Spodoptera eridania: Current and emerging crop threats from another invasive, pesticide-resistant moth

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With 5 figures and 1 table

Abstract: *Spodoptera eridania* (Stoll), a polyphagous lepidopteran pest from the Americas, has recently invaded western and central Africa. Like its congeners, *S. eridania* has developed pesticide resistance. The rapid global spread and impacts of *Spodoptera frugiperda* (J.E. Smith) has raised concerns about whether *S. eridania* is set to do the same. Here we fit a CLIMEX niche model for *S. eridania* and apply a climate change scenario for 2050 to investigate the sensitivity of the pest threat. We find that *S. eridania* can potentially expand its range throughout the tropics and into the sub-tropics, threatening a range of important commercial and subsistence crops. An important feature of the pest threat posed by *S. eridania* is the extent of its ephemeral habitat during warmer months. Modelled climatic changes will mostly expand this species potential range poleward by around 200 km by 2050, indicating a moderate sensitivity. These areas of emerging potential expansion are mostly into subtropical climates, supporting diverse cropping systems, including at risk crops beans, groundnut, potato, soybeans, tomato and sweet potato. The potential distribution of *S. eridania* in the Amazon basin and the southern boundary of the Sahara Desert appear set to contract substantially due to increasing heat stress. While it may not be as invasive as some of its congeners, nor acquire pesticide resistance as readily, *S. eridania* does have some of these traits, and the current and emerging pest threat posed by this moth deserves closer attention, especially in relation to intercontinental phytosanitary measures to slow its spread.

Keywords: Biosecurity, climate change, CLIMEX, invasive species, Noctuidae, southern armyworm

1 Introduction

Widespread mega-pests including noctuid moths such as *Helicoverpa armigera* (Kriticos et al. 2015b) and species of *Spodoptera* (Yonow et al. 2018, Du Plessis et al. 2019) are threatening global food security, and their spread appears largely human-mediated, in association with trade in goods (Tay & Gordon 2019). The genus *Spodoptera* includes many notorious agricultural pests such as fall armyworm *S. frugiperda* J.E. Smith, 1797, beet armyworm *S. exigua* Hübner, 1808, and tobacco cutworm *Spodoptera litura* (Fabricius, 1775). *Spodoptera frugiperda* has recently become a global invader, spreading throughout Africa and Asia in only two years, and arriving in Australia in 2020 (IPPC 2021). These highly polyphagous moths threaten a wide variety of crop species, are highly mobile, and have demonstrated the ability to readily develop resistance to many popular pesticides (Yainna et al. 2021).

The southern armyworm, *S. eridania* (Stoll, 1781) appears to be joining the ranks of several of its congeners as a significant invasive pest. In recent years, *S. eridania* has become a significant pest of cotton and soybean in Brazil (Montezano et al. 2014), though it is unclear what has driven this change. *Spodoptera eridania* has been recorded as an

invasive insect when it spread to western Africa (Goergen 2018), and it has been listed as an A1 quarantine pest for Europe (Bragard et al. 2020).

Spodoptera eridania, like its congeners, is highly polyphagous and feeds on both vegetative and reproductive stages of attacked crops (Montezano et al. 2014). It can survive on around 200 different host plants, and some of the most affected crops include alfalfa, soybean, sweet potato, and tomato (CABI 2021). It poses a serious threat to both commercial horticultural (tomato) and field crop (soybean) production, as well as subsistence farming (sweet potato). *Spodoptera eridania* is native to central and north America. It is a strong flyer, expanding its range poleward during the warmer months, contracting its range to the sub-tropics during the colder months. In the USA, this ephemeral habitat extends from South Carolina up to Massachusetts on the eastern seaboard and Southern Ontario in Canada, though most of the summer observations have been limited to 36.5°N. While it is a strong flyer, *S. eridania*'s dynamic range may not be as widespread as *S. frugiperda*. In South America it is mostly regarded as an outbreak pest on soybean, though in Cerrado State and southern Brazil it is regarded as the most important pest of soybeans (Luz et al. 2019, de Sousa et al. 2019, Machado et al. 2020).

Spodoptera eridania has developed an extremely high tolerance to the popular *Bacillus thuringiensis* protein Cry1Ac (Bernadi 2014). In some cases, *S. eridania* may even increase larval growth when feeding on genetically modified plants that express this protein alone. So far, transgenic soybean plants that express both Cry1A and Cry1F proteins appear effective in suppressing *S. eridania* (Machado et al. 2020). If *S. eridania* follows the pattern observed in *S. frugiperda* and *S. litura* it is likely to acquire further pesticide resistance as it expands its range into regions where poor pest management practices are prevalent and it is subject to strong selection pressure. Thus, as it invades it may become even more difficult to control.

Knowing the potential distribution of an invasive pest can assist in planning and implementing a range of biosecurity risk mitigation and preparedness activities such as invasion pathway attenuation, targeted surveillance, pesticide registration, development of resistant crop germplasm and even preemptive testing and approval of biological control agents (Charles et al. 2019). Bioclimatic models are frequently used to estimate the potential distribution of invasive pests to support pest risk assessments (Venette et al. 2010). As species invade new regions and continents, they tend to expand their range to fill their climatic niche. One effect of climatic changes is to shift where the climatic boundaries lie. It is therefore prudent when formulating biosecurity strategies to consider the influence of likely anthropogenic climate changes on the potential distribution of the pest.

In this paper we use CLIMEX (Hearne Scientific Software, Melbourne; Sutherst & Maywald 1985, Kriticos et al. 2015a) to model the global potential distribution of *S. eridania* under recent historical climatic conditions, considering the effects of irrigation in extending the range of its hosts. We then overlaid the known distribution of the major crop hosts to highlight the threats posed by this invasive moth in each continent, providing advanced warning so that biosecurity preparedness activities can be undertaken prior to the arrival of the moth. Finally, we apply a set of "business as usual" climate change scenarios for later this century to assess whether the threats are likely to change materially because of projected global climatic changes.

2   Methods

2.1   Modeling package

The Compare Locations model in CLIMEX V4.1 (www.hearne.software, Sutherst & Maywald 1985, Kriticos et al. 2015a) was used to fit a niche model for *S. eridania*. This system allows the modeler to adjust parameters describing the species responses to temperature and soil moisture. Trapezoidal temperature and soil moisture response functions accord with the ecological Law of Tolerance, and are combined multiplicatively in accord with the ecological Law of the Minimum.

