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Where and when? How phenological patterns of armyworm moths (Lepidoptera: Noctuidae) change along a latitudinal gradient in Brazil

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Abstract

The phenological patterns exhibited by different organisms are known as adaptive responses to the cyclical environmental conditions. However, only a limited number of researches explore which factors are responsible for these phenological patterns in pest species. In the current study, abundance patterns were studied in the phenology of three *Spodoptera* Guenée, 1852 species, along the 29° latitudinal gradient in South America. The goal was to test whether widely distributed and abundant crop pest species would exhibit different phenological responses to seasonal meteorological variables and host plant availability. To test this, 13 light traps were set up in Brazil to collect adult *Spodoptera* samples at the time of the new moon, every month, from June 2015 to May 2016. The time of occurrence and intensity of the phenology were determined for each species, employing circular statistics. Both metrics revealed significant variations among the different species, as well as the factors associated with them. Latitude was found to affect the period of occurrence in *Spodoptera cosmioides* (Walker, 1858) and *Spodoptera albula* (Walker, 1857), whereas in *Spodoptera frugiperda* (J. E. Smith, 1797) its effect was evident only in the intensity of its phenology. Further, both meteorological variables and host plant availability in the sampling sites produced predictive models to account for the phenological patterns expressed. These findings suggest that different species of *Spodoptera* exhibit different adaptive strategies in their life cycles in response to environmental conditions, thus necessitating specific management practices regarding their seasonal population fluctuation.

Keywords: period of occurrence, intensity of phenology, abiotic factors, host plant availability, *Spodoptera*

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Introduction

From an agricultural perspective, knowledge regarding the factors that induce phenological patterns in pest species is crucial for proper pest control and management (Dennis *et al.*, 1986). Two main parameters have been used to identify and quantify phenological events: the periods of occurrence and intensity of phenology (Morellato *et al.*, 2000; Zar, 2010). The first represents the period when over which the phenological event is expressed. The second is not related to the period of the phenological event itself, but to how long it occurs throughout the year (Morellato *et al.*, 2000; Ting *et al.*, 2008). Therefore, the intensity of phenology is a parameter positively related to the total abundance of observations throughout the

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year and negatively related to the duration of this phenomenon.

Latitudinal gradients represent an optimal scenario to study the way the organisms regulate their phenological patterns (either the occurrence period and/or phenological intensity) given the temporal fluctuations in climate and food availability (Garibaldi *et al.*, 2011; De Frenne *et al.*, 2013). In this context, the Noctuid moth pests have been identified as suitable models for these studies, as they enable comparisons to be made of the different phenological responses of the same species in different sites. Insect pests adversely impact many crop species, causing average annual economic losses of up to 18% (Oerke, 2006), as seen in genus *Spodoptera*, for instance. The genus includes 30 species, most of them having wide geographical distribution and at least 50% of these are economically significant, as they consume many of the principal crop species across the world (Pogue, 2002).

While information on the geographic distribution and host plants of the South American *Spodoptera* species is available (Pogue, 2002; Specht & Roque-Specht, 2016), data regarding the duration and period of occurrence are very limited (Murúa *et al.*, 2006). When available, most of the documentation comes from laboratory experiments, which are usually limited to local findings, not taking into account the natural fluctuations across a wide latitudinal scale (Bavaresco *et al.*, 2004; Zenker *et al.*, 2010; Montezano *et al.*, 2013; Almeida *et al.*, 2014; Montezano *et al.*, 2014). Some meteorological factors, such as temperature, precipitation, and photoperiod, may be linked to insect phenology (Garibaldi *et al.*, 2011). They may directly influence phenology when they affect the pest itself or indirectly when they affect the availability and quality of its food source (Porter *et al.*, 1991; Cammell & Knight, 1992; Garibaldi *et al.*, 2011), both in the natural and agricultural habitats (Altermatt, 2010). On the other hand, food availability may be a predominant factor when vast quantities of the food sources previously available through, for example, monoculture, become limited due to changes in cropping and harvesting patterns (Cocu *et al.*, 2005).

The annual population dynamics exhibited by the *Spodoptera* species along the 29° latitudinal gradient in Brazil are used in this study to test the following null hypotheses: (1) as these species are abundant in the agricultural ecosystems and can be recorded throughout the year, they all reveal similar phenological patterns along the latitudinal gradient; (2) meteorological factors and host plant availability similarly influence the period of occurrence and phenology intensity of all armyworm species.

