Temperature based phenology model for predicting establishment and survival of *Spodoptera litura* (Fab.) on groundnut during climate change scenario in India

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ABSTRACT

Studies were conducted to develop temperature-based phenology model for *Spodoptera litura* on groundnut, at both constant and fluctuating temperatures and to predict the possibility of pest risk in future climate change scenarios of India using 'stochastic simulation tool' in Insect Life Cycle Modelling (ILCYM) software ,which is based on rate summation and cohort up-dating approach. Phenology model predicted temperatures between 25°C and 30°C as the favourable range for *S. litura* development, survival and reproduction. The intrinsic rate of increase (*rm*), and finite rate of increase (») increased with increase in temperature from 15°C to 30°C and decreased with increase in temperature. Intrinsic rate of increase (*rm*), varied from 0.05 females/female/day at 15°C to 0.17 females/female/day at 30°C. *S. litura* population attained a maximum net reproductive rate 'R_o' (334.09 females/female/generation) and total fecundity (1041.88 individuals/ female/generation) at 27°C temperature. Simulated life table parameters were used to determine indices such as the establishment risk index (ERI), the generation index (GI), and activity index (AI) by using the 'Population distribution and risk mapping' module of software during present and future climatic scenarios and significant increase in AI and ERI with higher GI at future (2050) climatic conditions compared to current (2000) climatic conditions indicating the strong suitability for establishment and survival of *S.litura* in India.

Keywords: Life table, S.litura, phenology model, temperature, establishment risk index

Spodoptera litura (Fabricius), tobacco caterpillaris a serious and devastating polyphagous insect pest causing considerable losses to many economically important cultivated crops including groundnut (Qin et al., 2004) and loss of major crops due to insect pest varies between 10 and 30%. To develop any pest management programme for a specific agro-ecosystem, information on abundance and distribution of pest in relation to weather parameters is a basic requirement (Patel and Shekh, 2006). Activity of S. litura in relation to weather factors have been investigated by many workers (Nandagopal et al., 2006; Prasad et al., 2013; Ramesh Babu et al., 2015). Incidence of insect pests is driven by various environmental factors and temperature is one of the most important factors that influences significantly. Temperature is a key abiotic factor influencing survival and reproduction rates in insects and hence strongly determines the pest's demographic parameters, which are essential for interpreting population dynamics, developmental rates and seasonal occurrence. Detailed knowledge on temperature effects on herbivore insect pests can be used to determine the range where the pest might develop (establish) and to predict the population's growth potential (i.e. intrinsic rate of increase) and dynamics. In fact, each pest management

programme requires authentic determination of the pest's population parameters (Zamani et al., 2006). The ability of an insect to develop at different temperatures is an important adaptation to survive in various climatic conditions, and its understanding is important for predicting pest outbreaks (Gilbert and Raworth, 1996). The temperature response phenology models simulate the variability in insect development times within a population based on the detailed laboratory assessments of the insect's life history and thus, can provide better results on future pest activity (Wagner et al., 1984). Phenology models that use non-linear functions of higher biological significance and include stochastic functions for simulating variability in development times within a population can provide better results than linear models (Sporleder et al., 2004). The pest forecasting models facilitate better preparedness to combat outbreaks of serious insect pests by developing effective pest management strategies well in advance.

The objective of present study was to develop an inclusive temperature-dependent population growth model for *S. litura*, which permits prediction of its population growth potential and will also help in future population growth potential under probable climate change.

MATERIALS AND METHODS

Insect cultures

During the rainy seasons of 2016 and 2017, egg masses and larval population of S. litura were collected from the groundnut fields of Hayathnagar Research Farm of ICAR-Central Research Institute for Dryland Agriculture (CRIDA), Hyderabad, Telangana in India (Location: 17.32° N, 78.59° E, Alt. 566 m). For mass multiplication of S. litura the insect culture was maintained in glass jars $(15 \text{ cm} \times 10 \text{ cm})$ at controlled temperature and humidity conditions of $27 \pm$ 2 °C and $65 \pm 5\%$ RH and natural photoperiod in the insectary of Entomology laboratory, ICAR-CRIDA, Hyderabad. The larvae were reared on groundnut leaves for one generation (from egg to egg) to obtain bulk population for further experimentation. The pupae were transferred to pupation jars containing a 2-3 cm layer of moist sterilized sand covered with filter paper. Just after emergence, the adults were shifted to oviposition jars similar to pupation jars but lined with filter paper on the inner side to facilitate egg laying. The adults were fed on water and honey solution (4:1 v/v) soaked on a cotton swab.

