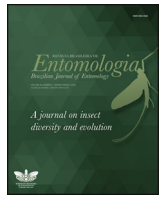




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Spodoptera cosmioides (Lepidoptera: Noctuidae) in Brazil: spatial distribution and relationship in the *S. latifascia* species group

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ABSTRACT

Spodoptera cosmioides (Walker, 1858) is an economically relevant polyphagous moth, widely distributed in the Neotropics and part of the *Spodoptera latifascia* (Walker, 1856) species group. In this study, we used extensive sampling from different regions to describe the spatial distribution of *S. cosmioides* in Brazil and evaluate its variability both from morphological and molecular perspectives. Variable coloration and several morphological similarities were found among *S. cosmioides* and congeners of the *S. latifascia* complex, diverging from each 0.5 to 3.5% of mitochondrial DNA. The genetic divergence at the species level of *S. cosmioides* was 0.5% throughout Brazil, and a geographic structure was absent, including shared haplotypes with *S. descoinsi* Lalanne-Cassou & Silvain, 1994. *Spodoptera cosmioides* was found in all six biomes of Brazil, with the highest abundance recorded in the Cerrado, followed by the Amazon, Atlantic Rainforest, Caatinga, Pantanal, and Pampa.

Introduction

Spodoptera Guenée, 1852 (Lepidoptera: Noctuidae) is a diverse group of noctuid moths globally distributed (Kergoat et al., 2021) of great economic importance, particularly in the tropical and subtropical regions. The morphological resemblance among adults at the specific level (Pogue, 2002) leads to difficulties in assigning specimens to a given taxon, in some cases neither using molecular tools, due to the recent diversification of this genus (ca. 10 Myr [Kergoat et al., 2021]). An example of a cryptic group in the Neotropics is the *Spodoptera latifascia* complex (Silvain and Lalanne-Cassou, 1997), which includes *Spodoptera cosmioides* (Walker, 1858), *Spodoptera descoinsi* Lalanne-Cassou & Silvain, 1994, *Spodoptera evanida* Schaus, 1914, and *Spodoptera latifascia* (Walker, 1856).

Spodoptera cosmioides had been a synonym of *S. latifascia* until Silvain and Lalanne-Cassou (1997) revalidated its specific status. The

distinction between *S. cosmioides* and *S. latifascia*, as well as these from *S. evanida*, is supported by stable differences in genitalia, and >3% of genetic divergence at the mitochondrial DNA level (Kergoat et al., 2021). On the other hand, differentiation of *S. cosmioides* to *S. descoinsi* is challenging, from either morphology (genitalia and wing coloration) or DNA sequences (Kergoat et al., 2012, 2021; Dumas et al., 2015). Concerning the biological perspective, experimental tests on pheromone composition suggested prezygotic differences between *S. cosmioides*, *S. latifascia*, and *S. descoinsi* (Lalanne-Cassou et al., 1994, 1999; Monti et al., 1995, 1997). In addition, hybridization between *S. descoinsi* and *S. latifascia* was demonstrated, and experiments on mating behavior suggested some level of post zygotic isolation between them (Lalanne-Cassou et al., 1999).

S. cosmioides presents one of the broadest distributions in the *S. latifascia* species complex, including sympatry to the other three species (Pogue, 2002). However, the intra and interspecific variation has never been explored throughout the occurrence of *S. cosmioides* based upon extensive sampling. Revealing the variability within the

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S. latifascia complex is relevant due to larval polyphagy; more than a hundred host plants are addressed to *S. latifascia* in Central and North America (Passoa, 1991; Heppner, 2007), and more than 120 to *S. cosmioides* in South America (Takahashi et al., 2003; Specht and Roque-Specht, 2016; Ferreira et al., 2019). The relevance of *S. cosmioides* (often referred to as *S. latifascia* or *S. ornithogalli*) as a pest is also reflected by corresponding publications for Argentina (Rizzo, 1977; Pastrana, 2004; Urretabizkaya et al., 2010), Bolivia (Rogg, 2000), Brazil (Gallo et al., 2002), Colombia (Posada Ochoa, 1989), Paraguay (Resquin-Romero, 2000), Peru (Dioses and Colchado, 2017), Venezuela (Salinas, 1967) and Uruguay (Biezanko et al., 1974; Bentancourt and Scatoni, 2006). In addition, subsidies for the management of this species have been provided, both in plant nurseries and large annual crops, such as cotton and soybean (Santos et al., 1980; Habib et al., 1983; Bavaresco et al., 2002, 2003, 2004; Fernández et al., 2004; Santos et al., 2010; Cabezas et al., 2013; Fronza et al., 2013; Bernardi et al., 2014; Lutz et al., 2018; Loureiro et al., 2020; Machado et al., 2020; Meriño-Cabrera et al., 2020; Barcellos et al., 2022).

In this study, we characterize spatial variation in *S. cosmioides* under an extensive sampling throughout its distribution range in Brazil. In addition, a comparative assessment was performed, including genitalia, wing coloration and size, and mitochondrial DNA haplotypes within the *S. latifascia* complex.

Material and methods

Spatial distribution and specific abundance

First, a search for specimens and information about the geographical distribution of species belonging to the *S. latifascia* complex was performed. Regarding bibliographic sources, all publications that provided collection sites, at least up to the municipal level, were used. Database queries were conducted using BOLD (Ratnasingham and Hebert, 2007). Data were obtained from the following collections: CLAM - Coleção Alfred Moser, São Leopoldo, Rio Grande do Sul, Brazil; CPAC - Coleção Entomológica da Embrapa Cerrados, Planaltina, Distrito Federal, Brazil; CVOB - Coleção Vitor O. Becker, Reserva Serra Bonita, Camacan, Bahia, Brazil; MCTP - Museu de Ciências e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil; MECB - Museu de Entomologia Ceslau Maria Biezanko, Universidade Federal de Pelotas, Pelotas, Rio Grande do Sul, Brazil; MUCS - Museu de Ciências Naturais da Universidade de Caxias do Sul, Caxias do Sul,

Rio Grande do Sul, Brazil; and UFSM - Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brazil. Variation in wing color and gross genitalia morphology of 45 specimens from these collections was analyzed.

In addition to this information, we used data on abundance for specimens identified as *S. cosmioides* collected in 16 localities in Brazil (Table 1). The collections were conducted through monthly samplings (five nights around each new moon) from July 2015 to June 2017, employing Pennsylvania traps equipped with a collection bucket and three liters of 96°GL ethyl alcohol. Spatial distribution maps were created using Quantum GIS 2.14.3 software. Representative materials were deposited in the DZUP - Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil, CPAC, and MUCS.

Maps were created using the software Quantum GIS 2.14.3 and vectorized with the software CorelDraw® X7, with points indicating the recorded presence of each of the four species, along with a table and a map illustrating the specific abundance of *S. cosmioides* at various sites. This analysis encompasses two years of collection in Brazil. In addition, a schematic map was developed, depicting the likely distribution of each species based on data gathered during the current study.

Morphology

For genitalia observations, the abdomen of specimens was detached, cleared in a 10% potassium hydroxide (KOH) solution, stained with Chlorazol black, and slide-mounted in glycerin following Brambila (2009). We performed observations with a Leica® M125 stereomicroscope and photographed with an attached Sony® DSC-H10 digital camera. All images were digitalized and vectorized with the software CorelDraw® and CorelPhotoPaint® X7. Comparisons at inter-specific levels were made with descriptions and photographs provided by Pogue (2002).

