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Research article

Geographical Distribution Patterns and Niche Modeling of the Iconic Leafcutter Ant *Acromyrmex striatus* (Hymenoptera: Formicidae)

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Abstract

Ants are considered one of the most successful groups in the planet's evolutionary history. Among them highlights the fungus-farming ants of the genera *Atta* and *Acromyrmex* that occur throughout most of the Americas. Within the *Acromyrmex* genus, the species *A. striatus* distinguishes from other *Acromyrmex* species as its morphology and karyotype differ from its congeners. This species is found in open environments of dry climate in the southern States of Brazil, Argentina, Paraguay and Uruguay; however, little is known about the current distribution of the species. This article aimed to investigate the current distribution of the species by compiling its known distribution and discussing its distributional range. To achieve this, published and unpublished data obtained through a literature search and active collections in various locations were compiled. Published and unpublished data revealed that 386 colonies were recorded, distributed across four countries where its occurrence is known. Environmental factors, such as temperature, humidity, soil type and vegetation, as well as historical geological and climate events that have modified Earth's surface may have influenced species distribution patterns. In the Neotropics, the environmental factors that most impacted the distribution of species were the glaciation periods that occurred in the Quaternary, leading to a great migratory process. These factors may have contributed to the current geographical distribution of *A. striatus*.

Key words: leaf-cutter ant, occurrence, species distribution, Attini

Ants are considered one of the most successful animal groups in Earth's evolutionary history, comprising a monophyletic group called Formicidae (Hölldobler and Wilson 1990, Ward 2014). With nearly 16,000 species (Bolton 2016), ants are a dominant part of almost all terrestrial ecosystems corresponding to ~20% of all animal biomass on the planet. It is estimated that this proportion is even larger in the tropical region of the Americas, representing no less than 25% of all animal biomass (Hölldobler and Wilson 1990).

The Neotropical region contains the greatest diversity and the highest level of endemism among all biogeographic regions (Fisher 2010). In the Neotropics, ants from the *Attini* tribe stand out, as they comprise 2,724 described species grouped into 45 genera (Bolton 2016). Among them, exclusive to the New World and involved in a symbiotic relationship with Basidiomycete fungi, are the fungus-growing ants (Schultz and Meier 1995). They depend on the growth of a symbiotic fungus as their main food source, and in return provide the fungus with protection against pathogens and competitors, while contributing to its dispersal (Weber 1972, Hölldobler and Wilson 1990, Ward et al. 2015). It is estimated that this symbiotic relationship emerged ~50 million years ago in South America (Schultz and Brady 2008), making fungus-growing ants one of the few known animal groups in evolutionary history to engage in the complex behavior of agriculture (Mueller et al. 2005). Further, among fungus-growing ants, the genera *Acromyrmex* and *Atta* are notable in their use of fresh plant material to grow the fungus gardens and for being the dominant herbivores in the Neotropics (Mikheyev et al. 2008).

Environmental factors, such as vegetation, soil type, temperature and pluviosity, contribute to determining the geographical distribution and frequency of ant species (Diehl-Fleig and Rocha 1998, Cardoso and Cristiano 2010, Cardoso et al. 2010, Meyer et al. 2011, Chaladze 2012, Gils and Vanderwoude 2012). Ants from the *Acromyrmex* genus are found from the southern USA (40°N latitude) to Argentina (44°S latitude), including all of tropical and subtropical South America, except for Chile (Weber 1966). It is suggested that this exception is due to the incapacity of organisms to cross the Atacama Desert and the up-lift of the Andes (Weber 1966).

Acromyrmex striatus (Roger 1863) is one of the species from the *Acromyrmex* genus, and is found in open environments in southern South America (Lopes 2005). This species is easily distinguishable within the genus due to its reddish brown colored workers, which measure 6.5 mm in length, have a head with multiple longitudinal striations, and a darker, smooth and tubercle-free gastral tergum (Gonçalves 1961). Additionally, different from its congeners, *A. striatus* possesses a smaller number of chromosomes than that of other *Acromyrmex* species. Besides, the diploid number of 22 chromosomes is equal to that verified in *Atta* species (Cristiano et al. 2013). *A. striatus* is common in farmlands and its nest is rather distinctive, as workers clean the soil surface above the fungal culture chambers, removing all vegetation and dead vegetable matter so that the site appears to have been weeded (Gonçalves 1961).

