Population dynamics of *Eldana saccharina* Walker (Lepidoptera: Pyralidae): application of a biophysical model to understand phenological variation in an agricultural pest

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Abstract

Understanding pest population dynamics and seasonal phenology is a critical component of modern integrated pest-management programs. Accurate forecasting allows timely, cost-effective interventions, including maximum efficacy of, for example, biological control and/or sterile insect technique. Due to the variation in life stage-related sensitivity toward climate, insect pest population abundance models are often not easily interpreted or lack direct relevance to management strategies in the field. Here we apply a process-based (biophysical) model that incorporates climate data with life stage-dependent physiology and life history to attempt to predict *Eldana saccharina* life stage and generation turnover in sugarcane fields. Fitness traits are modelled at two agricultural locations in South Africa that differ in average temperature (hereafter a cold and a warm site). We test whether the life stage population structures in the field entering winter and local climate during winter directly affect development rates, and therefore interact to determine the population dynamics and phenological responses of *E. saccharina* in subsequent spring and summer seasons. The model predicts that: (1) *E. saccharina* can cycle through more generations at the warm site where fewer hours of cold and heat stress are endured, and (2) at the cold site, overwintering as pupae (rather than larvae) confer higher relative fitness and fecundity in the subsequent summer adult moths. The model predictions were compared with a large dataset of field observations from scouting records. Model predictions for larval presence (or absence) generally overlapped well with positive (or negative) scout records. These results are important for integrated pest management strategies by providing a useful foundation for future population dynamics models, and are applicable to a variety of agricultural landscapes, but especially the sugarcane industry of South Africa.

Keywords: Sugarcane borer, overwintering life stage, fitness, temperature stress, climate variability, weather

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Introduction

Lepidopteran borers are food crop pests of economic significance in sub-Saharan Africa (Davis & Pedigo, 1990; Cardwell *et al.*, 1997; Kfir, 1998). The African sugarcane stalk borer, *Eldana saccharina* Walker (Lepidoptera: Pyralidae), poses a great threat to commercial, emerging and small-scale sugarcane growers in South Africa, Zimbabwe, Uganda, Ethiopia, and maize and sugarcane farmers in most of the west African countries (Girling, 1972; Conlong, 2001; Assefa *et al.*, 2010). Larval boring (i.e. feeding) causes direct and indirect revenue losses through stalk damage and secondary fungal stalk infections (Butterfield, 2002; Goebel & Way, 2006). Control strategies for *E. saccharina* include cultural practices, chemical control and biological intervention (e.g. Webster *et al.*, 2006). Most recent developments include integrated pest management (IPM) programs that are followed by commercial sugarcane growers (Webster *et al.*, 2006), intensive research and the implementation of area-wide IPM programs (Conlong & Rutherford, 2009; Webster *et al.*, 2009; Conlong *et al.*, 2016).

In South Africa, the first pest outbreak of *E. saccharina* in sugarcane occurred in 1939 on 2-year-old sugarcane (cultivar: POJ 2725) planted in the warm Umfolozi flats of KwaZulu-Natal (Dick, 1945; Carnegie, 1974; Atkinson, 1980). Previous studies concluded that low winter temperatures could limit the stalk borer distribution by reducing adult reproductive performance, larval development, and survival (Dick, 1945; Atkinson, 1980; Atkinson *et al.*, 1981; Way, 1994). However, since this first outbreak on the Umfolozi flats, *E. saccharina* has spread rapidly into areas formerly thought to be too cold for the completion of the larval life stage (Webster *et al.*, 2006; Assefa *et al.*, 2008). As such, the current known geographic distribution of *E. saccharina* stretches across several distinct climate zones (e.g. Conlong, 2001; Kleynhans *et al.*, 2014*b*) beyond the coastal sugar belt to inhabit the warm sub-tropical summer climates in Thohoyandou in Limpopo (northern limit), cool winter sites in the Mkambati Nature Reserve in the Eastern Cape (southern limit) and cold winter sites with occasional frost at Boskop dam in the North-West province (western limit) (fig. 1; Conlong, 2001; Assefa *et al.*, 2008).

Across the geographic distribution of *E. saccharina*, populations at different climatic locations could represent different biotypes that differ ecologically (see Conlong, 2001) or physiologically (Sinclair *et al.*, 2012). These differences might result in phenotypic (Maes, 1998) and genetic differences between populations (e.g. King *et al.*, 2002; Chown *et al.*, 2007; Kleynhans *et al.*, 2014*b*). Frequent cold spells resulting in frost in the northern Midlands possibly limit *E. saccharina* presence early in the season (see table 1 in Webster *et al.*, 2006, 2009), however, the species is now spreading and possibly adapting to the cooler climates of the northern and southern Midlands of KwaZulu-Natal. Indeed, there is marked phylogenetic differentiation between *E. saccharina* populations along geographical lines in broader Africa (Lange *et al.*, 2004; Assefa *et al.*, 2006). Evidence for phenotypic variation of climate stress resistance traits of *E. saccharina* exists within South Africa likely due to the effects of local, fine-scale climate variation (Kleynhans *et al.*, 2014*b*) and perhaps also host plant differences (Kleynhans *et al.*, 2014*a*).

To further complicate understanding the processes facilitating the spread of *E. saccharina* into cooler regions of South Africa, the different life stages of this pest vary in their thermal tolerances, their ability to sustain activity in the face of climate extremes, and their capacity to overcome lethal conditions.

Laboratory trials, for example, reveal stage-specific critical thermal temperatures and lower developmental thresholds (LDT) (Way, 1995; summarized in table 1). At low temperatures (11.00 °C for 14 days) larvae were completely inactive and did not feed, but, when returned to 20.00–25.00 °C they revived and continued to develop (Dick, 1945). This suggests that larval development can be arrested, but larvae can survive a typical cold winter. While larvae appear to have a relatively low freezing point of -7.01 ± 0.30 °C (mean ± SE given throughout), their specific freeze tolerance strategy remains unstudied. Moreover, *E. saccharina* pupae are able to withstand laboratory temperatures down to a much colder -17.00 ± 1.80 °C before they freeze, conditions that would likely not be encountered in the field in Africa (Kleynhans *et al.*, 2014*a*). Given these different thermal sensitivities, the life stage that coincides with cold temperatures during winter may be the key to whether a population persists or perishes in a newly invaded, cold, location.

Here we aim to develop a better understanding of the effect of local climate on population phenology, fitness and abundance of *E. saccharina* in South Africa. We test the null-hypothesis that the life stage and population age structure entering a given winter determines the resulting downstream spring and summer population phenology and age structure. We apply a mechanistic (process-based) population model, following the methods described in Barton & Terblanche (2014), to predict population abundance and performance at two geographic locations currently occupied by *E. saccharina*: a warm site (-25.46S, 31.57E decimal degrees given throughout; average minimum temperature of the coldest month (July) = 8.50 °C; average annual temperature = 21.60 °C) and a cold site (fig. 1; -29.91S, 30.63E; average minimum temperature of the coldest month = 7.60 °C; average annual temperature = 17.00 °C) (Hijmans *et al.*, 2005 calculated 50 year (1950–2000) averages). The two sites were chosen to represent a typical warm and cold site in the current thermal range of *E. saccharina*, at least within South Africa (fig. 1). More specifically, stage-specific developmental rates and critical temperature thresholds were integrated with hourly temperature data to predict how seasonal fluctuations in thermal conditions at the two study sites may affect *E. saccharina* phenology, and quantify thermal stress, survival, population turnover, relative abundance and fecundity. In addition to modelling the outcomes at the two climatically-distinct geographic locations, we consider two separate freeze-intolerant overwintering life stage scenarios (larvae vs. pupae). This is due to field scouting data revealing the presence of both life stages in the sugarcane at the two study sites during mid-winter but it remains unclear if this would significantly influence downstream population dynamics the following spring of summer season. Additionally, thermal thresholds estimated by Way (1995), which may overestimate actual values because they are estimated from a linear model, for all life stages are below average winter temperatures (in July). Together with lower freezing points, this suggests that larval and pupal stages of *E. saccharina* can theoretically survive and develop throughout the year in all regions. The biological and population implications of overwintering stage however remain unstudied.