Materials and methods

Sampling

Spodoptera adults were sampled from June 2015 to May 2016, in 13 locations, positioned along the latitudinal gradient of −2° to −31°, covering four Brazilian biomes (table 1) (IBGE, 2004). At each location, a Pennsylvania type light trap was installed (Frost, 1957) provided with a BL T8 15W Black Light fluorescent lamp, having wavelengths from 290 to 450 nm, and a maximum of about 340 nm. The traps set at about 3.0 m height above the ground were operated for around 12 h, from twilight until dawn, for five nights per new moon cycle (Yela & Holyoak, 1997), for 12 months, or 60 nights of sample collection per trap.

Table 1. Sampling sites and abundance of *Spodoptera* spp. sampled in a latitudinal gradient in Brazil.

	Biome	State	Locality	Latitude	Longitude	TS	PS	*S. albula*	*S. cosmioides*	*S. frugiperda*
1	Amazon	Pará	Mojuí dos Campos	−2.017	−54.07	618	69	131	47	126
2	Amazon	Acre	Rio Branco 1	−10.02	−67.12	706	57	9	230	771
3	Amazon	Acre	Rio Branco 2	−10.02	−67.03	712	58	–	83	337
4	Brazilian Savanna	Distrito Federal	Planaltina 1	−15.1	−47.04	1012	87	44	13	179
5	Brazilian Savanna	Distrito Federal	Planaltina 2	−15.1	−47.07	994	86	42	18	187
6	Brazilian Savanna	Minas Gerais	Uberaba 1	−19.15	−47.13	1659	81	51	30	67
7	Brazilian Savanna	Minas Gerais	Uberaba 2	−19.15	−47.12	1682	81	13	5	89
8	Atlantic Forest	Paraná	Londrina 1	−23.02	−51	2666	46	34	56	510
9	Atlantic Forest	Paraná	Londrina 2	−23.02	−51	2666	46	19	28	296
10	Atlantic Forest	Rio Grande do Sul	Passo Fundo 1	−28.05	−52.07	3005	15	1	52	84
11	Atlantic Forest	Rio Grande do Sul	Passo Fundo 2	−28.05	−52.07	3005	15	–	33	457
12	Southern Grassland	Rio Grande do Sul	Bagé 1	−31.14	−53.15	3492	12	–	11	78
13	Southern Grassland	Rio Grande do Sul	Bagé 2	−31.02	−54	3477	9	–	13	43

Numbers beside localities discriminate trap sites.
TS, temperature seasonality (standard deviation × 100); PS, precipitation seasonality (coefficient of variation). Climatic data extracted from Hijmans *et al.* (2005).

However, the light traps could vary in efficiency as they were affected by abiotic factors, including wind velocity, temperature, and, principally, the lunar luminosity (Yela & Holyoak, 1997). To minimize this sampling effect, only three nights for each trap during the new moon cycle were considered, selecting the three samples which showed the largest number of individuals collected. The insects collected daily were sorted, identified (Pogue, 2002), and prepared in the laboratory. Voucher specimens were deposited in the 'Coleção Entomológica da Embrapa Cerrados' and Coleção Entomológica Pe. Jesus Santiago Moure, Departamento de Zoologia, Universidade Federal do Paraná, Brazil.

Predictor variables

With the objective of identifying the predictive power of the factors responsible for the phenological patterns exhibited by the species, the data were collected on the availability of food surrounding (e.g. host plant area) each trap and climatic region. Food availability was estimated using buffer zones with two different scales of 100 and 400 m. Employing the Google Earth Pro (2017) software, the cultivated and uncultivated parts of the regions within each buffer zone were quantified.

The cultivars were distinguished in terms of the vegetative species and cultivation period (from planting time to harvest), while the uncultivated areas were considered perennial. Therefore, the size of the areas was multiplied by the number of days that the plants were present, thus quantifying the food availability for the *Spodoptera* populations (Supplementary table S1). Most of the sampling sites had a predominantly agricultural landscape supporting the annual soybean (*Glycine max* (L.) Merril) and maize (*Zea mays* L.) crops, each cultivated for 3–4 months. Secondarily, there were other species such as *Sorghum bicolor* ((L.) Moench) and several species of pasture crops including *Andropogon* spp., *Panicum* spp., *Brachiaria decumbens* Stapf., *Melinis multiflora* (P. Beauv.), *Pennisetum purpureum* (Persoon), *Avena* spp., and *Lolium multiflorum* (Lam.) (Montezano *et al.*, 2013; Specht & Roque-Specht, 2016).

Furthermore, latitude and climate seasonality were also used as predictors of *Spodoptera* phenology. The climate metrics were represented by annual temperature seasonality and annual precipitation seasonality. The first represents the amount of temperature variation over a given year based on the standard deviation (SD) (variation) of monthly temperature averages, while the second is a measure of the variation in monthly precipitation totals over the course of the year. This index is the ratio of the SD of the monthly total precipitation to the mean monthly total precipitation (also known as the coefficient of variation) and is expressed as a percentage (O'Donnell & Ignizio, 2012). These variables are available in WorldClim database (Hijmans *et al.*, 2005).

