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Analysis of the invasiveness of spotted wing *Drosophila* (*Drosophila suzukii*) in North America, Europe, and the Mediterranean Basin

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Abstract The polyphagous Asian vinegar fly *Drosophila suzukii* (spotted wing *Drosophila*) is a native of Eastern and Southeastern Asia. It emerged as an important invasive insect pest of berries and stone fruits in the Americas and Europe beginning in 2008. Species distribution models are commonly used for analyzing the extant and potential range expansion of invasive species. Previous modeling efforts for *D. suzukii* include a degree-day model, a MaxEnt

ecological niche model, a demographic model incorporating the effects of temperature, and a preliminary mechanistic physiologically-based demographic model (PBDM). In the present analysis, we refine the PBDM for *D. suzukii* based on biological data reported in the literature. The PBDM is used to assess the effects of temperature and relative humidity from a recently published global climate dataset (AgMERRA) on the prospective geographic distribution and relative abundance of the pest in the USA and Mexico, and in Europe and the Mediterranean Basin. Our focus is on areas of recent invasion and of predicted higher invasiveness in these areas. Although the species is native to Asia and is of putative temperate origins, it has established in subtropical to north temperate zones worldwide where it infests a wide range of wild and domesticated berries and stone fruits. The model captures the observed phenology of *D. suzukii* at specific locations, as well as the potential geographic distribution and relative favorability across larger regions. The main limiting factor is cold winter temperature in northern areas, though high temperatures and low relative humidity may be limiting in arid areas. The effect of greater cold tolerance in winter morph adults is explored.

Electronic supplementary material The online version of this article (doi:10.1007/s10530-016-1255-6) contains supplementary material, which is available to authorized users.

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Key message

- A physiologically based demographic model (PBDM) of the spotted wing *Drosophila* (*D. suzukii*) was developed using data from the literature. The PBDM is used to estimate the prospective geographic distribution and abundance of the species in the USA and Mexico in North America, and in Europe and the Mediterranean Basin, with focus on areas of recent invasion and of high predicted invasiveness.
- The analysis explains the role of weather, especially winter temperatures, on the phenology and dynamics of *D. suzukii* at the local scale and in the aggregate across larger regions.
- The model suggests that regional dispersal could be an important factor in its buildup during late summer in north temperate latitudes where winter survival is low.

Introduction

The polyphagous Asian vinegar fly *Drosophila suzukii* (Matsumura) (Diptera: Drosophilidae) (spotted wing *Drosophila*) is a native of Eastern and Southeastern Asia (Walsh et al. 2011), and emerged as an important invasive insect pest of wild and domesticated berries and stone fruits in the Americas and Europe in the late 2000s (Walsh et al. 2011; Cini et al. 2014; Lee et al. 2015; Poyet et al. 2015). *D. suzukii* was detected in Hawaii in 1980 (Kaneshiro 1983) and was first found in California in 2008 (Walsh et al. 2011). Its biology and dispersal were reviewed extensively by Asplen et al. (2015), but unanswered questions remain as to why the pest rapidly expanded its range.

Models are commonly used to find explanation for the extant and potential range expansion of invasive species such as *D. suzukii*. For example, a degree-day model for *D. suzukii* phenology was developed for the Pacific areas of the USA and Canada (Coop 2010), and Damus (2009) produced a MaxEnt ecological niche model to predict its range (Walsh et al. 2011). Demographic models incorporating the effects of temperature were developed by Wiman et al. (2014, 2016) using data from Tochen et al. (2014) to serve as the basis for pest management of the fly. Langille et al. (2016) report a well done mechanistic site specific model that relies in part on the preliminary

mechanistic physiologically-based demographic model (PBDM) reported by in Asplen et al. (2015) by A.P. Gutierrez and L. Ponti (*cf.* Gutierrez 1996; Gutierrez and Ponti 2013).

Scientific consensus expressed by the Intergovernmental Panel on Climate Change (IPCC 2014) indicates that ecological niche models, when used to assess climate effects on biological systems, have important shortcomings, among which are a lack of physiological mechanisms and the inability to account for population processes. PBDMs circumvent many of these problems as they are a mechanistic summary of the available information on the weather driven biology of species such as *D. suzukii* (e.g., Gutierrez and Ponti 2013; Ponti et al. 2015b). In this paper, we update the PBDM introduced in Asplen et al. (2015) and use it to assess the geographic range and relative abundance of *D. suzukii* across much of North America (USA and Mexico), Europe and the Mediterranean Basin. The focus of the analysis is on areas of recent invasion and of predicted high invasiveness.

Biology of *D. suzukii*. Like other *Drosophila* species, *D. suzukii* has multiple generations per year (Izquierdo 1991; Wiman et al. 2016), but does not have a true diapause stage, and overwinters as “reproductively quiescent” long-lived melanized winter morph adults (Dalton et al. 2011; Shearer et al. 2016; Toxopeus et al. 2016). Jakobs et al. (2015) found an absence of additional cold tolerance imparted by developmental plasticity, and that adults are chill-susceptible and are killed by exposure to low temperatures. In contrast, Toxopeus et al. (2016) and Shearer et al. (2016) found that acclimated winter morph adults have enhanced cold tolerance. Furthermore, winter survival of adults is enhanced in natural refuges and around built structures (e.g., Harris et al. 2014; Lee et al. 2015; Zerulla et al. 2015).

During favorable periods, growth, development and reproduction of *D. suzukii* life stages depend on temperature, the drying power of the air, and host quality and availability (Tochen et al. 2014, 2015). Zerulla et al. (2015) followed via dissection of field collected females the lack of ovary development in *D. suzukii* during winter and the resumption of ovary development in spring (see Wiman et al. 2016; Toxopeus et al. 2016). Plantamp et al. (2016) found that cold treatments had a strong impact on adult survival but had no effect on female’s fertility. The

magnitude and pattern of age-specific fecundity in *D. suzukii* contrasts sharply with other drosophilids such as *D. melanogaster* that have oviposition rates an order of magnitude higher during the first 20 days of adult life, but unlike *D. suzukii* reproduction falls off dramatically after 40 days (Asplen et al. 2015). Toxopeus et al. (2016) found that acclimated winter morph adults have delayed reproductive maturity, and can remain active at lower temperatures than summer morph adults. These above attributes suggest that *D. suzukii* is able to maintain population pressures longer and under more adverse conditions than other drosophilids (see Tochen et al. 2014; Wiman et al. 2014).

The above biology is further enhanced in temperate areas by the fly's ability to attack a wide range of hosts, some of which are available year around (Lee et al. 2015; Kenis et al. 2016). In Europe, Kenis et al. (2016) reared SWD from 84 plant species belonging to 19 families, 38 of which are non-native. While development, fecundity and mortality rates vary with hosts (Lee et al. 2015; Tochen et al. 2014, 2015; Jaramillo et al. 2015; Hamby et al. 2016), modeling the dynamics of these hosts (e.g., Gutierrez and Ponti 2013) and their effects on *D. suzukii* is vexing. In the PBDM, we assume hosts are available for *D. suzukii* reproduction when temperatures are in the favorable range.

Methods

The model

The mathematical underpinnings of age structured PBDM for *D. suzukii* are based on the distributed maturation time models of Manetsch (1976) and Vansickle (1977) reviewed briefly in the "Appendix" (see Gutierrez 1996, pp. 82; DiCola et al. 1999, pp. 523–524). The biological data used to formulate the bio-demographic functions of the PBDM (cf. Gilioli et al. 2016) for *D. suzukii*, the source of the weather data used to drive the model, and the simulation procedures are reviewed below.

