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Important pest species of the *Spodoptera* complex: Biology, thermal requirements and ecological zoning

José Roberto Postali Parra[1] · Aloisio Coelho Jr[1] · Johanna Bajonero Cuervo-Rugno[1] · Adriano Gomes Garcia[1] · Rafael de Andrade Moral[2] · Alexandre Specht[3] · Durval Dourado Neto[4]

Abstract

In South America, especially in Brazil, four members of the *Spodoptera* complex, *Spodoptera albula* (Walker, 1857)*, S. cosmioides* (Walker, 1858)*, S. eridania* (Stoll, 1782)*,* and *S. frugiperda* (J.E. Smith, 1797) are important pests of many crops, in particular corn, soybean and cotton crops. *Spodoptera eridania* and *S. frugiperda* have recently invaded Africa and caused serious crop damage, and *S. frugiperda* has invaded Asia and Oceania. The present study tested the effect of a range of seven temperatures (18–34 °C) on these four *Spodoptera* species simultaneously, assessing several biological variables. Based on the thermal tolerances obtained experimentally, the ecological zoning of each species in Brazil was mapped and compared spatially, according to the crop calendar of three important crops in different regions (first and second corn harvest, soybean and cotton). Our results showed that *S. eridania* had the lowest temperature threshold (T_t), i.e., it is favored in regions with more moderate temperatures; and did not tolerate the warmest temperature, failing to complete its development at 34 °C. In contrast, *S. albula* did not complete its development at 18 °C and may be more successful in warmer regions. In general, *S. frugiperda* and *S. cosmioides* were able to develop over a wide range of temperatures, and *S. frugiperda* showed a higher biological potential at all temperatures evaluated. Our biological data and the computational code are available online. The extensive data produced here can help other entomologists to delimit the spatial distribution of the *Spodoptera* complex and forecast outbreaks of these pests.

Keywords Invasive pest · Spatial modeling · Fall armyworm · Integrated pest management

Key message

- The comparative biology of four Spodoptera species is described for the first time

- Spodoptera frugiperda and S. cosmioides were least affected over the temperature evaluated
- Spodoptera eridania were related to colder, and S. albula to warmer temperatures
- Use of crop calendar and thermal requirements allowed a more realistic pest zoning
- Our dataset could help entomologists to understand the invasion potential of these pests

✉ Aloisio Coelho Jr
aloisiocoelho@usp.br

1 Department of Entomology and Acarology, University of São Paulo (USP)/Luiz de Queiroz College of Agriculture (ESALQ), Piracicaba, SP, Brazil

2 Department of Mathematics and Statistics, Maynooth University, Logic House, Maynooth, Co. Kildare, Ireland

3 Embrapa Cerrados, Planaltina, DF, Brazil

4 Department of Crop Science, University of São Paulo (USP)/Luiz de Queiroz College of Agriculture (ESALQ), Piracicaba, SP, Brazil

Introduction

Most of the 30 species of *Spodoptera* Guenée, 1852 are serious agricultural pests, mainly in the tropics and subtropics (Pogue 2002). Seven of the 15 species of *Spodoptera* in the Americas are considered to be pests: *S. albula* (Walker, 1857), *S. cosmioides* (Walker, 1858), *S. eridania* (Stoll, 1782), *S. exigua* (Hübner, 1808) (introduced in North America), *S. frugiperda* (J.E. Smith, 1797), *S. latifascia* (Walker,

1856) and *S. ornithogalli* (Guenée, 1852) (Pogue 2002; Brito et al. 2019). Four of these (*S. albula, S. cosmioides, S. eridania* and *S. frugiperda*) are serious pests in Brazil, where they are known as the "*Spodoptera* complex" (Parra and Omoto 2004). Recently, *S. eridania* and *S. frugiperda* have been reported in Africa, and *S. frugiperda* has also appeared in India (Goergen et al. 2016; Ganiger et al. 2018; Sharanabasappa et al. 2018) and in Oceania (Australia) (EPPO 2020). *S. frugiperda* is categorized as A1 (quarantine pest) in Europe (EPPO 2019).

All species of the *Spodoptera* complex are polyphagous, utilizing many different host plants (Pogue 2002). For instance, *S. frugiperda* has more than 60 host species (Knipling 1980; Nagoshi 2009) and *S. albula, S. cosmioides* and *S. eridania* may attack 55, 202 and 126 hosts, respectively (Cabezas et al. 2013; Montezano et al. 2013a, b a, 2014a, b a; Specht & Roque-Specht 2016). These wide host ranges are maintained in new areas, where the species become invasive pests (Goergen et al. 2016; Ganiger et al. 2018; Sharanabasappa et al. 2018). Besides having a wide range of host plants, *Spodoptera* species easily move between host plants of the same or different species (Garcia et al. 2019; Malaquias et al. 2020).

Under Brazilian conditions, the members of the *Spodoptera* complex cause significant crop damage, particularly to corn, soybean and cotton (Knippling 1980; Pogue 2002; Montezano et al. 2013a, b; da Silva et al. 2017; Specht and Roque-Specht 2018). *Spodoptera frugiperda* damages all stages of the corn plant, reducing production by up to 57% (Cruz et al. 1999). First, second and third instar *Spodoptera* larvae feed on the upper surface of leaves, causing superficial damage (scratch marks). Fourth instar and older larvae produce holes in the leaves and may destroy young plants. *Spodoptera frugiperda* larvae can also feed on the corn culm, and in older plants on the ear stalk as well, affecting grain production (Vickery 1929; Cruz 1995). *Spodoptera eridania* and *S. cosmioides* are well known for feeding on soybean pods and cotton bolls (Gazzoni and Yorinori 1995; da Silva et al. 2017).

In addition to the diversity of host plants attacked, the members of the *Spodoptera* complex have high biotic potential in controlled conditions (Montezano et al. 2013b, 2014a, b b, 2019; Specht and Roque-Specht 2018). These pest populations are managed primarily through intensive use of pesticides and GMO plants (Adamczyk and Sumerford 2000; Bernardi et al. 2014; Fatoretto et al. 2017), which may result in selection of resistant populations (Carvalho et al. 2013; Bernardi et al. 2014). Taken together, the biological characteristics of this complex, the few control techniques available and the characteristics of

tropical Brazilian agriculture (large continuous crop areas) are extremely favorable for insect pests such as the species that constitute the *Spodoptera* complex. To increase the efficiency of pest control, it is essential to develop new strategies based on the principles of integrated pest management (IPM) (Norris et al. 2003). Detailed information about the bioecological characteristics of these insect pests, as well as the study of population dynamics in different crops, is required to support decision-making (Lacerda et al. 2019; Garcia et al. 2019).

The present study evaluated biological variables and the thermal requirements of the four most economically important pest species of the *Spodoptera* complex in South America (*S. albula, S. cosmioides, S. eridania* and *S. frugiperda*). Each of these species was reared on an artificial diet at one of seven temperatures. Although different studies have investigated each member of the *Spodoptera* complex individually (Parra et al. 1977; Beserra and Parra 2005; Montezano et al. 2013a, b, 2014 a, b; Favetti et al. 2015; Garcia et al. 2018; Specht and Roque-Specht 2018; da Silva et al. 2019), an experimental design to compare the species simultaneously has not yet been implemented. Based on the thermal requirements, we were able to estimate and spatially represent the number of generations of each species in different production areas throughout Brazil, considering the crop calendars (planting schedules) for corn, soybean and cotton. This ecological zoning provides useful information about the most suitable areas (on a continental scale) for the development of the species, based on their thermal tolerances. This information is extremely helpful for implementing IPM strategies. Studies of thermal requirements may provide useful insights into the distribution of species, based on degree-day models (Honék 1996; Trudgill et al. 2005; Garcia et al. 2017). For instance, Garcia et al. (2017) delimited strategic zones for the development of *S. frugiperda* on corn in the state of Florida, using the thermal constant and the lower temperature threshold for this species. Using a degree-days approach, Westbrook et al. 2015) modeled the seasonal migration of fall armyworm in the USA. Use of predictive models based on the extensive data presented here may help to understand the bioecological potential of each *Spodoptera* species in an agricultural context, and also to develop IPM programs. Given the importance of the *Spodoptera* complex, the present results are useful to determine the potential for damage caused by each species and to visually represent the effects of a wide range of temperatures on the biological variables and number of generations, for the different growing seasons of corn, soybean and cotton.

Materials and methods

Insect sources

Spodoptera albula, S. cosmioides and *S. eridania*

The populations of *S. albula, S. cosmioides* and *S. eridania* were obtained from commercial companies. All species were collected in the 2015–2016 growing season. *Spodoptera albula* and *S. eridania* were collected from cotton, and *S. cosmoides* was collected from soybean. All the companies reared each species according to reliable standardized techniques, using the diet developed by Greene et al. (1976) at 25 ± 2 °C, 60 ± 10 RH and natural photophase. The companies also maintained quality control procedures for insect rearing, e.g., they periodically introduced wild-type insects into the colonies (Leppla 2009). The species were originally collected from unknown municipalities and crops in the Brazilian Savanna (Cerrado) Biome in central-western Brazil. These stocks were kept in laboratory conditions for at least four generations (< 6 months).