Experiments on life tables were conducted at temperatures of 15, 20, 25, 27, 30, 33 and 35°C. In order to construct life tables, a group of newly laid eggs of S. litura were placed on a piece of wet filter paper in Petri dish (75 x 10 mm). These Petri dishes were maintained at seven different temperatures (15, 20, 25, 27, 30, 33 and 35°C) in growth chambers (I 36LL; Percival Scientific, Inc. Perry, USA) at 75 \pm 5% relative humidity with a photoperiod ratio of 14:10 (14 hours of light: 10 hours of dark). After egg hatching, the egg period was recorded at different temperatures. Freshly hatched neonates (thirty) were collected and experimental trials were initiated. Freshly hatched thirty neonates were reared individually in Petridishes (75 x 10 mm) till the adult stage. Larvae were fed with fresh groundnut leaves collected from fields. The data on durations of egg, larval, pupal and adult and total development periods at each temperature were recorded.

Modelling and simulation tools

The Insect Life Cycle Modelling (ILCYM) software version 3.0, developed by the International Potato Centre, Lima, Peru(https://research.cip.cgiar.org/ confluence/displayilcym/Downloads (Tonnang *et al.*, 2013) was used for the development of process-based temperature-driven and age-stage structured *S. litura* phenology model.

Development time and its distribution

The cumulative frequencies of development times of each life stage and temperatures were plotted against normalized developmental times by fitting a complementary log-log (CLL) distribution curve for all stages. The mathematical expressions of distribution function (Tonnang *et al.*, 2013) is given as: CLL distribution: $F(x)=1-\exp(-\exp(a_i + b \ln x)))$, where, F(x) is the probability to complete development at time x, lnx is the natural logarithm of the days observed, a is the intercept corresponding to temperature i, and b is the common slope of the regression model. The best fit model was selected based on Akaike's Information Criterion (AIC), a well-known goodness of fit indicator (Akaike, 1973).

Development rate

Inverse of durations of immature development and adult survival (1/days) were taken as rates of development and survival, respectively. The non-linear regression model was fitted to establish the relationship between development rate and temperature (Zajac *et al.*, 1989). The modified fourteen parameter version of Sharpe and DeMichele model was used for estimating rates of egg development(Sharpe and DeMichele, 1977) and Janish 2, function was fitted to larvae and pupa of *S.litura* at various constant temperatures.

Immature stages mortality and adult senescence

Mortality was calculated from the frequency of cohort mortality. The mortality in immature stages of *S. litura* at various constant temperatures was estimated by applying modified version of the Wang model (Wang *et al.*, 1982). The relationship between senescence of adults of *S. litura* at various constant temperatures was determined by fitting a modified fourteen parameter version of Sharpe and DeMichele model (Stinner *et al.*, 1974).

Temperature dependent reproduction

The oviposition was modelled considering the three temperature dependent functions: temperature dependent total fecundity, age-related oviposition frequency and agespecific adult survival. Anon-linear regression model, Taylor 2was fitted to find out the effects of various constant temperatures on total number of eggs produced by a female adult during her whole life span (Kim and Lee, 2003). The relationship between cumulative oviposition rate and female age was well described by the Gamma function.

Estimation of life table parameters at constant temperatures

Using 'stochastic simulation tool' in ILCYM which is

based on rate summation and cohort up-dating approach (Curry *et al.*, 1978), the life table parameters *viz.*, gross reproductive rate (GRR), net reproductive rate (Ro), intrinsic rate of natural increase (rm), finite rate of increase (\rangle), mean generation time (T) and doubling time (Dt) were estimated. The estimates were based on the developed phenology model at seven constant temperatures ranging 15 - 35°C with five repetitions each.

Comparison of life tables at constant and fluctuating temperatures

The life table data on *S. litura* obtained from fluctuating temperature experiment were compared with model outputs produced using constant temperature experiments. The stochastic simulation based on rate summation and cohort updating approach (Curry *et al.*, 1978) was used in estimating life history parameters.