There are records of the occurrence of *A. striatus* in Brazil, Argentina, Uruguay and Paraguay, distributed mainly in sandbanks along the southern coastline of Brazil, and sandy plains throughout the Pampas and parts of the Chaco (Argentina and the extreme south of Paraguay) (Delabie et al. 2011). In Brazil, *A. striatus* is restricted to the States of Santa Catarina and Rio Grande do Sul; however, there are no recent surveys on its geographical distribution. Hence, this article aimed to investigate the distribution of *A. striatus* using available published and unpublished data.

Materials and Methods

The distribution survey of *A. striatus* was performed using published and unpublished data, gathered through literature review and active collections in various locations during the months of January and February 2010, January to March 2011 and November 2013.

Two hundred and ninety-six colonies of *A. striatus* were collected in 44 locations in Brazil, Argentina and Uruguay (Supp Table 1 [online only]), encompassing most of the area where the species is distributed. Specific permission for collections in Brazil was granted by the Chico Mendes Institute for Conservation of Biodiversity (Instituto Chico Mendes de Conservação da Biodiversidade, ICMBio), permission SISBio26441-1. All samples from Argentina and Uruguay were kindly ceded by Dr. Stela Quirán and Dr. Martin Bollazzi, respectively.

Regarding published data, information from collections made by several authors in three different countries was used (Supp Table 2 [online only]). Additionally, AntWeb online database (www.antewb.org) was used to gather information concerning the species locations. When coordinates of collection localities were not indicated by the authors, they were obtained using the Google Earth program (Google Inc., Mountain View, CA). All provided information about nest location in each of the publications was used, aiming for the highest possible precision.

ArcGIS, version 10.2 (ESRI, Redlands, CA), was used to elaborate an *A. striatus* distribution map, with the adoption of the SIRGASS 2000 projection system. We also generated South America temperature and pluviosity maps using data obtained from Worldclim (version 1.4) (Hijmans et al. 2005). For Species Distribution Modelling (SDM) we used five models: BIOCLIM, DOMAIN, Generalized Linear Model (GLM), Support Vector Machines (SVM), and Boosted Regression Trees (BRT), which were subsequently independently validated and summarized in a mean, providing a consensus between models. These models were used aiming to define, based on climatic conditions and altitude, the species' environmental requirements (Guo et al. 2005, Bombi et al. 2009, Elith et al. 2009). Climate and altitude data were obtained from WorldClim. The selected environmental predictors were: annual mean temperature (BIO1), mean diurnal range (mean of monthly (max temp−min temp)) (BIO2), isothermality (BIO3), temperature seasonality (standard deviation×100) (BIO4), temperature annual range (BIO7), mean temperature of driest quarter (BIO9), annual precipitation (BIO12), precipitation seasonality (BIO15), Precipitation of Driest Quarter (BIO17), precipitation of warmest quarter (BIO18), precipitation of coldest quarter (BIO19). All analysis was carried out in the R program (R-Core Team 2014).

Results

Collections in Brazil were concentrated mainly along the coastlines of states where the species occurs; encompassing 22 coastal cities and nine inland cities of the State of Rio Grande do Sul. Samples from 12 colonies were also collected in five cities from two Argentinean provinces (La Pampa and Buenos Aires), and one colony in the Uruguayan province of Riviera.

The combination of published and unpublished data resulted in 386 colonies distributed across four countries where species occurrence is known (Fig. 1). In Argentina, where the species is more widely distributed, records of *A. striatus* were verified in 10 out of 24 Argentinean provinces (Buenos Aires, Formosa, Jujuy, La Pampa, La Rioja, Mendonza, Salta, San Luis, Santa Fe e Santiago del Estero), encompassing a large part of the species' known distribution area, which, according to collected data, extends from Paraguay (22°S latitude) to Argentina (38°S latitude).