2.2   Climate Data

We used the CliMond CM30 World (1995H V2.0) climate dataset to fit models under a natural rainfall scenario (Kriticos et al. 2012). This global dataset consists of 30-year averages centered on 1995 for daily minimum and maximum temperatures, monthly rainfall totals, and relative humidity (at 09:00 and 15:00 h), at a spatial resolution of 30 arc minutes. We use a future climate scenario for the average 20-year period centered on 2050. We use the results from a single climate model (Australian Community Climate and Earth-System Simulator, ACCESS 1.0) forced with the RCP 8.5 emission scenario. This scenario is variously labeled as extreme (Hausfather & Peters 2020) or business-as-usual (BAU) (IPCC 2014). In choosing this scenario we aim to highlight the direction of changes in climate suitability, recognizing that this will have substantial uncertainties in the magnitude and rate of the changes expected by 2050. Our intention here is not to predict changes, but rather to inform risk assessments and adaptive management of cropping and pest management.

2.3   Species distribution data

The distribution data of *S. eridania* was compiled from a variety of sources. Distribution data for the Americas was taken from the GBIF website (GBIF.org 2020). Additional records were assembled from the iNaturalist (www.inaturalist.org/) and Symbiota Collections of Arthropods Network (SCAN) (www.scan-bugs.org) websites. For Africa, co-ordinates of four distribution records in Western and Central Africa from Goergen (2018) were estimated using Google Earth. Records

in Cameroon originate from a field survey conducted from November to December 2019 in the southern part of the country (Fagbohoun, unpub. data).

2.4   Host distribution

The major crop hosts of *S. eridania* were identified by intersecting the major hosts listed in the CABI Invasive Species Compendium with those available in the Mapspam dataset (You et al. 2006). This resulted in a list of eight crops including both commercially important species and those of importance for subsistence agriculture (beans, cotton, cowpea, groundnut, potato, sweet potato, soybean, and tobacco). Unfortunately, spatial production maps for tomatoes are not presently available in the MapSpam dataset. The distribution of the production areas for the major crops was overlain upon the climate suitability maps to understand the nature of the pest threat patterns from *S. eridania* posed to different production areas.

2.5   Model fitting

We chose the CLIMEX model for *S. frugiperda* reported in Du Plessis et al. (2018) as a starting point for hand-fitting a CLIMEX Compare Locations model. The distribution data in North America and scientific literature were used to fit the model. A critical issue with the distribution data was the interpretation of the poleward range boundary. Two citizen science platforms (iNaturalist and SCAN) were used to estimate the overwintering geographical boundary, using time-stamped and geocoded records. This process is described in full in the Supplementary Material.

Mitchell & Tumlinson (1994) report the results of a pheromone lure survey in Alachua County, northern Florida, moderately close to the northern range boundary for *S. eridania* persistence. The seasonal and interannual variation in temperature and rainfall in this location during this period provided an opportunity to fine-tune several parameters, based on the relationship between the trap catches and the climate experienced. The CLIMEX Compare Locations/ Years model was used to compare the model results with these field reports using concurrent weather data.

The model-fitting procedure follows those described in Kriticos et al. (2015a). The stress parameters were mostly fitted to the distribution data, and the Growth Index parameters were informed by laboratory experiments and the phenological observations of Mitchell & Tumlinson (1994). The distribution data in Africa were reserved from model-fitting so as to be used to validate the model. The fitted parameters are detailed in Table 1.

2.6   Stresses

2.6.1   Cold stress

The cold stress parameters were fitted to the estimated overwintering limit in the southern USA. Mitchell & Tumlinson

Table 1. CLIMEX parameter values for *Spodoptera eridania* (see text for details of sources).

Parameter	Description	Parameter values
Moisture		
SM0	Lower soil moisture threshold	0.1
SM1	Lower optimum soil moisture	0.5
SM2	Upper optimum soil moisture	1
SM3	Upper soil moisture threshold	1.75
Temperature		
DV0	Lower threshold	12 °C
DV1	Lower optimum temperature	23 °C
DV2	Upper optimum temperature	27 °C
DV3	Upper threshold	35 °C
Cold Stress		
TTCS	Cold stress temperature threshold	2 °C
THCS	Temperature threshold stress accumulation rate	0.1
DTCS	Degree-day stress cold stress threshold*	20 °C day
DHCS	Degree-day stress cold stress accumulation rate	-0.001 week^{-1}
Heat Stress		
TTHS	Heat stress temperature threshold	35 °C
THHS	Temperature threshold stress accumulation rate	0.005 week^{-1}
Dry Stress		
SMDS	Soil moisture dry stress threshold	0.1
HDS	Stress accumulation rate	-0.005 week^{-1}
Wet Stress		
SMWS	Soil moisture wet stress threshold	1.75
HWS	Stress accumulation rate	0.002 week^{-1}
Threshold Heat Sum		
PDD	Number of degree-days above DV0 needed to complete one generation	380 °C Day
Irrigation Scenario	2.5 mm day^{-1} as top-up throughout the year	

*CS accumulates if there are fewer than the threshold number of degree-days above DV0 experienced in the week.

(1994) notes that adult *S. eridania* can withstand several days with minimum temperatures falling below freezing, though prolonged temperatures below 10 °C and frosts that kill host plants appear to limit the northern range in the USA. During December of 1989 and early January of 1990, there were three days of continuous sub-freezing temperatures during which there were zero trap captures in Alachua County, Florida (Mitchell & Tumlinson 1994). It was unclear

whether subsequent trap catches in January 1990 arose from *S. eridania* overwintering as pupae, or were migrants from warmer, more southerly populations. We believe that the latter explanation is more plausible because temperatures would not have risen sufficiently above the development threshold (12 °C) for pupae to complete development. In contrast, the winter of 1989-90 was milder, and *S. eridania* adults were trapped during December and January.