Estimation of pest risk indices

Using values of the life table parameters, we calculated Establishment risk index (ERI), Generation index (GI) and Activity index (AI) for possible pest risk at each data point (Tonnang *et al.*, 2013):

Spatial mapping of risk indices

The risk indices thus estimated were employed in the "potential population analysis and mapping" module of ILCYM for visualizing the risk maps. The module facilitated spatial simulations of pest populations through grid-based within a deûned area according to grid-speciûc monthly temperatures interpolated from available databases (worldclim in this case) (Tonnang *et al.*, 2013). The process generated ASCII ûles (.asc) which were converted to grid format (.grd) for visualizing the risk maps by importing in DIVA-GIS (an open source geographic information system, downloadable at http://www.diva-gis.org).

RESULTS AND DISCUSSION

Effects of temperature on development time and survivorship

At different temperatures, the data on development duration for immature and adult stages of *S. litura* are presented in Table 1. The temperatures within the evaluation range have a greater influence on the development of the immature life stages of *S. litura*. Results indicated that, the duration of the immature stages and the time required completing the cycle from egg to adult decreased significantly with increasing temperatures within the temperature range of $15-33^{\circ}$ C (Table 1) and became non-

Table 1: Mea	un developmer.	it time (Days±	SE) of immatur	e and adult life	stages of S. liti	ura at differen	t constant temp	eratures (Fitte	d function: clog	glog)
Temperature	Εį	38	Lar	va	Pup)a	Fem	ale	Mal	e
$(^{0}C)+0.5$	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed
15	10.573 ± 0.39	12 ± 0.512	49.323 ± 0.465	51 ± 0.655	33.778 ± 0.393	36 ± 1.916	35.673 ± 0.527	38±0.805	32.771 ± 0.478	36 ± 0.675
20	5.903 ± 0.25	6 ± 0.497	28.284 ± 0.265	29 ± 0.269	17.639 ± 0.249	18 ± 0.428	21.586 ± 0.351	23 ± 0.587	19.704 ± 0.344	21 ± 0.539
23	2.333 ± 0.09	3 ± 0.109	18.877 ± 0.170	19 ± 0.161	12.436 ± 0.131	13 ± 0.124	17.171 ± 0.275	18 ± 0.551	13.773 ± 0.228	14 ± 0.436
21	2.094 ± 0.08	3±0.116	16.642 ± 0.166	17 ± 0.183	11.269 ± 0.150	12 ± 0.167	10.710 ± 0.213	11 ± 0.396	9.644 ± 0.186	10 ± 0.328
30	1.922 ± 0.07	3 ± 0.097	14.960 ± 0.146	16 ± 0.242	8.470 ± 0.125	9 ± 0.186	10.542 ± 0.187	11 ± 0.378	7.768 ± 0.161	8 ± 0.340
33	2.367 ± 0.09	2 ± 0.138	12.365 ± 0.127	13 ± 0.246	8.079 ± 0.116	8 ± 0.266	8.106 ± 0.150	8±0.417	6.370 ± 0.134	6 ± 0.346
35	2.318 ± 0.05	3 ± 0.235	15.138 ± 0.129	16 ± 0.733	10.483 ± 0.143	10.5 ± 0.573	8.057±0.151	8±0.485	6.263 ± 0.130	6±0.395

Table 2: Estimated life table parameters of S. litura at different constant temperatures

Temperature	Intrinsic	Net	Gross	Mean	Finite	Doubling
(°C)+0.5	rate of	reproductive	reproductive	generation	rate of	time
	increase (rm)	rate (R0)	rate (GRR)	time(T)	increase(?)	(days)
15	0.05	0.01	1.70	73.23	0.94	12.79
20	0.05	30.83	445.00	61.98	1.05	12.53
25	0.13	291.82	991.57	42.75	1.14	5.22
27	0.15	334.09	1041.88	37.09	1.16	4.42
30	0.17	185.33	825.46	30.55	1.18	4.05
33	0.13	40.55	552.36	27.74	1.14	5.19
35	0.06	8.07	323.99	32.02	1.06	6.63



Fig.1: Temperature-dependent developmental rates (1/day) for immature stages of *S. litura*. (a)Egg; Sharpe & DeMichele 14. (b) Larva and (c) Pupa; Janish 2. The bold solid line is the selected model output and dashed lines above and below represents the upper and lower 95% confidence bands. Bars represent standard deviation of the mean.