Statistical analyses

Circular statistical tools are recommended to identify and discern phenological patterns of different species (Morellato *et al.*, 2000; Brito *et al.*, 2014). These tools transform value categories into angles ranging from 0 to 360° in a circle, whose '0' value is arbitrarily established (Zar, 2010). Hence, the occurrence dates of a phenological observation are transformed to an angle proportional to the circularity of the 365 days in a year (e.g. $n°$ days $\times 360/365$). The phenological parameters estimated in this study included (a) period of occurrence and (b) intensity of phenology. These indices were identified, based on the non-uniformity of the abundance distributions over time, which implied validation of the phenological variation present. Rao's Spacing test was employed to accomplish this for the data that did not show unimodal distribution (Bergin, 1991; Ribeiro *et al.*, 2010), as is evident. All the samples lacking significant values for the Rao's Spacing test were excluded from further analyses. After rejecting the hypothesis of uniform yearly abundances, the mean angle (μ) can be used to represent the concentration of abundances for a specified period of the year. This means that if the higher species abundance is related to a specific part of the year, it can be understood to be the period of occurrence exhibited by a particular species. Besides, once the mean angle is used to determine the period of occurrence, the SD of the mean angle can be calculated to represent the intensity of this phenomena (Morellato *et al.*, 2000; Ting *et al.*, 2008; Brito *et al.*, 2014). Therefore, SD determines the degree to which *Spodoptera* species are available throughout the year.

Two analyses were performed to test for the predictive factors responsible for the variations observed in the period of occurrence of the species. The first verified whether the average angle that represents the period of occurrence of the species is associated with the latitude at which each trap had been set up. As these variables are circular and linear, respectively, a circular–circular correlation test was used. The second analysis tested whether the period of occurrence for each species was synchronous with the time when the main crops (e.g. soybean, corn, wheat, sorghum, and pastures) were present in each site. The average angle of each crop available at the location of each trap (100 and 400 m scales) was calculated through its own circular average, assessed between the angles of the months during which the crops were present. In this analysis, the V test available in the Oriana 4.0 program was used (Kovach, 2011).

Likewise, we tested whether the same parameters described above influenced the intensity of phenology of the different *Spodoptera* species. In this analysis, the SD of the mean angle for each species, in each sample, drawn from the circular analyses was used as a surrogate of phenological intensity (Morellato *et al.*, 2000). But because this is a linear variable, it could be determined using linear regression models. The variables chosen as predictors included the period of occurrence of the soybean and maize crops (in days), seasonality of temperature and precipitation, as well as latitude. In addition, a null model was added using the random values, resulting in a total of six models for each species, each one having a single predictor variable. For each species, the best model produced for the intensity of phenology was chosen based on the Corrected Akaike Information Criterion (AICc) (Burnham & Anderson, 2004; Burnham *et al.*, 2011).

The weights drawn from the AICc varies from 0 to 1, in which the closer the value is to 1 the greater the predictive power yielded by the model. The support provided by alternative models is determined by the differences in the AICc values, in which a difference value of below 2 implies equally plausible models (Burnham & Anderson, 2004; Burnham *et al.*, 2011). As all the models are classified according to this value, the null model acts as a reference, enabling the identification and quantification of the variables having the best predictive power. Circular statistics, linear models, and comparisons of AICc were done using CircStats (Agostinelli, 2012) and bbmle (Bolker, 2017) package in R environment (R Core Team, 2015).

Table 2. Descriptive statistics derived from circular analysis of the abundance of *Spodoptera* collected with light traps, in the three most abundant nights on each new moon per locality.

	S. albula				*S. cosmioides*				*S. frugiperda*			
Locality	N	μ	CSD	U	N	μ	CSD	U	N	μ	CSD	U
Mojuí dos Campos	131	89°	30°	**	47	113°	23°	**	126	60°	69°	**
Rio Branco 1	9	63°	48°	**	230	91°	63°	**	771	68°	76°	**
Rio Branco 2	0	–	–	–	83	157°	103°	**	337	309°	90°	**
Planaltina 1	44	130°	58°	**	13	95°	60°	**	179	1328°	59°	**
Planaltina 2	42	156°	45°	**	18	102°	60°	**	187	23°	72°	**
Uberaba 1	51	174°	69°	**	30	126°	69°	**	67	118°	76°	**
Uberaba 2	13	113°	63°	**	5	145°	78°	n.s	89	199°	101°	**
Londrina 1	34	153°	66°	**	56	329°	67°	**	510	256°	75°	**
Londrina 2	19	169°	30°	**	28	135°	79°	**	296	183°	79°	**
Passo Fundo 1	1	121°	–	–	52	338°	61°	**	84	47°	58°	**
Passo Fundo 2	0	–	–	–	33	47°	64°	**	457	40°	40°	**
Bagé 1	0	–	–		11	29°	40°	**	78	56°	42°	**
Bagé 2	0	–	–	–	13	12°	34°	**	43	19°	60°	**

N, moths abundance; μ, mean circular vector; CSD, circular standard deviation; U, Rao's Spacing test.
**<0.01 Significant values.