CLIMEX can simulate a range of different cold stress mechanisms. As suggested in Mitchell & Tumlinson (1994), *S. eridania* appears to be limited by both low temperatures (frosts) that kill host plants, and by the lack of degree days above their activity threshold. A long-term monthly average for a daily minimum temperature of 2 °C equates to one or two days of frost each week. To simulate the frost limit, we use this value for the threshold temperature for lethal cold stress accumulation (TTCS) and fit the stress accumulation rate (THCS) at the assumed northern boundary. See the Supplementary information for details on how the northern limit for establishment of *S. eridania* was estimated. The second limit mentioned in Mitchell & Tumlinson (1994) regards the need for species to meet basal metabolic needs. If a species does not experience sufficient heat during the middle of the day, it cannot acquire sufficient metabolic resources to meet this need. In this case we fitted the threshold (DTCS) and accumulation rate (DHCS) parameters to the same estimated range limit in the USA. In our model, if *S. eridania* does not experience a minimum of 20 °C days per week above DV0, then stress starts accumulating at a rate of 0.001 week^{-1}.

2.6.2   Heat stress
The temperature threshold for heat stress (TTHS) was set to 35 °C in accord with the maximum temperature limit for development (Sampaio et al. 2021). The stress accumulation rate (THHS) was set to a moderate level of 0.005 week^{-1}. This combination of parameters limited the range in the west of Texas and on the border of Texas and Mexico, making the location records at those sites marginally suitable (1<EI <5) due to heat stress.

2.6.3   Wet stress
Mitchell & Tumlinson (1994) noted that for January through July 1991, rainfall in Gainesville was above average, and surmised that the "…torrential rains that often occurred during this period possibly helped keep the armyworm populations low, by destroying young larvae soon after they hatched, and also by increasing the level of natural control via disease organisms". To translate this into CLIMEX terms, we ran the Compare Locations/Years model and adjusted the Wet Stress threshold downwards to 1.75 to achieve a moderate reduction in suitability in this part of Florida during this period.

2.6.4   Dry stress
The threshold soil moisture level (SMDS) was set to 0.1 to reflect host plant stress as soil moisture fell below the permanent wilting point. The dry stress accumulation rate (HDS) was adjusted to barely allow persistence at the driest known distribution locations in the southwestern USA.

2.7   Growth Indices

2.7.1   Temperature Index
In accordance with Mitchell & Tumlinson (1994), the lower temperature threshold for development (DV0) was set to 12 °C. Foerster & Dionizio (1989) found that 17 °C and 30 °C were suboptimal for *S. eridania* development. The lower optimal temperature (DV1) was set to 23 °C, and the upper optimal threshold (DV2) was set to 27 °C. The upper temperature for development (DV3) was set to 35 °C, in accord with the estimated upper limit for development (Sampaio et al. 2021). Although eggs failed to hatch at 35 °C (Sampaio et al. 2021), this was under constant temperature conditions, and likely does not closely reflect survival under fluctuating temperature conditions.

2.7.2   Moisture Index
The plant hosts of *S. eridania* are relatively shallow-rooted herbs and shrubs that are susceptible to drought and waterlogging. Accordingly, SM0 was set to 0.1 to accord with the permanent wilting point, and SM2 was set to 1.0 to accord with field capacity. SM1 was set to 0.5 as an intermediate value. Based on the observations of Mitchell & Tumlinson (1994) and the model fitting for SMWS described above, SM3 was adjusted to 1.75.

2.8   Minimum Annual Heat Sum
Mitchell & Tumlinson (1994) indicates that 30 to 40 days are required for *S. eridania* to complete a generation. In the model, we fitted the minimum annual heat sum required to complete a generation (PDD) as 487 °C days above a base temperature of 12 °C (Sampaio et al. 2021).

2.9   Migration distances
To estimate *S. eridania*'s spatial pattern of seasonal dispersal, the distribution data in the USA from the GBIF, iNaturalist and SCAN datasets was used to assess the minimum distance from each point outside the area modelled as climatically suitable for population persistence. To reduce biases, records with the same geographical coordinates were removed, leaving 80 records in the sample. The distances were used to create a histogram and to estimate a series of quantile distances. These critical distances were used to buffer the area that was modelled as suitable for establishment (EI > 0) and 75th and 100th quantile zones were added to the maps to indicate the areas that may be accessible for migrat-

ing populations and may be suitable, at least under average climate conditions.

2.10 Climate suitability under historical and future climates

The current potential distribution was estimated by a composite natural rainfall and irrigation scenario. The global map of irrigated areas (GMIA, Siebert et al. 2013) is used to define where the irrigated scenario is applied. The method for creating the composite climate suitability map is described in Yonow et al. (2019). By overlaying the current known distribution of major crop hosts we can appreciate the invasion risks in the near term. A climate change scenario is explored using the ACCESS 1.0 RCP 8.5 future climate scenario dataset. We acknowledge the extreme uncertainty associated with projecting future climates, most of which is due to uncertainties in the pattern of emission of greenhouse gases through time. Our intention here is not to predict the future potential distribution, but rather to indicate the areas of sensitivity that biosecurity managers and agricultural producers should be aware of in the short to medium term. To assist in this task, we produce change maps between the 1995 and 2050 scenarios.

3 Results

The CLIMEX model of *S. eridania* under historical climate indicates the potential for substantial further spread throughout the tropics and sub-tropics, beyond Africa to Asia and Australia (Fig. 1). The suitability patterns have two main components, areas suitable for persistent occupation (coloured orange-red), and those only suitable for ephemeral occupation during the favourable season (shades of green). The dynamically suitable areas are quite extensive in the northern hemisphere (Fig. 1).

Considering the observed dynamics in North America, we might presume that in most years a zone of approximately 250 km into adjacent ephemeral climate suitability habitat may be accessible in most years; although the record in Ontario suggests seasonal range expansions of more than 1 300 km may be possible (Fig. 2).