Five hundred (250 males and 250 females) field-collected moths of different locations (including the north, center-west, south, and southeastern regions of Brazil) were pinned and dried for analysis of wing color. In order to make comparisons representative of space (all biomes) and time (seasons), 8 to 10 of the most intact specimens (4 to 5 females/males), from each month and location were randomly evaluated. Specimens with color variation were photographed with a Sony DSC-H10 digital camera. We compared the external coloration with the images of types from *S. cosmioides*, *S. descoinsi*, *S. evanida*, and *S. latifascia*, also using Pogue (2002).

Table 1 Brazilian biomes, states, municipalities, geographic coordinates (latitude and longitude), altitude, and the number of specimens (n) of *Spodoptera cosmioides* captured with light traps in agricultural areas on monthly collections (July 2015–June 2017).

Biome	State	Municipality	Latitude	Longitude	Altitude	Specimens collected (n)
Amazon	Roraima (RR)	Alto Alegre	02°56' N	61°00' W	87	287
Amazon	Pará (PA)	Mojú dos Campos	02°41' S	54°34' W	114	103
Amazon	Acre (AC)	Rio Branco	10°01' S	67°37' W	207	678
Amazon	Mato Grosso (MT)	Sinop	11°52' S	55°35' W	380	84
Caatinga	Pernambuco (PE)	Petrolina	09°03' S	40°10' W	365	1078
Cerrado	Tocantins (TO)	Porto Nacional	10°30' S	48°18' W	262	128
Cerrado	Bahia (BA)	Luis Eduardo Magalhães	12°06' S	45°45' W	742	630
Cerrado	Distrito Federal (DF)	Planaltina	15°36' S	47°42' W	1000	26
Cerrado	Mato Grosso do Sul (MS)	Chapadão do Sul	18°46' S	52°31' W	806	656
Cerrado	Minas Gerais (MG)	Uberaba	19°39' S	47°58' W	819	54
Pantanal	Mato Grosso do Sul (MS)	Miranda	20°06' S	56°37' W	120	219
Atlantic Rainforest	Espírito Santo (ES)	Domingos Martins	20°22' S	41°03' W	950	09
Atlantic Rainforest	Espírito Santo (ES)	Alegre	20°45' S	41°29' W	120	223
Atlantic Rainforest	Paraná (PR)	Londrina	23°11' S	51°10' W	594	127
Atlantic Rainforest	Rio Grande do Sul (RS)	Passo Fundo	28°13' S	52°24' W	682	81
Pampa	Rio Grande do Sul (RS)	Bagé	31°18' S	53°59' W	242	44

To address the wingspan variation, the forewings of 175 specimens collected in a latitudinal gradient in Brazil were measured from base to apex with a caliper (precision = 0.02 mm). We performed an ANOVA to test for differences in wing size between males and females. To determine whether wing size is related to latitudinal gradient and sex, we performed a linear regression analysis with the software R version 3.4.2. We adopted an alpha of 0.05 for all tests.

DNA analysis

DNA was extracted from 40 field-collected specimens of *S. cosmioides* from nine collection sites in Brazil (Table 2) by grinding part of the thorax in a PureLink Genomic DNA kit (Thermo Fisher Scientific, Waltham, USA). We amplified 650 base-pair fragments of the Cytochrome oxidase subunit I gene (COI) using primers Lco1490 and Hco2198 under conditions described by Folmer et al. (1994). The resulting PCR products were treated with enzymes (exonuclease and alkaline phosphatase) and sequenced in the forward strand with the Big Dye Terminator version 3.1 Cycle Sequencing Kit (Thermo Fisher Scientific, Waltham, USA); runs were performed on an ABI3730 XL automatic sequencer. We edited and aligned sequences using the software Codon Code Aligner version 9 (CodonCode Corporation, USA).

We characterized the genetic variation based on COI haplotypes using the software DnaSP version 6 (Rozas et al., 2017). In addition to the 13 sequences generated in this study for *S. cosmioides*, homologous COI sequences were mined from BOLD Systems and NCBI, including 48 recognized as *S. cosmioides* from Brazil, Costa Rica, and French Guiana, and nine identified as *S. descoinsi* from French Guiana (Table 2). To estimate the degree of divergence in the *S. latifascia* complex, we incorporated 10 sequences of *S. evanida*, and 29 sequences of *S. latifascia*, the closest related species to the *cosmioides+descoinsi* clade (Kergoat et al., 2021). The relationships among haplotypes were

inferred based on a median-joining approach (Bandelt et al., 1999) using the NETWORK version 10.0.0 software (Fluxus Technology Ltd., Sudbury, Suffolk, UK). Also, the evolutionary relationships of sequences were inferred through a maximum likelihood (ML) tree, implemented in PHYML v3.0 (Guindon et al., 2010), using 1000 replicates of heuristic search with random addition of sequences and TBR branch swapping. We performed a molecular variance (AMOVA) analysis based on haplotype frequencies using Arlequin v3.5 to evaluate the partition of variation at a population level, i.e., grouping specimens by geographic locality, such as Brazil vs. French Guiana, given their phylogenetic proximity. In addition, we calculated the genetic distance among pairs of species using the Kimura 2-parameter model with 1000 bootstrap replications.

Results

Distribution and spatial abundance of Spodoptera latifascia complex

All specimens examined, both from scientific collections in several institutions and those monthly collected in Brazil, indicated only the species *S. cosmioides* across the entire Brazilian territory, except one specimen of *S. evanida* collected in Espírito Santo (CVOB), Southeastern Brazil. Regarding bibliographic sources and databases, *S. cosmioides* is reported for the entire South America, excluding Chile, and Central America, and also in Panama and Southern Trinidad (Pogue, 2002). Additionally, the results of genetic comparisons indicated the presence of *S. cosmioides* in Costa Rica. *Spodoptera descoinsi* is reported in a non-specific location in Peru, various locations in the coastal area of French Guiana (Pogue, 2002), and near the tri-border area between French Guiana, Brazil, and Suriname (MNHN & OFB, 2023). *Spodoptera evanida* is reported in Colombia, Venezuela, French Guiana, and from south Amazonia to Espírito Santo state in Brazil. *Spodoptera latifascia* occurs from the southern United States, south to Costa Rica, and throughout the Caribbean, excluding Trinidad (Pogue, 2002) (Figs. 1 and 2).

Table 2

Samples used in the molecular analysis, including species as originally identified/deposited in databases, BOLD ID, locality, and occurrence of the four haplotypes observed in the *cosmioides-descoinsi* clade (see Fig. 9).