Materials and methods

Input climate data

A process-based, deterministic population model (see Barton & Terblanche, 2014) was applied to high resolution
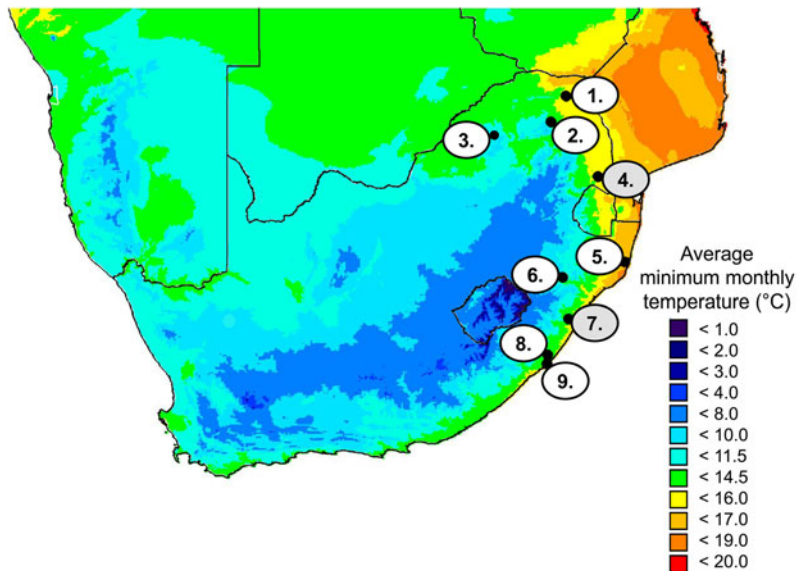
Site	Coordinates in decimal degrees (latitude, longitude)	Elevation (m)	Average minimum monthly temperature in June (°C)	Average maximum monthly temperature in December (°C)	Annual precipitation (mm)
1. Thohoyandou, Limpopo	-22.937, 30.572	567	10.6	30.8	746
2. Hans Merensky Dam, Tzaneen, Limpopo	-23.749, 30.108	917	6.1	27.0	1192
3. Boskop Dam, Potchefstroom, North West	-26.541, 27.121	1413	0.2	28.0	625
4. TSB Sugar Mill, Malelane, Mpumalanga	-25.457, 31.575	362	8.5	30.6	735
5. St Lucia Estuary, KwaZulu Natal	-28.118, 32.404	29	11.1	28.8	987
6. Wartburg, Midlands North, KwaZulu Natal	-28.600, 30.474	1119	3.0	26.7	757
7. Eston, Midlands South, KwaZulu Natal	-29.885, 30.654	614	7.6	25.5	934
8. Port Edward, KwaZulu Natal	-30.999, 30.003	40	9.1	23.7	1100
9. Mkambati Nature Reserve, Flagstaff, Eastern Cape	-31.295, 29.980	156	11.5	25.1	1120

Fig. 1. Site details where *Eldana saccharina* has been recorded present (1, 3, 9) on the range edges of its distribution. Warm permanent site locations: 2, 4, 5 and permanent cold site locations: 6, 7, 8. The two sites used in the model are numbered 4 and 7 (shaded in grey).

Table 1. Thermal constant (*K*) and lower developmental threshold (LDT) estimates for the different stages, obtained from Way (1995), and estimates of the theoretical optimal temperature (T_{opt}) for development of each life stage (following Briere *et al.*, 1999).

Stage	Name	*K*	LDT	T_{opt}
1	Egg	119.0	4.5	28.0
2	Larva 1	80.0	11.2	29.0
3	Larva 2	70.0	9.7	29.0
4	Larva 3	69.0	9.0	29.0
5	Larva 4	74.0	9.5	29.0
6	Larva 5	86.0	11.0	29.0
7	Larva 6	129.0	11.0	29.0
8	Larva 7	116.0	12.3	30.0
9	Pupa	160.0	11.6	29.0
10	Adult	200.0	11.0	28.0

time-series climate data for two point locations in South Africa, where *E. saccharina* is currently found in sugarcane: a warm site near Malelane in the province of Mpumalanga and a cold site near Eston in the province of KwaZulu-Natal. Daily maximum, minimum and average temperatures were compared for the period 1 July 2013–31 July 2014. For each site, hourly temperature fluctuations were interpolated from measurements of daily average minimum and maximum temperatures with a sinusoidal wave according to the equation in Campbell & Norman (1998). Daily temperature records were obtained from the SASRI Weather Data Acquisition and Processing System (WeatherWeb). Data for the warm site in Mpumalanga was collected at Mhlati (station number 465: 25.467S, 31.517E) at 301 m above sea level. Data for the cold site in KwaZulu Natal was collected at Hayfields (station number 458: 29.867S, 30.517E) at 785 m above sea level. The SASRI weather station is within a 6 km radius from the scouted sugarcane fields at the warm site and within a 15 km radius from the scouted sugarcane fields at the cold site. We assumed that the body temperatures (T_b) for *E. saccharina* life stages were equal to ambient temperature for the purpose of modelling the population responses throughout the season, i.e. the thermal effects of radiation, metabolism and evaporation on body temperatures of this species were assumed to be negligible (see Watt, 1968; Kingsolver & Moffat, 1982; see Supplementary information). Microsite temperatures did not differ significantly from that recorded by the weather station (see Supplementary information).

Physiological and life history traits and model parameters

Physiological data of each life history stage were called into the model while it was stepping through the temperature data. Thermal constants and LDT for the life history stages were obtained from work published by Way (1995). A Briere model (i.e. quadratic temperature-dependent equation) was used to estimate a theoretical optimal temperature for each life stage (Briere *et al.*, 1999). The input parameters for the model are given in table 1. These parameters remained constant for each model iteration.

During the larval phase, *E. saccharina* transitioned through 5–8 instars, depending on their diet and gender (Waiyaki, 1968; Girling, 1978; Atkinson, 1980). We modelled a seven-instar larval life stage, which corresponds to findings by Atkinson (1980), and age-related head capsule size studies completed by Way (1995). The temperature-dependent rates of egg-production were also obtained from Way's (1995) work

and corresponded to 205, 417, 432 and 183 eggs at 15, 20, 25 and 30 °C, respectively. These egg counts were however more conservative than those published recently by Walton & Conlong (2016) but sufficient to explore the potential impact of temperature on population dynamics.

Model setup and simulations

For each geographic location, we ran two model simulations to explore the outcomes of overwintering as either pupae, or larvae. We set the model to commence on 1 July 2013 with accumulated DD units set to 624.0 and 160.3 for larvae and pupae overwintering scenarios, respectively (table 1). At each hourly time step, the model calculated the number of degree-day (DD) units obtained according to the ambient temperature above the LDT temperature for each particular life stage (Way, 1995). Thus, as the model progressed through the simulation period, DD units were allowed to accumulate until the threshold DD (for that particular stage) was reached, at which point the model transitioned into the next life stage. Once the adult stage was reached (see Feng *et al.*, 2010), the model remained as an adult for 14 days, after which it transitioned back to an egg, the accumulated DD total was reset to zero, and an additional generation was tallied (Barton & Terblanche, 2014).