Under the historical climate scenario, the modelled potential distribution of *S. eridania* in the USA closely matches the known range dynamics. In the southern part of the USA, populations can persist year-round, as indicated by a positive value for EI (Histogram in Fig. 2). North of a diagonal line from central Texas (lat 31°N) to South Carolina (33°N), our model supports the observations that *S. eridania* expands its range northwards each year during the warmer months. During winter, the range contracts southwards, likely involving southwards migration as observed with *S. frugiperda* (Krauel et al. 2015). Occasionally, *S. eridania* has been detected as far north as southern Ontario in Canada. The model accurately reflects these seasonal range dynamics with a positive annual growth index GI_A with more than one potential generation extending into northern Canada (Histogram in Fig. 2). Irrigation increases the modelled
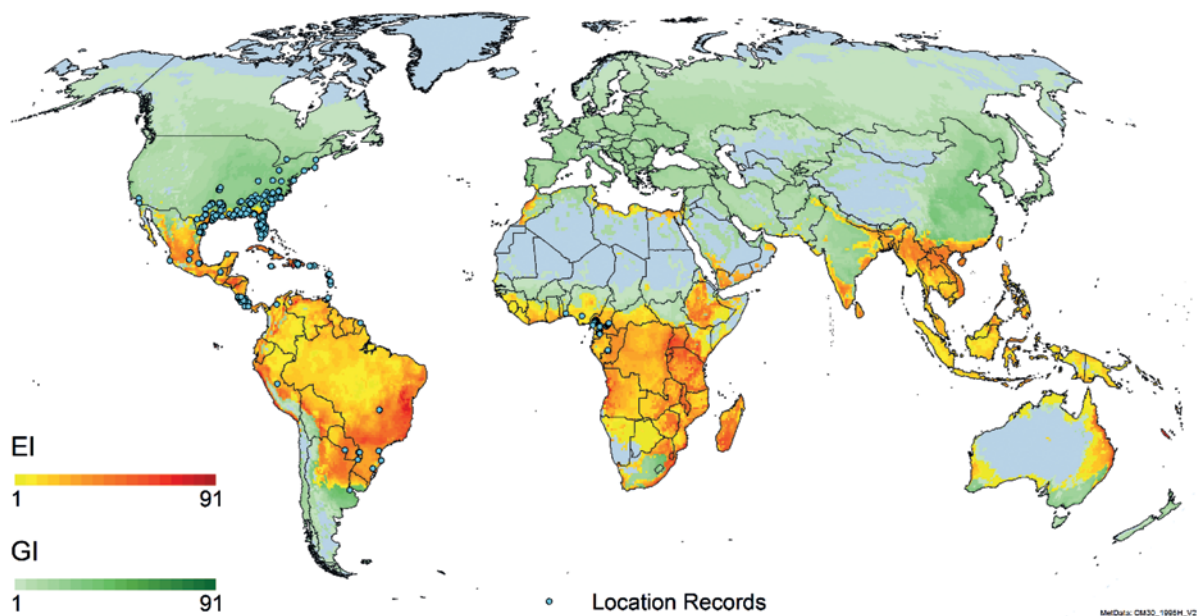

Fig. 1. Known global distribution and climatic suitability for *Spodoptera eridania* modelled using CLIMEX run with CM30_1995H climate data and a composite irrigation scenario (2.5 mm day^{-1} applied as top-up). Source of distribution data: GBIF, Goergen (2018) and (GG, JRF and GT-Y unpublished data).
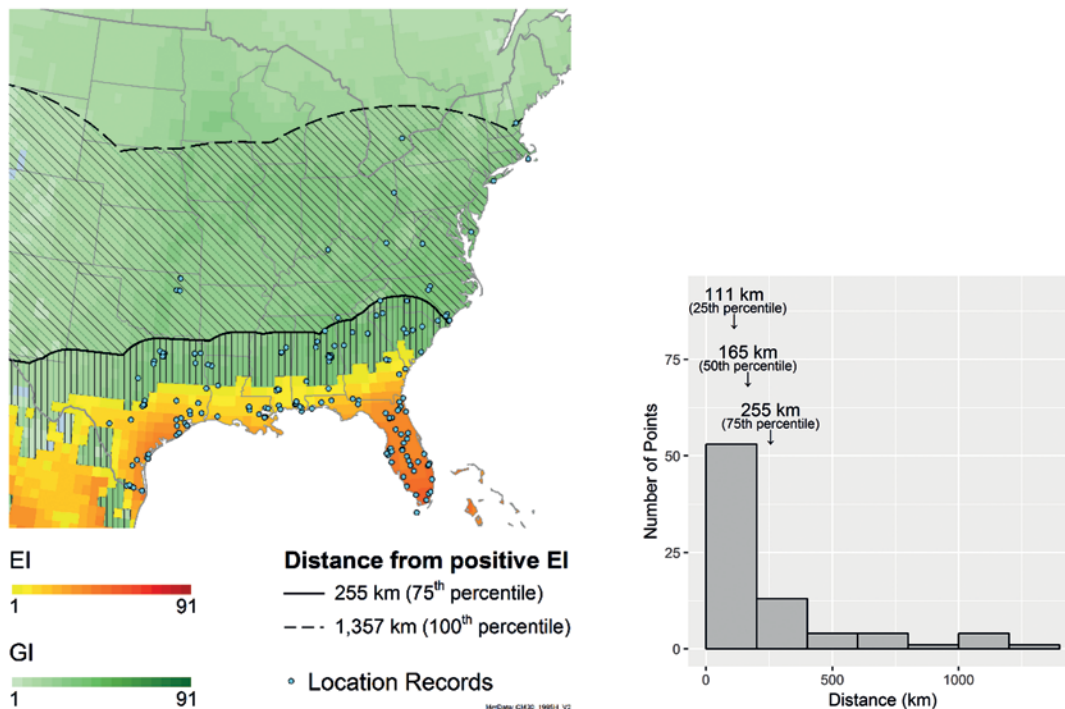
Fig. 2. Known distribution and climatic suitability for *Spodoptera eridania* in North America modelled using CLIMEX run with CM30_1995H climate data and a composite irrigation scenario (2.5 mm day-1 applied as top-up). Dispersal frequency zones are indicated using cross-hatching. Vertical hatching indicates the buffer zone where 75% of observed US records fell adjacent to the area modelled as suitable for persistence. Diagonal hatching indicates the zone that includes the maximum observed dispersal distance from the area modelled as suitable. Source of distribution data: GBIF, iNaturalist and SCAN. Histogram of distances of observed records of *Spodoptera eridania* in North America from areas modelled as suitable for persistence (Ecoclimatic Index > 0). Source of distribution data: GBIF, iNaturalist and SCAN.

potential range of *S. eridania* in Mexico and the south-western USA.