Spodoptera frugiperda

The populations of *S. frugiperda* were collected from cornfields in the Municipality of Piracicaba, São Paulo, in Tropical Seasonal Forest vegetation (part of the Atlantic Forest Biome), southeastern Brazil. The stock colony was kept in laboratory conditions for two years (approximately 20 generations).

Biology of the four species of the *Spodoptera* complex in different temperatures

To evaluate the effect of temperature on the biological performance of the members of the *Spodoptera* complex, seven climate-controlled chambers were maintained at the following temperatures: 18, 22, 25, 28, 30, 32 and 34 ± 1 °C, with $70 \pm 10\%$ RH and a photoperiod of 14:10 [L:D] h. The development stages were evaluated as follows:

Egg stage

Selected egg masses containing approximately 75 eggs were placed in plastic Petri dishes (35 mm). The bottom of the dish was covered with moistened filter paper to increase the humidity, and the rim of the dish was sealed with PVC film to prevent neonate larvae from escaping. Five replicates were prepared for each of the four *Spodoptera* species at each test temperature. The dishes were checked daily to count the number of larvae hatched and determine the duration and viability of the egg stage.

Larval stage

To evaluate the effect of the different temperatures on the duration and viability of the larval stages, newly hatched larvae were placed in 2.3 cm (diameter)×8 cm (height) glass tubes containing 20 ml of artificial diet (Greene et al. 1976) and closed with a cotton plug. The tubes were maintained in the climate-controlled chambers at the seven different experimental temperatures. For each species at each temperature, 120 glass tubes were prepared. Three days after the larvae were placed in the tubes, they were inspected to determine the number of larvae that fed on the diet (phagostimulation). After this period, the tubes were inspected daily to determine the duration and viability of the larval stage.

Pupal stage

After metamorphosis, each pupa (< 24 h) was weighed on an analytical balance (0.01 g). Then, males were separated from females based on the pupal morphological characteristics proposed by Butt and Cantu (1962). Each pupa was placed in an individual 50-ml polyethylene cup. The cups were placed on a metal tray covered with filter paper that was moistened daily and were maintained in a climate-controlled chamber regulated at one of the seven experimental temperatures. The pupae were maintained under these conditions until the adults emerged, and the duration and viability of the pupal stage were determined for each treatment.

Thermal requirements and maps

Calculating the temperature threshold and the thermal constant

Based on the data for each of the four species, the durations of the development stages (D) at different temperatures were determined. Then, the lower temperature threshold (T_t) and the thermal constant (K) were calculated using the following linear equation (Worner 1992; Haddad et al. 1999):

$$\frac{1}{D} = aT + b \tag{1}$$

where $1/D$ is the development rate, and T is the temperature (°C) at which the insect developed. The lower temperature threshold T_t was calculated as the ratio between angular (a) and linear (b) coefficients of the line ($-a/b$), and the thermal constant (K) was obtained using the quotient $1/b$ (Bean 1961; Campbell et al. 1974). The performance of the linear model in fitting the data was tested using the coefficient of

determination (R^2). Model fitting and parameter estimation were carried out using linear regression with the mean values, in R software version 3.5.3 (R Core Team 2019).

Calculating the number of generations

Based on the lower developmental temperature threshold and the thermal constant, we estimated the number of generations in a particular region, using the following equation (Arnold 1959).

$$G = \frac{N_d(T_a - T_t)}{K} \quad (2)$$

where G is the number of generations, N_d is the number of days that a particular crop remains in the field during one year, T_a is the mean temperature at that location, T_t is the lower temperature threshold, and K is the thermal constant.

Maps of producing regions

We created a computational program, written in Visual Basics version 6.0 (Supplemental data 1), to estimate the number of generations of each species in three different crops (corn, 1st and 2nd season; soybean; and cotton) grown in different locations, considering the crop calendar (planting schedule) for each plant. We used a dataset of 230 municipalities in Brazil with their respective crop calendars, i.e., the length of time that a given crop remains in the field (N_D) and the mean temperature (T_a) as inputs to our software (Brasil 2016) (Supplemental data 2). Using this information and Eqs. 1 (calculation of T_t and K) and 2 (calculation of G), the program calculated the number of generations of each species for each of the three crops, according to the locality. Although we used a specific dataset here, the program is flexible and datasets from different countries and regions could be input, producing their respective estimates of the number of generations.

Next, we used the ArcMap application in ArcGis Pro (ESRI 2018) to organize and represent the estimated number of generations for each *Spodoptera* species in each crop and municipality in Brazil.

Data analysis

Viability variables

Embryo viability is a discrete proportion. We fitted quasi-binomial generalized linear models (GLM) (McCullagh and Nelder 1989), including a different quadratic predictor over temperature per species of *Spodoptera*. We assessed the significance of the effects using F tests, since the dispersion parameter was estimated. We assessed the difference between the curves for each species by comparing nested models. The larval and pupal viability variables are binary. We fitted a Bernoulli GLM, including a different quadratic predictor over temperature for each species. We assessed the significance of the effects using Chi-squared tests for the difference of deviances. We assessed the difference between species' curves by comparing nested models. We assessed the goodness-of-fit using half-normal plots with simulation envelopes for all models (Moral et al. 2017) (Supplemental data).

Duration variables

The durations of the embryonic, larval and pupal periods are measured in days, and each is therefore a positive continuous random variable, as is the total duration of development. Since there is no censoring, i.e., all survival times are observed, we fitted the gamma GLM including a different linear predictor over temperature for each species. We assessed the significance of the effects using F tests (Supplemental data).

Other variables

The deformation, sex ratio and phagostimulation variables are binary. We fitted a Bernoulli GLM, including a different quadratic predictor over temperature per species for deformation, and a linear predictor for sex ratio and phagostimulation. We assessed the significance of the effects using Chi-squared tests for the difference of deviances. We assessed the difference between species curves by comparing nested models. We assessed goodness-of-fit using half-normal plots with simulation envelopes for all parameters (Moral et al. 2017). The weight variable is continuous. We fitted a Gaussian model, including a different quadratic predictor over temperature for each species. We assessed the significance of the effects using F tests. We assessed the difference between species curves by comparing nested models.

Results

Biology of the *Spodoptera* complex in different temperatures

The interaction between the *Spodoptera* complex and temperature was significant ($F_{3;104} = 5.60$; $P < 0.001$; Supplemental data 3) for embryo duration. *Spodoptera albula* had the longest embryonary period (10 days at 18 °C). At the warmest temperatures (≥ 30 °C), the embryonary periods of all four species were the same length (3 days) (Fig. 1).

For the larval period, a significant interaction between the four species and temperature was also found ($F_{3; 1772} = 28.38$;
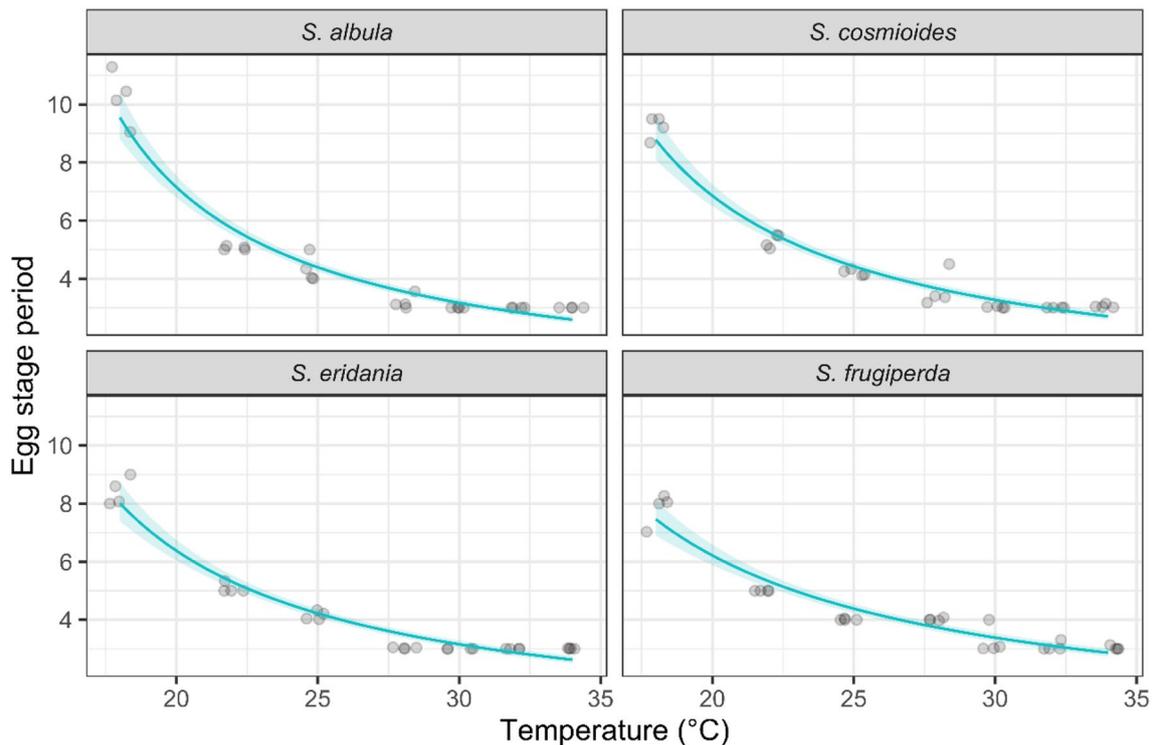
Fig. 1 Durations of the egg stage periods of *Spodoptera albula*, *S. eridania*, *S. cosmioides* and *S. frugiperda* fed on artificial diet (Greene et al. 1976) in different temperatures (Photophase 14 h, RH 70 ± 10%). Solid lines represent the estimated mean duration, and shaded areas represent the 95% confidence intervals for the true means