Fig.2: Temperature dependent mortality rate of immature life stages of *S. litura*. (a) Egg(b) Larva; Wang 8 and (c)Pupa; Wang 7. Fitted curves: Non-linear model for all immature stages. The upper and lower 95% confidence intervals of the model are indicated.

linear at 35°C temperature. The cumulative frequencies of development times of each life stage and temperatures were plotted against normalized development times by fitting a linear binomial distribution curve for immature stages and adult stages of *S. litura*. Decrease in immature development

time from low to high temperatures till 33°C was noted. The observed mean development times for all the immature life stages were fastest at 33°C (Egg: 2 ± 0.13 ; Larva: 13 ± 0.24 ; Pupa: 8 ± 0.26), and lowest at 15°C (Egg: 12.0 ± 0.51 ; Larva: 51.0 ± 0.65 ; Pupa: 36.0 ± 1.19).



Fig.3: Change in abundance and damage potential of *S. litura* in groundnut production areas of India based on activity index (AI) for (a) current (b) future climatic conditions and (c) difference between the current and future climatic conditions.

Among various abitoic factors that influence insect pests, temperature plays a vital role on different life history traits; including development time, longevity and fecundity. Thus, reduction of longevity or duration of an insect with increase in temperature occurs due to the accelerated use of energy (Tommaso et al., 2007) and similar trend of reduction of duration was observed in our study. The developmental durations of S. litura immature stages observed at different constant temperatures were in conformity with earlier reports of Fand et al.(2014) and Srinivasa Rao et al.(2014). The mean development time (days) of each stage and total life span decreased from 15°C to 33°C temperature. A similar decrease in development period with an increase in constant temperatures was reported in case of other lepidopteran insect pests such as Elasmopalpus lignosellus (Hardev et al., 2013) and S. litura (Srinivasa Rao et al., 2014). The life table parameters of lepidopteran insect pests are influenced by kind of host plant (Yasar and Güngör, 2005; Kumar et al., 2009) and quality of the diet (Jallow and Matsumara, 2001). The availability of quality host plant will play significant role in insect pest population dynamics by influencing the different life stages (Yasar and Gungor, 2005).

Effects of temperature on development rate

Inverse of durations of immature development and adult survival (1/days) were taken as rates of development and survival, respectively. Development rate as a function of temperature, increased monotonically for all the immature stages (egg, larva and pupa) until 33°C. For describing the temperature dependence of development rate of egg stage fourteen parameters version of the Sharpe and DeMichele was used (Sharpe and DeMichele, 1977) and Janish 2, function was fitted to larvae and pupa of *S.litura* at various constant temperatures. The thermal reaction norms were well fitted by the modified fourteen parameter version of Sharpe and DeMichele model as indicated by the smallest value of AIC (-16.0) and highest value of coefficient of determination (> 0.92) for egg stage, Janish 2 were well fitted for larvae and pupa with smallest value of AIC (Larva: AIC of -53.28; Pupa:AIC of -51.04)and highest valueof coefficient of determination(Larva: $R^2>0.91$; Pupa: $R^2>0.92$), respectively (Fig 1). The senescence rate for both the female and the male adults increased linearly from low to high temperatures. The modified fourteen parameter version of Sharpe and DeMichele model for male and female provided a good fit to the observed mean senescence rates for both the adult sexes.

Immature survival at constant temperatures

The temperature dependent mortality rates for egg and larva of *S. litura* were well fitted by the Wang 8 model as indicated by the smallest value of AIC (Egg: < -14.3; Larva: < -21.6) and highest value of coefficient of determination (Egg:>0.97; Larva:>0.96) respectively and for pupal stage of *S. litura*, Wang 7 model were well fitted as indicated by the smallest value of AIC(Egg: < -7.4) and highest value of coefficient of determination(Egg :> 0.95). The optimum temperature for survival of immature life stages of *S. litura* within the range of 25 to 33 °C (>70% survival of all the immature stages). Temperature significantly influenced immature survival in *S. litura*. At constant temperature of 15°C, the egg and larval survival ranged between 18-23%, whereas only 5.0% of the pupae could survive to become adults at this low temperature. The survival rates of *S. litura* immature stages varied significantly at various constant temperatures. The constant temperatures below 20°C and above 33°C were highly unfavourable for survival of all the immature life stages, where increased mortality rates were observed. In the present study, we could obtain highest percentage of survival (65.0%) in *S. litura* larva when reared at constant temperature of 30°C in laboratory. Manimanjari *et al.* (2014) reported the similar trend in survivorship of *S. litura* wherein they found lowest and highest survival at 20°C and 30°C temperatures, respectively when reared on sunflower. Further, the survival rates of immature stages of *S. litura* are highly dependent on host plants used for larval feeding (Xue *et al.*, 2010).