Rate of development of *D. suzukii*

The data and bio-demographic function for *D. suzukii* developmental rates (R_{e-a}) for the egg to adult period

(subscript *e-a*) on temperature (T) are illustrated in Fig. 1 (Eq. 1; cf., Brière et al. 1999).

$$R_{e-a}(T) = \frac{0.0044 \cdot (T - 5.975)}{1 + 4.5^{(T-31)}} \quad (1)$$

A lower thermal threshold ($\theta = 5.975$ °C) was estimated with the developmental rate ($R_{e-a}(T(t))$) declining to zero at about 31.5 °C (C. Plantamp (unpub; see Asplen et al. 2015); Tochen et al. 2014; Kinjo et al. 2014; Kanzawa 1939; Ryan et al. 2016; see Hamby et al. 2016). $R_{e-a}(T(t))$ is the proportional development at temperature T at time t with development completed when $\int R_{e-a}(T(t)) dt = 1$. We note that the model may be formulated using either proportional development or degree-days (dd). For heuristic purposes and for use by biologists, we first compute the average developmental times for the life stages in dd in the linear midrange of favorable temperatures (e.g., $dd = \text{days}(T - \theta)$, but use Eq. 1 to adjust the daily values (i.e., $\Delta a_{e-a}(T(t))$) used to drive model dynamics (see below). Specifically, the daily increment of dd for development at time t is computed as $\Delta a_{e-a}(T(t)) = 243R_{e-a}(T(t))$ using the average egg to adult period (243 dd) as the reference value. The egg stage requires an average of 19.03 dd , larvae 121.76 dd , pupae 93.22 dd , reproductive adult females 1200 dd (approximately ~ 86 days at 20 °C) and 1275 dd for winter morph adults. Some adult flies may live 100–110 days at 21 °C (Kinjo et al. 2014; Dalton et al. 2011; Ryan et al. 2016).

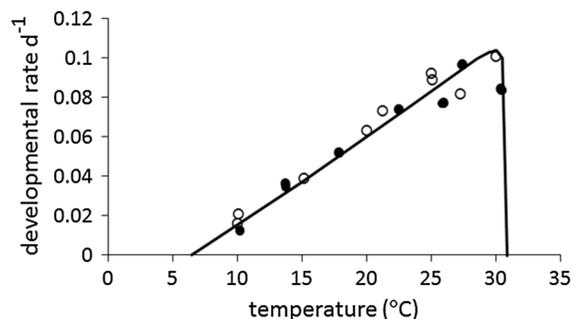


Fig. 1 Developmental rate of the egg to adult period (1/days) plotted on temperature. Data (open circle) courtesy of C. Plantamp (unpub; reported in Asplen et al. 2015) and Tochen et al. (2014) (filled circle)

Temperature and relative humidity on mortality

Temperature effects

The mortality rates of *D. suzukii* life stages across temperatures (Fig. 2a) were estimated from survivorship data provided by C. Plantamp (unpub) for the egg to adult stage in the range 10–30 °C, from adult survival at temperatures in the range –2 to 10 °C (Dalton et al. 2011), and from adult data at higher temperatures (25–33 °C) (Kinjo et al. 2014). Dalton et al. (2011) exposed cohorts of adults from different temperature regimes to –2 °C for 7 days, but the mortality rates of survivors were roughly the same after the cold temperature treatment as before. The mortality rates computed from Tochen et al. (2014) at 10 and 18 °C were similar to the Dalton et al. (2011) and C. Plantamp (unpub.) data. However, estimates of mortality rates from Tochen et al. (2014) were higher in the upper range of temperature than those reported by C. Plantamp (unpub.) and Kinjo et al. (2014) and were not included in the model. Average adult mortality rates in the field estimated from Zerulla et al. (2015) are shown in Fig. 2, but were also not used to fit the model (see discussion).

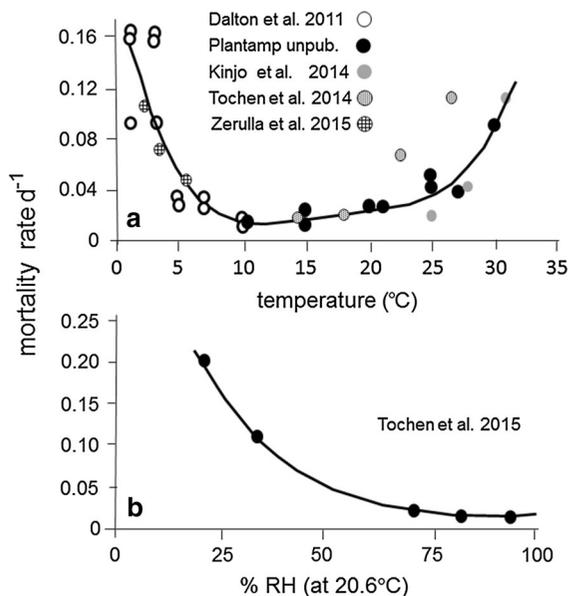


Fig. 2 Mortality rate per day **a** temperature estimated using data from various authors (see figure) and **b** relative humidity at 20.6 °C (Tochen et al. 2015) (see text)

A convex polynomial function (Eq. 2i) captures the mortality data of adults on mean daily temperature (T) well despite the inconsistencies in the data at 1° and 3 °C, (see Fig. 2).

$$\begin{aligned} \mu_T(T(t)) &= 0.000002T^4 - 0.000161T^3 + 0.004191T^2 \\ &\quad - 0.046696T + 0.20067 \leq 1 \\ R^2 &= 0.79 \end{aligned} \quad (2i)$$

The data from Dalton et al. (2011) and Tochen et al. (2014) are from an Oregon population, and a simple convex function provides a good fit for these data (Eq. 2ii).

$$\mu_T(T(t)) = 0.000675 \times (T - 15)^2 + 0.01 \leq 1 \quad (2ii)$$

However, because (2i) captures most of the data, it is used in the model to estimate temperature-dependent mortality.

Partial data on winter morph adult survival at 1° and 5 °C suggest phenotypic plasticity may significantly increase survival at low temperatures (Shearer et al. 2016; Toxopeus et al. 2016). Shearer et al. (2016) exposed winter morph adults to temperatures in the range 0–28 °C, while Toxopeus et al. (2016) estimated summer and winter morph adult survival at 0 °C, and adult survivorship after an hour exposure to temperatures in the range 0 to –13 °C. The data in Toxopeus et al. (2016) suggest that the mortality function for the winter morph is displaced to lower temperatures by approximately 5–6 °C. The data, however, are insufficient to characterize fully the effect of low temperatures on winter morph mortality (see supplemental materials Fig. S1), and hence the effects on the distribution and abundance of *D. suzukii* are explored heuristically in the discussion section with the results summarized in supplemental materials Figs. S2, S3.

Relative humidity effects

The drying power of the air affects mostly the free-living adult stage. The effect of relative humidity on adult mortality per day ($\mu_{RH}(RH(t))$) in the range 20–94 % RH were estimated from Tochen et al. (2015) (Fig. 2b; Eq. 3).

$$\begin{aligned} 0 \leq \mu_{RH}(RH(t)) &= 42.895RH^{-1.759} \\ R &= 0.98 \end{aligned} \quad (3)$$

Reproduction

On lab media, maximum fecundity of females from a French population was about 4.5 eggs per day at 21 °C (Chabert et al. 2013), and 5.7 eggs per female per day at 22 °C and 25 % RH (Emiljanowicz et al. 2014; see also Ryan et al. 2016; Hamby et al. 2016). In sharp contrast, Kinjo et al. (2014) reported 25eggs/female/day at 25 °C, while Tochen et al. (2014) reported a maximum rate of about 20eggs/female/day at 22 °C. Differences in the fecundity data collected for European and North American populations may be due to experimental methods or may have genetic roots (see Adrion et al. 2014). We opted to use the higher fecundity figure of 20 eggs day⁻¹ as a conservative hypothesis in terms of risk assessment, but note that the choice of values does not affect the predicted geographic distribution or patterns of favorability for *D. suzukii*.