For each modelling scenario, estimates of phenology and fitness were subsequently tracked throughout the 365-day simulation period. Model output parameters included: the number of generations per year (and showing the life stage transitions throughout the season), number of stress hours encountered through each life stage and for the season, relative fitness of adult moths, relative adult abundance and female fecundity. Parameters were compared between sites and overwintering life stage. Briefly, for each hour, DD were calculated where temperatures did not exceed 35.00 °C or dropped below the LDT. Stress-hours were calculated as the total number of hours during which T_b dropped below an arbitrary stress-inducing cold temperature set to 2.00 °C below the LDT (cold stress) or rose above 35.00 °C (heat stress). The thermal safety margin (TSM = T_{opt} − T_b, where T_{opt} is the stage-specific optimum temperature for development, listed in table 1 were calculated for each hour. Relative population fitness was calculated for emerging adult moths, based on the average developmental TSM, where relative fitness = 1/TSM, so adults that had developmental periods closest to the optimum were assumed to be the fittest. The relative abundance was calculated as the total number of adult female emergences over the previous 14 day period, assuming female moths survive for 9 days in total, multiplied by the relative fitness at that hour. Female fecundity predictions were estimated based on a linear model of the relationship between temperature and egg-production (see above for data). The number of reproducing 2-day old adult moths on each day were determined, and then multiplied by the potential number of eggs laid during that hour, depending on the T_b, and the temperature-dependent function for egg production. All modelling simulations and validations were performed in R (R Development Core Team, 2010; v. 3.1, R Foundation for Statistical Computing, Vienna, Austria).

Model output validations

Model predictions were validated against weekly-obtained scout records (expressed as a % larvae (all instars included)

scouted per 100 stalks) obtained from 29 sugarcane fields (>3 ha average, 16 different cultivars) in and around the Eston weather station, and >400 sugarcane fields (>8 ha average, 7–19 month old sugarcane, 14 different cultivars) in and around the Malelane weather station. We used predictions of life stage transition and stress (cold and heat) at the Eston site with a larval overwintering stage scenario, because scouted larval numbers returned high in-field infection during the initial winter months of this particular season. Scout records were obtained from the South African Sugarcane Research Institutes' extension specialist in the Midlands South region of KwaZulu-Natal, and the Lowveld Pest, Disease and Variety control specialist in the Malelane area. Surveys for *E. saccharina* larvae are done by Pest and Disease survey teams that pluck 100 stalks at random from a <10 ha sugarcane field. The stalks are sliced in half, lengthwise, and the number of larvae found are expressed as a percentage infestation, i.e. indication of larval relative abundance; and damage as percentage internodes bored, i.e. the total number of internodes damaged in the stalk, divided into the total number of internodes on the stalk multiplied by 100. The field age and cultivar were always recorded. The cultivars included in the scout records obtained from the field specialists were amongst others the high risk varieties: N16, N28, N31, N35, N36, N37, N40, N45, N47, N48, N49, N50, N52, and low risk varieties: N12, N39, N41 (Leslie, 2013). The sugarcane ages at fields where scouting was done ranged between 7 and 31 months.

Statistical analyses

All statistical analyses were performed in R (v. 3.1, R Foundation for Statistical Computing, Vienna, Austria; Packages 'MASS' and 'car'). A comparison of maximum, minimum and average daily temperatures was made between the geographic locations using the Wilcoxon–Mann–Whitney rank sum test as data were not normally distributed. The effect of geographic location and overwintering life stage on the number of generations, cold- and heat-stress hours is compared, with Poisson distribution of errors and log link function, while fecundity, relative moth abundance and fitness were compared, with Gaussian distribution of errors and identity link function, in generalized linear models. The models were corrected for over-dispersion by square root transformation of count data (quasi- family distribution of errors did not stabilize the variance in the data) and log transformation of continuous data. The models were checked for over-dispersion by inspection of residual deviance and degrees of freedom (following Crawley, 2007). The model predictions were validated against scout records of larval abundance using an area-under-the-curve (AUC) function that calculates the area under the response operating characteristic (ROC) curve (following Mason & Graham, 2002 with the pROC package). The *P*-value obtained from the AUC function is related to the Mann–Whitney *U* statistic that addresses the null hypothesis stating that the area under the ROC curve is 0.5 i.e. the model prediction has no relevance to actual observations. Values statistically >0.5 are considered to be models better than random.

Results

Population responses were modelled at two geographic sites, initiated from a larval or pupal overwintering life stage. Statistical analyses of the daily maximum, minimum

and average temperature verified that the Malelane site (22.34 ± 0.15 °C) was significantly warmer than the Eston site (18.60 ± 0.16 °C) (Wilcoxon rank sum test, *W* = 84,540, *P* < 0.0001). Daily maximum temperatures were significantly higher at Malelane than at Eston (29.57 ± 0.18 °C vs. 24.45 ± 0.22 °C respectively) and daily minimum temperatures were significantly lower at Eston than at Malelane (12.75 ± 0.15 °C vs. 15.11 ± 0.20 °C, respectively). Variation in ambient temperatures between the two sites resulted in significant differences in the predicted fitness traits of *E. saccharina* as described below.

The number of predicted generations completed for *E. saccharina* across the season was higher at the warm site than at the cold site (fig. 2a, b). Three complete generations were predicted at the warm site, irrespective of the life stage (larval or pupal) overwintering, while at the cold site larval overwintering resulted in a single generation during the season and pupal overwintering resulted in two complete generations (fig. 2a, b). The interaction effect between the site and overwintering life stage on the number of generations completed was significant (table 2), reflected by an additional generation following pupal overwintering at the cold site (fig. 2a, b). At the warm site (fig. 2c, d), overwintering stage had no impact on the timing of life history transitions; adult moths were predicted to appear earlier in Spring, and be present in October, January and March–April (fig. 2c, d) irrespective of overwintering stage. At the cold site adult moth abundance peaks were predicted in January following larval overwintering (fig. 2c) and in December, as well as March following pupal overwintering (fig. 2d). Overwintering larvae were, however, exposed to increased cold and heat stress at the cold site, in comparison with the warm site (fig. 3a, b). Ultimately, larval overwintering in the cold site reduced adult moth abundance, probably through an increased amount of thermal stress hours experienced in the field during the larval life stage.

The accumulated number of cold and heat stress hours depended on overwintering stage, climate (site) and stage sensitivity (table 2). In general, the larval life stage experienced more stress in a cold environment following larval overwintering in comparison with a warm site and pupal overwintering (fig. 3a, b). For example, the first and second instar larvae experienced the highest amount of cold stress hours when the larval life stage overwintered at the cold site, followed by pupae then the third instar larva. In contrast, when pupae overwintered at the cold site, the final larval instar experienced the highest amount of cold stress, perhaps partly owing to its relatively high LDT (table 1). Interestingly, adult moths experienced the highest amount of heat stress when larvae overwintered at the cold site, while pupae experienced more stress hours (both heat and cold stress) at a cold site following larval overwintering, than in a warm site (fig. 3a, b). As expected, for pupal overwintering, all *E. saccharina* stages experienced a higher incidence of heat stress at the warm site in comparison with the cold site, and more cold stress at the cold site in comparison with the warm site (fig. 3c, d). Given the relatively cold LDT of *E. saccharina* eggs (table 1), this life history stage did not experience any hours of cold stress at either site, however during the height of summer, several hours of heat stress at the warm site were endured, irrespective of overwintering stage (fig. 3).