$P < 0.001$; Supplemental data 4). The longest larval period was that of *S. albula* at 18 °C (57.5 days), and the shortest period was that of *S. cosmioides* at 32 °C (9.5 days). The larvae of all species except *S. eridania* developed more slowly at 34 °C, i.e., the larval period was slightly longer (Fig. 2).

Pupal development also showed a significant interaction between species and temperature ($F_{3; 1053} = 29.530$, $P < 0.001$; Supplemental data 2). Pupae of *S. albula* died at 18 °C, and and pupae of *S. eridania* died at 34 °C (Fig. 3, Supplemental data 5). The duration of the pupal stage was shortest for *S. frugiperda*, at 34 °C (5.9 days), and longest for *S. cosmioides* at 18 °C (34.2 days) (Fig. 3).

For all stages combined (egg + larva + pupa), *S. cosmioides* had the longest egg-adult period, 93 days at 18 °C; and *S. frugiperda* had the shortest period, 19.2 days at 32 °C (Supplemental data 6). The egg-adult period was longer in *S. frugiperda* (19.06 days) and *S. cosmidoides* (25.0 days) at 34 °C than at 32 °C. In *S. albula*, the egg-adult duration was 0.4 days shorter at 34 °C than at 32 °C (Supplemental data 6). At 34 °C, *S. eridania* did not complete the egg-adult period, whereas *S. albula* did not complete the egg-adult period at 18 °C.

For embryo viability, the factors *Spodoptera* and temperature showed a significant interaction ($F_{6; 100} = 3.4758$; $P = 0.003667$) (Supplemental data 7). Colder temperatures

(18 and 22 °C) negatively affected the egg viability of *S. cosmioides*, but at temperatures between 25 and 34 °C, the egg viability of this species was higher than 84%. The egg viability of *S. frugiperda* decreased slightly at extreme temperatures (18 and 34 °C), although still relatively high at approximately 85%, and reached its maximum between 22 and 32 °C (~91%) (Fig. 4). *Spodoptera eridania* showed a similar pattern, but with lower viabilities (51% at 18–22 °C and 85% at 25–30 °C). *Spodoptera albula* and *S. cosmioides* showed similar levels of egg viability, i.e., below 59% for temperatures between 18 and 22 °C and higher levels (> 71%) between 25 and 34 °C.

A significant interaction was also found between *Spodoptera* species and temperature for larval viability ($F_{6; 3350} = 157.92$; $P < 0.001$) (Supplemental data 8). Extreme temperatures, whether colder (18 and 22 °C) or warmer (32 and 34 °C), reduced the larval viability of *S. cosmioides* to less than 45% (Fig. 6). The temperatures of 18 and 34 °C were not favorable for *S. frugiperda* (42 and 68% viability, respectively), but the larval viability was higher than 85% for this species at 22 and 32 °C. Larval viability of *S. eridania* showed a downward trend with rising temperatures from 18 °C to 34 °C, with the highest larval viability at 18 °C and the lowest viability at 34 °C (38%). For *S. albula*, the maximum larval viability was observed at 28–30 °C (56–58%),
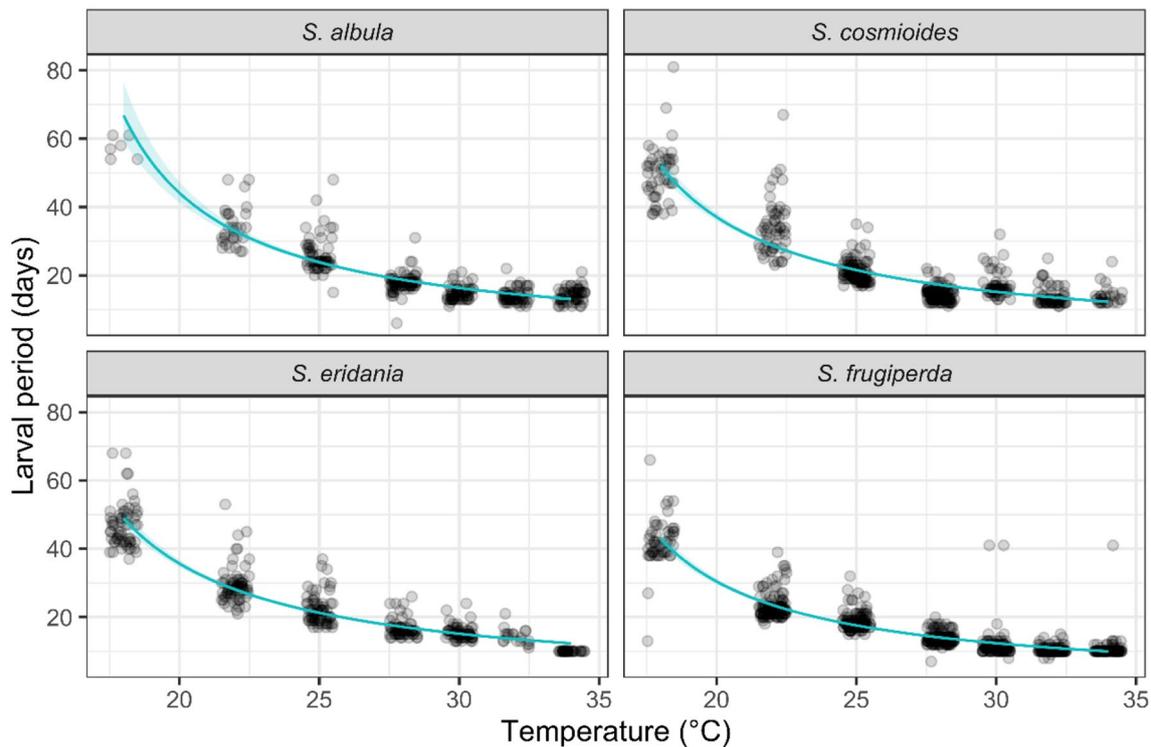
Fig. 2 Durations of the larval periods of *Spodoptera albula*, *S. eridania*, *S. cosmioides* and *S. frugiperda* fed on artificial diet (Greene et al. 1976) in different temperatures (Photophase 14 h, RH 70 ± 10%). Solid lines represent the estimated mean duration, and shaded areas represent the 95% confidence intervals for the true means

dropping to 5% at the coldest temperature of 18 °C and to 40% at the highest temperature of 34 °C (Fig. 5).

Pupal viability also showed a significant interaction between *Spodoptera* species and temperature ($F_{6;\ 1740} = 55.10$; $P < 0.001$) (Supplemental data 9). Pupal viability was strongly reduced at 34 °C (3.7%) for *S. cosmioides*, with the highest viability at 28 °C. Pupae of *S. frugiperda* exhibited higher survival rates at temperatures between 22 and 34 °C (> 81%). Overall, the pupal viabilities of *S. eridania* were low at all temperatures (< 50%) and no pupae were produced at 34 °C (Fig. 6). Although *S. albula* produced pupae at 18 °C, no adult moths emerged from these pupae; in general, for *S. albula*, the pupal viability at other temperatures was also low (< 58%) (Fig. 6).

Egg-adult viability was estimated based on the viabilities for the egg, larval and pupal phases (Supplemental data 6). These data indicated an overall negative effect of extreme temperatures on viability, although there were differences among the species. Because the egg-adult viability was affected by temperature, we can define a range for "optimal viability" using this estimated parameter. The highest viability levels were observed for *S. frugiperda*, which also showed a wide optimal temperature range for egg-adult

viability of 22–32 °C. *Spodoptera cosmioides* showed the second-highest egg-adult viability levels, with the optimal temperature range from 25 to 28 °C. The last two species showed the lowest viabilities, with optimal temperature ranges from 25 to 28 °C for *S. eridania* and 22 to 25 °C for *S. albula* (Supplemental data 6).