Species	BOLD Sequence ID	Locality	5-COI haplotype			
			H1	H13	H14	H15
<i>S. cosmioides</i>	BIGLE010-23, BIGLE011-23	Brazil, Sinop	X			
	BIGLE022-23	Brazil, Uberaba	X			
	BIGLE021-23	Brazil, Porto Nacional	X			
	BIGLE020-23	Brazil, Planaltina	X			
	BIGLE019-23	Brazil, Passo Fundo	X			
	BIGLE018-23	Brazil, Petrolina	X			
	BIGLE014-23, BIGLE015-23	Brazil, Londrina	X			
	BIGLE013-23	Brazil, Espírito Santo	X			
	BIGLE012-23	Brazil, Bahia	X			
	GBGL12601-13 to GBGL12603-13, GBGL12605-13 to GBGL12629-13; GBGL12604-13	Brazil, Pelotas	X		X	
	BLPDV1040-11; BLPDV4477-18, BLPDB111-09	Costa Rica, Area de Conservacion Guanacaste	X			
	INCTA730-10, BIGLE016-23, BIGLE017-23	Brazil, Para, Mojuí dos Campos	X			X
	LEMMZ013-10, LEMMZ014-10, LEMMZ121-10 to LEMMZ123-10, LEMMZ125-10, LEMMZ126-10, LEMMZ372-10	Brazil, Paraná, Serra do Mar	X			
	MHMYN5949-14	Costa Rica, Alajuela, Area de Conservacion Guanacaste	X			
	GBGL12581-13	French Guiana			X	
	GBGL12578-13, GBGL12577-13, GBGL12579-13; GBGL12580-13, GBGL12582-13	French Guiana	X			
	<i>S. descoinsi</i>	GBGL12570-13 (HQ177309), GBGL20223-15, GBGL12572-13, GBGL12573-13, GBGL12574-13, GBGL20222-15, GBGL20221-15	French Guiana			X
GBGL12571-13, GBGL12575-13		French Guiana	X			

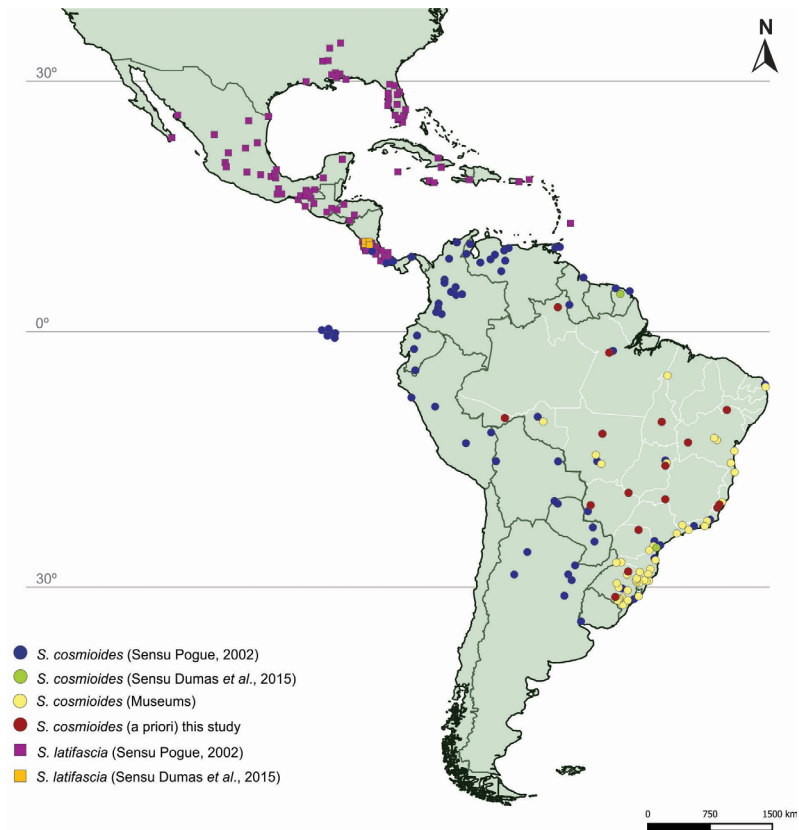


Figure 1 Geographical distribution of *Spodoptera cosmioides* and *S. latifascia* from the literature (Pogue, 2002; Dumas et al., 2015), field collection, and museum records obtained in the present study.



Figure 2 Geographical distribution of *Spodoptera evanida* and *S. descoinsi* from the literature (Pogue, 2002; Dumas et al., 2015; GBIF Secretariat, 2023).

The specific abundance of monthly and simultaneous collections conducted between 2015 and 2017 both indicated *S. cosmioides* found in all six biomes of Brazil, with the highest abundance recorded in the Cerrado (1500). The Amazon was the second region with significant abundance (1150 specimens), followed by the Caatinga (1078 specimens). In the Pantanal, Atlantic Rainforest, and Pampa, specimens were also collected, but the abundance was comparatively lower (220, 450, and 40 specimens, respectively) (Table 1, Fig. 3).

Genitalia and wing morphology

The morphology of genitalia of *S. cosmioides* specimens (Fig. 4) was nearly invariant among individuals collected from different regions of Brazil. Minor differences were limited to specimens exhibiting slightly more pronounced degrees of sclerotization, though without consistently affecting the shape or size of the structures.

The genitalia of *S. cosmioides* collected in Brazil were invariable and consistent with the typo's description. In males, the uncus is curved, elongated, and slightly widest at the base, gradually narrowing towards the apex. The costal process, situated sub-basally on the costa of the valva, is elongated and well-sclerotized, with the apex narrower and recurved (Figs. 4A, B). The cucullus has a rounded apex. The ampulla, a part of the clasper, is transverse to the coastal process; the basal sclerite of the clasper is a reduced plate, forming an inverted Y. The clavus has a base narrower than the apex, and numerous sensory setae are present at the apex (Fig. 4B). The coremata are bilobed (Fig. 4A). The basis of the vertical projection of the juxta is narrower, and the median projection is elongated, forming a triangle (Fig. 4C). The aedeagus is slightly sinuous, the vesica is elongated, and the cornuti are in the form of minute flat granules (Fig. 4D).

In females, the ventral plate of the ostium bursae is longer than wide, the distal margin narrow and U-shaped, and the ductus elongated and sclerotized, as in the appendix. Corpus bursae are large with striated membranes (Figs. 4E-G). Single signum, elongated with approximately 1 mm of length (Figs. 4E, H).

Regarding wing morphology, the adults evaluated in this study exhibit sexual dimorphism in both coloration and the size of the forewings (Fig. 5). The ground coloration of the male forewings ranges from ochre, light brown, to purplish gray. A white, oval, orbicular spot is adorned with light-brown scales in the center, located in the median region of the wing. Variation in the background color is noticeable, especially on the inner margin of the forewing, with intense ochre coloration observed in specimens collected at lower latitudes (e.g., Fig. 5A, C) and lighter tones in specimens collected at higher latitudes (Fig. 5I, K). Although not quantified, it was observed variation in tones of color among specimens collected at different times of the year. Specimens preserved for a long time either in alcohol (more than five years in this study) or pinned-dried (decades or even centuries) in scientific collections exhibit faded coloration, which suggests that such differentiation should be cautiously considered.

Females are slightly dark, with brown and gray tones, with a pattern of spots typical of that described in Pogue (2002). The hind wings are white, and a small patch of scales is found in the apex, pale brown in males and dark brown in females. The hind wings were similar to those found in the lectotype of *S. cosmioides* and the paratype of *S. descoinsi* (Figs. 6A, 6B and 5). Females had significantly larger forewings (15–21 mm) than males (13–19 mm); one-way ANOVA, $F = 35.64$, $p < 0.005$ (Fig. 7).

A linear regression that considered the interaction between latitude and sex showed that ca. 22% of the variation in size was explained by these factors in conjunction ($r^2 = 0.2257$, $p < 0.05$).

