.e., the most common crop type and trapping method (**Figure 4**). Generally, there is an increase in abundance from mid-summer which peaks around November or May for the Northern hemisphere and Southern hemisphere, respectively, and then drops dramatically. The effects of 50 and 100 °C/month accumulated DD below 5 °C are shown as large visible reductions in both early and maximum abundances, while there was practically no effect of 5 or 10 °C/month accumulated DD below 5 °C compared to 0. In exploring the connection between early and maximum abundances, we found a weak but significant negative relationship between the day of first detection and the maximal daily number of flies caught during the season, i.e. earlier first catch resulted in a higher peak abundance ($F_{1,393} = 38.9$, $p < 0.001$; **Figure 5**).

5. Discussion

Regional studies on the population biology of *D. suzukii* have been accumulating since its invasion through Europe, North and South America, but so far, no effort has been made to synthesize field abundance data on a broader scale. Here, we reviewed published local data on seasonal trap catches to investigate the general mechanisms of seasonal population dynamics of *D. suzukii* across local contexts, across its global distribution, both in its native and invasive range [11,12]. Knowledge on both geographical range and population abundance is crucial to undertake predictive modelling and improve novel management strategies that are proactive, sustainable [36], and benefit farmers, practitioners, and horticulture industry members.

As expected, our meta-analysis confirmed that population dynamics are very seasonal, similar to the findings of all the local studies we have reviewed [13–22,37–45], but show a global pattern. Our results indicated increasing trap catches from early March to the end of November in the Northern hemisphere and around early September to the end of May in the Southern hemisphere, also in line with regional findings.

In relating seasonal abundances to environmental predictors, specifically temperature, we found no strong effect of the mean temperature of the preceding month, however we found strong negative effects of exposure to high and low temperatures during the preceding month. This is consistent with the idea that extreme temperatures are more important than average temperatures in determining limits of development and survival, especially for ectotherms. It has been shown for *Drosophila* species that tolerance to extreme temperatures (e.g. during winter cold spells or summer heat waves), constrain species distributions [46–48], and correlative models also suggest that the distribution of *D. suzukii* is limited by low temperatures, especially at the northern and southern range limits [10,11,49]. Rather than simply using a single thermal threshold limit, we employed the widespread concept of degree-days, as it combines severity of the thermal exposure with the duration. This is a standard method in crop management, such as timing insecticide treatments to coincide with predictions of high pest pressure [50], and recently, physiologically based predictive DD models have been employed to forecast local *D. suzukii* phenology with varying success [27,28,44,51]. These models typically ignore temperature accumulation outside of extremes and, rather, focus on temperature accumulation within the range that permits development. For example, Kamiyama *et al.* (2020), implemented temperature accumulation between a lower limit of 7.2 ˚C and an upper limit of 30 ˚C, as *D. suzukii* development ceases outside of those temperatures [52]. This is akin to using optimum temperatures as described above. We argue that thermal extremes should not be disregarded in the explanation of population dynamics, which is supported by our finding of the strong association of seasonal abundance with accumulated DD below 5 ˚C and above 25 ˚C in the preceding month. Outside the optimum temperature range, temperature stress accumulates at much higher rates as recently shown for a range of drosophilids including *D. suzukii* [53]. This is consistent with our observations of near-linear decreases of trap catches with increasing number of DDs below 5 ˚C and above 25 ˚C.

Our results indicate prolonged periods of intense heat (e.g. a summer heat wave) will reduce population abundances. Several studies have found that *D. suzukii* populations grow in the early spring, then decline during the hottest summer months where rainfall is low and temperatures exceed 30 ˚C, and then peak again during autumn [15,17,22,24,51,54]. The lack of captures at high temperatures and the model predicting lower abundance with accumulated DDs above 25 °C could be due to reduced survival and/or reproduction at these temperatures [52,55], lack of activity and dispersal at temperatures between 25-30 °C [37], or migration to higher altitudes to other food sources and colder conditions as suggested by Mitsui *et al.* (2010).