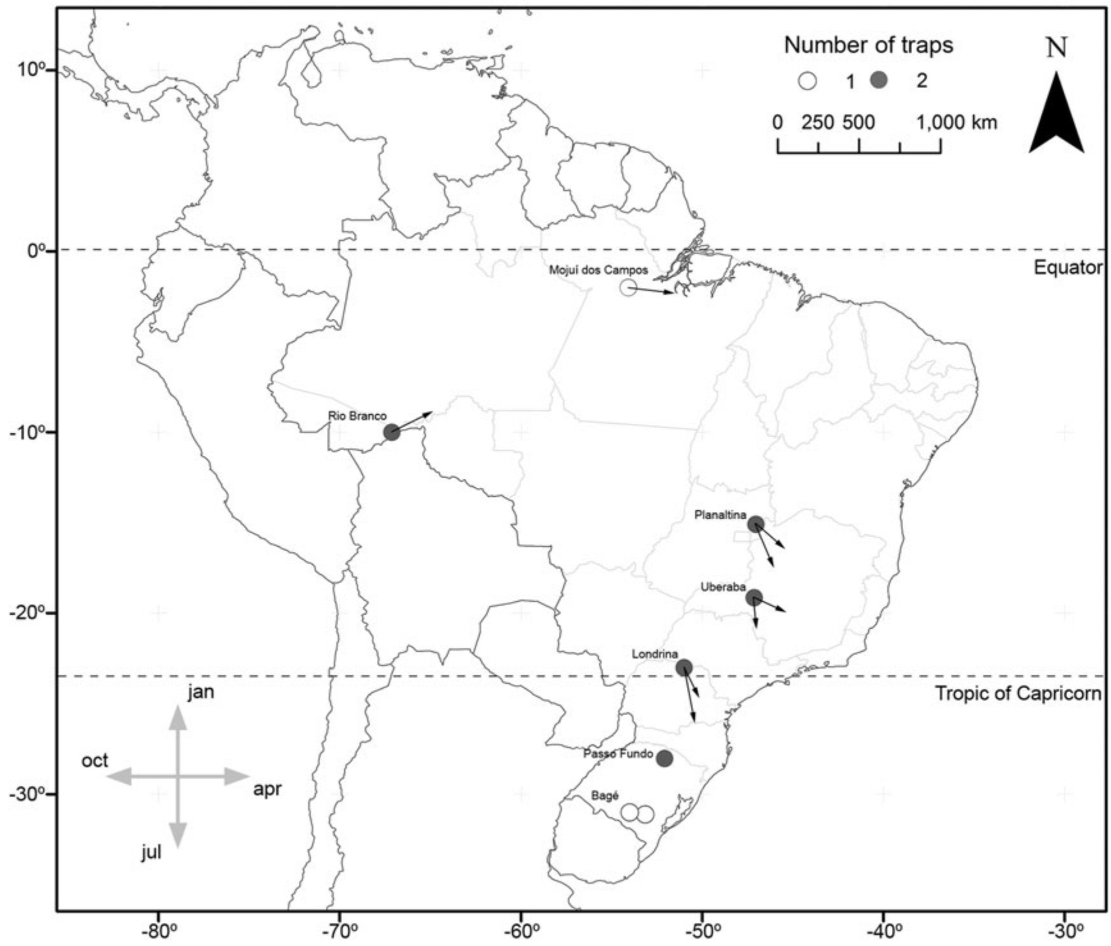

Fig. 1. Map illustrating the geographical distribution of sample sites, representing one (white) or two (gray) traps each. Vectors (arrows) point mean occurrence period, while its length represents the phenology intensity exhibited by *Spodoptera albula.*