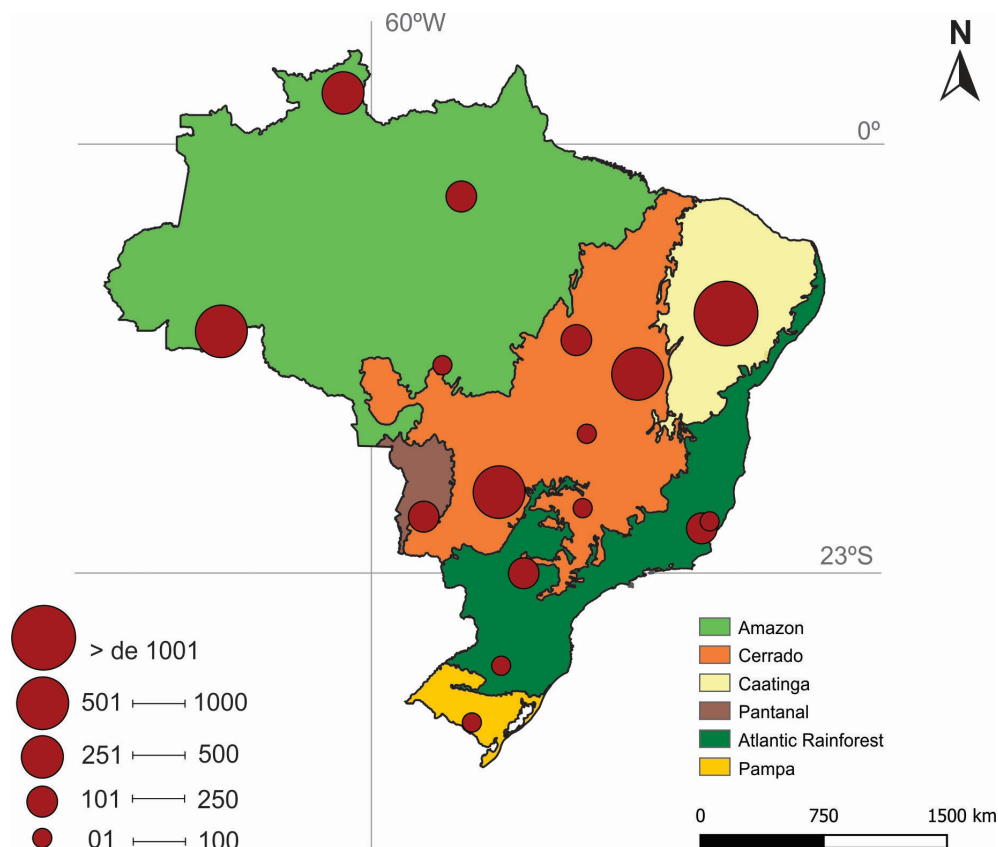


Figure 3 Variation in the number (red circles) of *Spodoptera cosmioides* sampled in this study for Brazil. For a complete description of localities and dates, see Table 1.

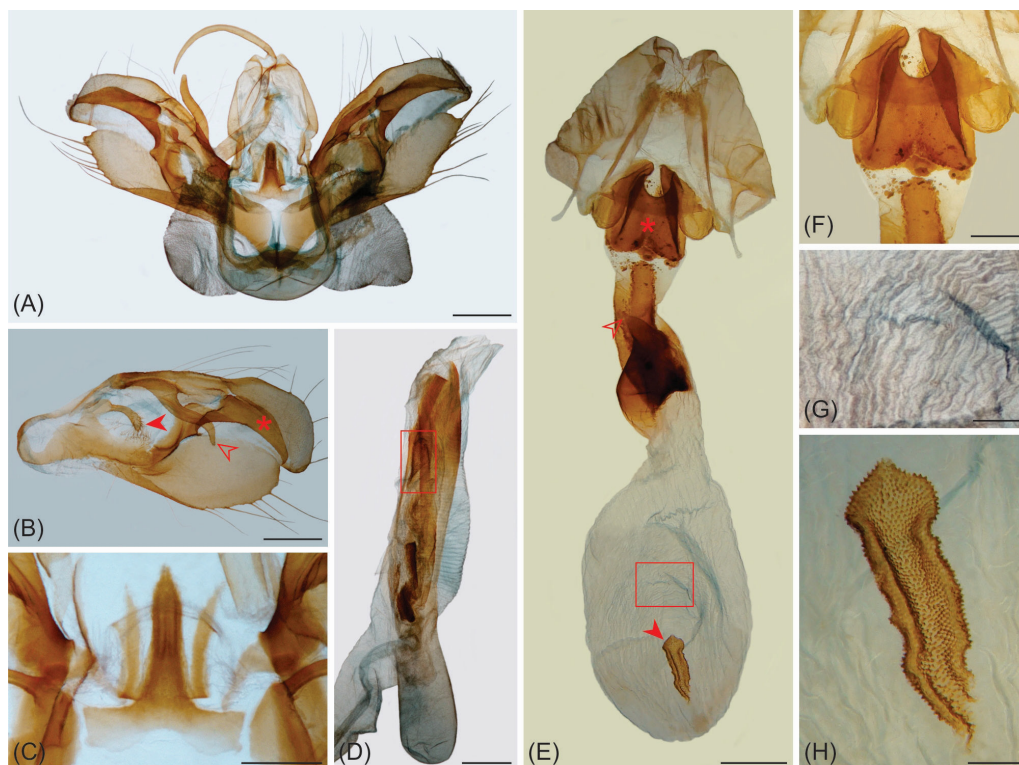


Figure 4 Genital morphology of *Spodoptera cosmioides* under light microscopy. Male genital, ventral view (aedeagus omitted) (A); right valva removed, open and closed arrow indicates coastal process and clavus, respectively, the asterisk indicates ampulla (B); detail of juxta in a triangle, ventral view (C); aedeagus, rectangle indicates flat granules in cornuti (D); female genital, ventral view (E), the asterisk indicates ventral plate of ostium bursae; open and closed arrow indicates the appendix bursae and the signum, respectively; the ventral plate of ostium bursae in detail (F); striated membranes of the corpus bursae (G), marked with a rectangle in (E); signum in detail (H). Scales bars: A, B, E = 1000 μ m; C, D, F = 500 μ m; G = 250 μ m, H = 200 μ m.