Similarly, the linear decrease of trap catches with accumulated DDs below 5 °C in the preceding month indicate that preceding periods of cold weather will significantly decrease abundance. Thus, our results support numerous observations of low temperatures being the limiting factor for both *D. suzukii* overall abundance as well as timing of first emergence (e.g. Dalton et al. 2011b; Tochen et al. 2014; Rossi-Stacconi et al. 2016; Thistlewood et al. 2018). The primary constraint on seasonal abundance is thought to be the number of overwintering adults [39,57], thus harsh winter conditions will slow down spring population build-up and severely restrict potential maximum abundance in the following season [13]. In support of this, we found a negative relationship between the timing of first trap catch and the maximum number of adult flies during the season, meaning that the later the first catch, the lower the peak season abundance. Similar results were found in a seven year monitoring data set, where maximum catches were predicted by the date of first catch, as well as by the trap catches in the previous years, suggesting overwintering populations [44]. Drummond *et al.* (2019) also found that the earlier *D. suzukii* were captured in a field, the higher the relative abundance in the following growing season. Given these effects of winter cold, there may be some capacity to develop an early-warning system in affected regions, which would benefit farmers who could use this risk-based approach to inform seasonal management planning.

Despite rather clear effects of high and low temperature extremes, the included predictors in the GAMM only account for approximately 22 % of the variance in seasonal abundance, suggesting that there are other significant drivers of abundance besides temperature. This is not surprising given the broad range of crops, management regimes, and trapping options encompassed by our compiled data set. Other important factors may include plant type, variety and availability [16,58], number of and distance to non-crop host plants [20,42,59], fruiting phenology, micro-climate refuges [60], and predators and parasitoids [61]. Similarly, other management related factors such as chemical usage [27], and harvest schedules [54(p201)] can have strong impacts on *D. suzukii* population abundances observed within crops.

It should be noted in the present study (and more generally in field pest abundance studies) that while trap catches are a measure of in-field abundance, they do not necessarily reflect true abundances and therefore crop risk [22,23,62]. During periods of abundant ripening fruits, the traps are in direct competition with crop and non-crop food sources for attracting adult flies. Hamby *et al.* (2014) found that while trap data often correlated with infestation rates, examples of high larval infestation with low trap captures were present in all seasons, cautioning the use of trap catches as the foundation for management decisions. Nevertheless, at present, trap data expressed consistently across studies represent the best available comparative data.

There are some important knowledge gaps and thus limitations of the modelling undertaken here, and in general for species distribution modelling. One important determinant of seasonal abundance that we could not account for in our study, and which most models to our knowledge fail to incorporate, is acclimation effects. The fact that *D. suzukii* have distinct summer- and winter morphs with significantly different thermal tolerances [52,63], and can induce a reproductive diapause in cold conditions [64] represent a crucial limitation in predictive models of seasonal abundance [27]. Another limitation widely acknowledged in predictive models is that the environmental temperature data used as predictors to link thermal tolerance to geographic distributions or abundances is overly simplistic [65,66]. The coarse estimates of environmental temperature, typically based on air temperature measured 2 m above ground do not adequately reflect the micro-climatic environment experienced by most smaller organisms. Such micro-climates are affected by vegetation cover, terrain, human structures, wind, solar radiation, soil moisture, etc. [66,67]. The difference between standard air temperature and temperature measured near the soil surface or inside vegetation can exceed 10 °C [68]. New developments in micro-climate models, software and databases [67,69,70] show promising future opportunities for more accurate species distribution and predictive abundance models.