In our model, an average age-specific ($x = \text{days}$) oviposition profile (i.e., $f(x)$ at 21 °C; Fig. 3a) using data from Chabert et al. (2013) was estimated using the function proposed by Bieri et al. (1983), but was

then scaled to the values reported by Tochen et al. (2014) (Eq. 4). Specifically, after a pre-oviposition period of less than a day at 21 °C, $f(x)$ increases to 20 eggs day⁻¹ at age $x = 20$ days, and then begins to decline.

$$f(x, T = 21 \text{ }^\circ\text{C}) = \frac{2.60x}{1.0475^x}, \tag{4}$$

Fecundity is affected by temperature, and data from Tochen et al. (2014) suggest that when normalized, fecundity is concave on temperature in the range 12.75–29 °C with a peak at 20.65 °C (Eq. 5, Fig. 3b; see Ryan et al. 2016).

$$0 \leq \phi_T(t) = 1 - \left[\frac{T(t) - 20.875}{8.125} \right]^2 \leq 1 \tag{5}$$

The total number of eggs ($E(t, T, RH)$) produced at time t (i.e., day) by the population of females ($N(t) = sr \cdot \int_{x_0}^{x_{\max}} N(x, t) dx$) is computed using Eq. 6,

$$E(t, T, RH) = \phi_T(T) \cdot \phi_{RH}(RH) \cdot \phi_C(N(t)) \cdot sr \int_{x_0}^{x_{\max}} f(x) \cdot N(x, t) dx \tag{6}$$

where $N(x, t)$ is the number of adults of age = x , $sr = 0.5$ is the sex ratio (Emiljanowicz et al. 2014), $\phi_T(T(t))$ scales for the effects of temperature (Eq. 5) and $0 < \phi_{RH}(t) = 1 - \mu_{RH}(RH(t)) \leq 1$ is a survivorship function that scales for the effects of relative humidity (see Eq. 3). In the absence of the limiting effects of host density, we introduce a decreasing function of female density to scale for intraspecific competition (i.e., $0 < \phi_C(N(t)) = 1 - \exp(-1/N(t)) < 1$) that keeps *D. suzukii* populations within reasonable bounds. Note that at $N = 1$, $\phi_C(N) = 0.63$ and may be viewed as the success rate of host finding.

Reproductive quiescence

In temperate areas, *D. suzukii* females reproduce when temperatures and host availability permit, but as temperatures cool in fall, winter morphs characterized by a darkened cuticle and underdeveloped or absent ovaries are produced (Toxopeus et al. 2016; Shearer et al. 2016; see also Wang et al. 2016; Wiman et al. 2016). Toxopeus et al. (2016) found that winter morphs develop when larvae are exposed to both short and long days at 11 °C, but not at 15 or 21.5 °C, and concluded that low temperature rather than photoperiod is the cue

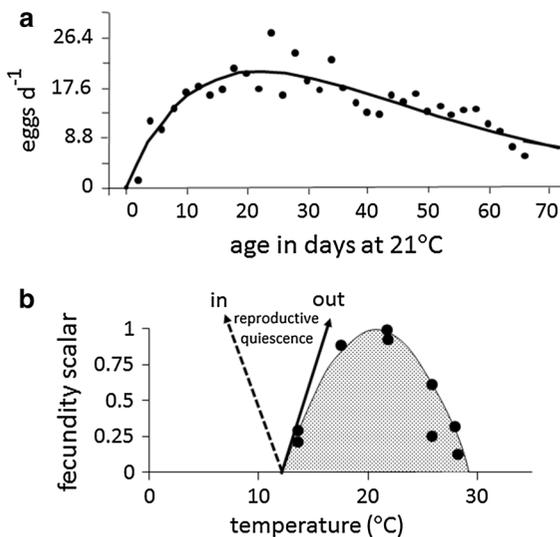


Fig. 3 Fecundity of *D. suzukii*: **a** age specific fecundity at 21 °C (from Chabert et al. 2013) scaled by $\times 4.4$ to fit the oviposition data reported by Tochen et al. (2014); and **b** the normalized effect of temperature on total reproduction (Tochen et al. 2014; the $\times 2$ outlier at 18 °C is not shown and was omitted in the analysis). Entry to or exit from reproductive quiescence is indicated by the dashed and solid arrows respectively (Fig. 3b)

for the increase in winter morph adults. Furthermore, winter morphs are unlikely to be in true diapause as females transferred from 11 °C (10:14 L:D) to 21.5 °C (13:11 L:D) 10 d post-eclosion become reproductively active within three days (Toxopeus et al. 2016).

A convenient way to model the two adult reproductive phases is to have population dynamics models for each. In our model, we assume that females enter and exit reproductive quiescence hinged on the oviposition temperature threshold of 12.75 °C (Fig. 3b; see Tochen et al. 2014). On a daily basis, a proportion of females of all ages at time t are assumed to enter the quiescent phase (P_{en}) in response to the previous five-day average temperature $T_{avg} < 12.75$ °C (Eq. 7i).

$$\text{if } T_{avg}(t) < 12.75 \text{ °C then} \\ 0 < P_{en} = 0.2 \times (12.75 - T_{avg}(t)) < 1.0 \quad (7i)$$

As average temperatures warm above 12.75 °C during spring, a proportion (P_{ex}) of females exit the quiescent phase and become reproductive.

$$\text{if } T_{avg}(t) \geq 12.75 \text{ °C then} \\ 0 < P_{ex} = 0.2 \times (T_{avg}(t) - 12.75) < 1.0. \quad (7ii)$$

Entry to or exit from reproductive quiescence in the model occurs as transfers between the same age classes of the two reproductive types, and the females continue to age and die overtime at temperature and humidity dependent rates. For example, adults of age x may enter reproductive quiescence at time t , but the survivors may become reproductive at some future time and age.

Weather data

Ambient weather data from the AgMERRA global weather dataset were used to drive the dynamics of the PBDM. The AgMERRA dataset was created as a baseline forcing dataset for the Agricultural Model Inter-comparison and Improvement Project (AgMIP, <http://www.agmip.org/>, see Ruane et al. 2015), and is a daily time series of max–min temperatures, solar radiation, rainfall and RH at ~25 km geographic resolution for the period of 1980–2010 (National Aeronautics and Space Administration 2015). We note that insects may experience temperatures and relative humidity in microhabitats that differ from ambient (e.g., Potter et al. 2013), but at least two factors limit estimating the appropriate corrections for *D. sukukii*: it has a very wide host range (>84) in diverse habitats

over a large geographic area, and the immature stages and the two adult morphs occupy different microhabitats (see discussion).

Simulation studies and GIS mapping

Unless indicated, the PBDM simulates the daily dynamics of all life stages continuously starting 1 January 1980–31 December 2010 for each of the 15,843 lattice cells (~25 × 25 km) for the USA-Mexico and the 17,791 lattice cells for Europe and the Mediterranean Basin. The relative densities of all life stages are predicted on a daily basis by the model, but only the cumulative annual densities are geo-referenced and written by year to batch files for mapping and statistical analysis. Means, standard deviations and coefficients of variation as a percent (CV truncated to 100) for each lattice cell are computed for all variables across years. However, in our analysis, we use cumulative annual pupal density as a metric of favorability at each grid cell. Populations of the fly may fall to very low values in the simulation, but are not allowed to go to zero for computational reasons. The model is assumed to be equilibrating during the first year, and hence the data for this year are not used in computing the summary statistics. Further, the summary variables should be viewed as indices of the time-place potential (favorability) and not as precise measures of *D. sukukii* abundance. To compare model predictions against field data, detailed daily simulations were made for the four locations in the western USA monitored by Dalton et al. (2011).

The simulation data were mapped using bi-cubic spline interpolation on a three-km raster grid using the GIS software GRASS (Geographic Resources Analysis Support System, GRASS Development Team 2014). Red on the color bar indicates high favorability and clear indicates very low favorability.