In Africa, the modelled potential distribution extends throughout most of sub-Saharan Africa (Fig. 3). The few distribution data currently available from Africa are limited to West and Central Africa. These are all located in areas with moderate to high EI values and serve to validate the modelled distribution under current temperature scenario. Regions particularly at risk in the humid tropics are large parts of central and southern Ghana and Côte d'Ivoire. In southern Africa, coastal areas, (the littoral of central Angola and the coastal regions of KwaZulu-Natal, Republic of South Africa and Maputo, Mozambique), are highly suitable. Similarly, in East Africa, coastal regions bordering Tanzania and Kenya with extensions up to southern Somalia appear suitable for *S. eridania* to establish. Within the main continent, almost all of Uganda and large parts of Democratic Republic of Congo appear highly suitable. In the north of Africa there is a narrow peri-coastal band that appears suitable for *S. eridania* persistence. The southern periphery of the Sahara Desert is suitable for *S. eridania* population growth only during the wet season.

The effect of irrigation in altering habitat suitability is most clearly apparent in the Nile valley corridor in Egypt and Sudan, snaking across the otherwise inhospitable Sahara Desert (Fig. 3). Here the suitability is ephemeral in the slightly cooler season in the southern portion of this area, with potential for high suitability and persistence in the northern Nile delta. According to the GMIA, there are other irrigated patches sprinkled throughout the Sahara Desert. In Saudi Arabia, pivot irrigation in the desert areas could provide suitable habitat for *S. eridania*.

In Europe, the threat from *S. eridania* is likely to be mostly ephemeral to southern Europe from populations in northern Africa and the Middle East should it become established there (Fig. 3). While the potential exists for the spread of *S. eridania* from sub-Saharan Africa to these northern African and the Middle Eastern beachhead locations, perhaps by the movement of goods, there is also the potential for natural spread along the Nile Valley and in Yemen and Saudi Arabia.

Spodoptera eridania can likely become established widely throughout tropical Asia (Figs. 3, S3). In the drier inland parts of India it could become a seasonal threat dur-
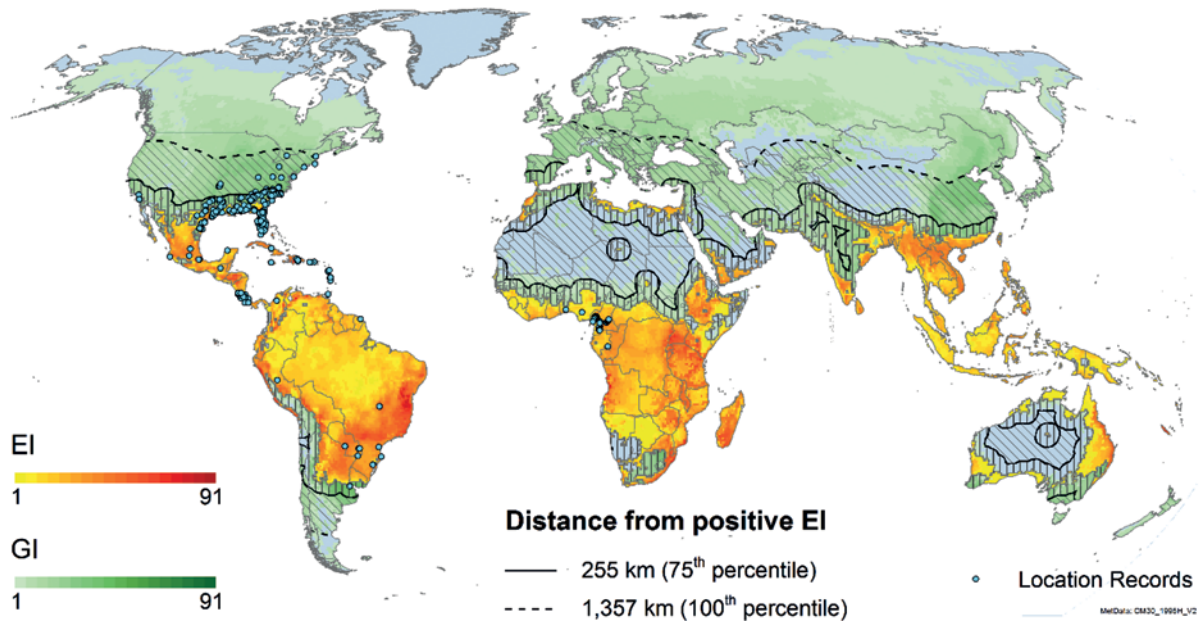
Fig. 3. Known distribution and climatic suitability for *Spodoptera eridania* in the world modelled using CLIMEX run with CM30_1995H climate data and a composite irrigation scenario (2.5 mm day-1 applied as top-up). Dispersal frequency zones are indicated using cross-hatching. Vertical hatching indicates the buffer zone where 75% of observed US records fell adjacent to the area modelled as suitable for persistence. Diagonal hatching indicates the zone that includes the maximum observed dispersal distance from the area modelled as suitable. Source of distribution data: Goergen (2018) and (GG, JRF and GT-Y, unpublished data).

ing the wetter periods of the year. In China it could become established in the south and migrate northwards during the warmer months to take advantage of the summer crops. While the seasonal threats are mostly restricted to the mid-latitudes (Zhejiang province), we might expect occasional incursions to extend as far north as Korea and Japan (Figs. 3, S3). The low-lying areas of Taiwan are likely highly suitable for *S. eridania*.

Under current climate, the risk posed to Australia by *S. eridania* is restricted mostly to the wetter exterior fringes of the continent (Fig. 3, S4). The warmer, generally more northerly areas appear suitable for *S. eridania* to establish. This risk area includes most of the cropping production zone. The southerly areas appear suitable for supporting ephemeral populations during the warmer months. The present threat to New Zealand is minimal. The climate is only suitable for supporting population growth during the warmer months. Because of its isolation from Australia and New Caledonia, the chance of regular natural migration is minimal.

Spodoptera eridania poses a substantial threat to crop production for all 8 species considered using the MapSPAM dataset (Fig. 4 for soybean, and Figs. S5 – S11 for the other 7 species). In the southern US, cotton and soybean are two high risk crops exposed to *S. eridania* populations annually. In the northern US cropping zone, soybeans, potatoes and beans are at risk from ephemeral populations. Much of South America, notably Brazil, experiences an optimal climate

for *S. eridania* where it threatens large-scale production of beans, cotton, soybean and tomato, and to a lesser extent sweet potato (Fig. 4, S5, S6 and S10).