6. Conclusion

In conclusion, we present a model that can be used to predict *D. suzukii* early season activity potential to the benefit of farmers and other industry practitioners. However, while trap catches are a measure of in-field abundance, they do not necessarily accurately reflect crop risk. Therefore, this model should be used to support, rather than replace, in-field monitoring efforts by enhancing knowledge of how climatic factors affect *D. suzukii* population activity. The negative impact of high temperatures suggest late-season management strategies focusing on manipulating the crop micro-climate to temperatures above 25 °C may reduce *D. suzukii* abundance. We show that early season abundance is modulated by climate, particularly the depth of cold extremes experienced in the preceding time period. Given these relationships, there may be some capacity to develop an early-warning system for affected crops and regions.

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8. Conflicts of interest

The authors have declared that no competing interests exist.

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10. Tables

Table 1. General Additive Mixed Model (GAMM) parametric coefficients, and approximate significance of smoothing functions of days after January 1 for the Southern hemisphere (or July 1 for the Northern hemisphere) following the incursion year (day), and parameters relating to the preceding 30 days of an observation; mean temperature (meanmonthlytemp), accumulated degree days below 5°C (ddmin), and accumulated degree-days above 25°C (ddmax). Approximate significance of the random effects term of main crop and trapping method are also shown. Edf: effective degrees of freedom, Ref.df: reference degrees of freedom, F: F-statistic, and p: p value with asterisks denoting significance levels: *** $p < 0.001$.

		Estimate	**Std. Error**	**t value**	**p**	
Intercept		-1.96	0.30	-6.43	1.34E-10	***
	k	**edf**	**Ref.df**	**F**	**p**	
s(day)	12	9.98	9.98	81.72	2.16E-164	***
s(meanmonthlytemp)	5	1.00	1.00	3.07	0.0795	
s(ddmax)	5	3.59	3.59	24.46	7.01E-18	***
s(ddmin)	5	1.00	1.00	27.25	1.82E-07	***
s(main crop)	-	10.09	20.00	3.15	8.81E-07	***
s(trapping method)	-	6.89	9.00	18.61	4.22E-16	***