Results

Model predictions

Prospective distribution of D. sukukii in the United States and Mexico

The reported geographic distribution of *D. sukukii* in the USA is wide but unevenly documented (CERIS

2015), while the distribution in Mexico is mostly unreported. PBDM predictions of relative densities across the USA and Mexico vary considerably [range 0, 7400] and were difficult to map using the same color scale. Hence, we used the boxplot function of *R* (R Core Team 2015) to identify statistical outliers (i.e., cumulative pupal densities $> \sim 3000$; cf., Tominski et al. 2008) and used a single darker shade of red to represent their distribution on the map for the US and Mexico (Fig. 4a). This procedure enabled better resolution of areas of known *D. suzukii* favorability in north temperate regions where densities are mostly less than half the predicted maximum in tropical Mexico and Hawaii (Fig. 4c).

Large areas of the western mountain states and northern Mexico have predicted low average densities (Fig. 4a) and high inter-annual variability as measured by the CVs (Fig. 4b) suggesting that both statistics are measures of low favorability. In contrast, much of the eastern and mid-western areas of the USA have relative high densities and $CV < 50\%$ suggesting variable but stable populations. A large transition zone extends northward through Texas to Wisconsin. A plot of mean density on CV shows an inverse relationship (Fig. 4d).

Low *D. suzukii* densities are predicted in the western USA (Fig. 4a) in areas where the fly is a known pest (e.g., coastal southern California, areas of northern California influenced by San Francisco Bay, and areas of Oregon and Washington). The data for this sub region were color clipped as described above at pupal densities < 819 (range [0, 1913]) to better illustrate the areas of relative favorability in the sub region (Fig. 4e, f). On a linear scale, the favorable areas in California are sevenfold less favorable than parts of tropical Mexico and Hawaii (Fig. 4c).

Maps of average annual cumulative daily mortality rates based on Eq. 2i above and below the midrange temperature of 16°C (i.e. $\mu_{\geq 16^\circ\text{C}}$, $\mu_{<16^\circ\text{C}}$) are shown in Fig. 5 for elevations below 2500 m that exclude the higher elevations of the Rocky Mountains. These cumulative values include mortality that occurs in the favorable range for *D. suzukii* development (see Figs. 1, 2). The areas of highest cold mortality are consistent with areas of low favorability in the central and northern regions of the USA and the high western deserts. In contrast, cumulative high temperature mortality rates are highest in the hot arid desert regions of southern California, Arizona and western Mexico where low relative humidity also increases mortality.

Using multiple linear regression, we summarize the effects of various abiotic factors on cumulative pupae per year across the US and Mexico. Note that daily changes in *dd* (i.e., Δdd) are computed using the nonlinear Eq. 1, and hence the yearly sums are measure of the total favorable physiological time (see text).

$$\begin{aligned} SWD_p = & -986.030 + 0.821rain_{mm} - 35.44\mu_{\geq 16C} \\ & + 2.083\mu_{<16C} + 0.041\mu_{\geq 16C} \times \mu_{<16C} \\ & + 0.409dd_{>5.975C} \quad R^2 = 0.72, \\ df = & 316, 854, \quad F = 161, 284 \end{aligned} \quad (8)$$

The independent variables, as yearly means with significance levels in brackets are $rain_{mm}$ (738.9, $p < 0.01$), $\mu_{\geq 16^\circ\text{C}}$ (6.484, $p < 0.01$), $\mu_{<16^\circ\text{C}}$ (31.84, $p < 0.01$) and $dd_{>5.975^\circ\text{C}}$ (3452, $p < 0.01$) (see full analysis in Table S1 in the supplemental materials). Because *D. suzukii* in some areas experiences significant mortality from both high and low temperatures, we included the interaction term $\mu_{\geq 16^\circ\text{C}} \times \mu_{<16^\circ\text{C}}$ (89.97, $p < 0.05$). Note that total rainfall in the analysis is a surrogate for the effects of relative humidity. Only the effects of high temperature across the region were on average negative with $\partial SWD_p / \partial \mu_{\geq 16^\circ\text{C}} = -35.41$ given the average effects of the other factors. This occurs because the mortality function is asymmetrical and increases with temperatures during periods of population growth (Eq. 2i, Fig. 2a). Analyses of regional subsets of the data could provide insights into local factors affecting *D. suzukii* densities.

Europe and the Mediterranean Basin

The same model was used to estimate prospective average *D. suzukii* population densities and CV across the Mediterranean Basin and Europe (Fig. 6a, b). The boxplot function from *R* (R Core Team 2015) was again used to identify statistical outlier densities (< 1295 with the full range [0, 2929]) in south coastal areas of Portugal-Spain and northwestern Morocco that are indicated with a darker shade of red (see Fig. 6c). The proportion of the area that is comparatively highly favorable is relatively small (see histogram in Fig. 6c). Note that the highest densities are about $< 1/2$ those in Hawaii and south central Mexico

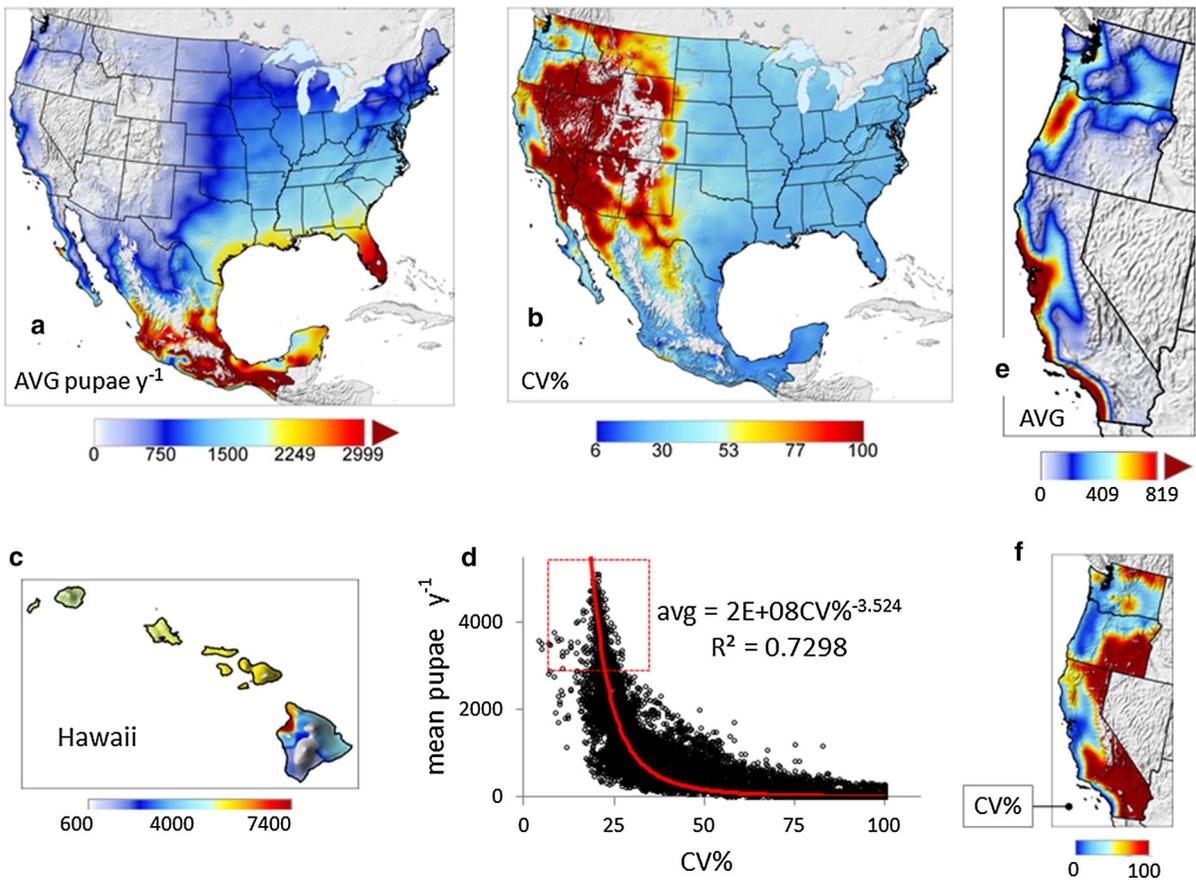
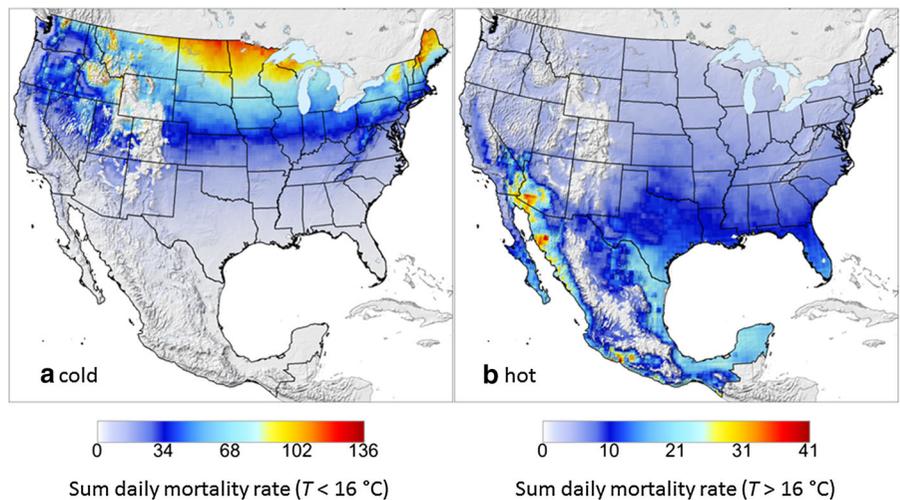