No interactions were found between temperature and the *Spodoptera* complex for phagostimulation; however, both temperature and species showed statistical significance (temperature $X_1 = 32.164$; $P < 0.001$; *Spodoptera* species $X_3 = 88.348$; $P < 0.001$). The proportion of larvae feeding on the third day after inoculation was higher than 80% for all species in all experimental temperatures, except *S. cosmioides* for temperatures higher than 28 °C and *S. albula* at 34 °C (Fig. 7a).

Pupal weight showed an interaction between weight, temperature and *Spodoptera* species ($F_{6;\ 1676} = 7.7552$; $P < 0.001$). Pupae of *S. cosmioides, S. frugiperda* and *S. eridania* were heavier in colder temperatures, whereas pupae of *S. albula* were heavier at 30 °C (Fig. 7b). *Spodoptera cosmioides* produced high proportions of deformed pupae at 22 °C (32%) and 18 °C (19%). Similarly, to the pupal weight, the proportion of deformed pupae showed an interaction with
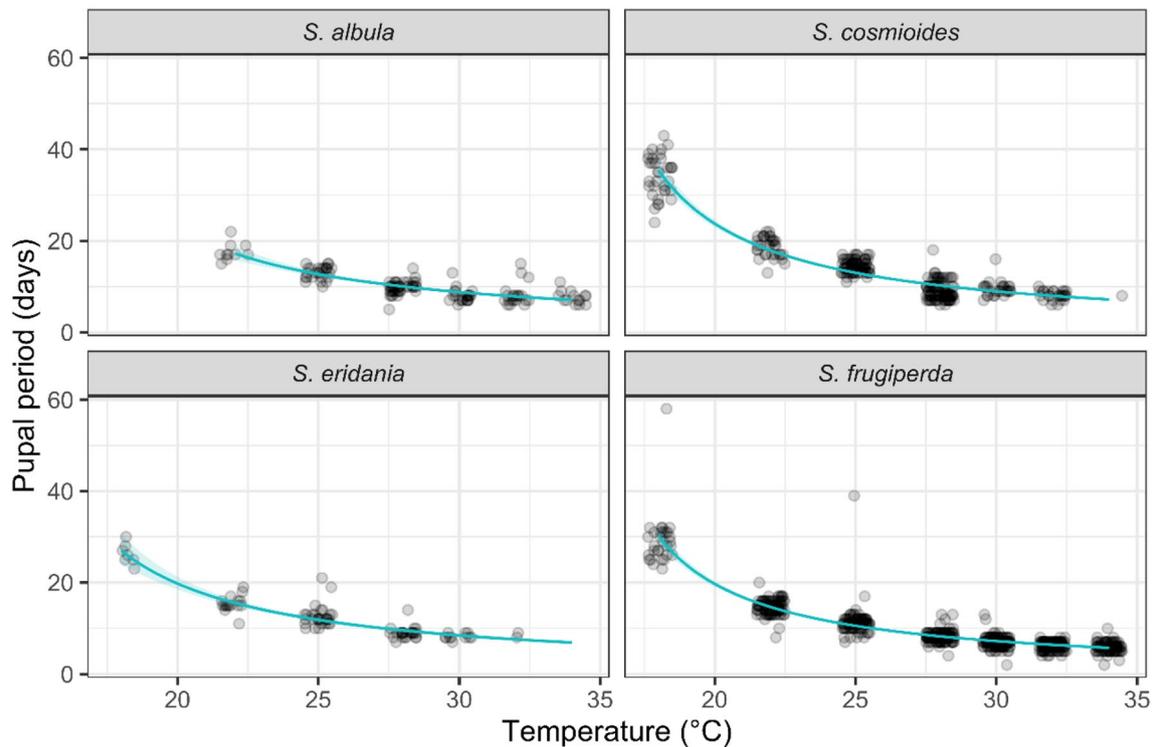
Fig. 3 Durations of the pupal periods of *Spodoptera albula*, *S. eridania*, *S. cosmioides* and *S. frugiperda* fed on artificial diet (Greene et al. 1976) in different temperatures (Photophase 14 h, RH 70 ± 10%). Solid lines represent the estimated mean duration, and shaded areas represent the 95% confidence intervals for the true means

temperature and *Spodoptera* species ($X_6 = 53.02$; $P < 0.001$). High proportions of deformities were also observed in *S. eridania* (up to 57.7% at 28 °C) and *S. albula* (up to 80% at 18 °C). In contrast, *S. frugiperda* pupae were in better condition at all temperatures (only 2.9% deformed pupae at 25 °C) (Fig. 7c).

Overall, *S. frugiperda*, followed by *S. cosmioides,* showed the best values for each of the variables evaluated over the range of temperatures tested. *Spodoptera eridania* performed poorly regarding most of the parameters evaluated, although slightly better in colder conditions. The sex ratio of these members of the *Spodoptera* complex did not differ among the species or over the different temperatures, ranging around 0.5 (Fig. 7d).

Thermal requirements of the *Spodoptera* complex

Spodoptera cosmioides showed the highest T_t, 13.23 °C, and *S. eridania* showed the lowest, 11.90 °C (Table 1). Regarding the thermal constant of the egg-adult period (K, the amount of heat energy that the insects need to mature), *S. frugiperda* needed the smallest amount, 390.06 DD (degree-days), and *S. eridania* the highest, $K = 495.96$ DD.

Bioecological zoning in different Brazilian areas according to crop calendars

Figures 8, 9, 10 and 11 show the number of generations estimated for each municipality, classified according to the *Spodoptera* species and crop. These members of the genus *Spodoptera* produce approximately 1–6 generations in each crop. *Spodoptera frugiperda* and *S. albula* showed the highest and the lowest number of generations in all crops, respectively. *Spodoptera frugiperda* showed the best combination of attributes to produce a large number of generations, i.e., high T_t and low K. This was clearly reflected in the larger number of generations estimated for *S. frugiperda* than for the other species (Table 2). The spatial distribution had a north–south gradient, with the number of generations increasing northward in all cases.

Discussion

Spodoptera cosmioides and *S. frugiperda* developed over the entire range of temperatures studied (from 18 to 34 °C). For both species, the egg-adult period was longer above 32 °C,
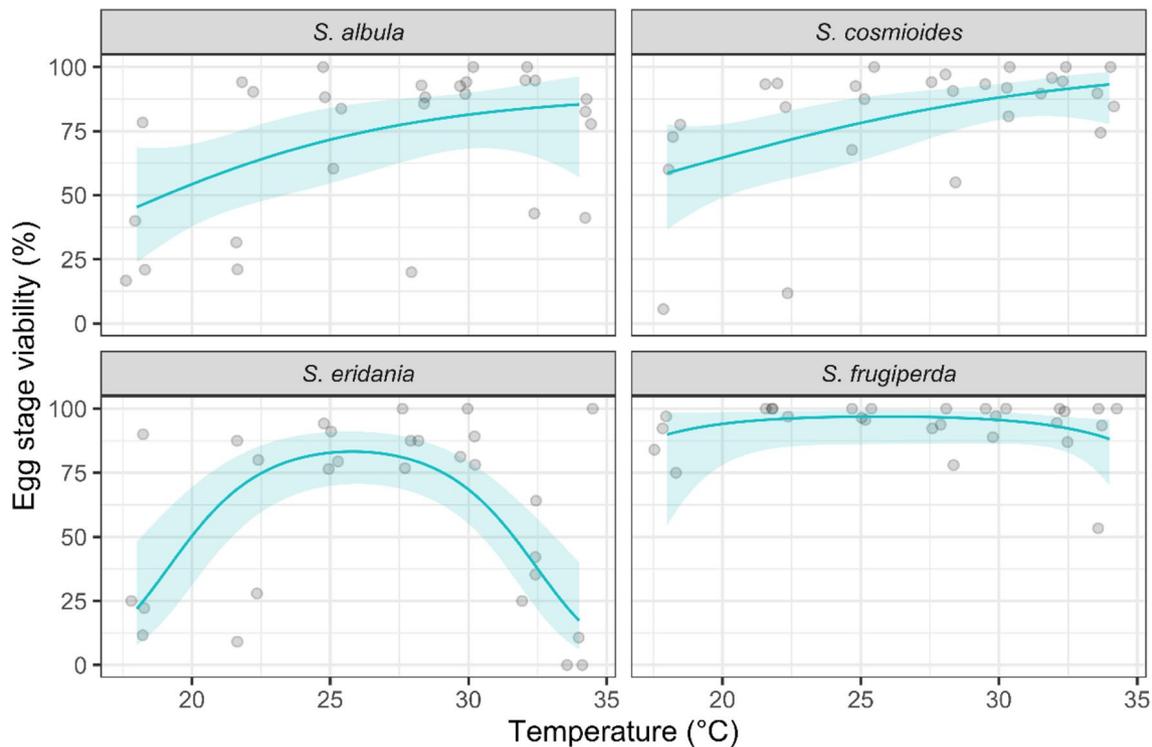
Fig. 4 Egg stage viabilities of *Spodoptera albula*, *S. eridania*, *S. cosmioides* and *S. frugiperda* fed on artificial diet (Greene et al. 1976) in different temperatures (Photophase 14 h, RH 70±10%). Solid lines represent the estimated mean viability, and shaded areas represent the 95% confidence intervals for the true means