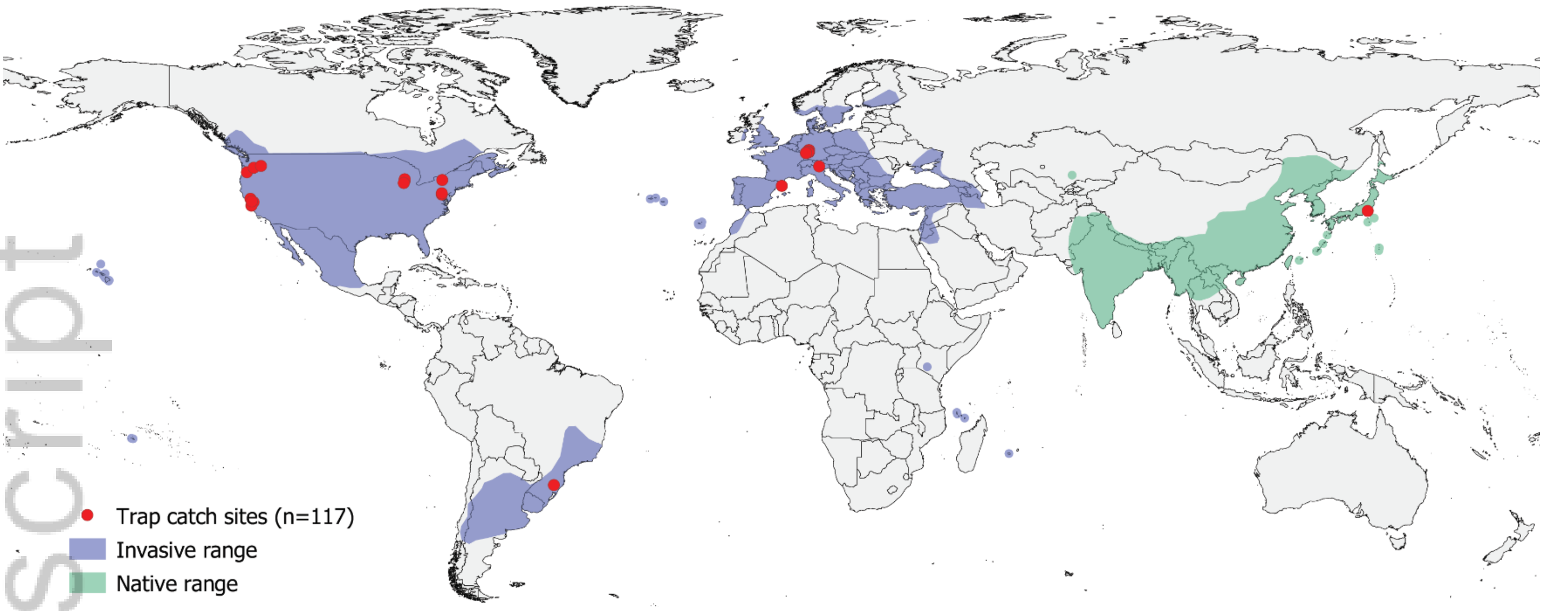

Figure 1. Geographic locations of seasonal abundance data and distributional range of *D. suzukii*

Geographic locations of the reviewed *D. suzukii* seasonal abundance data (117 trap catch sites; red dots), and approximate distributional range, divided into its native range (in green), and its invasive range (in blue) across Europe, North- and South America, and Africa. Island records and isolated mainland occurrences far from a cohesive range are buffered by 1 degree for increased visibility. The distributional range is approximated using previously published data sets of *D. suzukii* occurrences (Ørsted and Ørsted 2018; Reyes and Lira-Noriega 2020) and recent records (Boughdad et al. 2020; NPPO Finland 2020; Kwadha et al. 2021).