Fig. 4 Prospective distribution and relative abundance of *D. suzukii* pupae in the USA and Mexico below 2500 m elevation: **a** the average density (AVG) and **b** coefficient of variation as a percent (CV %) truncated to 100 %; **c** AVG for Hawaii, **d** plot

of AVG on CV % across all locations; and **e** AVG and **f** CV % in California, Oregon and Washington. The values in the *dashed box* in **d** are the outliers from **a** from the full data interval [0, 7401], and similarly [0, 1913] for **e**

Fig. 5 Distribution of cumulative daily mortality rates per year below 2500 m elevation: **a** below 16 °C, and **b** above 16 °C based on Eq. 2i



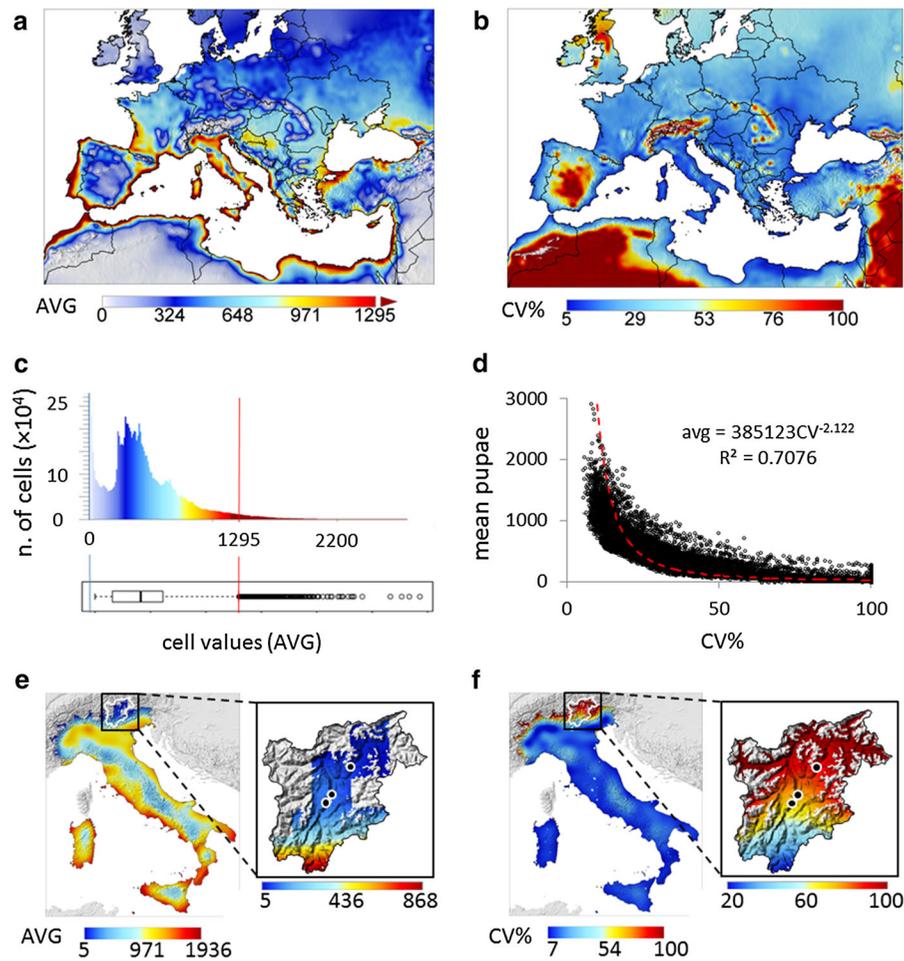


Fig. 6 Prospective distribution and relative abundance of *D. suzukii* pupae in Europe and the Mediterranean Basin below 2000 m elevation: **a** average pupae/year (AVG); **b** coefficient of variation as a percent (CV %); **c** histogram of cell values mapped in **a** with a box plot indicating outlier values (*empty circles*) that are shown as the *darkest shade of red* in **a** for

and are more comparable to coastal southern California. Densities of ~ 600 to 1295 pupae year $^{-1}$ are quite common across wide areas of southern Europe. *D. suzukii* populations decrease northward in Europe due to cold winter temperatures and in the south Mediterranean due to high summer temperatures and low humidity. The predicted low but consistent populations in northern areas of Europe are less than half those predicted for northern areas of the central USA where the fly currently causes damage. Note that except in arid areas of North Africa, the Middle East and parts of Spain; the CV (Fig. 6b) tends to be less than 50 % (see Fig. 6a). As in North America, average

improved data visualization; **d** plot of AVG on CV % across all locations; and **e** AVG and **f** CV % for Italy with insets for the Trentino-Alto Adige region with locations surveyed by Zerulla et al. (2015) indicated. The full data interval for Fig. 6a is [0, 2929]

pupal densities are inversely related to the inter-annual variability as measured by the CV (Fig. 6d).

The model predicts the presence of *D. suzukii* in South Tyrol (i.e., Alto Adige, a district within the Italian region of Trentino-Alto Adige) and in Switzerland (Fig. 6e, f; see insets for Trentino-Alto Adige) with relative low densities comparable to those predicted for part of California and Oregon (Figs. 4e vs. 6e). The occurrence of the fly in South Tyrol varies greatly from year to year as indicated by the high CV (Fig. 6f). The approximate locations in South Tyrol monitored by Zerulla et al. (2015) were derived from the metadata reported in their study (see insets in

Fig. 6e, f), and at those locations the model predicts average pupal densities in the range 43.8–94.3 with respective CVs of 89.1–72.3. Microclimatic conditions in mountain areas with complex topography are important in *D. suzukii* buildup (Zerulla et al. 2015), but the 25 km resolution of the weather data used for our sub-continental level analysis has limitations at this finer microclimate scale. A finer scale weather data set such as the Land Surface Temperature data with a 250 m resolution (Metz, Rocchini and Neteler 2014; <http://www.geodati.fmach.it/eurolst/>) would be required to model the influence of microclimatic conditions in Alpine areas. Although the *D. suzukii* model can be implemented at this scale, the analysis is outside the scope of our paper.