Temperature dependent reproduction

The temperature influenced significantly the reproductive traits in *S. litura*. Eggs were produced by females from temperature regimes between 15-35°C, with the minimum number of total eggs per female at 15°C (116.3) and peak egg laying at 27°C (1701.1) in their gonotrophic cycle. Egg laying was lowest at 15°C decreased with increase in temperature after 30°C, indicating the unsuitability of temperatures below and above this range for its oviposition.

A linear response was observed for fecundity with a maximum at 27°C and decreasing at lower temperatures. This demonstrates that prevalence of optimum temperature can play a bigger role in determining the suitability of climate for the mating and oviposition of *S. litura* adults. Fairly similar trend in temperature dependent fecundity of *S. litura* was reported by earlier workers, who found temperatures between 25-30°C as suitable range for *S. litura* reproduction, and temperatures >33°C were highly detrimental (Manimanjari *et al.*, 2014). Accordingly, a significant effect of temperature on mean total fecundity was identified by fitting Taylor 2 model.

The relationship between cumulative oviposition rate and female age was well described by the Gamma function. This study presents only the effect of temperature on *S. litura* fecundity on groundnut. However, fecundity is also influenced by several other factors such as host nutritional quality, food availability, nutrition of immature stages, and abiotic factors like light intensity, relative humidity, etc. (Garad *et al.*, 1984; Shahout *et al.*, 2011; Patil *et al.*, 2014).

Life table parameters at constant temperature

Finite (w) and intrinsic rates of increase (r_m) , net reproductive rate (R_a) , mean generation time (T) and doubling

time (DT) of S. litura varied significantly with temperature and were found to have quadratic relationship with temperature (Table 2). Finite rate of increase (») which is the indicator of reproductive value of new egg was highest at 30°C and thereafter showed a negative relationship with temperature. The intrinsic rate of increase (rm), and finite rate of increase (») increased with increase in temperature from 15°C to 30°C and decreased with increase in temperature. Intrinsic rate of increase (rm), varied from 0.05 females/female/day at 15°C to 0.17 females/female/day at 30°C. The findings of study are in agreement with Tuan et al., (2013) who reported 'r_m' values of S. litura in the range of 0.13-0.18 on groundnut. An increase in mortality with decrease or increase in temperature indicates the non-linear relationship. The suitable range for S. litura reproduction was observed between 25-30°C.S. litura population attained a maximum net reproductive rate 'R_a' (334.09 females/female/generation) and total fecundity (1041.88 individuals/ female/generation) at 27°C temperature. After that the net reproductive rate and gross reproductive ratedecreased with increase in temperature; at higher temperatures less fecundity was recorded. Similar finding were also reported by Guang et al., (2000).

Intrinsic rate of increase (r_{i}) and finite rate of increase (») were maximum at 30°C with values of 0.17 ± 0.002 and 1.18 ± 0.003 , respectively. Discrepancies occurred between r_m and Ro (r_m is a function of Ro) predicted from this study and those reported in literature. It seems that these discrepancies are largely due to the deviations from the selected sub-model for development and mortality of immature stages and total fecundity per female, which are considered to be the most variable factors (Sporleder et al., 2004). Besides, host material i.e. groundnut leaves used in rearing S. litura adds further to the variability in life cycle (Xue et al., 2010; Fand et al., 2014). Values estimated for 'T' indicate that the mean length of generations decreased from 73.23 days at 15°C temperature to minimum of 27.74 days at 33°Cand shortest doubling time was observed at $33^{\circ}C(5.19\pm0.05 \text{ days})$. Fitting of a polynomial model to the estimated life table parameters predicted temperatures between 27-33°C as a favourable range for S. litura development, survival and reproduction, where high reproductive potential and shorter generation length were observed. From our findings it is understood that the 'r_m' and '»' increased with increase in temperature from 15°C and later started declining from 33°C with increase in temperature. The 'r_m' gradually increases with temperature until some threshold, after which it decreases abruptly. Decrease of development time with increase in temperature causes increase in ' r_m ' with temperature as reported by Iranipour (2010) and sugar cane pest *Elasmopalpus linosellus* (Hardev *et al.*, 2013).