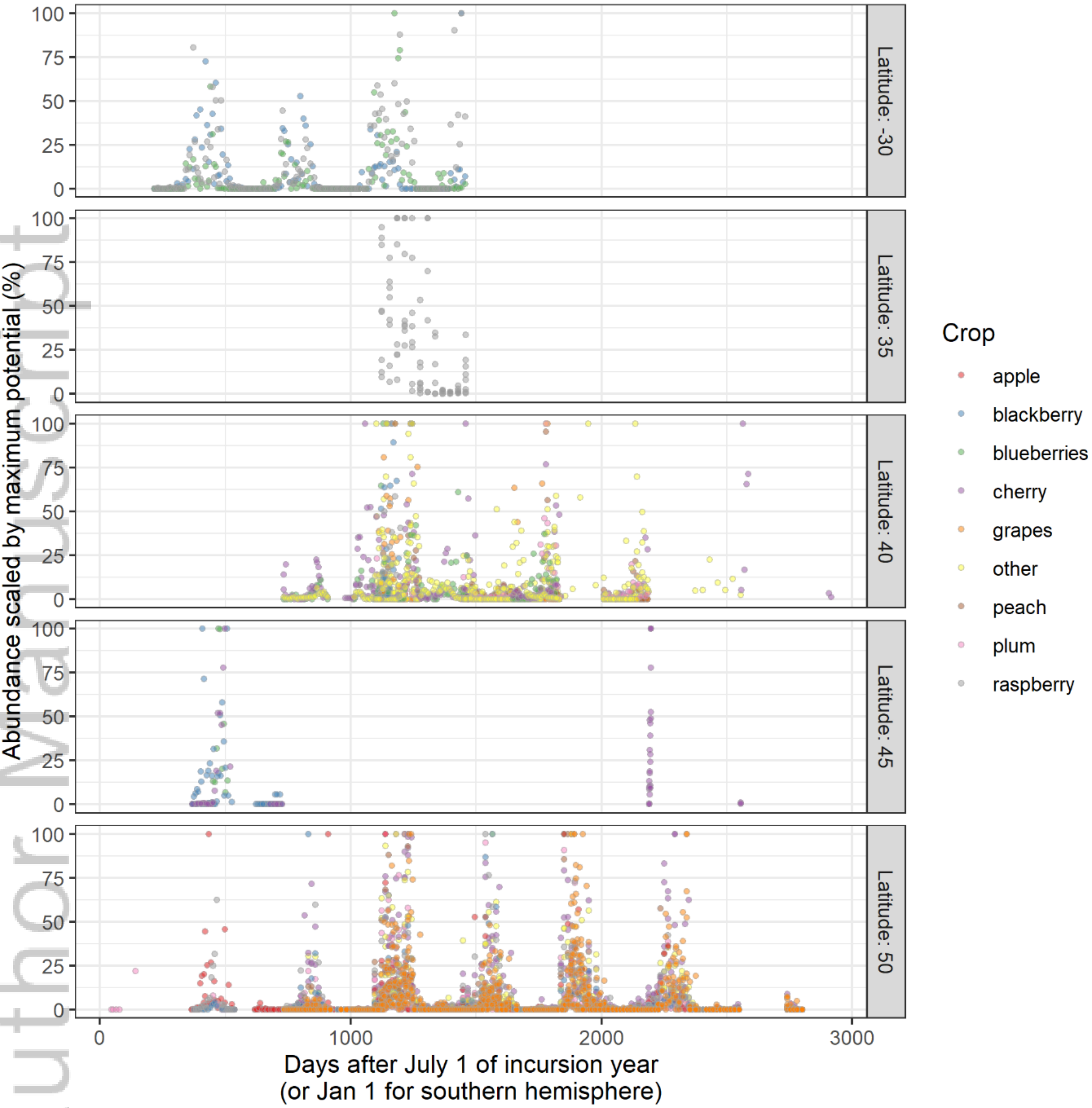

Figure 2. Seasonality of *D. suzukii* abundance across latitudes and crops

Scaled trap abundance data included in the compiled data set across latitudes rounded to nearest 5 degrees from -30 degrees (Brazil) to 50 degrees (Germany). The crop in which the trap was located is indicated by the colour of the marker. Here non-crop hosts have been excluded and hosts accounting for less than 5% of entries in the dataset are categorised as “other”.