Discussion

The recent literature speaks to the urgent need for approaches to estimate the geographic distribution and relative abundance of native and exotic species that may experience novel climate due to range expansion or climate change. Specifically, Sect. 4.3 (“Assumptions about future trends”) by Working Group II in the assessment reports (AR4; see also AR5) of the Intergovernmental Panel on Climate Change (IPCC 2014) outlines the shortcomings of widely used standard methods based largely on the climate envelope approaches (i.e., ecological niche models) commonly used to assess the impact of climate change on ecosystem. Among the gaps identified in IPCC AR4 were: the “inability to account for species interactions, the lack of physiological mechanisms, and the inability to account for population processes” (IPCC 2014). Single species and multi-trophic PBDM circumvent some of these problems (e.g., Gutierrez & Baumgärtner 1984; Gutierrez et al. 2010; Ponti et al. 2015a) and often challenge assumptions on how field data should be interpreted (e.g., Gutierrez and Ponti 2014; Gutierrez et al. 2014), especially where data gaps exist (see below).

The polyphagous spotted wing *Drosophila*, *D. suzukii*, is a native of Eastern and Southeastern Asia (Walsh et al. 2011). Phylogenetic analysis by Ometto et al. (2013) indicates that the species originated during the late Miocene when its native Asian range was characterized by extended mountain temperate forests. This finding is compatible with its observed

current distribution in mountain temperate climates (Ometto et al. 2013). Kimura (2004) found that *D. suzukii* had one of the broadest geographic ranges among the drosophilids of Japan, ranging from Hokkaido in the north to Iriomote Island east of Taiwan. The fly has extended its range in temperate and tropical areas in North America and Europe and the Mediterranean Basin where hosts are abundant (Kimura 2004; Lee et al. 2015; Kenis et al. 2016), including areas where weather may be only moderately suitable for population development.

Several biological attributes appear to enhance the fly’s ability to expand its range. For example, it has a very wide host range (e.g., Kenis et al. 2016); unlike most drosophilid larvae that develop on relatively protein-rich rotting fruit, *D. suzukii* larvae uniquely develop on protein-poor, carbohydrate-rich ripening fruit (see Jaramillo et al. 2015); and its thermal characteristics are conducive to its range expansion. Specifically, laboratory data on developmental rates were consistent across studies and predicted a lower thermal threshold of 5.95 °C (see text) and an upper threshold of ~31 °C (Tochen et al. 2014). Ryan et al. (2016) estimated a lower threshold of 8.1 °C and found that no adults emerged above 30.9 °C. The differences in threshold estimates likely reflect differences in experimental methods. A low threshold for immature stages (i.e., 5.95 °C) enables the species to be active early in the spring and to complete development of immature stages in the fall to produce winter morph adults (see Toxopeus et al. 2016), while the high threshold for reproduction would appear to delay reproduction until hosts are available in spring.

Reproduction potential in *D. suzukii* is relatively low, approximately half that of *D. melanogaster* (David and Clavel 1965; Tochen et al. 2014; Ryan et al. 2016; Hamby et al. 2016). Reported differences in reproductive rates observed in European and North American populations may be due to experimental conditions or may have some genetic roots (Adrion et al. 2014). In our analysis, we used the higher fecundity figure, noting that it has little impact on the prospective geographic range and patterns of relative abundance.

The effects of temperature on *D. suzukii* mortality on summer adults were variable among reported studies, especially at low (Dalton et al. 2011) and high temperatures (Fig. 2a; Tochen et al. 2014; C. Plantamp, unpub; Kinjo et al. 2014). Tochen et al.

(2015) characterized the effects of relative humidity and temperature on reproduction and mortality of summer adults, and the combined effects were incorporated in the PBDM (see Figs. 2, 3; Eq. 6). There is general agreement in the literature that cold winter temperatures are the major limiting factor for the fly in north temperate regions. Based on laboratory and field studies, Jakobs et al. (2015) concluded that adult *D. suzukii* phenotypic plasticity alone is insufficient to allow *D. suzukii* to overwinter in northern temperate areas. Stephens et al. (2015) studied cold hardiness of winter-acclimated *D. suzukii* in the laboratory, and concluded that the species is chill-intolerant, and further stressed that while the winter-morph adult is the most cold-tolerant life stage, both summer and winter-morph adult forms could not overwinter in cold climates without microclimate refuges (e.g., see below). Using available data on summer morphs survival with temperature, the PBDM predicts a wide distribution for the fly in the USA and Mexico with highest densities in warmer tropical areas of Mexico = Hawaii > Florida > coastal southern California with lower year round populations in temperate areas of Northern California (e.g., Stockton and Winters, CA; see Harris et al. 2014), and mid- to late-summer populations developing in Oregon and Washington (Dalton et al. 2011). Similar mid to late summer populations develop in the north Central USA with highest densities found in woodlands relative to crop fields such as raspberry (Pelton et al. 2016).

Recent, albeit incomplete, studies on winter morph adult survival at 1 and 5 °C suggest phenotypic plasticity may significantly increase survivorship at low temperatures (Shearer et al. 2016; see supplemental materials Fig. S1). Data from Toxopeus et al. (2016) on summer and winter morph adult survival at 0 °C and after 1 h exposure to temperatures from 0 to -13 °C suggest that the mortality function (Eq. 2i) for winter morph adults is displaced approximately 5–6 °C to lower temperatures (Fig. S1). For example, survivorship of the winter morph at 0 °C is about the same as for the summer morph at 5 °C. We explored heuristically the effect of shifting mortality Eq. 2i leftward 5.5 °C in the PBDM and found that this does not radically change the prospective geographic distribution of *D. suzukii* in the USA and Mexico, but because more adults survive the winter, densities increase in many areas such as coastal California and

in northern areas such as Maine and Wisconsin (Fig. 4 vs. Supplemental Materials Fig. S2).

In south and central Europe and the Mediterranean Basin, fly densities increase more widely to levels (>900) predicted for coastal California (Fig. S2), and inter annual variability declines (text Fig. 6 vs Supplemental Materials Fig. S3). The effect of increased winter morph survival on the density dynamics of egg production and summer and winter morph adults were explored for the cold location of Benton, WA (see Fig. S4). The results show the increase in winter survival, a modest increase in population densities, but no changes in population phenology. In colder areas such as Benton WA, the favorable season is limited by cool average temperature below ~12.75 °C (see Fig. 3b) that delay reproduction in spring and that induce the development of non-reproducing winter morph adults in fall (Toxopeus et al. 2016; Shearer et al. 2016). Data to characterize fully winter morph adult mortality are currently unavailable, but can easily be incorporated in the PBDM when they become available, and a complete analysis will be performed.

The effects of cold temperatures on field trap catch data were demonstrated at three locations in South Tyrol, Italy (Schlossleiten at 300 m elevation; Barbican at 900 m; and Kurtatsch at 200 m) during a 48-day winter period of 23 December 2013–13 March 2014 (Zerulla et al. 2015). In this study, hour degrees (*hd*) were recorded under mulch at six temperature intervals [i.e., $T \leq 0$ °C, $0^\circ < T \leq 2$ °C, $2^\circ < T \leq 5$ °C, $5^\circ < T \leq 7$ °C, $7^\circ < T \leq 10$ °C, and $T > 10$ °C]. The summed *hd* from the first four temperature intervals below the fly's developmental threshold of 5.96 °C were converted to *dd* and used to estimate roughly the average temperature ($\hat{T}_{<\theta}$) below the threshold experienced by the fly adults (Eq. 9).

$$\hat{T}_{<\theta} = \theta - \frac{\sum hd/24h}{48d} = \theta - \text{obs average temp} \quad (9)$$

From $\hat{T}_{<\theta}$ we computed the average daily mortality rate $\mu(\hat{T}_{<\theta})$ during the 48-day period using Eq. (2i) (see Fig. 2), and by taking the survivorship term to the 48th power, we estimated the winter survival (*lx*) at the three locations.

$$lx = (1 - \mu(\hat{T}_{<\theta}))^{48} \quad (10)$$

The estimated average temperatures and survivorship values (in brackets) are respectively 5.4 °C ($lx = 0.110$) at Schlossleiten; 3.72 °C (0.023) at Barbian; and 1.95 °C (0.002) at Kurtatsch. These values correspond to the relative levels of favorability of each area reported by Zerulla et al. (2015) and by our model (inset Fig. 6e). The three values of $\mu(\hat{T}_{<\theta})$ are plotted in Fig. 2a and are consistent with estimates from laboratory data. Flight activity was recorded at Schlossleiten during the winter period from January to March, while at Kurtatsch the flights mostly ceased in December with sporadic catches recorded only in January 2014. At Barbian, the flights stopped at the end of November 2013. The field results and our rough estimates of survivorship suggest that the fly can survive at Schlossleiten and could serve as a reservoir of infestation migrants during spring to the less favorable nearby areas of Barbian and Kurtatsch.