In sub-Saharan Africa *S. eridania* threatens both commercial (beans, cotton, tobacco and tomato) and subsistence (groundnuts, cowpeas, sweet potato) crops (Figs. S5, S6, S7, S8, S10 and S11). In Europe, the threat scenario posed by *S. eridania* is mostly via ephemeral migration in warmer months into all eight crops, though there is a small area in southern Spain that can likely support an established population of *S. eridania* where bean, cotton, potato, sweet potato and tobacco are presently grown. Southern and south-eastern Asia experiences some of the most highly suitable climates for *S. eridania*, and all crops assessed here are at risk within the zone suitable for establishment. Most of the cropping zone in China (North of approximately 25°N) faces a threat from ephemeral populations of *S. eridania*. This area contains extensive plantings of all crops examined here except cowpea. Similarly, India faces an ephemeral threat pattern in its interior, where the dynamics are driven by rainfall. As with China, all crops examined here are threatened except for cowpea.

Under the 2050 future climate scenario, the changes of greatest interest are areas indicating the potential for range expansion, and a likely range contraction (Fig. 5). In the US, the potential for a moderate (~250 km) northward shift in the overwintering limits is indicated (Fig. 5). The slight con-
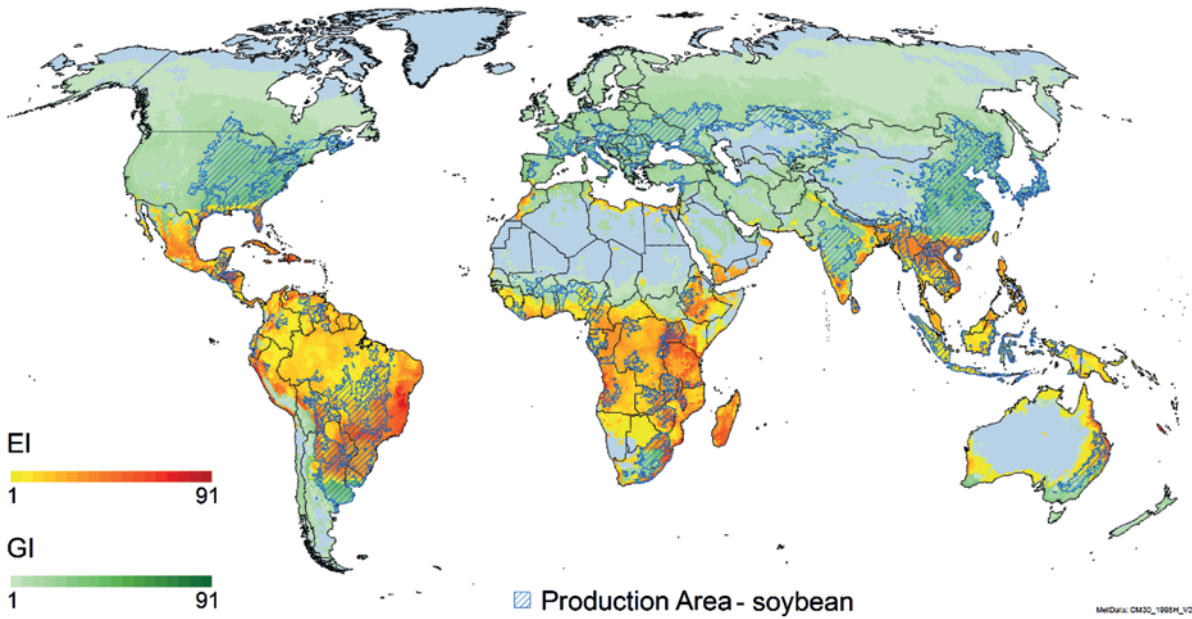
Fig. 4. Composite climate suitability for *Spodoptera eridania* in relation to production area of soybean, one of major crop hosts. Climate suitability modelled using CLIMEX **run with CM30_1995H climate data and a composite irrigation scenario (2.5 mm day-1 applied as top-up)**. Ecoclimatic Index (EI) indicates suitability for persistent populations, Growth Index (GI) indicates suitability for ephemeral populations. Cropping areas taken from MapSpam (You et al. 2006).
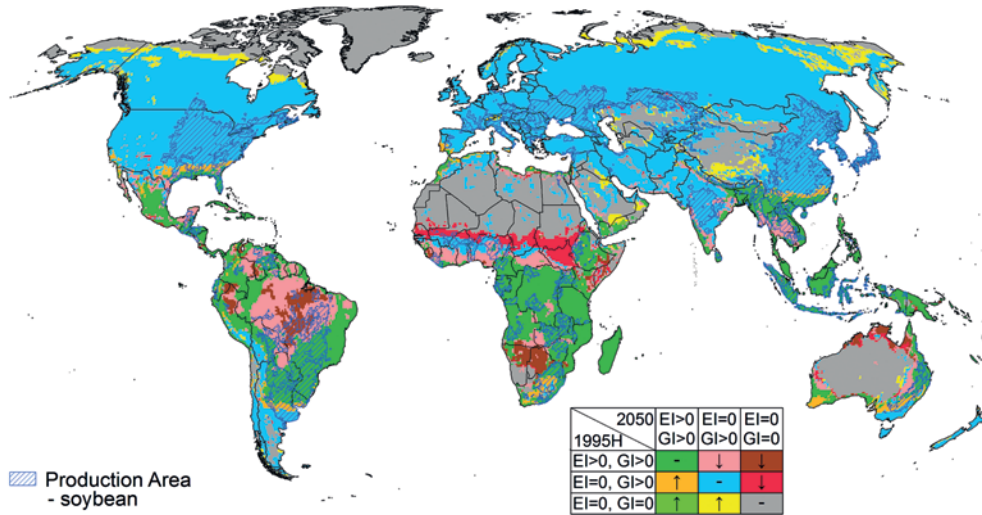

Fig. 5. Classified changes in global climate suitability for *Spodoptera eridania* modelled using CLIMEX comparing the 1995 historical climate suitability with that for 2050 under the RCP 8.5 scenario forcing the ACCESS 1.0 global climate model. The cropping area for soybean from the MapSPAM dataset is included (You et al. 2006). The symbols in the legend indicate the trend in climate suitability.

traction of the suitable range in the southern US indicates a shift from a climate that is suitable for persistence to an ephemeral climate. This feature is anomalous and is most likely due to noise in the future climate scenario. There is a small potential for the ephemeral range limits in Canada to be extended (yellow area in Fig. 5) though this is likely of

little consequence due to the shortness of the season and the paucity of cropping in this region due to skeletal soils.