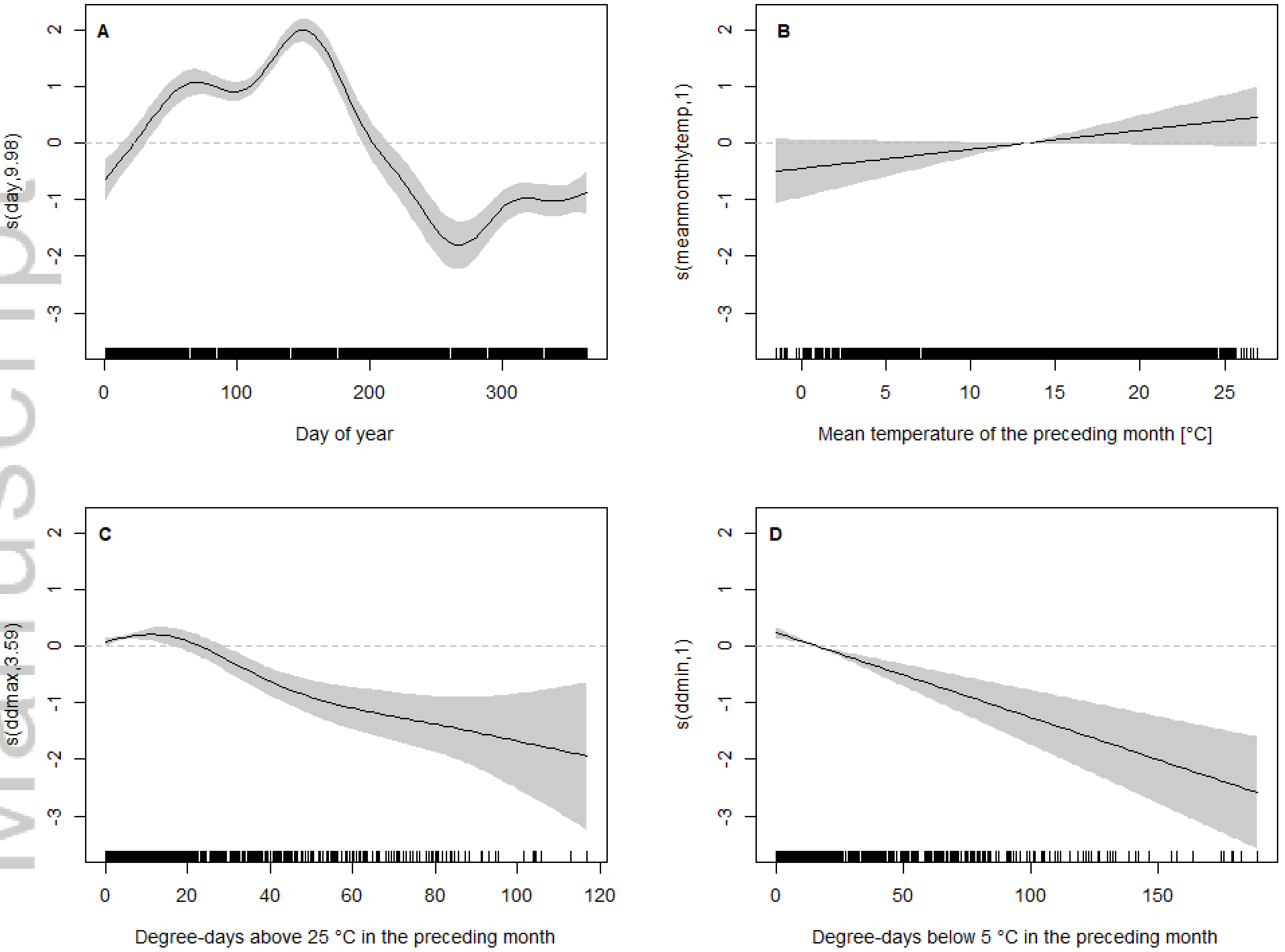

Figure 3. Effects of individual covariates on scaled abundance of *D. suzukii*

Partial dependency plots showing the marginal response of smooths of scaled abundance to **A.** s(day): days after July 1 in the Northern hemisphere (or January 1 in the Southern hemisphere), **B.** s(meanmonthlytemp): mean temperature of the preceding month, **C.** s(ddmax): accumulated degree-days above 25 °C in the preceding month, and **D.** s(ddmin): accumulated degree-days below 5 °C in the preceding month. Y-axis labels in all plots contain the covariate name and the estimated degrees of freedom for a given smoother. Horizontal dashes lines are displayed at response = 0 for reference, to differentiate increasing and decreasing effects of covariates.