more significantly for the larval stage, i.e., in the case of *S. cosmioides,* the larval period was 4 days longer at 34 °C than at 32 °C. The warmest temperature of 34 °C sharply reduced the viability of *S. cosmioides* (<1%), whereas *S. frugiperda* was able to reach almost 50% viability at the same temperature. *Spodoptera eridania* and *S. albula* failed to complete their biological cycles at 34 and at 18 °C, respectively. According to several authors, this *Spodoptera* complex originated in tropical and subtropical regions of the Western Hemisphere (Sparks 1979; Pogue 2002; Kergoat et al. 2012). Nevertheless, we did not observe development of *S. eridania* and *S. albula* at 34 °C and 18 °C, which indicates a more limited range of temperature conditions needed to support these species. According to Pogue (2002), *S. eridania* occurs in temperate regions of North America (colder conditions), *S. cosmioides* occurs in temperate regions of South America, and *S. frugiperda* occurs in temperate regions of South and North America (USA). *Spodoptera albula* is reported from the southern USA (southern Texas and Florida) to southern Brazil and in the warmer regions of Chile (Pogue 2002; Angulo et al. 2008; Kergoat et al. 2012; Montezano et al. 2014b). According to Montezano et al. (2013b), *S. albula*

showed a preference for feeding on dry diets, on which the egg-adult viability was higher than 80%, suggesting that this species prefers dry regions, such as the Brazilian savanna (Cerrado). The wide range of temperatures over which *S. cosmioides* and *S. frugiperda* successfully develop may explain why both species are serious crop pests in South America.

Although it does not enter diapause (Luginbill 1928; Sparks 1979), *S. frugiperda* has a wide geographic distribution, including areas with a temperate climate. Since this species is highly mobile in terms of both short-range movement within a particular crop and migrations over long distances, it is able to reach more areas that are suitable for development (Westbrook et al. 2015; Garcia et al. 2019). For instance, in North America, *S. frugiperda* populations overwinter in reservoir areas in Florida but expand their geographical distribution when climate conditions are favorable (Westbrook et al. 2015; Garcia et al. 2018). For the other species of the *Spodoptera* complex (*S. albula*, *S. cosmioides* and *S. eridania*), few studies have examined their migratory movements or their distributions through the year according to climate conditions.
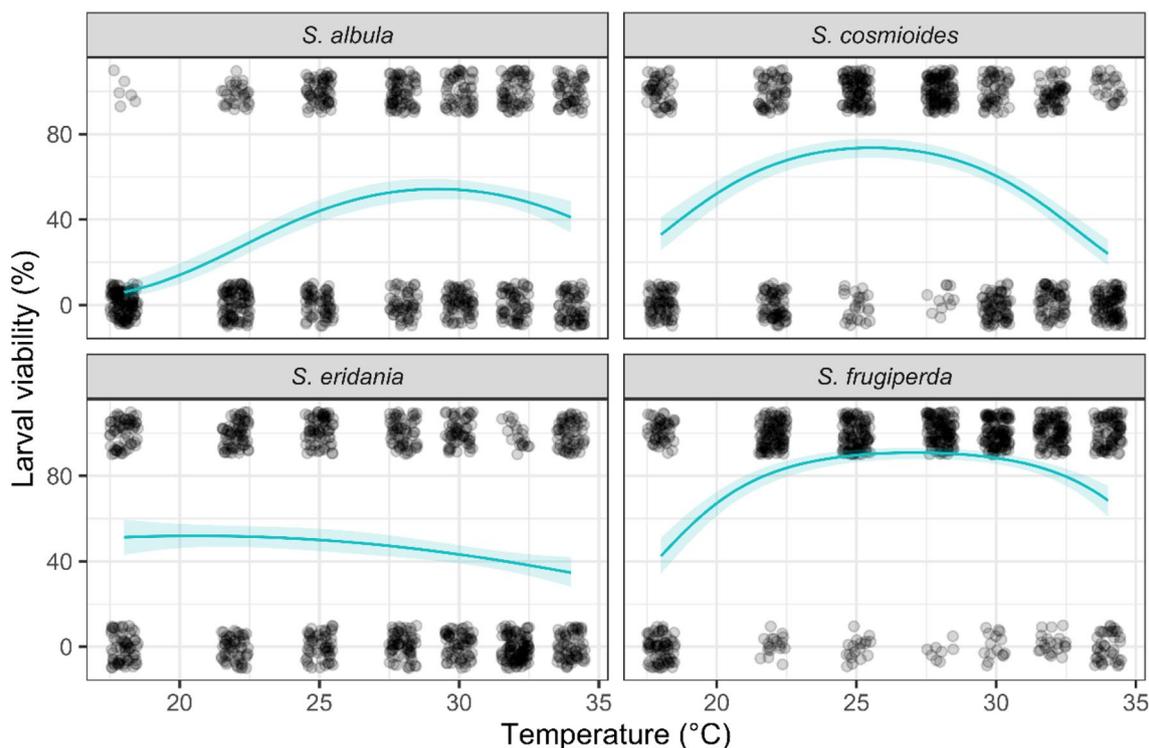
Fig. 5 Larval viabilities of *Spodoptera albula*, *S. eridania*, *S. cosmioides* and *S. frugiperda* fed on artificial diet (Greene et al. 1976) in different temperatures (Photophase 14 h, RH 70±10%). Solid lines represent the estimated mean viability, and shaded areas represent the 95% confidence intervals for the true means

According to Honèk (1996), the geographic location is strongly correlated with the level of the lower temperature threshold. Species with temperature thresholds below 8 °C are associated with cold regions, whereas species with thresholds higher than 12 °C are more associated with warmer regions (Trudgill et al. 2005). The T_t of *S. eridania* (11.9 °C) is closer to the value observed for subtropical species (~ 10.5 °C), i.e., this species is associated with lower temperatures. On the other hands, *S. frugiperda*, *S. cosmioides* and *S. albula* showed T_t values above 13 °C, indicating that they are more associated with tropical climates (Honèk 1996).

The values of the thermal constant indicated that *S. frugiperda* ($K = 390$ DD) requires less energy to complete its life cycle than the other species, which is a biological indicator of its greater importance as an insect pest. *Spodoptera cosmoides* showed a somewhat higher K (462 DD). *Spodoptera eridania* showed the highest K value, which may indicate a lower pest potential when combined with its observed failure to develop in the warmest temperatures (Honèk 1996).