On the global scale, the most apparent changes in suitability are a decreasing suitability and likely range contractions in South America (Amazonia), Africa on the southern border of the Sahara Desert and the horn of Africa (Somalia)

and the edges of the xeric interior of Australia (Fig. 5). There are apparent potential range increases in Argentina, South Africa, southern Australia and China, as well as small pockets around the Mediterranean Sea (Fig. 5). Northland in New Zealand may become marginally suitable for *S. eridania* to establish by the 2050s (Fig. 5, Fig. S22). If *S. eridana* were to become established in Northland it could easily migrate throughout the cropping zones in New Zealand during the warmer months.

4   Discussion

The CLIMEX model reflects the dynamic niche of *S. eridania* in its native range, distinguishing between the area where it can maintain populations throughout the year, and the region in which it can temporarily extend its range during favourable seasons. Surprisingly, for a pest species that impacts a wide variety of crops, the geographical overwintering limits of *S. eridania* have not been reported, and we were unable to find any experts who could give us a precise estimate of where that dynamic limit might lie. Fortunately, citizen science efforts to capture the presence of *S. eridania* throughout the year in mid-latitude locations in the USA provided a useful means of gauging the northern extent of the zone in which it is established. The *S. eridania* location records in South America all fall within areas modelled as being climatically suitable. The location records of *S. eridania* in Africa were reserved from model-fitting and provided a means of validating the model. All of these invaded range records fell within areas modelled as being climatically suitable. This concordance gives us some confidence in the model, though more extensive invaded range distribution data will be necessary to judge how robust the model is.

The potential distribution of *S. eridania* under historical climate conditions extends throughout the tropics and subtropics. We expect that its dynamic seasonal migration patterns in the Americas may be reflected elsewhere in the world, with tropical and subtropical areas that are suitable for establishment, surrounded by a buffer of areas that may only be suitable for temporary range expansion (Fig. 1). We have used the same seasonal buffer as was fitted to the North American distribution data but it is not clear to what extent the observed patterns in North America reflect biological and ecological characteristics of *S. eridania* or meteorological characteristics of the region where strong low-level jets may transport moths (and other lightweight organisms) over long-distances into higher latitudes (Drake 1985, Westbrook et al. 2019). Hence, the buffer distances should be considered as hypothetical guidelines to indicate the potentially accessible region within the ephemeral habitat zone. Any under-estimates may have relatively little consequence as the growing season in such high latitude areas would be very short and the number of generations very low.

Irrigation plays an important role in extending the potential distribution of *S. eridania* into xeric environments. Suitable host crops in these areas may be under threat from *S. eridania*, and provide a stepping-stone invasion route linking areas of suitable habitat. Visually, this is highly apparent in the Nile Valley and the Arabian Peninsula. Irrigation in these areas combined with moderate temperatures creates the warm, wet conditions favoured by many tropical and sub-tropical pests that would otherwise find these areas too dry, and lacking hosts. Considering the effects of irrigation in a spatially explicit manner allows these risks to be exposed. Ignoring the effect of irrigation has led some authors to misapply the CLIMEX model, fitting biologically inappropriate soil moisture parameters (e.g., Shabani & Kotey 2016), resulting in unreliable models with very poor specificity, with widespread desert areas being incorrectly modelled as being climatically suitable.

The future climate scenarios exhibit changes in suitability that accord with theoretical expectations, with poleward and altitudinal range expansions, and contractions from the warm end of its range. In North America, the likely poleward range extension under a warming climate is likely to see *S. eridania* become established in regions where all of the crops assessed here are grown, and the shifting base for seasonal migration means that it is likely to have even greater potential impact on the mid-latitude crop production belt in the USA. Much like the southern United States, the majority of Mexico is presently suitable for annual persistence of *S. eridania*, continuing into the 2050 scenario, though with a reduced EI due to decreased temperature suitability and increased heat stress. Hence, parts of southern Texas, northern Mexico and the southernmost tip of Mexico (Merida, Campeche, and Chetumal) may see a future range contraction if temperatures continue to rise beyond the 2050 scenario. Canada may see more frequent migrations of *S. eridania* in the south-eastern provinces, though the growing season remains short in the scenario we explored.

In South America, the most notable feature of the future climate scenario is that in northern Brazil there is likely to be a very large range contraction due to heat stress (Fig. 5). In Argentina and Uruguay, the modelling suggests that the area suitable for persistence is likely to expand polewards by approximately 200 km.

In Africa, it appears that *S. eridania* may be set to expand its range throughout sub-Saharan Africa. The area modelled as suitable for establishment includes all the agricultural production areas in sub-Saharan Africa. As the climate warms, much of western, eastern, and southern Africa are likely to decrease in suitability for *S. eridania* persistence. Along the southern border of the Sahara Desert, increasing dry stress may make this area unsuitable for even ephemeral occupation by *S. eridania* in the future. Unfortunately, this also reflects a grim scenario of deteriorating conditions for crop production in this area where irrigation is unavailable. In Central Africa, the climate remains suitable for *S. eridania*

under this future scenario, indicating that the pest risks are likely to persist. There is a wide variety of mostly subsistence crops being grown in Central Africa that are hosts for *S. eridania*, and they will face on-going pest pressure.

In South Africa, under the future climate scenario there is an increase in the potential range of *S. eridania* in the Highveld grasslands and eastern Karoo. The northern portion of this area of increasing suitability encompasses a great deal of the area presently growing most of the crops explored here, especially soybeans.