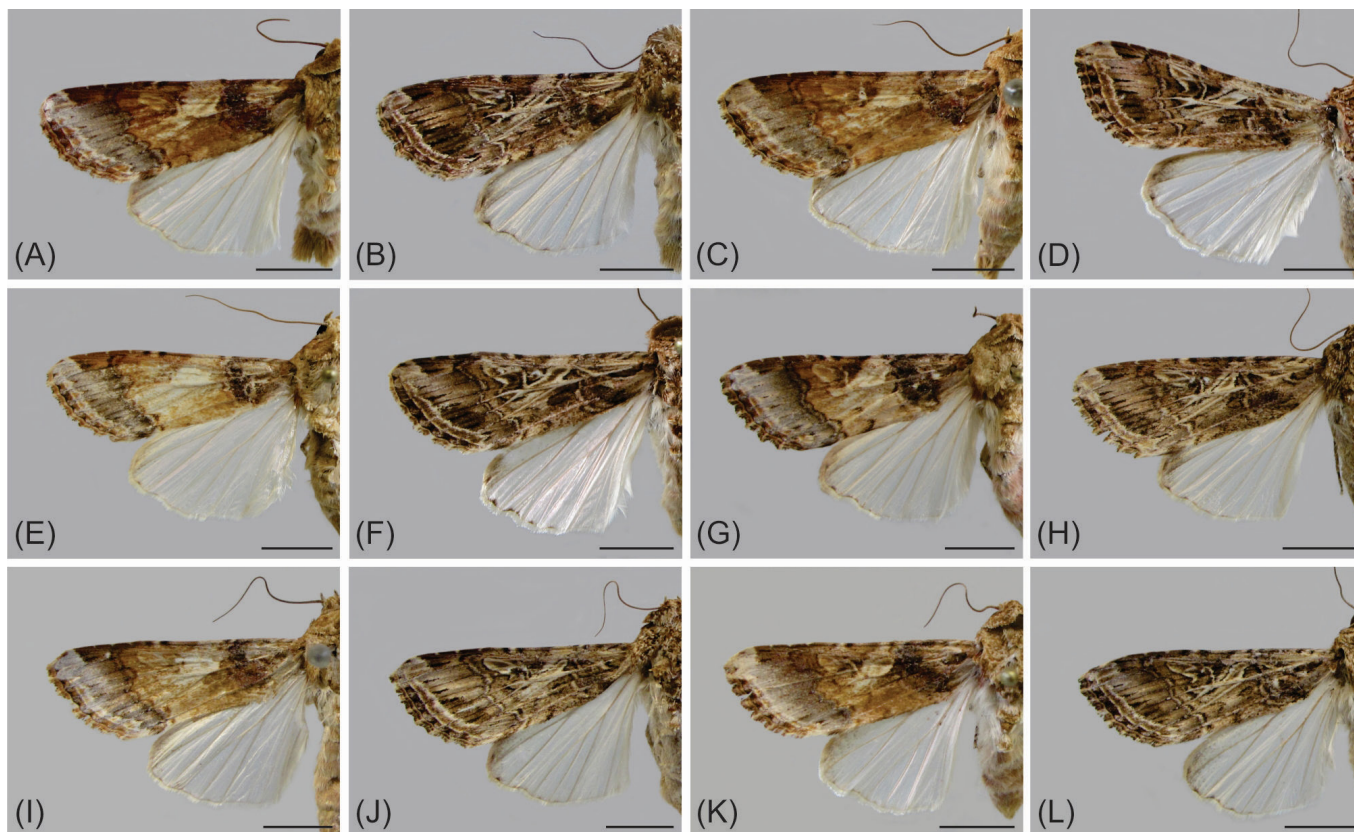


Figure 5 Variation in dorsal wing color pattern in *Spodoptera cosmioides*. A-B Rio Branco: A #m, B #f (left forewing); C-D Planaltina: C #m, D #f (left forewing); E-F Chapadão do Sul: E #m, F #f (left forewing); G-H Alegre: G #m, H #f (left forewing); I-J Londrina: I #m, J #f (left forewing); K-L Passo Fundo: K #m, L #f (left forewing). Scale bars: 5 mm, respectively.

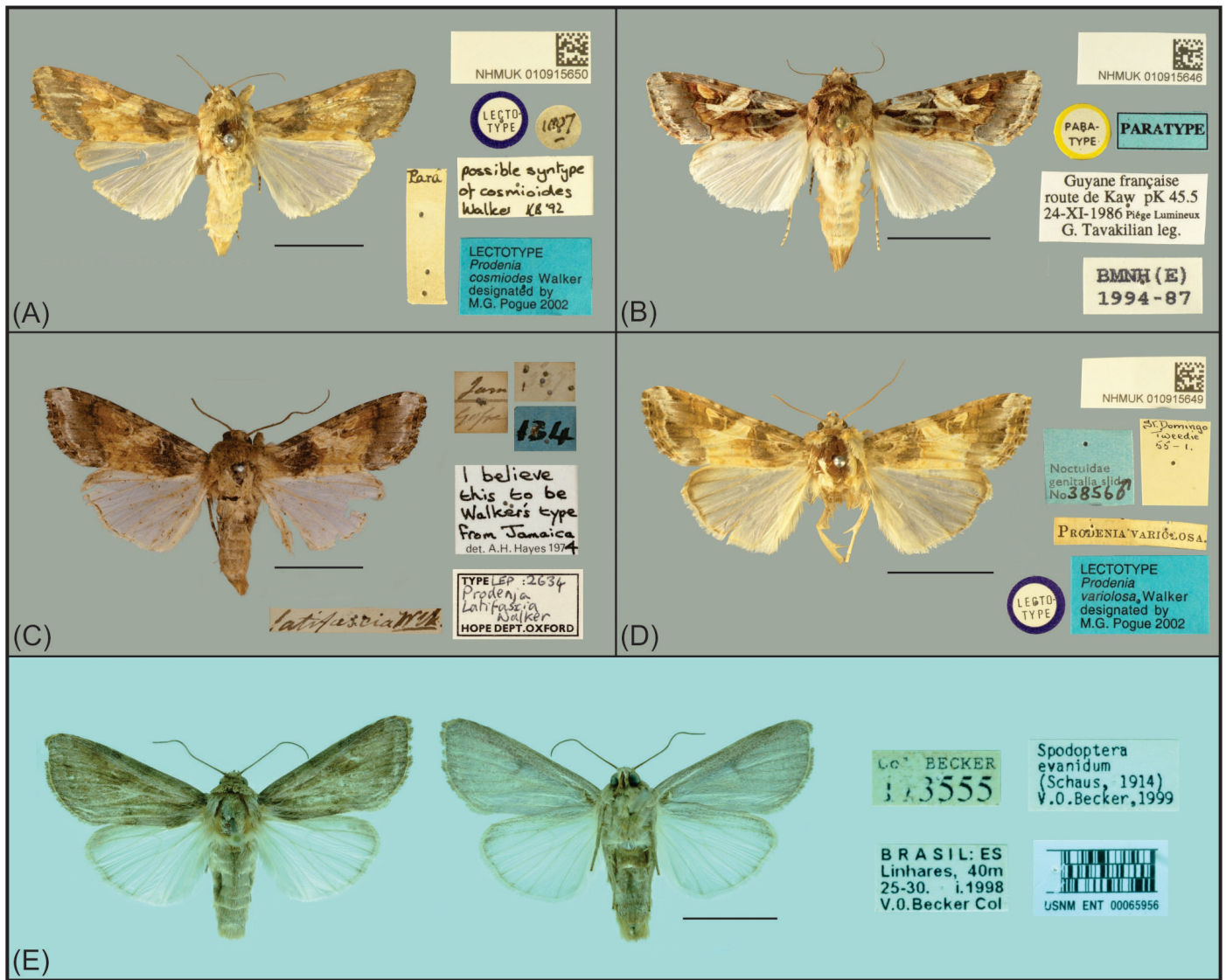


Figure 6 Lectotype of *Spodoptera cosmioides* (A), paratype of *S. descoinsi* (B), possible (syn)type of *S. latifascia* (C), and lectotype of *Prodenia variolosa* Walker, a junior synonym of *S. latifascia* (D), under dorsal view. Dorsal and ventral views of a specimen of *S. evanida* (E). Scale bar: 10 mm.