The number of generations found in our study (1–6 per crop) is substantially below the number estimated per year in other studies that did not consider the crop calendars, e.g., 10 for *S. albula* (Montezano et al. 2014a, b b), 8 for *S. cosmioides* (Specht and Roque-Specht 2018) and 12 for *S. frugiperda* (Garcia et al. 2018). This demonstrates the importance of considering the crop calendar in calculating this value, since the number of generations can be overestimated. Our results more closely resemble those of Garcia et al. (2018), who estimated the number of generations of *S. frugiperda* in one year, considering a dynamic crop area (5–6 generations). Independently of the crop species, *S. frugiperda* is more benefited by the local temperatures than the other three *Spodoptera* species, in agreement with its importance for agriculture. Regarding the spatial distribution, the estimated number of generations was higher for the North and Northeast regions of Brazil. In Brazil, high incidences of *S. frugiperda* have been reported in Altamira, state of Pará in the north (Almeida et al. 2013), and of *S. cosmioides* and *S. eridania* in the northeastern states of Bahia, Sergipe and Alagoas (Teodoro et al. 2013).
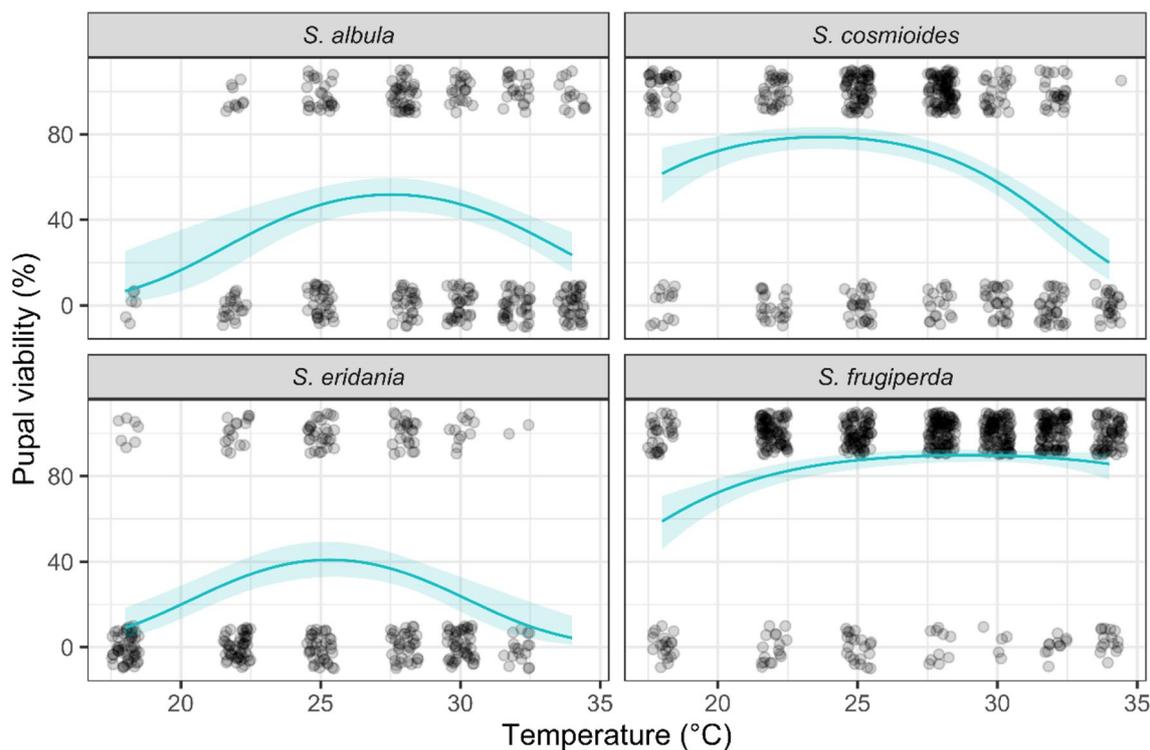
Fig. 6 Pupal viabilities of *Spodoptera albula*, *S. eridania*, *S. cosmioides* and *S. frugiperda* fed on artificial diet (Greene et al. 1976) in different temperatures (Photophase 14 h, RH 70±10%). Solid lines represent the estimated mean viability, and shaded areas represent the 95% confidence intervals for the true means

Based on the biological variables and distribution maps, we conclude that *S. frugiperda* and *S. cosmioides* have the highest pest potentials, since they showed more appropriate biological attributes, with higher viabilities over a wide range of temperatures and wider distributions. Although Brazil is generally thought of as a tropical country, 9.1% of its area is subtropical (Alvares et al. 2013). The Brazilian subtropical zone includes the states of Paraná, Rio Grande do Sul, southern São Paulo and a small portion of Mato Grosso do Sul, which produce large amounts of soybean and corn and small amounts of cotton. It is predictable that

S. eridania may be a more serious problem in this area, as well as in the colder parts of the states of Mato Grosso do Sul, Goiás and Bahia. Overall, considering the invasions of *S. frugiperda* and *S. eridania* into Africa and *S. frugiperda* also into India, *S. eridania* may become a larger problem in colder regions, such as the higher-elevation areas of Kenya and southern Africa, and *S. frugiperda* may expand its distribution into both cold and warm areas.

Although the maps constructed in the present study, based on the biology of the insect pests, are informative and helpful tools for management, one limitation must be addressed.
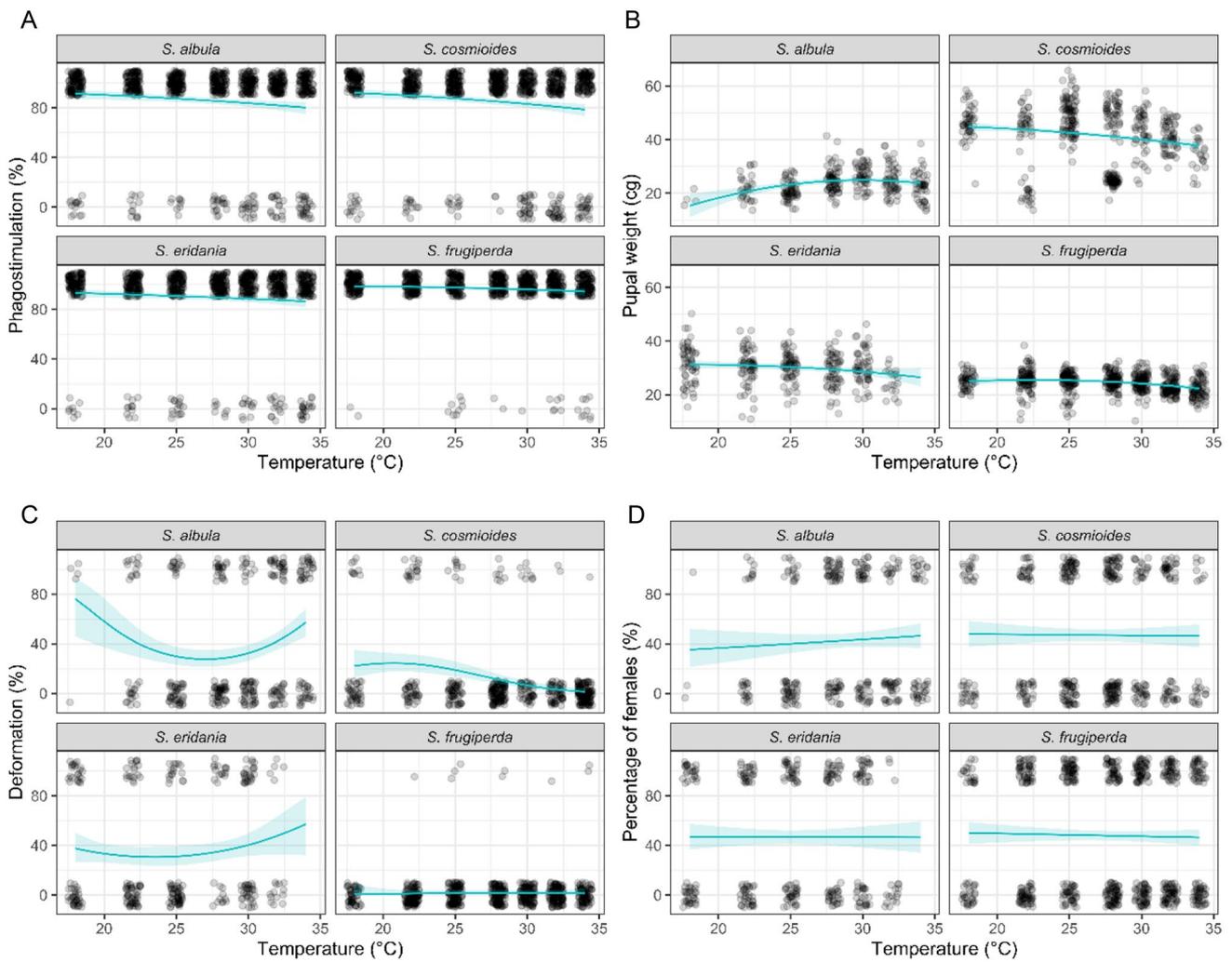
Fig. 7 **a** Larvae feeding after the 3rd day in artificial diet (phagostimulation %), **b** pupal weight, c) proportion of deformations and d) sex ratio of *Spodoptera albula*, *S. eridania, S. cosmioides* and *S. frugiperda* fed on artificial diet (Greene et al. 1976) in different temperatures (Photophase 14 h, RH 70 ± 10%). Solid lines represent the estimated mean viability, and shaded areas represent the 95% confidence intervals for the true means

Table 1 Thermal requirements of the *Spodoptera* complex

Species	T_t (°C)[a]	K (DD)[b]
S. frugiperda	13.04	390.06
S. eridania	11.90	495.96
S. cosmioides	13.23	462.02
S. albula	13.19	478.49