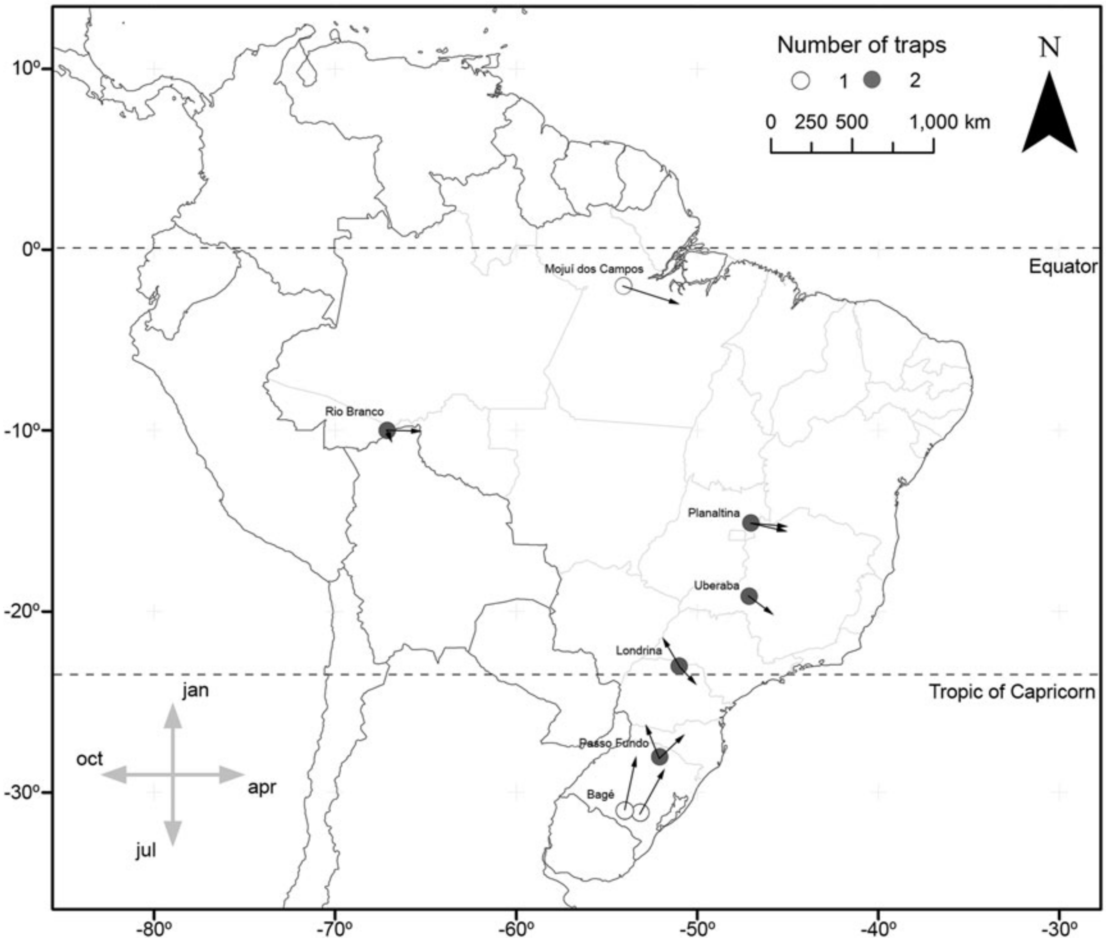

Fig. 2. Map illustrating the geographical distribution of sample sites, representing one (white) or two (gray) traps each. Vectors (arrows) point mean occurrence period, while its length represents the phenology intensity exhibited by *Spodoptera cosmioides*.

Results

Along the entire latitudinal gradient, a total of 5277 *Spodoptera* adults were collected from all the traps, with an average of 11 individuals captured per trap/night. Low numbers and/or presence in a few localities made it impossible to assess the phenological patterns of *S. marima* (Schaus, 1904), *S. eridania* (Stoll, 1782), *S. dolichos* (Fabricius, 1794), and *S. androgea* (Stoll, 1782). In most of the samples, these species revealed abundances in non-uniform distributions through the year, and their non-significant values were normally related to the occasional poor numbers of specimens captured. Hence, the results for *S. albula*, *S. cosmioides*, and *S. frugiperda* only are reported (table 2).

Period of occurrence

In the cases of *S. albula* and *S. cosmioides*, the occurrence periods showed significant correlation with latitude ($R^2 = 0.72$, $P < 0.05$; $R^2 = 0.64$, $P < 0.05$). Therefore, at the lower latitudes, *S. albula* was found between February and April. But as the latitudes increases, the period of occurrence of this species extends from April to June (fig. 1). *Spodoptera cosmioides*, at the lower latitudes, occur mostly between April to July. However, with the increase in latitude, this period of occurrence shifts from December to May (fig. 2). On the other hand, *S. frugiperda* exhibited no relationship between the period of occurrence and latitude (R^2 -0.2, $P > 0.05$) (fig. 3). Additionally, the mean occurrence of *Spodoptera* species corresponded to the time span when the main host plant species were grown throughout the year. Soybean and corn, in particular, showed the greatest correlation with their period of occurrence. From among all the crop species cultivated, *S. albula* showed the least number of correlations (30% of the cultivated species; 50% of the sampled localities), followed by *S. cosmioides* (34% of the cultivated species; 73% of the sampled localities) and finally *S. frugiperda* (75% of the cultivated species; 83% of the sampling sites) (Supplementary table S2).