The present results revealed that the association between temperature and life table parameters was nonlinear relation. Many empirical models by incorporating ' r_m ' as a key parameter were used for prediction of population dynamics of insect pests. Similar approach of using laboratory measurements of temperature was adopted by Tshiala *et al.* (2012) to model the empirical relationship between life table parameters and temperature and assessed the impact of climate change on leaf miner. Temperature driven phenology models developed using laboratory information can be used for projection of status of future insect population (Vincent *et al.*, 1997). The present study aimed to quantify the relationship between life table parameters and temperature and further used for predicting the pest population under present and future climate change scenarios.

Validation of phenology model at fluctuating temperatures

The range of diurnal temperature fluctuations used in generating life table data for *S. litura* extended between 21.7-30.2°C with a mean temperature of 25.5 ± 0.4 °C. Validation of the phenology model was conducted by comparing modeling results with experimental one-cycle life-table data obtained from fluctuating temperature studies.

Estimation of pest risk indices

Simulated life table parameters were used to determine indices such as the establishment risk index (ERI), the generation index (GI), and activity index (AI) by using the 'Population distribution and risk mapping' module of ILCYM software. The ERI index characterizes geographical areas by their capacity to assure S. litura survival. The maximum value of ERI is 1, means that all the immature stages are able to survive throughout the year at varied proportions. The likelihood of survival and establishment reduces considerably for the areas deviating from this ERI maximum. Similarly, GI is an estimate of the mean number of generations that a given insect pest can produce within a year. At high temperatures, the generation duration decreases meaning more generations per year and an increment of population gross number (Tonnang et al., 2013; Fand et al., 2015). The average number of generations that S. litura population can complete in a year under the current (2000) and the future (2050) climatic conditions are determined using the third module of ILCYM. The results indicated significant increase in activity index and establishment risk index at future (2050) climatic conditions compared to current climatic conditions (Fig 3). There is increase in the average number of generations of *S*. *litura* population under future (2050) climatic conditions compared to the current (2000) climatic conditions.

According to the model predictions, under the current climate conditions S. litura can produce maximum of 10-12 generations per year in India. An additional two mean number of generations produced per year by S. litura under the future climatic conditions (2050 scenario) in India. These findings greatly support our predictions on S. litura number of generations per year under both current and future climatic scenarios. Every increase in GI by a value of 1.0 indicates completion of an additional generation per year and thus increases in the abundance and the damage potential of S. litura. The relationship between aspects of an insect life-history (development, survival, reproduction, etc.) and environmental variables (temperature) can be well described by process-based phenology models. These models can be used to identify environments where insects might persist and are realistic and preferable tools to predict the risks of establishment and population growth potential of insects' species. These index values will act as potential indicators to understand the distribution and abundance of insect pest. The present results indicate that temperature is vital in influencing the growth and life table parameters of S. litura and that pest incidence is likely to be higher in the future.

CONCLUSION

This study indicated that the growth and development of S. litura are significantly influenced by temperature. Both lower and higher temperatures limited the survival and development of insect pest and the ideal condition for the growth of the pest is at 27°C temperature, while the development rate increases with temperature upto 33°C. However the life table parameters are sensitive to temperature which is major factor of climate change. In the present study pest risk indices are simulated using the pests' process-based phenology model that describes the basic physiological principals of insect species' growth, i.e. its development, survival and reproduction. The model discussed here might be used as a tool for specific pest risk assessments and for improving pest management strategies for S. litura. Furthermore, all other possible sources of uncertainty (e.g. predictions of climate change, future host plant distribution,

etc.) in making the predictions on *S. litura* distribution, abundance and its response to future climatic changes warrant more detailed insights into the abiotic and biotic factors that impact the species population growth and spatiotemporal abundance.

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