[a]T_t Temperature threshold

[b]K thermal constant

The experiments were performed under laboratory conditions; therefore, these maps, as well as our assumptions, need to be verified under real conditions in future studies. Model validation is an important step in the modeling process (Garcia et al. 2019), and we are aware that other variables such as relative humidity and rainfall may affect the distribution and number of generations of each species. Even so, we decided to use a degree-days approach, since it has been successfully applied in other studies involving *Spodoptera* species (Westbrook et al. 2015).
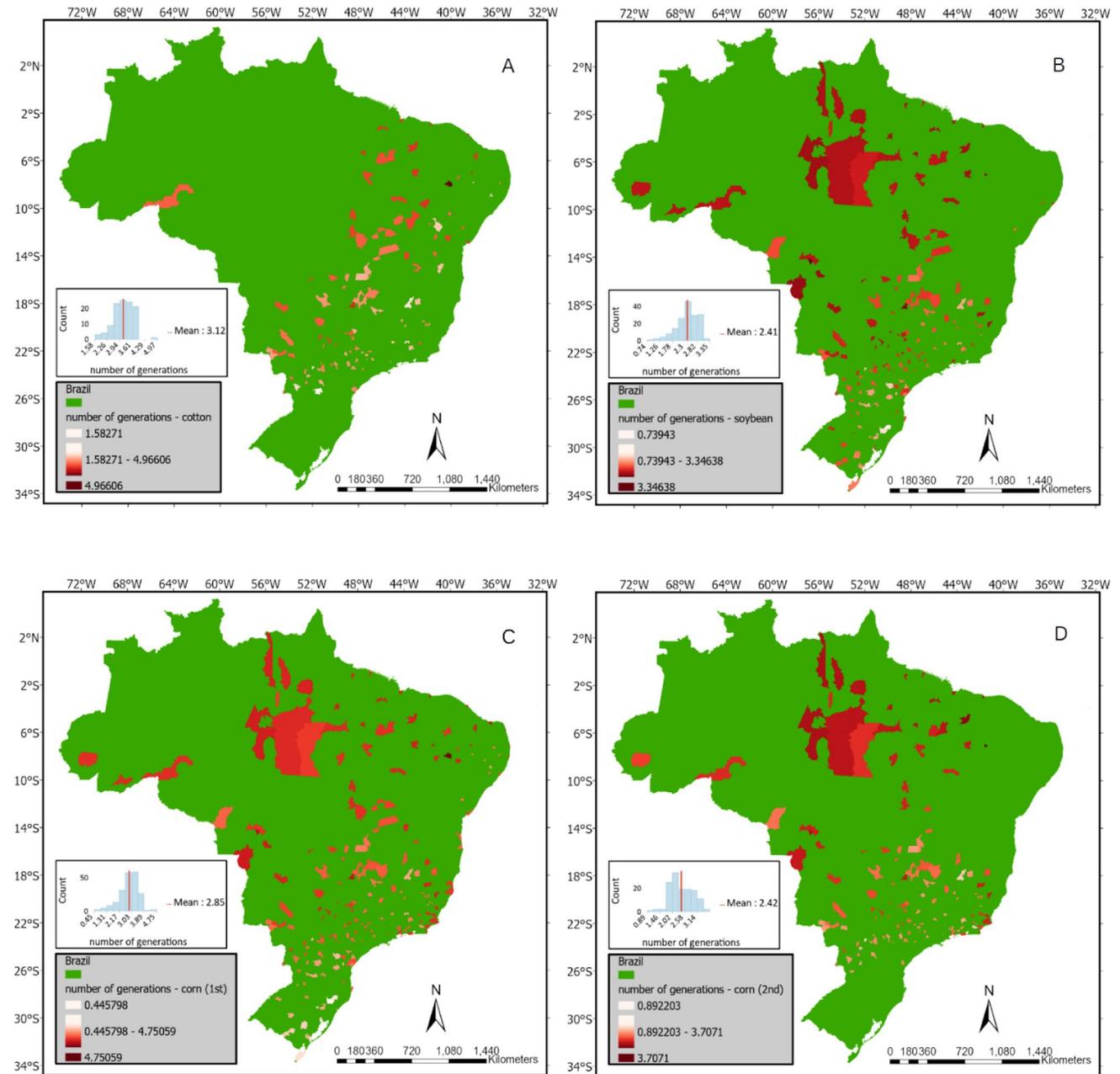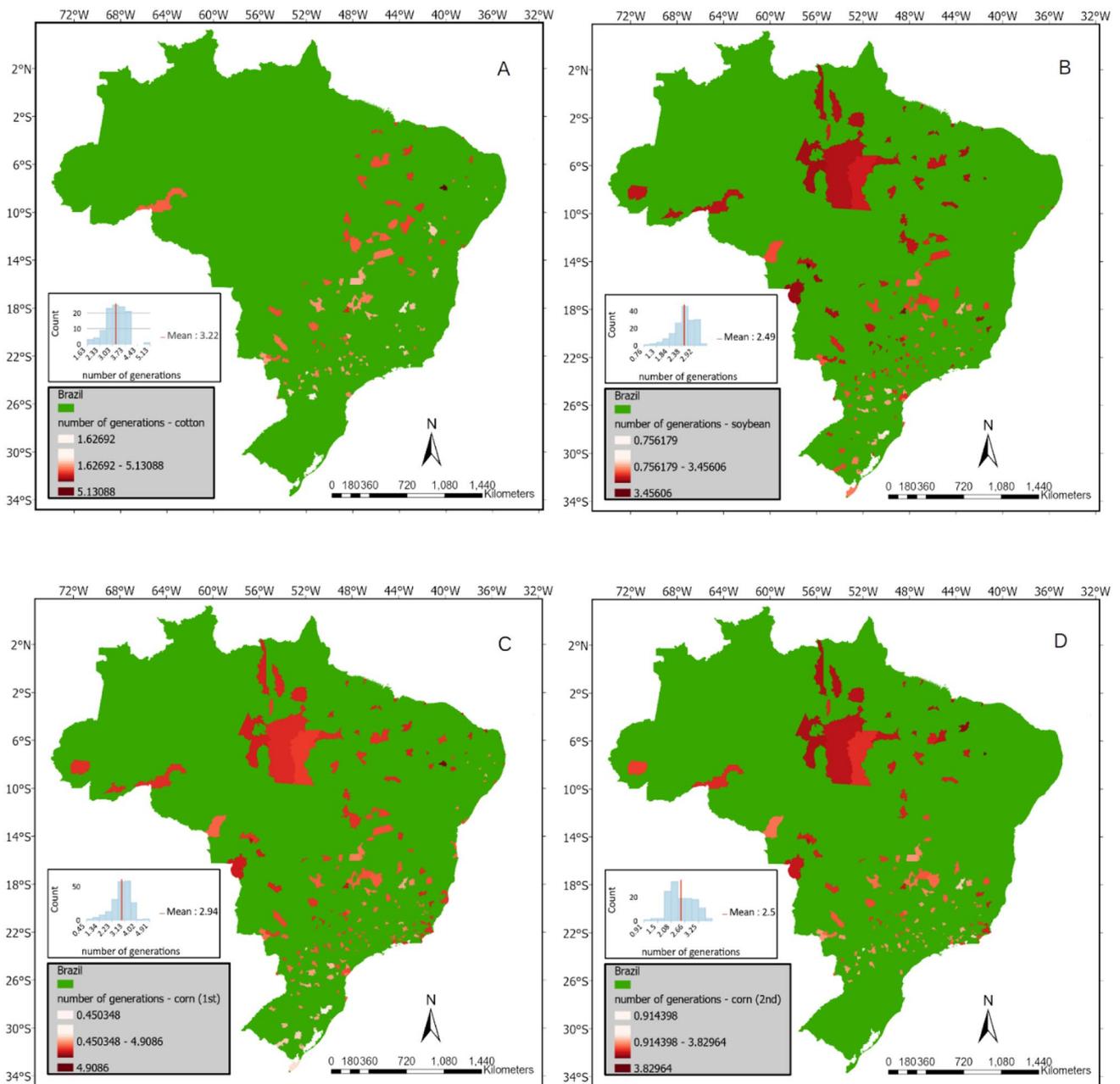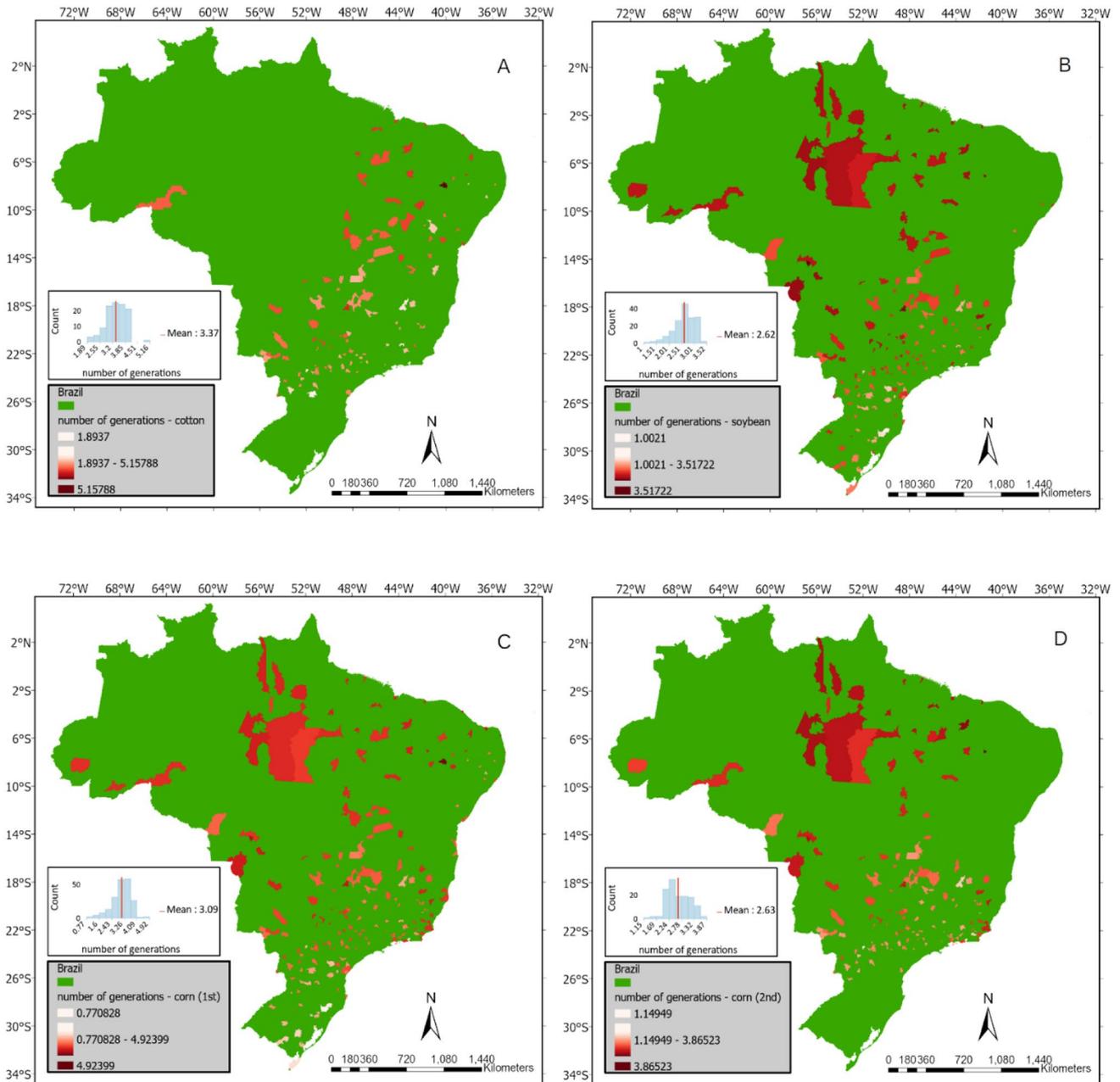
Fig. 8 Interpolated maps indicating the estimated number of generations per year for *Spodoptera albula* according to the corresponding thermal requirements and crop calendar. Color tones indicate different numbers of generations (darkest red, highest number of generations; white, lowest number of generations). Each of the four maps indicates the number of generations for a particular crop in different municipalities: **a** cotton, **b** soybean, **c** corn (1st season) and **d** corn (2nd season)
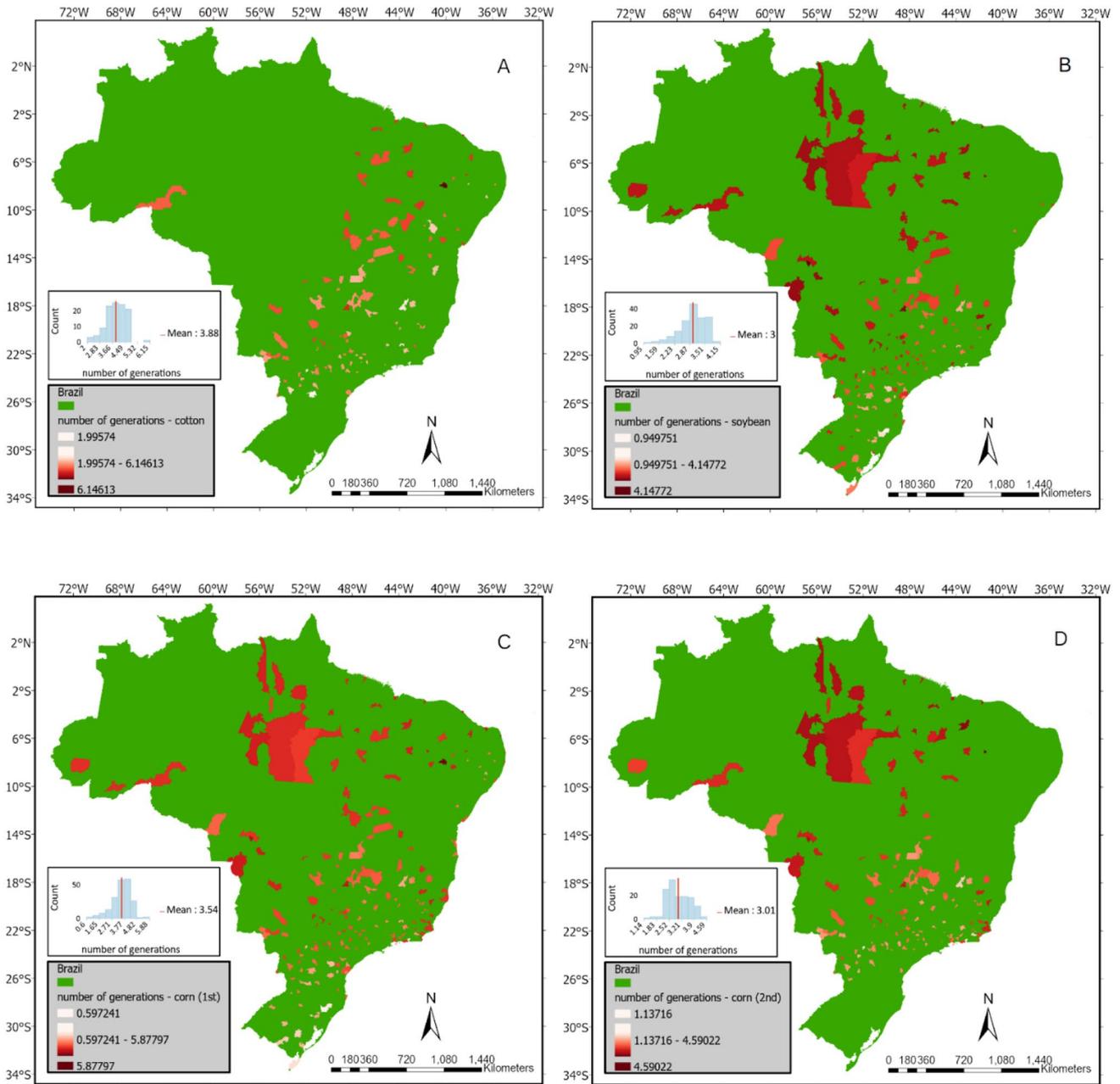
Fig. 9 Interpolated maps indicating the estimated number of generations per year for *Spodoptera cosmioides* according to the corresponding thermal requirements and crop calendar. Color tones indicate different numbers of generations (darkest red, highest number of generations; white, lowest number of generations). Each of the four maps indicates the number of generations for a particular crop in different municipaliies: **a** cotton, **b** soybean, **c** corn (1st season) and **d** corn (2nd season)