The potential for damage to African tomato production from *S. eridania* is significant as all of the top-15 tomato-producing countries in Africa (Arah et al. 2015) are modelled as having moderate to high climate suitability for this pest. It is unclear what the additive effects of *S. eridania* may be on crop pest management in areas already invaded by *Tuta absoluta*, which also favours tomatoes as a host (Desneux et al. 2010).

For *S. eridania,* the Sahara Desert separates the bulk of the climatically suitable region of sub-Saharan Africa from the small peri-coastal areas along the Mediterranean Sea and Atlantic Ocean that are climatically favourable for *S. eridania*. Apart from areas that are irrigated, the Sahara is largely unsuitable for supporting any population growth of *S. eridania*. Thus, the desert may form a hindrance to the natural wind-dispersed spread of *S. eridania* to the areas suitable for supporting persistent populations in North Africa. Based on the observed patterns of migration in North America, long-distance dispersal by *S. eridania* appears to be infrequent, and even with irrigation along the Nile River supporting seasonal populations of *S. eridania*, migration from sub-Saharan Africa to the Nile Delta seems unlikely. However, the movement of contaminated produce along the Atlantic coast, up the Nile Valley and through the Red Sea/Suez Canal may prove to be the more effective invasion route, allowing *S. eridania* to establish beachhead populations in suitable habitats from which it can migrate northwards into Europe during favourable seasons.

Currently, *S. eridania* is not known to be present in the European Union (EU). The invasion risk posed by *S. eridania* to Europe is similar to that posed by *S. frugiperda* (Du Plessis et al. 2018), with a potential zone of establishment along the Mediterranean coast in northern Africa and some areas in Spain, Italy and Greece. Elsewhere in Europe agricultural production may be threatened by seasonal populations of migrating *S. eridania* adults. The magnitude of these threats will probably depend on the size of the overwintering populations as well as proximity and seasonal wind patterns. The marginal climate suitability of these Mediterranean areas for both *S. frugiperda* and *S. eridania* means that should they get established in this region, the present threat may be low, though it seems likely to increase in the future.

Southern European countries (Portugal, Spain, Italy and Greece) account for the majority (76.5%) of European field-cropped tomato production area (EU Fruit and Vegetables Market Observatory – Tomato subgroup, 2021). Very little of this production area may be threatened by persistent field populations of *S. eridania* under historical climate conditions because only small areas of Spain are modelled as being climatically suitable for *S. eridania* to establish. However, the emerging threat with climate change is appreciable, with substantial areas of Portugal and southern Spain becoming climatically suitable for *S. eridania* establishment. Mediterranean islands and southern areas of Italy, Greece, Cyprus and Turkey are likely to become suitable for establishment sometime this century (Fig. S23).

The potential distribution of *S. eridania* in Asia is largely in the Southeast. In the future climate scenario, most of this area will continue to be suitable for annual persistence of *S. eridania*, with contraction in suitability in regions of Thailand, Myanmar, and parts of Laos. Here, the suitability changes from establishment to ephemeral. The potential distribution of *S. eridania* in China is likely to expand poleward (northwards), and the ephemeral zone is likely to expand to the west and into higher elevations. In southern Asia, parts of India, Myanmar, Thailand and Cambodia may become too hot in the near future for *S. eridania* to persist.

The potential range of *S. eridania* in Australia includes most of the primary horticultural area in the eastern states and the areas where beans, cotton, soybeans, sweet potato, tomato and tobacco are grown. The modelled climatic changes expand the potential range polewards (southwards) to encompass most of the remaining areas presently growing these crops.

There is now compelling evidence that the global spread of *S. eridania*'s congener, *S. frugiperda* has been via a mixture of trade-related inter-continental spread and natural migratory spread within continents (Tay et al. 2020). Effective phytosanitary measures are therefore likely critical to slowing the spread of *S. eridania* globally. Thankfully, its observed spread in Africa has not followed the explosive pattern of *S. frugiperda*. Nonetheless, apart from the Sahara Desert, there are no apparent dispersal barriers within Africa, and as our modelling indicates, there is potential for natural spread northwards through the irrigated areas along the Nile Valley and the Arabian Peninsula into the Middle East. The irrigated areas along the south-eastern Mediterranean coast (Egypt, Israel, Lebanon) may then pose a seasonal threat to tomato production in Turkey and southern Europe. The widespread use of greenhouses for growing tomatoes in Turkey may extend the duration of the seasonal threat from *S. eridania* into the cooler months.

The trade in agricultural produce between the Americas and Asia is a potentially important westward invasion pathway for *S. eridania*. Once established anywhere in Asia, there is little to stop it spreading throughout Asia and into Oceania. The genomic evidence in 3rd-party interception data from Asia suggests that *S. frugiperda* from South America preceded the arrival of material from Africa (Tay et al. 2020). While the actual spread of *S. frugiperda* into China may not

have initially come via Myanmar as has been widely claimed (e.g. Sun et al. 2021), these studies have highlighted the potential for this invasion pathway for migratory moths from south-western Asia into China and eastern Asia via wind dispersal. Hence, throughout Asia and Australasia we should be vigilant to the spread of *S. eridania* via trade and natural dispersal pathways.

The detection of *S. eridania* in fields and in agricultural produce is complicated by the existence of morphologically similar species that co-occur including *S. frugiperda, S. litura, S. exigua* and *Mythimna separata* (Walker). This underscores the importance of expert assessment of entries in image-based databases such as iNaturalist and SCAN, and the need for assessment categories that reflect uncertain taxonomic resolution. To assist in the interception of infested produce and to track the spread of *S. eridania* it will be necessary to develop cheap, accessible detection and diagnostic tools such as e-nose detectors and LAMP assays as well as more precise genomic tools such as whole genome sequencing.

There is value in an ongoing program to monitor the spreading populations of *S. eridania* for the presence of alleles with resistance to pesticides. This information could be used to help inform producers of what classes of pesticides to avoid to reduce pesticide wastage and selection pressure for the resistance alleles. Since most of the area at risk of spread of *S. eridania* is in developing countries in Africa and Asia, there is perhaps a case to be made for an important role of a body such as FAO to collate information on the spread and resistance status of *S. eridania* and other invasive moths that threaten smallholder crops and making this information freely available using real-time web-mapping.

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The pdf version (Adobe JavaScript must be enabled) of this paper includes an electronic supplement:
Fig. S1–S26, Distrubution records