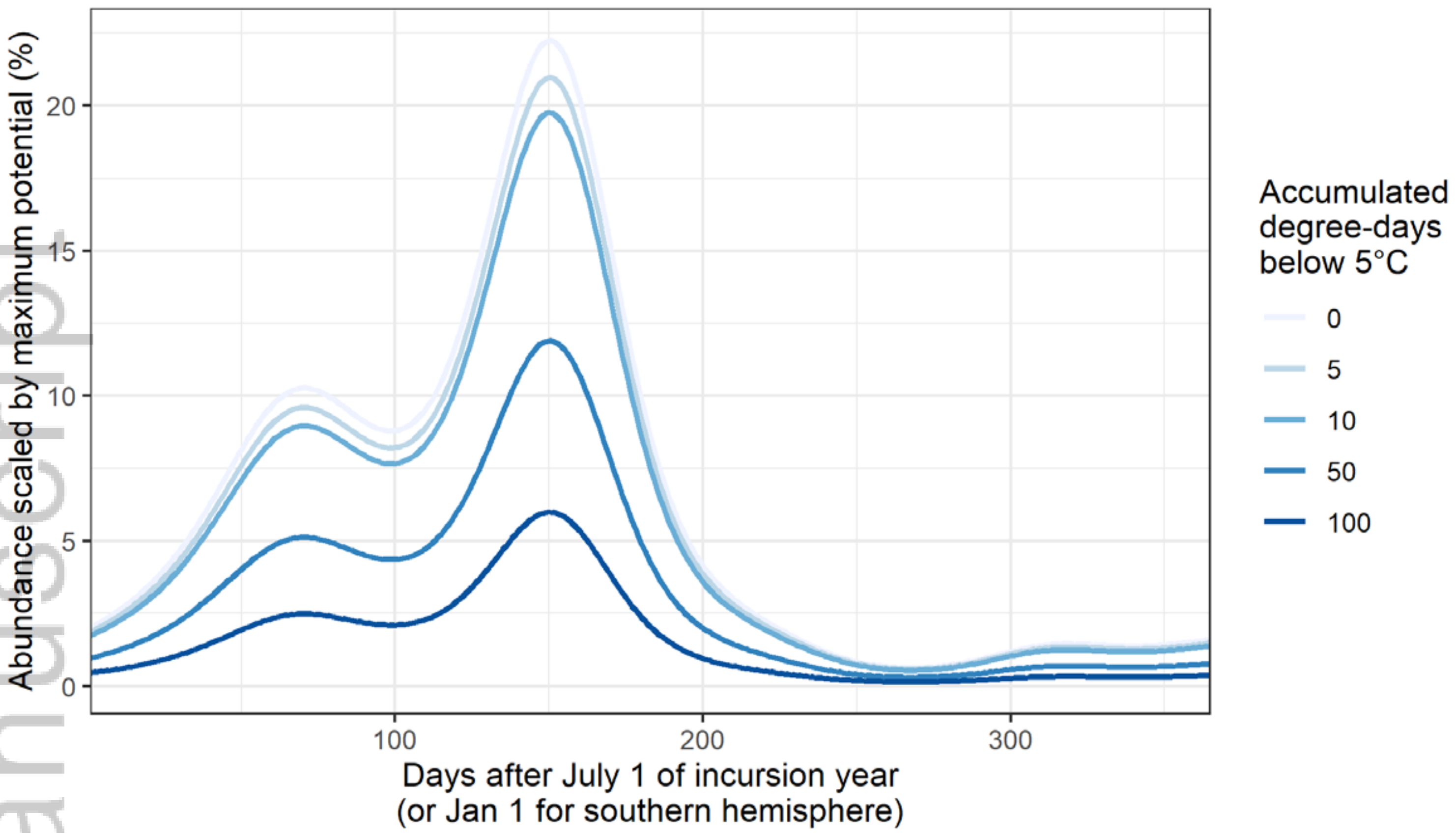

Figure 4. Predicted effects of accumulated degree days below 5 °C on abundance

Predicted scaled seasonal abundance (maximum observable for a given location), assuming a mean monthly temperature of 10 °C, accumulated degree-days above 25 °C of 10, accumulated degree-days below 5 °C of 0, 5, 10, 50, and 100, using apple cider vinegar traps in a grape crop.