All five models used in the SDM analysis showed high values for the area under the receiver operating characteristic curve ($AUC > 0.9$), demonstrating high predictive capacity (Bioclim, $AUC = 0.955$; Domain, $AUC = 0.983$; GLM, $AUC = 0.983$; SVM, $AUC = 0.977$; BRT, $AUC = 0.972$). The potential distribution of *A. striatus* for each model and the mean model are presented in Fig. 2. The five models have generated different probabilities for the potential distribution pattern of *A. striatus*. The green areas on the maps represent locations with higher probability for the species' occurrence that have included the most areas were *A. striatus* was actively recorded.

Discussion

According to the results obtained, the distribution pattern of *A. striatus* was as expected, and encompassed sandy environments from the Brazilian Atlantic Forest to portions of the Pampas and Chaco regions. The occurrence of the species in these environments is probably linked to preference patterns regarding soil selection when females establish new colonies. In fact, it has been demonstrated that the selection of an adequate soil type for establishing the colony is particularly important among leafcutter ants (Bollazzi et al. 2008). According to Diehl-Fleig and Rocha (1998), newly fertilized *A. striatus* queens are selective regarding soil type for establishing the nest, preferring sandy and clay soils poor in organic matter. This preference matches the soil types determined in the environments where records of occurrence were compiled, such as the sandy coastal plains in the States of Santa Catarina and Rio Grande do Sul, which are composed of quartzite and nutrient-poor soil (Araújo and Lacerda 1987). Thus, the selectivity in choosing the soil type for establishing the nest is likely to be a major driver in the distribution pattern of *A. striatus*.

Abiotic factors, such as temperature and humidity, also influence species spatial distribution patterns (Ricklefs 2003, Chaladze 2012).