Fig. 10 Interpolated maps indicating the estimated number of generations per year for *Spodoptera eridania* according to the corresponding thermal requirements and crop calendar. Color tones indicate different numbers of generations (darkest red, highest number of generations; white, lowest number of generations). Each of the four maps indicates the number of generations for a particular crop in different municipalities: **a** cotton, **b** soybean, **c** corn (1st season) and **d** corn (2nd season)

Fig. 11 Interpolated maps indicating the estimated number of generations per year for *Spodoptera frugiperda* according to the corresponding thermal requirements and crop calendar. Color tones indicate different numbers of generations (darkest red, highest number of generations; white, lowest number of generations). Each of the four maps indicates the number of generations for a particular crop in different municipalities: **a** cotton, **b** soybean, **c** corn (1st season) and **d** corn (2nd season)

Table 2 Range of the number of generations of each *Spodoptera* species estimated for each crop according to crop calendars

Species	Crop			
	Cotton	Soybean	Corn (1st season)	Corn (2nd season)
S. albula	1.6–5.0	0.7–3.3	0.5–4.8	0.9–3.7
S. cosmioides	1.6–5.1	0.8–3.5	0.5–4.9	0.9–3.8
S. eridania	1.9–5.2	1.0–3.5	0.8–4.9	1.1–3.9
S. frugiperda	2.0–6.0	1.0–4.0	0.6–5.9	1.1–4.6

Author contributions

JRPP, ACJr, JBCR, AGG and DDN conceived the study. JRPP, ACJr, JBCR designed the experiments. ACJr and JBCR conducted the experiments. JRPP, ACJr, AGG, RAM and DDN analyzed data. JRPP, ACJr, JBCR, AGG, RAM, AS and DDN wrote the manuscript, and all authors read and approved the manuscript.

Compliance with ethical standards

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