Intensity of phenology

The intensity of phenology was predicted in a similar manner, using the two scales analyzed (100 and 400 m). However, in this case, the null model revealed the best predictive power for the intensity of phenology for *S. albula* and *S. cosmioides*. On the contrary, the seasonality of the precipitation and temperature predicted the higher intensity of phenology in *S.*

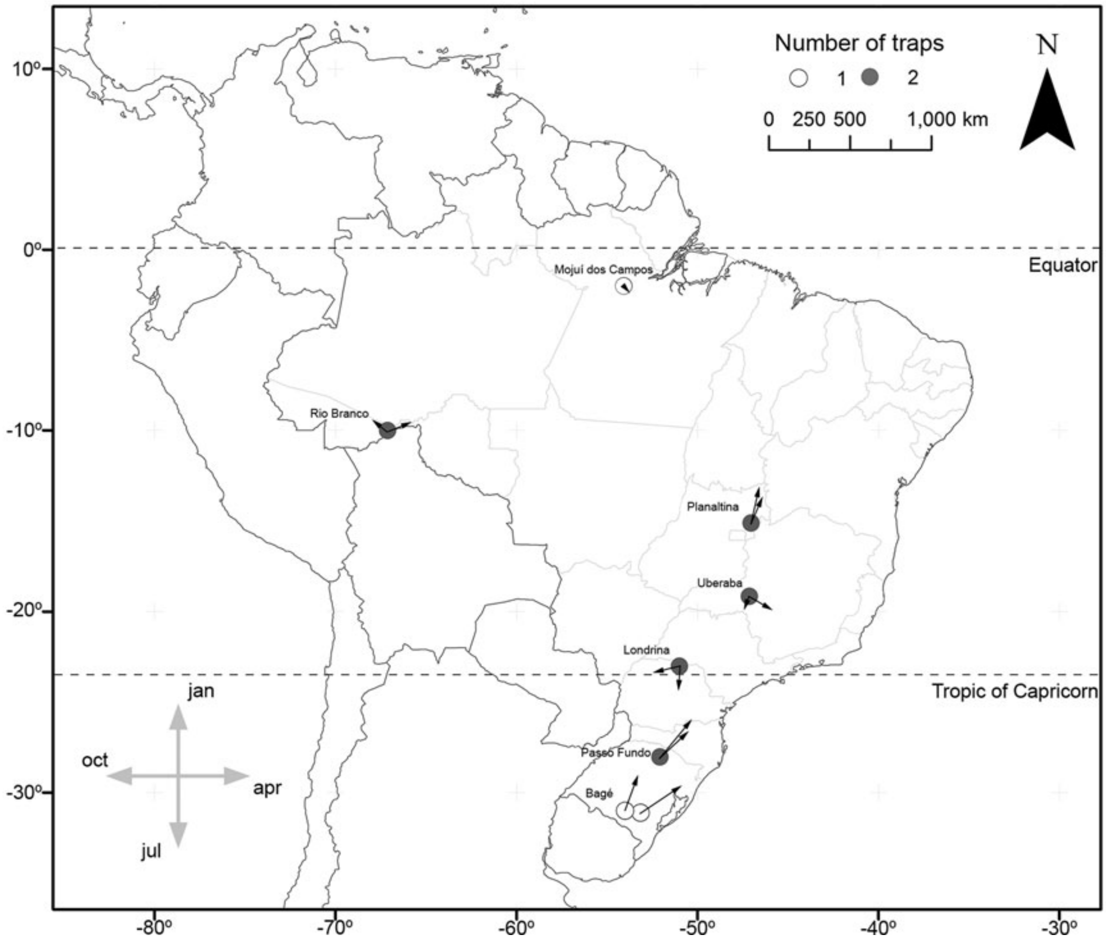

Fig. 3. Map illustrating the geographical distribution of sample sites, representing one (white) or two (gray) traps each. Vectors (arrows) point mean occurrence period, while its length represents the phenology intensity exhibited by *Spodoptera frugiperda*.

frugiperda along the entire latitudinal gradient (table 3), supporting the concept that each species of *Spodoptera* has its own specific response to the abiotic and biotic factors.

Discussion

Period of occurrence

In contrast to natural environments (Wolda, 1988; Kishimoto-Yamada & Itioka, 2015), only a few phenological studies related to latitude have been conducted in agricultural ecosystems (Cocu *et al.*, 2005). Usually local studies restricted to minor latitudinal gradients do not contribute understanding of the phenological plasticity of a particular species (Fielding *et al.*, 1999). Therefore, the period of occurrence for several widespread pest species remains unknown, despite such understanding being highly relevant for global food production (Régnière & Sharov, 1998; Donatelli *et al.*, 2017). The phenological responses of organisms can reveal variations along the entire latitudinal gradient and the factors usually linked to this phenomenon include temperature, precipitation, and photoperiod (here represented as latitude). As the latitudes move away from the tropics, greater seasonality in the temperature and photoperiod is observed, but less seasonality in precipitation (De Frenne *et al.*, 2013).