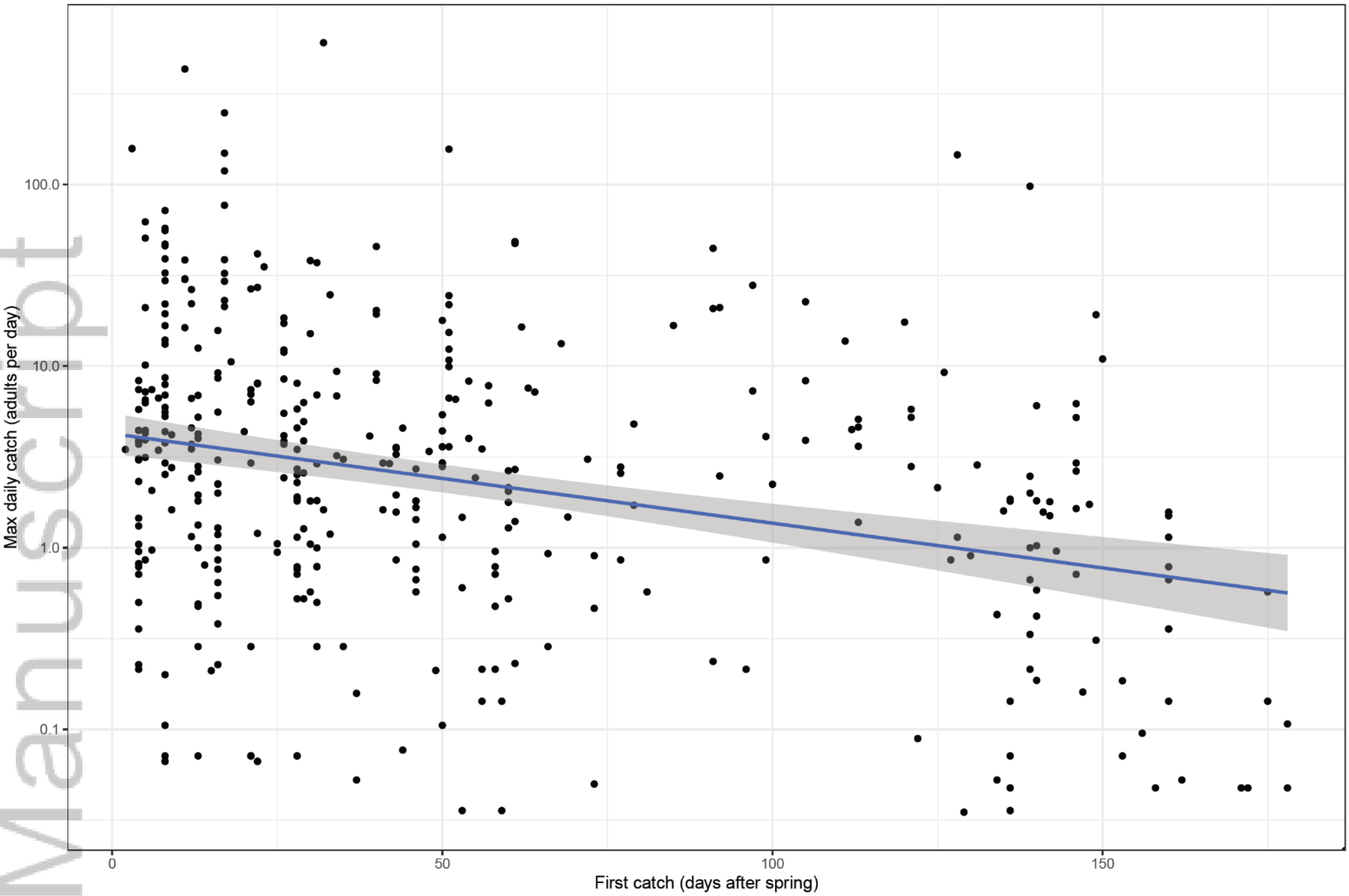

Figure 5. Relationship between the date of first catch and maximum daily catches

Scatterplot showing the maximum daily catch of adults caught per trap per day (log-transformed), summarised for each study, crop and year as a function of time of first catch in number of days after spring (March 1 for the Northern hemisphere or September 1 for the Southern hemisphere). The blue solid line represents the linear regression and the grey shaded area represents the 95 % confidence interval around the regression.

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Global analysis of the seasonal abundance of the invasive pest *Drosophila suzukii* reveal temperature extremes determine population activity potential

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Pest management is limited by the inability to predict seasonal outbreaks. Identifying climatic drivers of population dynamics in critical in developing early-warning systems for affected crops and regions.