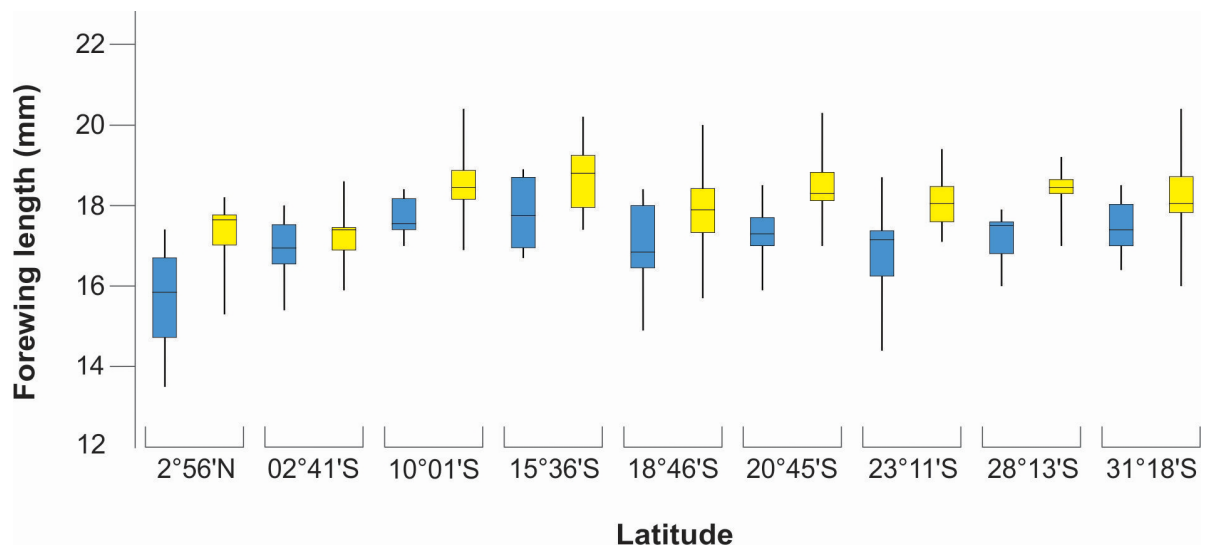


Figure 7 Variation in *Spodoptera cosmioides* wing length for populations distributed along a latitudinal gradient in Brazil. Blue and yellow colors correspond to male and female, respectively. Box plots represent medians and quartiles.

Mitochondrial DNA variation

In the phylogenetic tree, *S. cosmioides* and *S. descoinsi* merged into a single clade, sister to *S. evanida*, a cluster related to *S. latifascia* (Fig. 8). The network analysis of the mitochondrial sequences showed 15 haplotypes arranged in three haplogroups: *cosmioides-descoinsi* (H1, H13–H15), *evanida* (H7–H9), and *S. latifascia* (H2–H6, H10–H12), separated by five to seven mutational steps (Fig. 9A). When considering the relationships within the *cosmioides-descoinsi* haplogroup, most haplotypes differed by a single mutation. The H1 showed the highest frequency, widely spread in Brazil, from the southernmost (Latitude 31° south) to Costa Rica (Latitude 10° North), including populations in French Guiana (Fig. 9B). The H14 and H15 were restricted to Pelotas municipality and Para state (Brazil), respectively. The H13 was exclusive to French Guiana, including sequences identified as *S. cosmioides* and *S. descoinsi*. Pairwise genetic distance evidenced a gradient of divergence, with a minimum of 0.5% between *S. cosmioides* and *S. descoinsi* and a maximum of 3.5% between *S. evanida* and *S. latifascia* (Fig. 10).

Results from the analysis of molecular variance (AMOVA) considering specimens in Brazil as a distinct population of specimens from French Guiana suggested that a majority of the genetic variance (66%) is attributed to variation within populations and the remaining (34%) to variation among populations (Table 3).

Discussion

The study of spatial distribution in pest crops is fundamental for the optimization of sampling techniques, determination of economic damages, and development of actions for its management (He et al., 2022). The high biotic potential, associated with the use of more than a hundred host plants by its larvae (Specht and Roque-Specht, 2016, 2019), gives support to *S. cosmioides* to be distributed approximately from latitudes 10° North in Costa Rica (this study), Panama, and Trinidad to 35° South, including Uruguay and southern Argentina (Pogue, 2002). In Brazil, *S. cosmioides* occurs in areas with different edaphoclimatic conditions, being abundant in sampling localities, including biomes with contrasting climates and, consequently, vegetation compositions: humid equatorial (Amazon), semiarid (Caatinga), tropical savanna (Cerrado), even temperate (Pampa), tropical rainy forest (Atlantic Forest) and tropical wetland (Pantanal).

It is important to note that the majority of studies until the 1980s and the records of specimens deposited in museums (Figs. 1-2) can be attributed to the historical pattern of Brazilian agricultural expansion, which commenced on the northern coast and primarily occupied areas with agriculture in the Southeast and South (Miranda, 2020). Despite this, the assessment of specific abundance (Fig. 3), coupled with larval polyphagy and studies on biology (Santos et al., 1980; Habib et al., 1983; Bavaresco et al., 2002, 2003, 2004; Fernández et al., 2004; Santos et al., 2010; Cabezas et al., 2013; Fronza et al., 2013; Bernardi et al., 2014; Specht and Roque-Specht, 2016, 2019; Lutz et al., 2018; Loureiro et al., 2020; Machado et al., 2020; Meriño-Cabrera et al., 2020; Barcellos et al., 2022), thermal requirements, and ecological zoning (Parra et al., 2022), suggest that this species may pose greater harm to cultivated plants in warmer (tropical and equatorial) areas of Brazil and other American countries. In this context, it is noteworthy that the agricultural occupation process of the Central-West and northern regions of Brazil only began in the 1970s and continues to expand northward (Miranda, 2020).

Except for *S. evanida*, which has a more uniform color, perhaps due to the small number of individuals available for study, all three other species in the *S. latifascia* complex present variable wing coloration (see adult photos in Pogue, 2002), especially due to different collection sites, as observed in this study (Fig. 5). It is important to emphasize

that the conspicuous coloration of the *S. descoinsi* paratype (Fig. 6B) (Lalanne-Cassou et al., 1994; Pogue, 2002) may not be present in all specimens (see. MNHN & OFB, 2023), whose color hardly differs from *S. cosmioides* and *S. latifascia*. The chromatic variability of these species is documented even in caterpillars of *S. latifascia* (Passoa, 1991) and *S. cosmioides* (Zenker et al., 2007). In these cases, it is observed caterpillars from the same egg mass with distinct color patterns, from entirely black, well-marked colored lines and triangular spots to light gray without (or with a reduced number) triangular spots and longitudinal stripes.