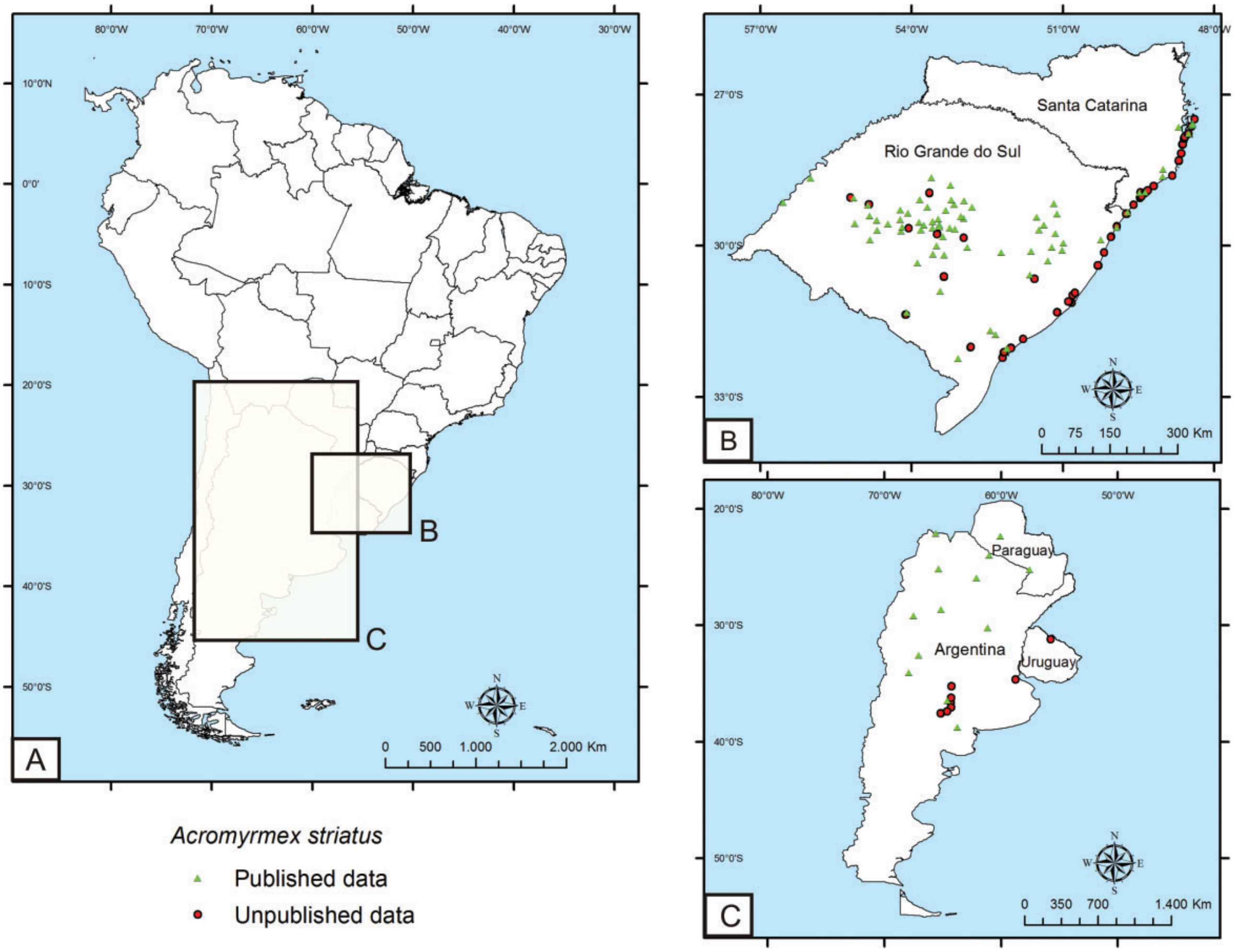

Fig. 1. Geographical distribution of *Acromyrmex striatus*. Map of the South American continent indicating the locations of occurrence (A), distribution of the species in Brazil (B), distribution of the species in Argentina, Paraguay and Uruguay (C). Each location is represented by a symbol referring to previously published or unpublished data (records from this article).

Similarities in the temperature and humidity profiles were observed in the regions where *A. striatus* was found to occur. The average temperature in these regions varies between 15 °C and 25 °C, and the maximum pluviometric means varied from 250 to 2,000 mm throughout the year (Fig. 3). Although pluviosity levels of regions where *A. striatus* occurs show a wide amplitude, the species distribution centers mostly where the maximum average rainfall is between 750 and 1,500 mm/year.

From the SDM analysis, it is possible to observe the influence of climatic factors in *A. striatus* potential distribution. The consensus model suggests that the areas with higher probability of occurrence of the species correspond to Southern Brazil, suggesting that this region presents adequate environmental conditions for its occurrence. The distribution pattern demonstrated in this article differs from that observed by Cristiano et al. 2016 estimated by maximum entropy, showing up to be much more restrict. Such more restrict potential distribution could be due to the higher number of models analyzed here together with higher number of climatic variables that may increased the accuracy of the mean model (Thuiller 2003).

An environmental condition such as temperature is also limiting factors for the growth of the symbiotic fungus, and directly affects colony development and survival. Powell and Stradling (1986) reported that the optimum growth temperature for *Attamyces bromatificus*, one of the symbiotic fungi cultivated by some species of fungus-growing ants, varies between 20 °C and 25 °C, and becomes lethal over 30 °C. The fungus can survive for some time at lower temperatures, down to 5 °C, though this results in the interruption of its metabolic activities. This temperature range coincides with that of *A. striatus* distribution, indicating that the optimum growth temperature for this species of symbiotic fungus is similar to that reported in the literature (Powel and Stradling 1986). In cold winters, members of our research group have sampled *A. striatus* colonies with extremely reduced fungus gardens and the workers in hibernating behavior (D. C. Cardoso and M. P. Cristiano, personal observations). Thus, the optimal conditions for the growth of the cultivated fungus by *A. striatus* may represent the limiting factor over its distribution, restraining the species in subtropical open areas.

Our study depicts *A. striatus* occurrence comprising the four neighboring South American countries of Brazil, Argentina, Paraguay and Uruguay. Its distribution extends from the city of Florianópolis, Brazil, as the northern edge of the species distribution, to the del Cadén phytogeographic district in the province of La Pampa, Argentina, as the southern edge. However, there are reports in scientific literature of its occurrence in Bolivia. Kusnezov (1953) mentioned the occurrence of *A. striatus* in Cochabamba (Bolivia); however, this is likely an inaccurate record in which the specimen is a sample of *A. silvestrii*; at that time, both species were considered