Relative population fitness and relative adult abundance are direct results of these population stress-predictions, and as such varied accordingly. The relative fitness of *E. saccharina* life stages was significantly affected by the climate of the two
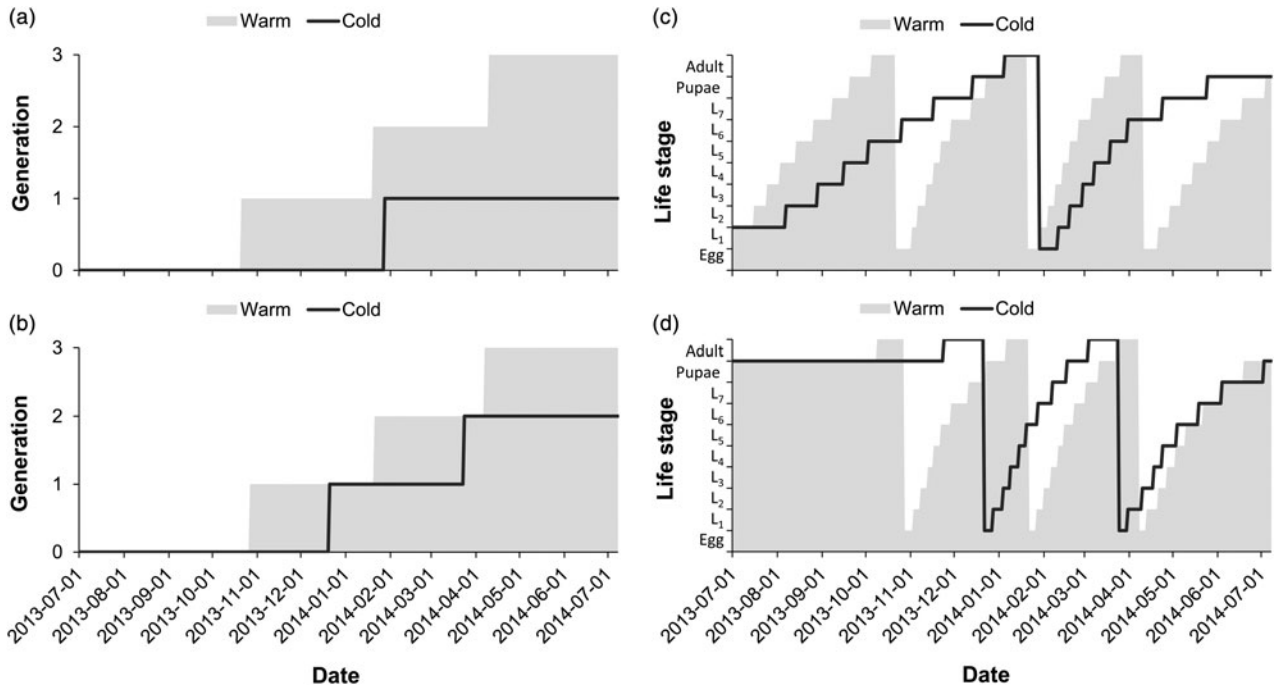
Fig. 2. The impact of local climate and overwintering stage on the number of generations (a, b) completed and life stage transition (c, d) predictions for *E. saccharina* in a warm (Malelane) and cold (Eston) climate. Model predictions were based on a larval (a, c) and pupal overwintering stage (b, d) and projected the dates of life stage transition or generation turn-over through time. In (c, d), 'L' on the *y*-axis represents larval instar stage (L_1 = first instar larva).

Table 2. Summary results from a generalized linear model testing the effects of warm or cold climate (site).

Model output	Effect	d.f.	χ^2	*P*-value
Number of generations	**Overwinter stage**	**1**	**87.47**	**<0.0001**
	Site	**1**	**2075.50**	**<0.0001**
	Overwinter stage × site	**1**	**326.93**	**<0.0001**
Cold-stress (h)	**Overwinter stage**	**1**	**1483.50**	**<0.0001**
	Site	**1**	**5339.60**	**<0.0001**
	Life stage	**9**	**3740.20**	**<0.0001**
	Overwinter stage × site	**1**	**997.90**	**<0.0001**
	Overwinter stage × life stage	**9**	**2041.90**	**<0.0001**
	Site × life stage	**9**	**2520.70**	**<0.0001**
	Overwinter stage × site × life stage	**9**	**2117.80**	**<0.0001**
Heat stress (hours)	**Overwinter stage**	**1**	**1568.11**	**<0.0001**
	Site	**1**	**493.52**	**<0.0001**
	Life stage	**9**	**273.51**	**<0.0001**
	Overwinter stage × site	**1**	**620.82**	**<0.0001**
	Overwinter stage × life stage	**9**	**511.78**	**<0.0001**
	Site × life stage	**9**	**515.66**	**<0.0001**
	Overwinter stage × site × life stage	**9**	**657.70**	**<0.0001**
Relative moth fitness (1/TSM)	Overwinter stage	1	2.65	0.1034
	Site	**1**	**1342.73**	**<0.0001**
	Overwinter stage × site	**1**	**6.88**	**0.0087**
Relative moth abundance (adults per day)	Overwinter stage	1	0.75	0.3872
	Site	**1**	**230.79**	**<0.0001**
	Overwinter stage × site	1	0.75	0.3872
Fecundity (eggs per day)	**Overwinter stage**	**1**	**4.10**	**0.0428**
	Site	**1**	**55.44**	**<0.0001**
	Overwinter stage × site	**1**	**7.68**	**<0.0100**

TSM, thermal safety margin.
Overwintering life stage (overwinter stage), which was pupae or larvae, particular life stage, which includes eggs, seven larval stages, pupae and adults (life stage) tested where applicable on the number of generations, cold- and heat-stress hours (Poisson distribution of errors and log link function), relative adult abundance, fecundity and relative fitness (Gaussian distribution of errors and identity link function). Interaction effects are presented with × and the degrees of freedom (d.f.), chi-square (χ^2) statistic, corresponding *P*-value are shown. Significant effects are shown in bold.
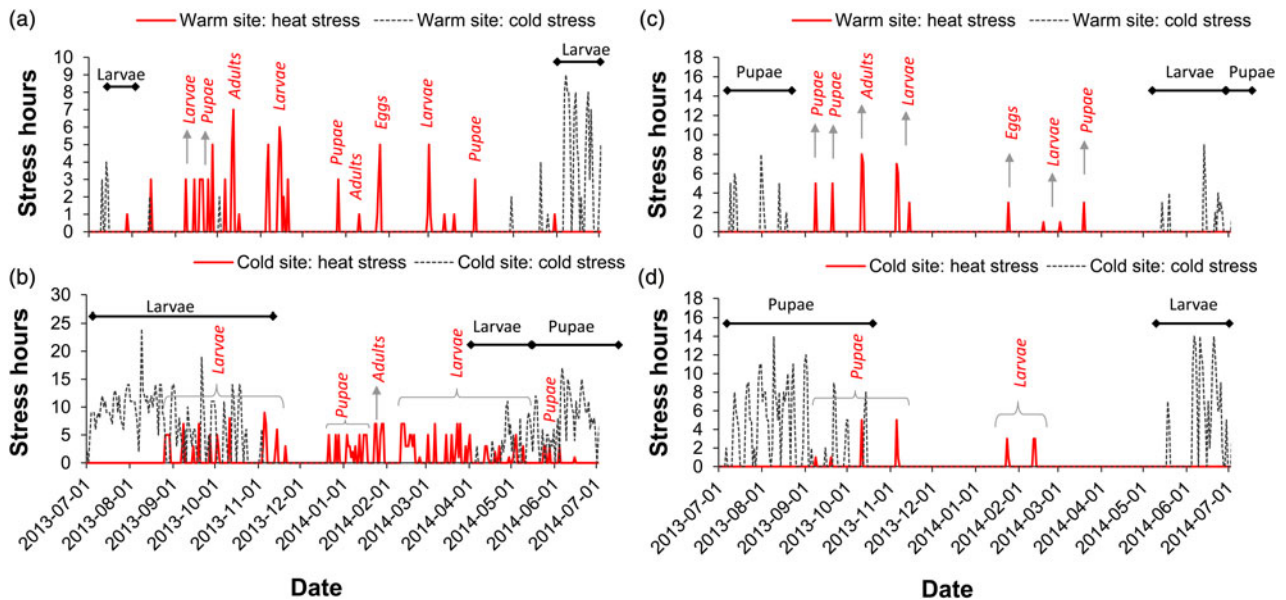
Fig. 3. The impact of local climate and overwintering stage on the number of stress hours per day for the specific life life history stages during the model simulation. Model outcomes were based on larval (a, b) and pupal (c, d) overwintering stages at a warm site and a cold site in South Africa. Horizontal bars denote the duration and life stage that experienced cold stress, while curly brackets and arrows show the heat stressed life stages throughout the season.

sites (table 2) such that relative fitness was higher at the warm site in comparison with the cold site (fig. 4a, b). The interaction effect between site and the overwintering stage on relative moth fitness was also significant, whereby fitness at the cold site was higher with pupal-overwintering in comparison with larval-overwintering. Relative moth abundance predictions for *E. saccharina* were also significantly affected by site, with higher abundance predicted at the warmer site (table 2, fig. 4c, d). Female fecundity (number of eggs laid per female per hour) was significantly affected by the overwintering life stage and the site (table 2), so that reproduction and/or egg laying commenced sooner at the warm site than at the cold site. Estimates of fecundity showed the first spikes during November at the cold site following pupal overwintering in comparison with January (42 days later) following larval overwintering. This lag effect between the overwintering stages resulted in 13, 552 more eggs being produced at the cold site following pupal overwintering vs. larval overwintering.