These variables are most often related to the insects' life cycles, and correspond to the periods of occurrence of *S. albula* and *S. cosmioides*. Interestingly, the periods of occurrence and variables influencing this phenological pattern are different for both these species along the entire latitudinal gradient investigated in this study. The occurrence of *S. albula* was observed to be delayed as the latitude increased. *Pieris rapae* (Linnaeus, 1758) (Gordo *et al.*, 2010) and *Cactoblastis cactorum* (Berg, 1885) (Hight & Carpenter, 2009) in the Northern Hemisphere exhibited similar patterns, although within a narrower latitudinal gradient. In regions where the temperature differences are well defined (e.g. Southern Brazil), insect activity is more evident during the hotter seasons (Wolda, 1988). However, temperature differences do not appear to significantly affect the period of occurrence for *S. albula*, as its occurrence in the highest latitudes corresponds with the months experiencing low temperatures.

The availability of crops also does not seem to be a determining factor for the period of occurrence for *S. albula*, as this coincides only with the period of cultivation of plants not utilized by the species (e.g. pasture and wheat) (Montezano *et al.*,

Table 3. Variables correlated to the phenology intensity of *Spodoptera* species, ranked by the Corrected Akaike Information Criterion (AICc), at 400 and 100 m buffer size.

	400 m						100 m				
	ΔAICc	df	Weight	AICc	C		ΔAICc	df	weight	AICc	C
S. albula											
Corn	0	3	0.31	68.84	(–)	Latitude	0	3	0.29	69.33	(–)
Latitude	0.5	3	0.24	69.33	(–)	PS	1.3	3	0.15	70.62	(+)
PS	1.8	3	0.13	70.62	(+)	Soybean	1.3	3	0.15	70.63	(+)
Null model	2	3	0.12	70.83	(+)	Corn	1.3	3	0.15	70.66	(–)
TS	2.2	3	0.1	71.04	(+)	Null model	1.5	3	0.14	70.83	(+)
Soybean	2.3	3	0.1	71.19	(–)	TS	1.7	3	0.12	71.04	(+)
S. cosmioides											
Null model	0	3	0.4	109.17	(+)	Null model	0	3	0.36	109.17	(+)
PS	2.1	3	0.14	111.3	(+)	Corn	1.1	3	0.2	110.29	(–)
TS	2.1	3	0.14	111.32	(–)	PS	2.1	3	0.12	111.3	(+)
Soybean	2.6	3	0.11	111.77	(+)	TS	2.1	3	0.12	111.32	(–)
Latitude	2.6	3	0.11	111.8	(+)	Soybean	2.6	3	0.1	111.75	(–)
Corn	2.7	3	0.1	111.86	(–)	Latitude	2.6	3	0.1	111.8	(+)
S. frugiperda											
PS	**0**	**3**	**0.57**	**109.54**	**(+)**	**PS**	**0**	**3**	**0.57**	**109.54**	**(+)**
TS	**2**	**3**	**0.21**	**111.54**	(–)	**TS**	**2**	**3**	**0.21**	**111.54**	(–)
Latitude	**2.6**	**3**	**0.16**	**112.11**	**(+)**	**Latitude**	**2.6**	**3**	**0.16**	**112.11**	**(+)**
Soybean	6.1	3	0.03	115.62	(+)	Null model	6.5	3	0.02	116.07	(+)
Corn	6.5	3	0.02	116	(–)	Corn	6.5	3	0.02	116.07	(+)
Null model	6.5	3	0.02	116.07	(+)	Soybean	6.5	3	0.02	116.08	(–)

The variables in bold indicate a higher predictive power when compared with the null model. ΔAICc, differences relative to the smallest AICc value in the model set; df, degrees of freedom as associated with hypothesis testing; weight, Akaike weight; C, correlation polarity; TS, temperature seasonality (standard deviation × 100); PS, precipitation seasonality (coefficient of variation). Climatic data extracted from Hijmans *et al.* (2005)

2013). Curiously, *S. albula* revealed the highest abundance in those areas showing marked seasonality of precipitation (dry season), which is in agreement with the results of Piovesan *et al.*, (2017). Even in the highest latitudes, the period of occurrence of *S. albula* corresponds with the months experiencing low humidity. Likewise, its sister species, *S. ochrea* (Hampson, 1909) occurs especially in the dry ecosystems of Peru and Ecuador (Pogue & Passoa, 2000; Pogue, 2002; Kergoat *et al.*, 2012) suggesting an adaptation of these species to highly seasonal environments or at least when any given season experiences low precipitation rates.