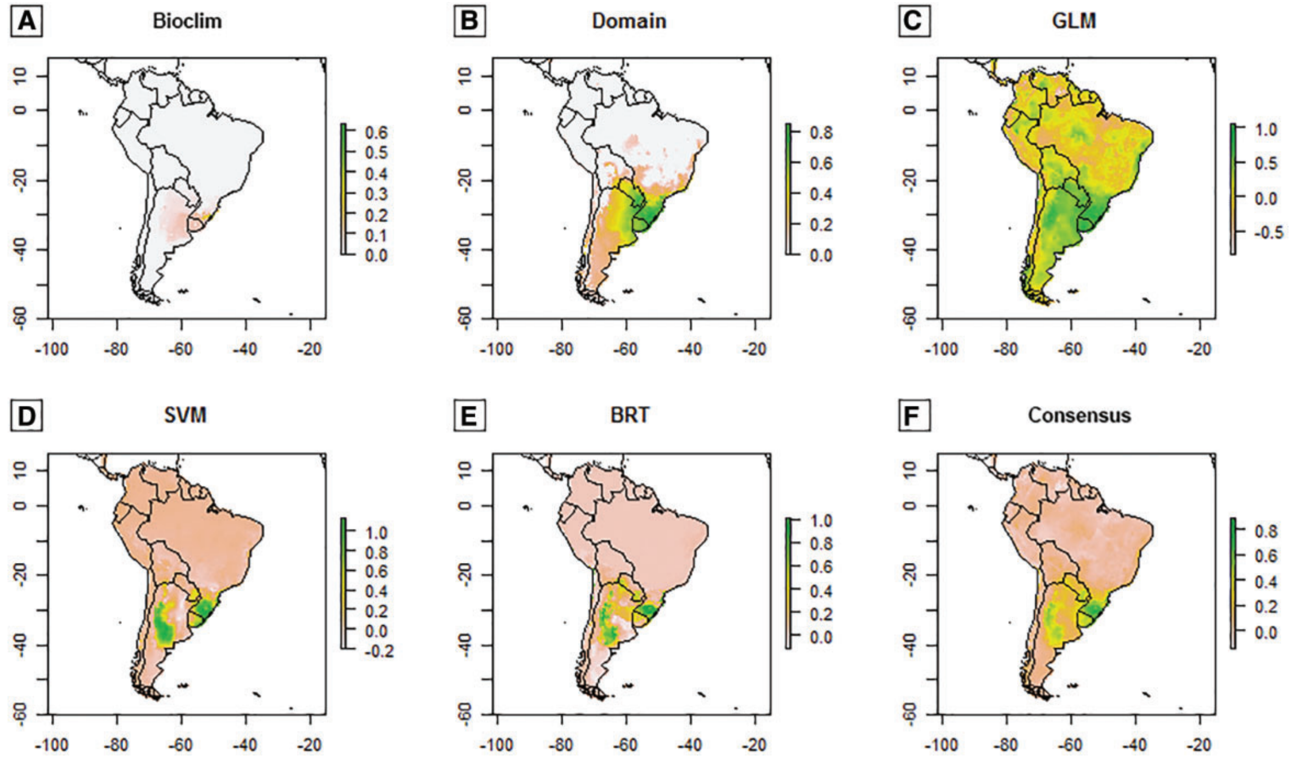

Fig. 2. Potential distribution models of *Acromyrmex striatus* recovered by Bioclim (A), Domain (B), GLM (C), SVM (D), and BRT (E). Consensus model obtained through the weighted average method (F). The darkness of the pixels is proportional to the habitat suitability value (grey: not suitable; dark green: highly suitable).