The availability of year-round in-field scout records enabled the verification of temporal model predictions. Here, model predictions for insect stress hours were plotted against scout records (expressed as average % larvae) in the field. We used larval overwintering model predictions for these validations because the larval scout data during winter revealed larval presence in the field from both model sites. Larval incidence was highest when the model predictions for insect stress in the environment were lowest and *vice versa* (Fig. 5a, c, cold stress: GLZ: χ^2 = 3740.20, d.f. = 9, P < 0.001; heat stress: GLZ: χ^2 = 273.51, d.f. = 9, $\underline{P}$ < 0.001). Furthermore, predictions for the adult stage corresponded with notable absences of larval observations in the scout records (fig. 5a), possibly further explaining population demographics observed at the cold site and during the second moth peak at the warm site. In summary, larval presence, according to the biophysical model, overlapped well with positive scout records averaged across

a matrix of sugarcane field ages and cultivars (fig. 5b, d). The AUC calculation resulted in a significant model ability to predict the observed outcomes (cold site AUC = 0.76 ± 0.127 c.i. and P = 0.003; warm site AUC = 0.63 ± 0.132 c.i. and P = 0.031). At the cold site, the model performed better in predicting larval presence and absence (overall performance = 67.39% accurate; false positive rate = 38.89%, false negative rate = 10.00%) than at the warm site (overall performance = 62.26% accurate; false positive rate = 44.83%, false negative rate = 29.17%).

Discussion

Modern IPM programs rely heavily on understanding the pest phenology in order to develop predictive tools to plan timely, cost-effective interventions, especially with biological control. Here we aimed to develop a better understanding of the effect of local climate on *E. saccharina* population phenology and fitness, since it is clear that temperature, through its effect on insect life-cycle duration, forms a critical part of any control program. For many tropical species that live at environmental temperatures close to their optimal performance temperatures, their relative fitness is expected to decrease with mild warming. In contrast, for species that occupy high-latitudes or altitudes have environmental temperatures far cooler than optimal, such that climate warming may enhance fitness (Deutsch *et al.,* 2008). The latter may be the case for *E. saccharina*, at least for the populations considered here. From the results obtained, different climatic locations affected different fitness traits that had significant outcomes ecologically (see also Conlong, 2001). We provide support for adult moth abundance variation across geographic sites that depend on the overwintering life stage and local climatic conditions. We specifically show that overwintering larvae resulted in a reduced adult moth occurrence in the field. Three generations were completed at a warm site. At a cold site one generation were
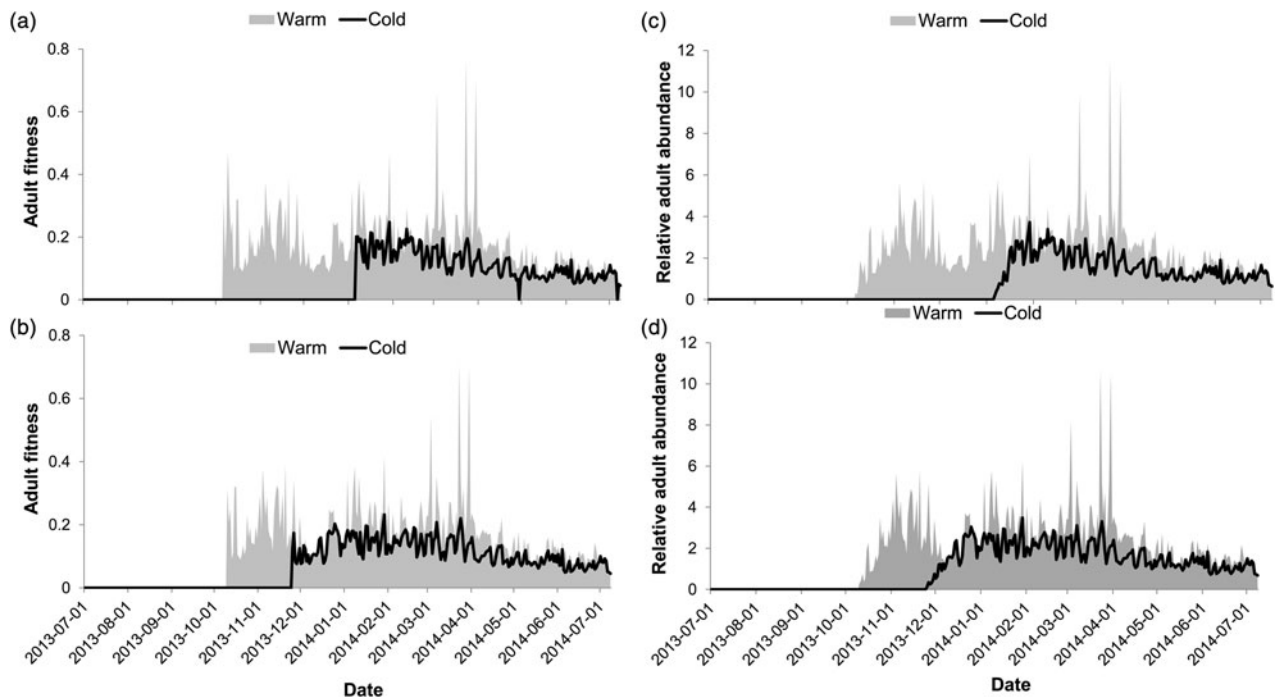
Fig. 4. The impact of local climate and overwintering stage on adult moth fitness (a, b) and relative adult abundance (c, d). Model predictions were based on a larval (a, c) and pupal (b, d) overwintering stage.

completed and more frequent cold and heat stress were observed when larvae overwintered here in comparison with pupae overwintering. Relative population fitness and abundance did not differ between the overwintering stages, however fitness and the resulting abundance was significantly lower at the cold site. In the context of Sterile Insect Technique (SIT) as part of an area-wide IPM control approach for *E. saccharina* (Conlong & Rutherford, 2009), the data generated from this model indicate that field releases of sterile moths in warm sites can be performed at the start of the first moth peak of the season, i.e. July–September, to bring down the peak predicted to occur during October, irrespective of overwintering life stage. In cold sites, however, these results suggest that releases should be delayed by approximately 1 month when the pupal stages are most abundant during winter-month scouting.

The model predictions of life stage timing and abundance were compared with a large in-field scout dataset. Here the model performed relatively well. For example, the number of predicted stress hours was high, or the model projected an adult life stage, which is unable to be surveyed or sampled in the scout data, during the times when larval scout data were zero. Model predictions for larval presence overlapped well with positive scout records averaged across a matrix of sugarcane ages and cultivars. Furthermore, earlier light trapping work showed that adult moth phenological cycles showed a definite September peak although with low moth numbers (Carnegie & Leslie, 1990), larger adult numbers peaked during November–December and March–May (Atkinson, 1982) and, specifically, in April (Carnegie & Leslie, 1990). Here, the model predictions, for both sites and overwintering stages, correspond well to these findings. Finally, definite low adult moth abundance was recorded by Atkinson (1982) and Carnegie & Leslie

(1990) during June–July, which the model reflected through an incomplete pupal period over these months. To conclude, the model corresponded well with adult moth peak events on the calendar (or Julian days), and larval abundance predictions were verified by on-farm scouting practices. In a broader context, these results hold important implications for field releases of SIT moths in different areas (Potgieter *et al.*, 2013, 2016), and or biological control agents targeting different larval instar ages and/or pupae (Conlong, 1990, 1994). These results can also be used to better predict the timing of insecticide applications targeting specific stages in the *E. saccharina* life cycle (Leslie *et al.*, 2006) and perhaps aid in understanding fitness cost in insecticide-resistant strains of insect pests, for example, diamond back moth (*Plutella xylostella* (Linnaeus) (Lepidoptera: Plutellidae)) when experiencing thermal stress (Zhang *et al.*, 2015). The application of this biophysical model can inform growers and pest management advisory staff to ensure accurate and timely management actions against this pest in the field.