By contrast, *S. cosmioides*, like other insects (Wolda, 1988), reveals an inverse period of occurrence to that of *S. albula*, which increases with the rise in latitude. Therefore, this species occurs in greater abundance during the hotter and wetter seasons, in places experiencing more seasonal temperatures. However, the greater synchronization between the availability of the host plant and occurrence periods of both *S. cosmioides* and *S. frugiperda* suggests that these species have developed more intrinsic relationships with the crop species in agricultural ecosystems although specific differences were identified between them. While *S. cosmioides* tended to be linked chiefly with the availability of soybean and corn crops, *S. frugiperda* was associated with many host plant species, regardless of the latitude or crop season. This indicates that these species are affected only secondarily by climatic conditions and that they are most abundant when their principal crop species are available (e.g. soybean, maize) (Thiéry *et al.*, 2014).

Interestingly, *S. frugiperda* displayed striking differences in occurrence in regions exhibiting only slight differences in latitude, similar climatic (clear-cut seasons) and agricultural conditions (same species cultivated during the same period). At present, it is still difficult to understand the population dynamics of *S. frugiperda*, as these variations may be linked to at least two biotypes present, known as the 'rice-strain' and 'corn-strain' (Pashley *et al.*, 1985; Nagoshi & Meagher, 2004). Nagoshi & Meagher (2004) report that both strains reveal sharp temporal variations in response to the seasonal conditions. However, it was not possible to study temporal variations among the various biotypes in the present work.

Another relevant phenomenon is the possibility that some *Spodoptera* species migrate along latitudinal gradients, as climate and host plant availability also changes accordingly. If such a phenomenon occurs, we would expect to find a similar population size occurring at different periods of the year, thus corroborating the patterns found for *S. albula* and *S. cosmioides*. However, it should be noted that unlike in the Northern Hemisphere (Nagoshi *et al.*, 2012; 2017), the central region of Brazil (covered by the savanna ecosystems) experiences extreme droughts during the winter (from May to September), thus probably isolating populations from Northern and Southern Brazil and suppressing migrant behavior. In this context, molecular studies are necessary to test this hypothesis.

Intensity of phenology

The variables of climate and food availability may also affect the intensity of the phenological pattern of the species, without actually impacting the time of their occurrence (Ting *et al.*, 2008). However, in this study, *S. frugiperda* was the only species to reveal a variation in the phenological intensity correlated with latitude. This species occurred in greater concentrations (e.g. with stronger phenological intensity) in the higher latitudes and, therefore, exhibited higher climatic seasonality (De Frenne *et al.*, 2013), but is likely to be more homogeneous at the lower latitudes where smaller temperatures are less variable (Wolda, 1988). Therefore, host plant availability appears to change their period of occurrence; however, the intensity or length of this period is linked to climatic factors.

These findings suggest that such dissimilarities in phenology may be related to biotic, abiotic, or both factors (Day, 1984; Eizaguirre *et al.*, 2002; Jang *et al.*, 2009; Garibaldi *et al.*, 2011; Ortega-López *et al.*, 2014; Doherty *et al.*, 2017), and will depend on the pest species. Yet, there are many other factors that can also influence the moth population variation measured in this study, for instance the presence and abundance of predators, parasitoids, and pathogens (Wolda, 1988; Kishimoto-Yamada & Itioka, 2015). However, there are still many challenges to quantify these kind of variables in tropical regions, as many of these ecological relationships are still poorly documented.

Conclusions

By assessing the period of occurrence and degree of phenological intensity, this study reveals that the species studied show unique adaptive strategies for the varying conditions generated by the global latitudinal gradient. Hence, pest management techniques should also take into account the latitudinal location of the host crops. For instance, strategies employed in the management of *S. albula* and *S. cosmioides* need to focus on specific months of the year, when these species are found along different latitudinal gradients. On the other hand, the management of *S. frugiperda* should focus on the period when soybean, corn, wheat, sorghum, and pasture crops are grown, regardless of the time of the year, at the various latitudinal sites. Furthermore, more intense monitoring is necessary at the higher latitudes, during the periods of higher temperatures, while uninterrupted monitoring is required at the lower latitudes, as the phenological intensity decreases. With the prospect of climate change (Peñuelas *et al.*, 2009; De Frenne *et al.*, 2013), a clear understanding of the phenological patterns of pest species becomes central to their management, as they will assist in the prediction of pest incidence in different geographical regions in the future.

Supplementary material

The supplementary material for this article can be found at https://doi.org/10.1017/S0007485318000822

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