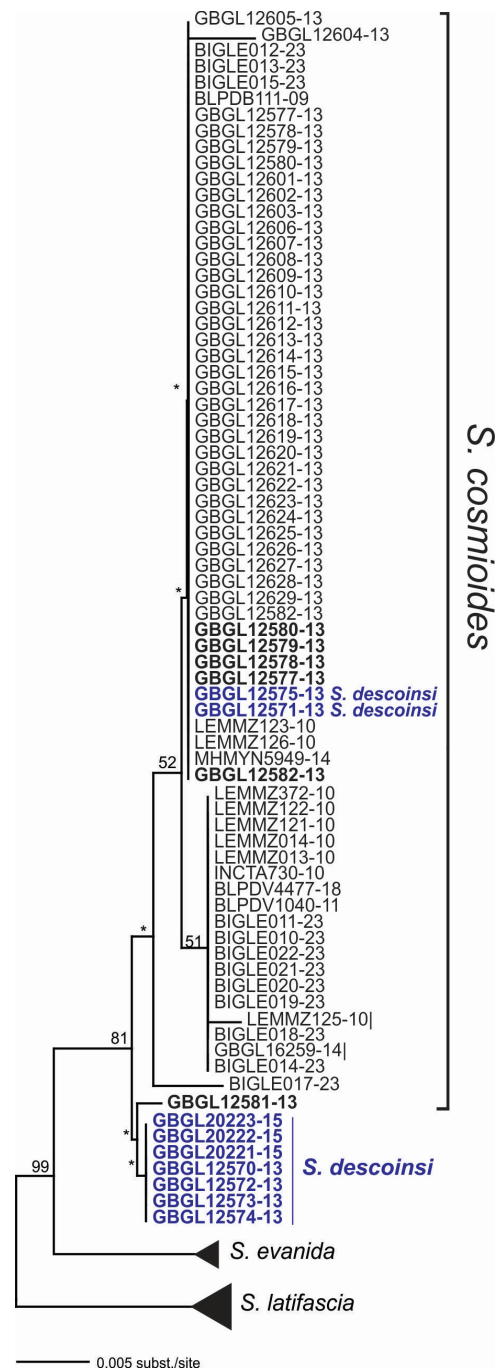


Figure 8 Maximum likelihood tree of *Spodoptera cosmioides* reconstructed based on sequences of the Cytochrome oxidase subunit I gene. Sequences of *S. descoinsi* (blue), *S. evanida*, and *S. latifascia* taken from BOLD Systems were also included. The numbers above the branches indicate bootstrap support (asterisk indicates values below 50%). Bold indicate sequences from French Guiana (blue, *S. descoinsi*; black, *S. cosmioides*).

Table 3

Analysis of molecular variance (AMOVA) using *F*-statistics based on mitochondrial sequences for *cosmioides* + *descoinsi* clade, under the geographic scenario: specimens from French Guiana (*S. descoinsi*) were grouped as a population and samples from Brazil (*S. cosmioides*) as another population.

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Among populations	1	4.004	0.13560	34.55
Within populations	70	20.524	0.39320	65.45
Total	71	24.528	0.52880	
Fixation Index	$F_{ST}: 0.34554$			

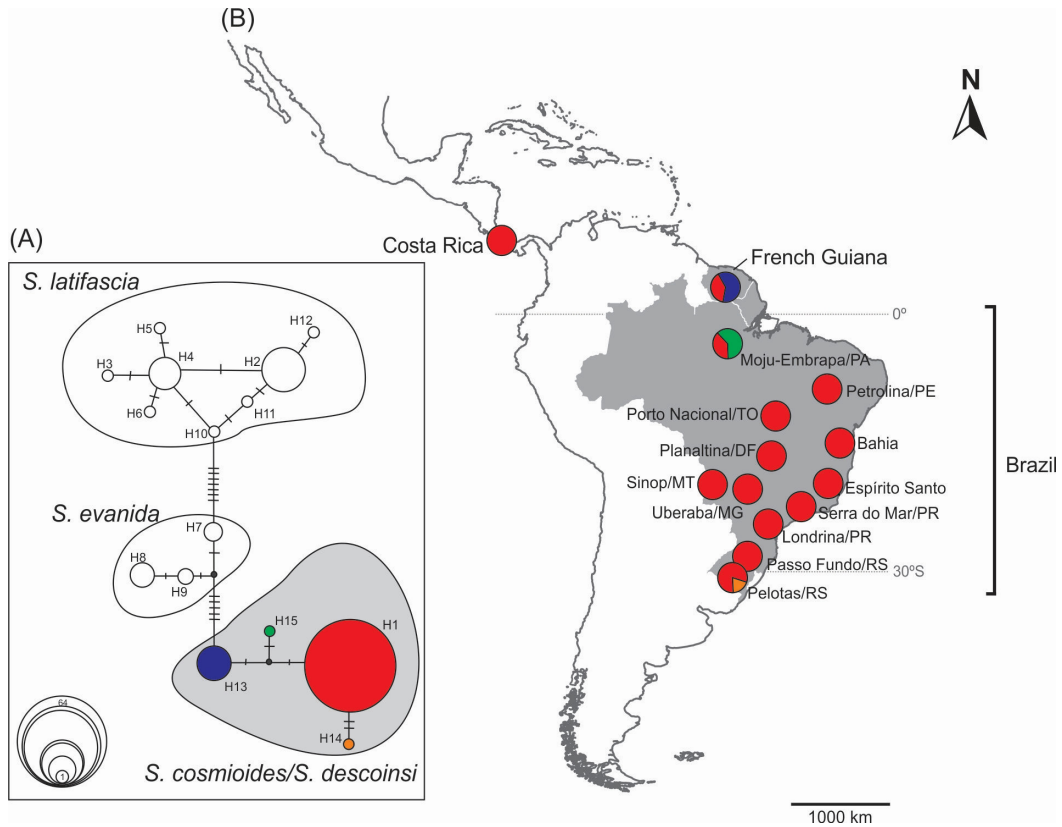


Figure 9 Evolutionary relationships within the *S. latifascia* group based on sequences of the Cytochrome oxidase subunit I gene (COI). Median-joining network among COI haplotypes (A). Haplotype frequency is indicated by the circle size (given in the inset). Distribution of the five haplotypes identified in *cosmioides*+ *descoinsi* clade indicated by circles of fixed size, colored, according to the proportion of occurrence for each site (B).

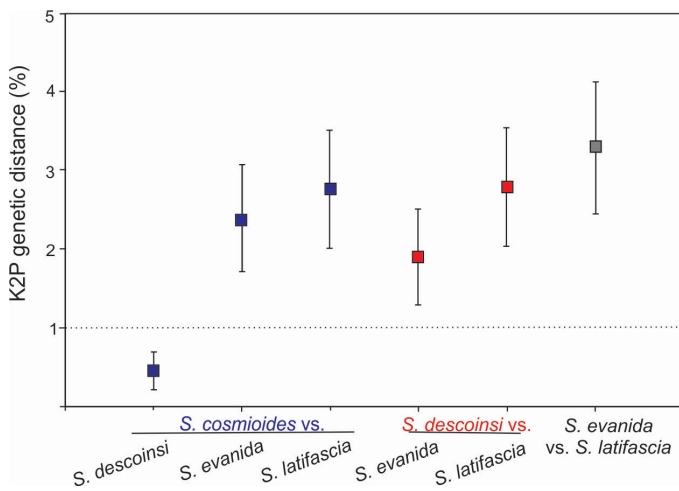


Figure 10 Pairwise genetic distance (mean and standard error) in the *S. latifascia* group (*S. cosmioides*, *S. descoinsi*, *S. evanida*, and *S. latifascia*) based on sequences of the Cytochrome oxidase subunit I (COI) gene fragment, using Kimura-2 parameters (K2P) model. The dashed line highlights a 1% threshold of distance.