Mechanistic (process-based) population modelling enables scenario-driven hypothesis testing. Here the overwintering life stage significantly affected the generation time in the cold, but not hot regions. In other words, the population's age structure at the end of a previous season, partly determines the population's phenology, age- and stage-structure of the following season. Warm climates are more stable and temperatures fluctuated closer to the thermal optimum of the insects, resulting in fewer stress hours experienced, in terms of both magnitude and frequency. Stress (i.e. sustained sub- or super-optimal temperatures), in turn, resulted in changes in overall population abundance and estimated fitness. We showed that larvae experienced more stress in a cold environment following larval overwintering in comparison with a warm site and pupal overwintering. This suggests
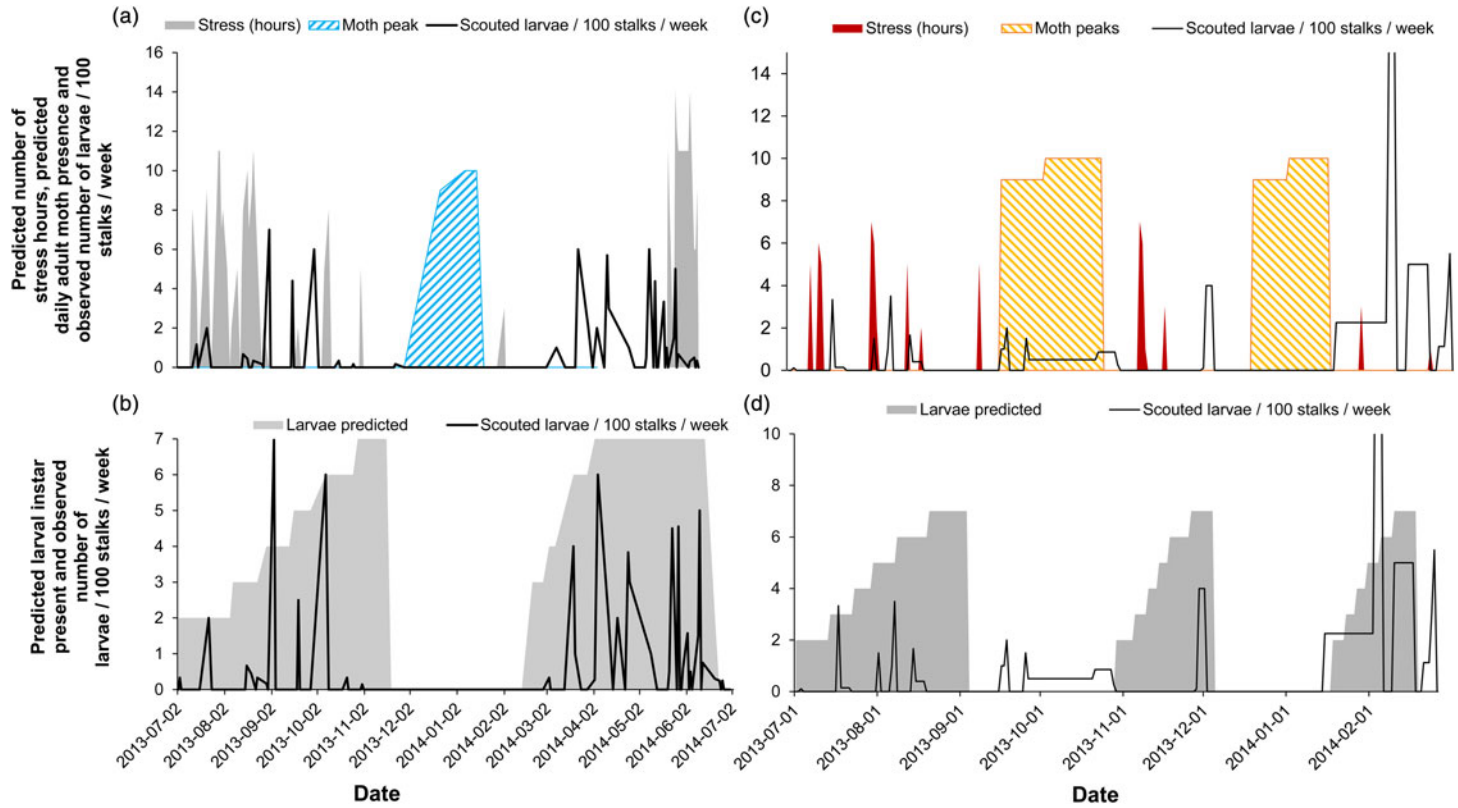
Fig. 5. Predicted thermal stress index (hours) and timing of the adult life stage (moth peaks) compared with weekly obtained scout records (expressed as the number of larvae per 100 stalks per week) for a cold site (a) and a warm site (c) and the predicted larval instars over time (tallied for a larval overwintering life stage) compared with obtained scout records at the two sites (b, d).

that, in cold environments, there might be consistent selective pressure for *E. saccharina* to develop greater cold resistance (e. g. seasonal acclimatization or genetic adaptation over the long term) during the larval stage or complete the final larval instar sooner in order to pupate and overwinter in this stage. Indeed, running model simulations across multiple seasons might alter the life history stage within which overwintering occurs. The model predicts that overwintering as pupae confers higher adult occurrence, increased generation number and reduced thermal stress. Microclimate temperature recordings at different locations relative to the sugarcane stalk showed that there was a significant interaction effect between season and location (GLZ: $\chi^2 = 7.30$, d.f. = 2, $P = 0.03$). In the winter, average temperatures recorded inside the sugarcane stalk were significantly cooler (16.32 ± 0.15 °C) than the base of the stalk (16.61 ± 0.10 °C) (see Supplementary information). Larvae can 'seek out' slightly warmer microsites by boring into the stalks during winter. Leaf sheaths – where adult moths and eggs are typically found – were warmer than the insides of the stalks but this difference was not significant during the winter months.

Further studies exploring where, and when, pupal overwintering occurs in the field would provide useful insights into *E. saccharina*'s physiology in its new and native ranges, and may help to forecast a population's potential for crop damage at a given location. For example, the detection of large numbers of overwintering pupae may serve as an early warning signal for more intense pest management practise in anticipation of relatively high adult performance in the following summer generations (as predicted here by the model).

The results obtained in this study are dependent on the incorporation of stage-specific trait data. This is not typically done for species abundance models, and the procedure outlined here is relatively novel, even to pest modelling literature. There are however limitations to the model as it currently stands. For example, here we modelled a single season to focus primarily on the effects of local climate and overwintering life stage on the model predictions. When more than one season's phenological and abundance responses are captured, it will likely sketch a better picture about the long-term stressors that work on the species in a particular environment. From a broader point of view, sophisticated models that have been developed to predict the outcomes of IPM intervention (Potgieter *et al.*, 2012, 2013, 2016) provide excellent insight into temporal population responses in the light of future pest management plans. Nevertheless, the mechanism-based model applied in this study provided novel insights into the effect of newly-invaded cold climates on *E. saccharina* survival and adult relative abundance. These results, in addition to many other observations concluding that *E. saccharina* will spread into novel areas, provide strong evidence for complete generation turnover and population fitness in cold climates. The model assumes (or rather constrains) overwintering larvae or pupae and hence does not allow for multiple overwintering stages, which might further advance adaptation to unpredictable climate.