Behavioral factors can also affect survival during adverse periods. For example, Tochen et al. (2015) posited that behavioral adaptation of short-distance migration enables *D. suzukii* adults to move towards favorable microclimates that enhance their survival and reproduction in otherwise marginal environments (see Zerulla et al. 2015). This point was clearly illustrated by Harris et al. (2014) during 2011–2013 using apple cider vinegar traps to monitor *D. suzukii* adults in multiple crops and associated fruiting plants at the Wolfskill USDA Germplasm Repository at Winters, CA, USA. During spring and summer, *D. suzukii* adults were trapped in the orchards, but during November through April, high trap captures were associated only with citrus, with highest numbers of flies found around a nearby house where fruiting ornamentals such as common myrtle (*Myrtus communis*) and firethorn (*Pyracantha* sp.) were present and had fruit until April 2013. Had the trapping occurred only in the orchard area, the results would have suggested that *D. suzukii* had decreased to very low numbers during winter when in fact adults were active nearly all year around with trap catches near the house during winter being nearly twice as high as those during the season in the orchards (Harris et al. 2014). In a mark-recapture study, *D. suzukii* adults were found to take refuge in wild habitat surrounding a cultivated raspberry field before migrating back to the field when the susceptible crop was present (Klick et al. 2015). This information suggests that

surrounding habitats with hosts, especially in sheltered areas, should be monitored for *D. suzukii* adult winter activity and survival (Lee et al. 2015). Fly movement makes accurate sampling of adult densities throughout the year vexing.

The trapping records of Dalton et al. (2011) during 2010 at five sites in Oregon, Washington and California likely had unknown sampling bias. As predicted by the PBDM, *D. suzukii* adults were found during much of the year at Stockton (San Joaquin Co.), CA (see Fig. 7) which is located about 40 miles south of Winters, CA where Harris et al. (2014) recorded *D. suzukii* year around (see also Kaçar et al. 2015). The climate at both locations has the moderating influence of San Francisco Bay (see Figs. 5a, 7). Specifically, the PBDM predicts that cold weather mortality [i.e., $\mu(T < 16\text{ °C})$] had little impact on *D. suzukii* at Stockton CA, but temperatures were often too low for reproduction ($T < 12.5\text{ °C}$ in Fig. 3b; grey areas in Fig. 7; see Tochen et al. 2014). Hot weather during summer (red areas in Fig. 7) caused some suppression of *D. suzukii*, but the effect was not large. Predicted cold weather mortality rates at Stockton, CA were 1/10th those at Marion and Wasco Counties of Oregon and Benton County in Washington where populations grew only after mid-summer (Fig. 7). This delayed phenology is due to cold temperatures in late fall and winter that drive *D. suzukii* populations to near zero (cf., Jaramillo et al. 2015) despite the presence of alternate hosts in the area (Lee et al. 2015), allowing populations to resurge only in mid- to late-summer. The impact of cold temperatures on reproductive quiescence occurred only during fall in Oregon and Washington, while mortality due to higher temperatures during summer did not appear to have much impact at any of the four western locations studied by Dalton et al. (2011). The delayed phenology of the fly in these colder areas suggests that, as occurs with aphids and other insects carried long distance as aeroplankton (e.g., Gutierrez et al. 1974), *D. suzukii* adults may be carried from more favorable near-coastal areas of the northwest to augment reinvasion of colder areas (e.g., Stephens et al. 2015). This possibly explains the earlier phenology of *D. suzukii* at Marion Co, OR compared to more inland areas of Wasco Co, OR or Benton Co, WA (see Dalton et al. 2011). Similar scenarios (sensu Dingle 1972) may also occur in the northern reaches of the central USA (e.g., Pelton

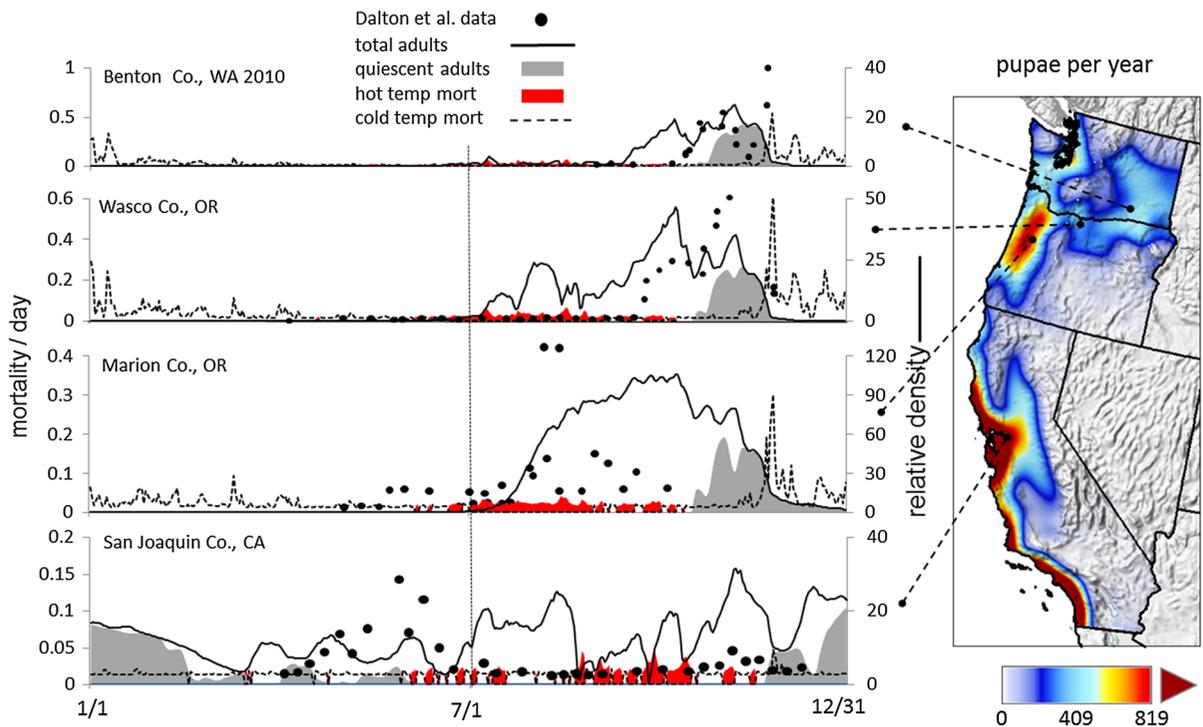


Fig. 7 Simulated and observed dynamics of *D. suzukii* at Benton Co., WA, Wasco Co., OR, Marion Co., OR and San Joaquin Co., CA. The dark solid line is the total adults, the grey area is the number of reproductively quiescent adults, the dashed line is the daily rate of cold weather mortality at

temperature $<16^{\circ}\text{C}$ and the red area is the rate of hot weather mortality. The symbols (filled circle) are the trap data for *D. suzukii* females (redrawn from Dalton et al. 2011) while the vertical dashed line indicates July 1

et al. 2016) that may be reinvaded from warmer southern areas, and in Europe into higher latitudes and elevations in mountainous areas (e.g., Switzerland and Northern Italy).