The variation in the wing coloration within the *S. latifascia* species complex is similar to those found in congeners, such as *Spodoptera albula* (Walker, 1857), *S. eridania* (Stoll, [1782]), *S. exigua* (Hübner, [1808]), and *S. ornithogalli* (Guenée, 1852) (Pogue, 2002; Brito et al., 2019). In this sense, it is common in *S. eridania* a black longitudinal streak that begins in the reniform spot and reaches out to the costal margin of the forewing in some individuals. Likewise, the orbicular spot on the forewing of some individuals of *S. eridania* and *S. albula* appears very conspicuous in some individuals and completely discolored, unnoticeable in others (Pogue, 2002). This is a known pattern in Noctuidae, where both individuals from different locations, or even from a single female, present forewings with different ground colors and spots (or spot patterns) either present, absent, or variable (Specht et al., 2021).

When added to sexual dimorphism, such differences have as consequences a great number of proposed synonymies and erroneous identifications in collections (Pogue, 2002). Corresponding variation indicates that taxonomic studies in this group should consider samples of large sizes, coming from a variety of localities, and when possible, based upon reared individuals where population variation if any can thus be detected.

The comparison of the genitalia of *S. cosmioides* collected in Brazil with *S. descoinsi* showed inconsistent differences, which might be explained by their phylogenetic proximity (Kergoat et al., 2012, 2021; Dumas et al., 2015). For this morphological comparison, images presented in the original description of *S. descoinsi* were used (Lalanne-Cassou et al., 1994), in addition to those kindly provided by Dr. Gael J. Kergoat (INRAE, CBGP, France). The males are similar in the uncus, costal process, cucullus, ampulla, juxta, coremata, and aedeagus, but slightly different when comparing the clasper and clavus. The base of the clasper is narrower in *S. cosmioides*, as is its width towards the ampulla. Besides, the clavus appears slightly longer in *S. descoinsi*; however, the number of sensory setae found in the apex of the clavus of both species does not differ. In females, the distal margin of the ventral plate of the ostium bursa appears to be slightly narrower than in *S. descoinsi*. In addition, the apex of the appendix also seems to be more pointed in *S. cosmioides*. The other structures have similar shapes and sizes. Consistent diagnostic divergences between the genitalia of *S. cosmioides* and *S. descoinsi* were not found. However, we here maintained the latter as a good species based on pre- and postzygotic isolation mechanisms existing among them, as already mentioned (Lalanne-Cassou et al., 1999), pending further sampling and data to be obtained regarding it.

Overall, a distinction based on stable morphological characters in the *S. latifascia* complex was found only between *S. cosmioides*/*S. descoinsi*, *S. evanida*, and *S. latifascia*. As already pointed out by Silvain and Lalanne-Cassou (1997) and Pogue (2002), males of these species differ regarding the ochreous patch in the forewing, between the antemedial and postmedial lines and below vein M. This patch is larger and more distinct in *S. cosmioides*. In males, the genitalia are mainly distinguished by the shape of the clasper, more trapezoidal in *S. cosmioides*, and that of the juxta, finer in *S. cosmioides*. In females, the lamella antevaginalis is less wide in *S. cosmioides*, and its anterior part is more sclerotized. The anterior part of the ductus bursae is less sclerotized in *S. cosmioides* than in *S. latifascia*. Accordingly, morphological comparison mirrored the results of mtDNA analysis, which shows the highest genetic divergence (3.5%) in the species complex.

From a molecular perspective, the evolutionary relationships first demonstrated by Dumas et al. (2015) and Kergoat et al. (2012, 2021) were recovered, grouping *S. cosmioides* with *S. descoinsi* in a single clade, with a shallow structure of two subclades. Three individuals (GBGL12581-13 *S. cosmioides*, GBGL12575-13 *S. descoinsi*, and HQ177308.1 *S. descoinsi*) were responsible for the non-reciprocal monophyly of the two species. It is likely that such spurious results recovered with mixed specimens of both species on the tree are due to the misidentification of sequences mined from the database. To clarify this scenario, those sequenced specimens should have their morphology examined, which is impracticable. Alternatively, specimens belonging to *S. descoinsi* should be re-collected in French Guiana, and examined from morphological and molecular perspectives. However, given the shallow divergence of the clade that abridges most sequences of *S. descoinsi* in our resulting tree, admixture with *S. cosmioides* may occur in some level, resulting from horizontal gene transfers, and incomplete lineage sorting of the mitochondrial gene used to infer relationships. Thus, a broader analysis of differentiation is necessary for these species. Individuals from French Guiana together with those *S. cosmioides* from Brazil should be further examined using distinct nuclear markers and/or SNPs to elucidate the degree, if so, of admixture. The genetic divergence at the species level of *S. cosmioides* was 0.5% throughout the distribution range. A lack of geographic structure was evident. From the four haplotypes of *S. cosmioides* revealed in this study, H1 was the most frequent and

widespread throughout the latitudinal scale; the others were restricted to certain regions, such as southernmost Brazil (H14), the Brazilian Amazon (H15), and French Guiana (H13). In the latter, the H13 was shared by representatives of *S. cosmioides* and *S. descoinsi* from the same area, which may indicate ancestral polymorphism and/or introgression. Similar to the congeneric *S. ornithogalli* (Brito et al., 2019), a more widely distributed haplotype was reported from Southeast and South Brazil, with others restricted to the extreme south, found from the center of the country to the south and shared with the Northern Hemisphere, the Amazon equatorial area, and French Guiana. Thus, the combined results of this study with those of Brito et al. (2019) indicate the existence of haplotype endemism for both species in similar locations. Specimens collected in this study, and those by Brito et al. (2019), were sampled in locations close to or within agricultural areas, which may have reduced the chance of collecting specimens associated with native plants.

In conclusion, data showed that as predicted, the distribution range of *S. cosmioides* is broader than that already known, partially overlapping with that of *S. latifascia* in Central America, for example in Costa Rica, and totally with those of *S. descoinsi* and *S. evanida* in South America. The higher abundance of *S. cosmioides* in tropical and equatorial areas detected here, when associated with its polyphagous feeding habit and pesticide tolerance in specific cases, indicate that expansion of human settlement towards the last agriculture frontiers in the north in Brazil may favor population increase and enhance pest status of this species, particularly in monocultures.

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Conflict of interest

The authors declare that they have no conflicts of interest.

Author contribution statement

RB and GLG Conceptualization (Supporting). RB, GRPM and WSA Data curation (Supporting). RB, VFERS and WSA Formal analysis (Supporting). RB Methodology (Equal), Software (Supporting), Writing – original draft (Lead). RB, GRPM and VFERS Writing – review & editing (Supporting). GLG and AS Formal analysis (Lead). GLG and WSA Investigation (Supporting). GLG, VFERS, WSA and AS Methodology (Supporting). GLG, GRPM and VFERS Project administration (Supporting). GLG and GRPM Supervision (Supporting). GLG Writing – review & editing (Lead). GRPM and AS Conceptualization (Lead). Investigation (Lead). GRPM Funding acquisition (Supporting). GRPM and VFERS Writing – original draft (Supporting). AS Data curation (Lead), Funding acquisition (Lead), Project administration (Lead), Supervision (Lead), Validation (Equal), Writing – original draft (Equal), Writing – review & editing (Equal).

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