Higher population turnover associated with warmer climates involve higher pest abundance and crop damage under regional global warming changes in climate. Locomotion performance, adult size, body mass, fecundity, growth rate and development time are temperature dependent and affect insect field fitness (Angilletta *et al.*, 2002; Terblanche *et al.*, 2006; Kingsolver & Huey, 2008). The planned SIT program against *E. saccharina* in the sugarcane industry (Conlong & Rutherford, 2009) will, for example, benefit from the use of this model, as already explained. However, to obtain maximum effect with minimum costs, sterile male moth releases should be conducted when the natural population of moths are low and in the initial stage of moth peak as mating ratios and released moth performance are critical aspects of SIT success (Chidawanyika & Terblanche, 2011; Sørensen *et al.*, 2013; Terblanche, 2014). In this way, sterile-male mating will optimize sterile egg production during the wild moth's peak so that the effect on the population is maximised towards reproductive suppression. Higher average temperatures might reduce the number of cold stress events (e.g. freeze thaw cycles), accelerate the development times and lead to range expansion into areas that are currently too cold for *E. saccharina* persistence. Management strategies should be tailored according to local climates, especially in areas where multiple generations are expected to occur and also in areas where the pest might expand its range.

The results also provide valuable insights into the management of *E. saccharina* in commercially grown sugarcane. Adult scouting practices could benefit from the model predictions in validation and forecasts. It would be valuable to verify the model predictions on adult moth abundance once such a scouting method has been developed. The predicted output parameters are directly relevant and interpretable to the general sugarcane grower in the specific site locations. It furthermore holds significance to the broader sugarcane industry through added insight into the effect of local climate and overwintering stage on *E. saccharina* population abundance. This work should aid in decision making when area-wide IPM strategies are employed in the field.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S0007485317000712

References

Angilletta, M.J. Jr., Niewiarowski, P.H. & Navas, C.A. (2002) The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* **27**, 249–268.

Assefa, Y., Mitchell, A. & Conlong, D.E. (2006) Phylogeography of *Eldana saccharina* Walker (Lepidoptera: Pyralidae). *Annales de la Société Entomologique de France* **42**, 331–337.

Assefa, Y., Conlong, D.E., van den Berg, J. & Le Rü, B.P. (2008) The wider distribution of *Eldana saccharina* (Lepidoptera: Pyralidae) in South Africa and its potential risk to maize production. *Proceedings of the South African Sugar Technologists' Association* **81**, 290–297.

Assefa, Y., Conlong, D.E., van den Berg, J. & Mitchell, A. (2010) Distribution of sugarcane stem borers and their natural enemies in small-scale farmers' fields, adjacent margins and

wetlands of Ethiopia. *International Journal of Pest Management* **56**, 233–241.

Atkinson, P.R. (1980) On the biology, distribution and natural host plants of *Eldana saccharina* Walker (Lepidoptera: Pyralidae). *Journal of the Entomological Society of Southern Africa* **43**, 171–194.

Atkinson, P.R. (1982) Phenology of *Eldana saccharina* Walker in Natal and use of light traps to monitor distribution and abundance. *Proceedings of the South African Sugar Technologists' Association* **56**, 90–94.

Atkinson, P.R., Carnegie, A.J.M. & Smaill, R.J. (1981) A history of the outbreaks of *Eldana saccharina* Walker, in Natal. *Proceedings of the South African Sugar Technologists' Association* **55**, 111–115.

Barton, M.G. & Terblanche, J.S. (2014) Predicting performance and survival across topographically heterogeneous landscapes: the global pest insect *Helicoverpa armigera* (Hübner, 1808) (Lepidoptera: Noctuidae). *Austral Entomology* **53**, 249–258.

Briere, J.F., Pracros, P., Le Roux, A.Y. & Pierre, J.S. (1999) A novel rate model for temperature-dependent development for arthropods. *Environmental Entomology* **28**, 22–29.

Butterfield, M.K. (2002) Genetic models to assess the development of counter-resistance in insect pests exposed to Bt-sugarcane. *Proceedings of the South African Sugar Technologists' Association* **76**, 329–335.

Campbell, G.S. & Norman, J.M. (1998) *An Introduction of Environmental Biophysics*. 2nd edn. New York, USA, Springer Science.

Cardwell, K.F., Schulthess, F., Ndemah, R. & Ngoko, Z. (1997) A systems approach to assess crop health and maize yield losses due to pests and diseases in Cameroon. *Agriculture, Ecosystems and Environment* **65**, 33–47.

Carnegie, A.J.M. (1974) A recrudescence of the borer *Eldana saccharina* Walker (Lepidoptera: Pyralidae). *Proceedings of the South African Sugar Technologists Association* **48**, 107–110.

Carnegie, A.J.M. & Leslie, G.W. (1990) *Eldana saccharina* (Lepidoptera: Pyralidae): ten years of light trapping. *Proceedings of the South African Sugar Technologists' Association* **64**, 107–110.

Chidawanyika, F. & Terblanche, J.S. (2011) Costs and benefits of thermal acclimation for codling moth, *Cydia pomonella* (Lepidoptera: Tortricidae): implications for pest control and the sterile insect release programme. *Evolutionary Applications* **4**, 534–544.

Chown, S.L., Slabber, S., McGeogh, M.A., Janion, C. & Leinaas, H.P. (2007) Phenotypic plasticity mediates climate change responses among invasive and indigenous arthropods. *Proceedings of the Royal Society B: Biological Sciences* **274**, 2661–2667.

Conlong, D.E. (1990) A study of pest-parasitoid relationships in natural habitats: an aid towards the biological control of *Eldana saccharina* (Lepidoptera: Pyralidae) in sugarcane. *Proceedings of the South African Sugar Technologists' Association* **64**, 111–115.

Conlong, D.E. (1994) A review and perspectives for the biological control of the African sugarcane stalk borer *Eldana saccharina* Walker (Lepidoptera: Pyralidae). *Agriculture, Ecosystems and Environment* **48**, 9–17.

Conlong, D.E. (2001) Biological control of indigenous African stemborers: What do we know? *Insect Science and its Application* **21**, 267–274.

Conlong, D.E. & Rutherford, S.R. (2009) Conventional and new biological and habitat interventions for integrated pest management systems: review and case studies using *Eldana saccharina* Walker (Lepidoptera: Pyralidae). ch. 10, vol. **1**, pp. 241–261 *in* Peshin, R. & Dhawan, A.K. (*Eds*). *Integrated Pest Management: Innovation-Development Process*. Dordrecht, The Netherlands, Springer. ISBN 978-1-4020-8991-6 (Print); 978-1-4020-8992-3 (online). DOI 10.1007/978-1-4020-8992-3_10.

Conlong, D.E., Webster, T.E. & Wilkinson, D. (2016) Ten years of area-wide integrated pest management with a push-pull component against *Eldana saccharina* (Lepidoptera: Pyralidae) in sugarcane in the midlands north region of Kwazulu-Natal. *Proceedings of the South African Sugar Technologists' Association* **89**, 70–84.

Crawley, M.J. (2007) *The R Book*. Chichester, John Wiley and Sons.

Davis, P.M. & Pedigo, P. (1990) Yield responses of corn stands to stalk borer (Lepidoptera: Noctuidae) injury imposed during early development. *Journal of Economic Entomology* **83**, 1582–1586.

Deutsch, C.A., Tewksbury, J.J, Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. & Martin, P.R. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the USA* **105**, 6668–6672.

Dick, J. (1945) Some data on the biology of the sugarcane borer (*Eldana saccharina* Wlk). *Proceedings of the South African Sugar Technologists' Association* **19**, 75–79.

Feng, H., Gould, F., Huang, Y., Jiang, Y. & Wu, K. (2010) Modeling the population dynamics of cotton bollworm *Helicoverpa armigera* (Hüber) (Lepidoptera: Noctuidae) over a wide area in northern China. *Ecological Modelling* **221**, 1819–1830.