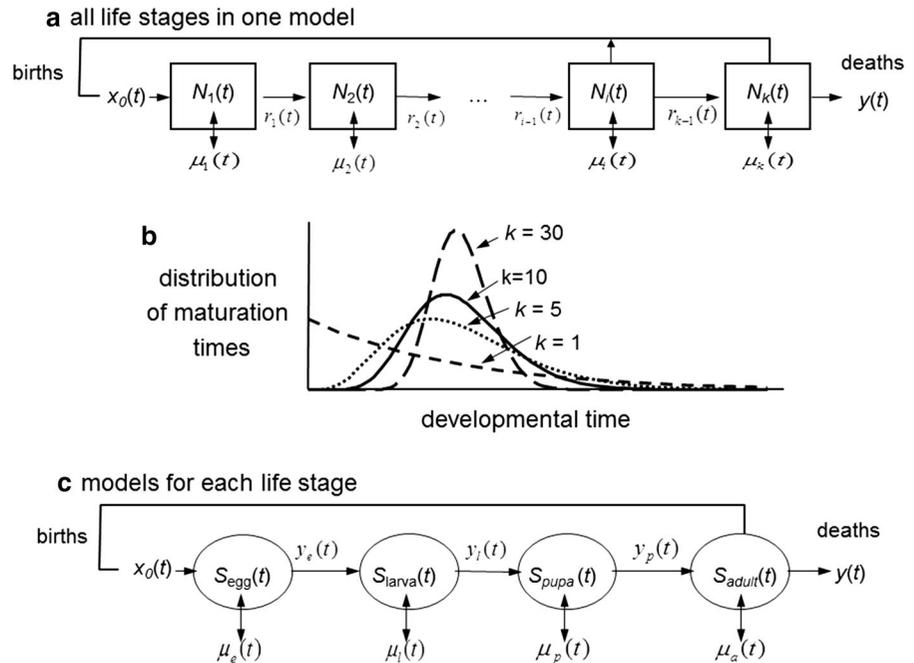
Climatic conditions in the Mediterranean Basin are more favorable and stable for *D. suzukii* (Fig. 6) where year-round survival is predicted. In contrast, *D. suzukii* is limited by high temperatures and low RH in hot dry areas of the southwestern USA and northern Mexico (Fig. 5), but cold winter weather can also be a factor in parts of this area. Similarly, high temperatures and low RH would also impact *D. suzukii* in inland North Africa.

In summary, *D. suzukii* is a cold intolerant invasive species that attacks a wide range of wild and domesticated berries and fruit. The cold resistant winter morph adults can survive winters and reproduce during spring in marginal north temperate climates (Toxopeus et al. 2016). The PBDM gave good predictions of the prospective distribution and relative favorability of climate for *D. suzukii* in North

America, Europe and the Mediterranean Basin. Despite not including the effects of host plants availability and microclimate effects, the PBDM was able to predict the relative dynamics and phenology of adult trapping data at four locations (Dalton et al. 2011; Fig. 7); data that were likely complicated by sampling bias and fly movement among potential hosts (Klick et al. 2015; Lee et al. 2015; Tochen et al. 2015) and possibly between sheltered habitats (e.g., Harris et al. 2014). The model suggests that in colder areas, the observed late-season buildup of the fly results from low winter survival and the movement of adults from areas with phenologically earlier populations.

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Fig. 8 A distributed maturation time model: **a** the general model across all life stages including flow rates between stages (r), net mortality rates [i.e. $\mu_i(t)$, $i = 1, \dots, k$] due to biotic and abiotic factors where $x_0(t)$ are births and $y(t)$ is death at maximum age, **b** the stylized distribution of cohort maturation times given different values of the Erlang parameter k , and **c** the general model with the dynamics of **a** specified for each life stage (S) including stage specific flow rates between stages (y_{stage}), net mortality (i.e. μ_{stage}) due to biotic and abiotic factors (see text)



System (GRASS) software, and making it available to the scientific community. Funding for the modeling/GIS analysis was provided by the Center for the Analysis of Sustainable Agricultural Systems (CASAS) and Agenzia nazionale per le nuove tecnologie, l'energia e lo sviluppo economico sostenibile (ENEA), Rome Italy. The experimental work on *D. suzukii* was supported at Oregon State University by the US Department of Agriculture National Institute of Food and Agriculture (USDA-NIFA) award #2010-51181-21167, the Oregon Blueberry Commission, and the Northwest Center for Small Fruit Research, and the Agricultural Research Foundation.

Author contributions A.P.G. and L.P. conceived and developed the PBDM/GIS system. D.D. developed field and laboratory data used in the analysis. All authors read and approved the manuscript.

Appendix

A review of physiologically based demographic model (PBDM)

Physiologically-based demographic system models (PBDMs) explicitly capture the mechanistic weather-driven biology and dynamics of species at all trophic levels to predict the weather driven phenology, dynamics and distribution of single and multiple species across wide geographic areas on a daily basis—a time step rarely used in macro-ecological

modeling (see Gutierrez and Baumgärtner 1984; Gutierrez 1996; Gutierrez and Ponti 2013). For some applications, the time step could be smaller or larger (Gilioli et al. 2016). The model captures via sub-models the processes of resource acquisition and allocation, and the birth–death rates in great detail or using simple functions that capture the relevant biology (see Gutierrez 1996; Gutierrez and Ponti 2013; Gilioli et al. 2016). PBDMs are sufficiently detailed to be realistic, and yet complexity is kept to a minimum by applying the same dynamics model and process sub models to all trophic levels. The complexity enters the model at the conceptual level and running the model requires minimal computational capacity. These models have contributed to basic theory and helped solve many applied field problems because they bridge the gap between purely theoretical analytic models and overly complicated simulation models. Physiological analogy across trophic levels is a powerful conceptual tool and is used as a way to tackle the huge challenges facing global ecosystem modeling.

A demographic dynamics model with distributed maturation times

The biology of resource acquisition and allocation is embedded in a demographic model with distributed

maturation times (Manetsch 1976; Vansickle 1977) and is used to simulate the dynamics of age (and mass) structured populations where time (t) is chronological time and age (a) is in physiological time units (e.g., proportional development, degree days). But other dynamics models could also be used (e.g., Gutierrez 1996; DiCola et al. 1999; Gilioli et al. 2016).

The general distributed maturation time model for the i th age class of a population as a rate (r_i) is

$$\frac{dr_i}{dt} = \frac{k \Delta x}{del} [r_{i-1}(t) - r_i(t)] - \mu_i(t)r_i(t). \quad (11)$$

The density of the i th cohort is $N_i(t) = \frac{del}{k} r_i$, where Erlang parameter k is the number of different age cohorts (stages), del is the expected mean developmental time, Δx is an increment in time varying physiological age, $\frac{k \Delta x}{del}$ scales the time varying flow rate of individuals between age classes, and $-\infty < \mu_i(t) < \infty$ is the proportional net loss rate that could include age-species death and net immigration and in mass dynamics model the age specific growth rate. Note that births enter the first age class with age zero. The density of all k cohorts is $N(t) = \sum_{i=1}^k N_i(t)$, but the density can also be summed by life stage. The maturation across the k age classes is depicted in Fig. 8a, while the patterns of emergence times for different values of k are depicted in Fig. 8b (see Manetsch 1976; Vansickle 1977). Assuming $k = 25$ age classes, the standard deviation of developmental times for the immature and adult life stages (i.e., $std = \sqrt{del^2/k}$) is $\sim 20\%$ of the mean. Similar schemes could be used for each life stages (Fig. 8c).

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