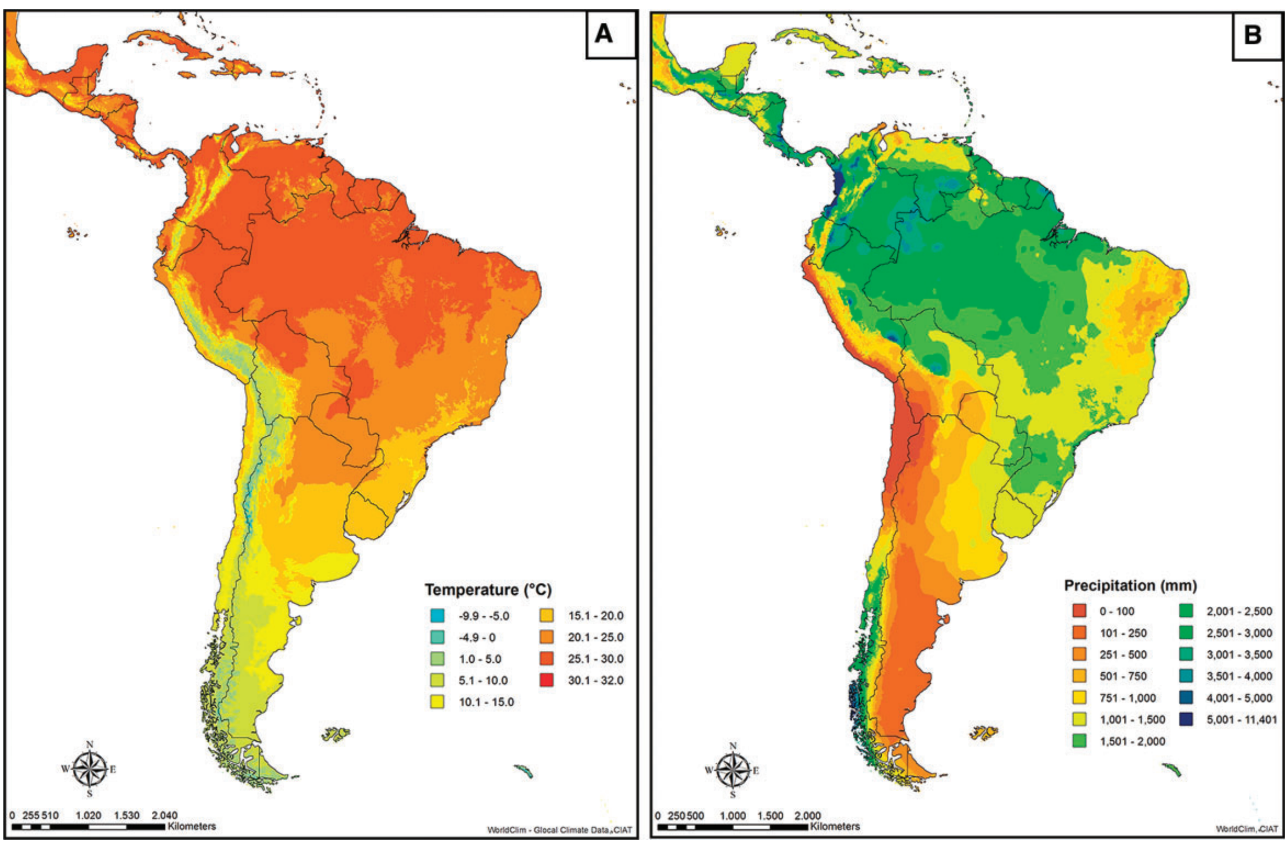

Fig. 3. Average temperature (A) and precipitation (B) in South America. Historical data referring to the years from 1950 to 2000, according to www.worldclim.org.

by the author as taxonomic synonyms. Nevertheless, we did not automatically discard the possibility that *A. striatus* may occur in Bolivian territory, as Bolivia borders other countries with confirmed records of the species and encompasses part of the Chaco region, one of the biomes where the species occurs.

Mistakes in the identification and records of occurrence of species are not rare in scientific literature and are an important source of bias in distribution surveys. Similar problem have been reported for *Mycetophylax simplex* that supposedly occurs only on sand dunes on the South Atlantic coast, but has been recorded in Paraguay. However, it was suggested that this record likely refers to the common inland species now placed as *Kalathomyrmex emeryi* (Wild 2007). Potential records mistakes of ant species occurrence was an issue raised by Wetterer et al. (2016). The authors criticize previously ranges of *Trachymyrmex*, *Mycetophylax* and *Mycocepurus* that includes Barbados islands, but none species from these genera has been collected on the island. They suggested that these records might be a mistake due inaccurately drawn maps.

From a general perspective, it is possible to conclude that the geographical occurrence of a species is directly linked to a number of historical and ecological processes, which over time end up shaping its distribution pattern. Regarding *A. striatus* its appear to be restricted to open-sandy subtropical environments of southern South America, but more studies are required to better trace its distribution, especially in locations from Paraguay and Uruguay, where its occurrence is poorly known and apparently much sparser.

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Insect Science* online.

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