Girling, D.J. (1972) *Eldana saccharina* Wlk. (Lepidoptera: Pyralidae), a pest of sugarcane in East Africa. *Proceedings of the International Society of Sugarcane Technologists* **14**, 429–434.

Girling, D.J. (1978) The distribution and biology of *Eldana saccharina* Walker (Lepidoptera: Pyralidae) and its relationship to other stem borers in Uganda. *Bulletin of Entomological Research* **68**, 471–488.

Goebel, F-R. & Way, M. (2006) Crop losses due to two sugarcane stem borers in Reunion and South African. *Proceedings of the South African Sugar Technologists' Association* **26**, 806–812.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**, 1965–1978.

Kfir, R. (1998) Maize and grain sorghum: Southern Africa. pp. 29–37 *in* Polaszek, A. (*Ed*.) *African Cereal Stem Borers. Economic Importance, Taxonomy, Natural Enemies and Control*. CAB International in association with ACP-EU Technical Centre for Agricultural and Rural Co-operation (CTA), Wallington, United Kingdom.

King, H., Conlong, D.E. & Mitchell, A. (2002) Genetic differentiation in *Eldana saccharina* (Lepidoptera: Pyralidae): evidence from the mitochondrial cytochrome oxidase I and II genes. *Proceedings of the South African Sugar Technologists Association* **76**, 321–328.

Kingsolver, J.G. & Huey, R.B. (2008) Size, temperature and fitness: three rules. *Evolutionary Ecology Research* **10**, 251–268.

Kingsolver, J.G. & Moffat, R.J. (1982) Thermoregulation and the determinents of heat transfer in *Colias* butterflies. *Oecologia* **53**, 27–33.

Kleynhans, E., Conlong, D.E. & Terblanche, J.S. (2014*a*) Host plant-related variation in thermal tolerance of *Eldana*

saccharina (Lepidoptera: Pyralidae). *Entomologia Experimentalis et Applicata* **150**, 113–122.

Kleynhans, E., Mitchell, K.A., Conlong, D.E. & Terblanche, J.S. (2014b) Evolved variation in cold tolerance among populations of *Eldana saccharina* (Lepidoptera: Pyralidae) in South Africa. *Journal of Evolutionary Biology* **27**, 1149–1159.

Lange, C.L., Scott, K.D., Graham, G.C., Sallam, M.N. & Allsopp, P.G. (2004) Sugarcane moth borers (Lepidoptera: Noctuidae and Pyraloidae): phylogenetics constructed using COII and 16S mitochondrial partial gene sequences. *Bulletin of Entomological Research* **94**, 457–464.

Leslie, G. 2013. Carry-over cane & Eldana control. pp. 8–9 *in* Leslie, G. (*Ed.*) *The Link*. South African Sugarcane Research Institute, Mount Edgecombe, South Africa. May edition.

Leslie, G.W., Stranack, R.A. & De Haas, O. (2006) Progress in the use of aerially applied fastac® (alpha-cypermethrin) for the control of the sugarcane borer *Eldana saccharina* (Lepidoptera: Pyralidae), and an assessment of its commercial impact. *Proceedings of the South African Sugar Technologists' Association* **80**, 236–244.

Maes, K.V.N. (1998) Pyraloidea: crambidae, pyralidae. pp. 87–98 in Polaszek, A. (*Ed.*) *African Cereal Stem Borers. Economic Importance, Taxonomy, Natural Enemies and Control.* CAB International in Association with ACP-EU Technical Centre for Agricultural and Rural Co-operation (CTA), Wallington, United Kingdom.

Mason, S.J. & Graham, N.E. (2002) Areas beneath the relative operating characteristics (ROC) and relative operating levels (ROL) curves: statistical significance and interpretation. *Quarterly Journal of the Royal Meteorological Society* **128**, 2145–2166.

Potgieter, L., van Vuuren, J.H. & Conlong, D.E. (2012) Modelling the effects of the sterile insect technique applied to *Eldana saccharina* Walker in sugarcane. *ORiON* **28**, 59–84.

Potgieter, L., van Vuuren, J.H. & Conlong, D.E. (2013) A reaction-diffusion model for the control of *Eldana saccharina* Walker in sugarcane using the sterile insect technique. *Ecological Modelling* **250**, 319–328.

Potgieter, L., van Vuuren, J.H. & Conlong, D.E. (2016) Simulation modelling as a decision support in developing a sterile insect-inherited sterility release strategy for *Eldana saccharina* (Lepidoptera: Pyralidae). *Florida Entomologist* **99**, 13–22.

R Development Core Team (2010) *R: A Language and Environment for Statistical Computing*. Vienna, Austria, R Foundation for Statistical Computing. ISBN 3-900051-07-0, http://www.R-project.org/. Packages: MASS: Venables, W.N. & Ripley, B.D. (2002) *Modern Applied Statistics with S*. 4th edn. New York, Springer. ISBN: 0-387-95457-0; Car: John Fox and Sanford Weisberg (2011) *An {R} Companion to Applied Regression*. 2nd edn. Thousand Oaks, CA, Sage. http://socserv.socsci.mcmaster.ca/jfox/Books/Companion; pROC: Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., Müller, M. (2011) An open-source package for

R and S+ to analyze and compare ROC curves. *BMC Bioinformatics* **12**, 77–84.

Sinclair, B.J., Williams, C.M. & Terblanche, J.S. (2012) Variation in thermal performance among insect populations. *Physiological and Biochemical Zoology* **85**, 594–606.

Sørensen, J.G., Addison, M.F. & Terblanche, J.S. (2013) Mass-rearing of insects for pest management: challenges, synergies and advances from evolutionary physiology. *Crop Protection* **38**, 87–94.

Terblanche, J.S. (2014) Physiological performance of field-released insects. *Current Opinion in Insect Science*. **4**, 60–66.

Terblanche, J.S., Klok, J.C., Krafsur, E.S. & Chown, S.L. (2006) Phenotypic plasticity and geographic variation in thermal tolerance and water loss of the tsetse *Glossina pallidipes* (diptera: Glossinidae): implications for distribution modelling. *American Journal of Tropical Medicine and Hygiene* **74**, 786–794.

Waiyaki, J.N. (1968) *The Biology and Control of the Principal Lepidopterous Borers Associated with Sugarcane at the Tanganyika Planting Company, Arusha-Chini. Miscellaneous report* No. 653. Tropical Pesticides Research Institute, Arusha, Tanzania.

Walton, A.J. & Conlong, D.E. (2016) General biology of *Eldana saccharina* (Lepidoptera: Pyralidae): a target for the sterile insect technique. Special issue 1: factors and variables that affects quality of lepidopterans use din SIT programmes. *Florida Entomologist* **99**, 30–35.

Watt, W.B. (1968) Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution* **69**, 1486–1496.

Way, M.J. (1994) A preliminary assessment of the effects of different constant temperatures on the reproduction of *Eldana saccharina* (Lepidoptera: Pyralidae). *Proceedings of the South African Sugar Technologists' Association* **68**, 16–18.

Way, M.J. (1995) Developmental biology of the immature stages of *Eldana saccharina* Walker (Lepidoptera: Pyralidae). *Proceedings of the South African Sugar Technologists' Association* **69**, 83–86.

Webster, T.M., Maher, G.W. & Conlong, D.E. (2006) An integrated pest management system for *Eldana saccharina* in the midlands north region of KwaZulu-Natal. *Proceedings of the South African Sugar Technologists' Association* **79**, 347–358.

Webster, T.M., Brenchley, P.G. & Conlong, D.E. (2009) Progress of the area-wide integrated pest management plan for *Eldana saccharina* Walker (Lepidoptera: Pyralidae) in the midlands north region of KwaZulu-Natal. *Proceedings of the South African Sugar Technologists' Association* **82**, 471–485.

Zhang, L.J., Jing, Y.P., Li, X.H., Li, C.W., Bourquet, D. & Wu, G. (2015) Temperature-sensitive fitness cost of insecticide resistance in Chinese populations of the diamondback moth *Plutella xylostella*. *Molecular ecology* **24**, 1611–1627.