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UNRAVELING AN OVERLOOKED RISK FACTOR FOR ENVENOMING: RELATIONSHIP BETWEEN LONOMIA CATERPILLARS AND THEIR HOST PLANTS

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Abstract. ***Introduction:*** The host plants are crucial for the survival of *Lonomia* spp. (Lepidoptera: Saturniidae), particularly during the larval stage, which is the sole phase associated with human envenomation after accidental contact with their spines. ***Objective:*** This work aims to contribute to the understanding of the relationship between the two caterpillar species involved in such cases – *Lonomia achelous* and *Lonomia obliqua*, restricted to the tropical forests of South America – and their respective host plants, mainly focusing on features that may increase the risk of envenoming. ***Methods:*** A bibliographical survey about specific interactions (biological characteristics, human uses, and geographical distribution) was conducted. The data was sourced from scientific literature and/or opinion from experts in the Saturniidae family, covering the period from 2020 backwards. ***Results:*** The findings revealed that both species are polyphagous. A common trait among their host plants is the presence of tannins in the leaves. Most host species have at least one human use, thereby increasing the risk of inadvertent contact with caterpillars. Additionally, the geographical distribution of both species aligns with the distribution of their native host plants, which are predominantly heliophilous. ***Conclusion:*** This work provides an extensive panoramic insight into the interactions between *Lonomia* spp., their hosts, and the environment, which is essential for designing effective prevention strategies for addressing *Lonomia* accidents in South America.

Keywords: geographic distribution; larva; *Lonomia*; Lepidoptera; human envenomation.

INTRODUCTION

Like any other lepidopteran, *Lonomia* species go through four developmental stages: adult, egg, larva (or caterpillar), and pupa. The adults exhibit notable sexual dimorphism, with the male being smaller than the female. Females are less agile than males, with wide and ornate wings, and some have long caudal extensions. Copulation usually occurs near a tree that will serve as a host for the offspring. After copulation, the female flies to the canopy of the host tree and deposits eggs on the leaves (Arocha-Piñango 1987, Lemaire 2002, Lorini 1999). The selection of a host plant for oviposition is influenced by various factors, such as availability in time and space, as well as the presence or absence of oviposition stimulants (Honda 1995). The choice of the host by the female is considered crucial for the continuity of the species because it allows the survival of her offspring (Lederhouse et al. 1992).

After hatching, caterpillars first eat their own eggshell, then begin feeding on host plant leaves, causing some damage (Odum & Barret 2015). They live in clusters of dozens of individuals that rest on the host tree trunk during the day, and feed during the nighttime, a strategy commonly employed by lepidopterans to evade diurnal predators (Bernays 1998, Chudzinski-Tavassi & Alvarez-Flores 2013, Heinrich 1971, 1979, Heinrich & Collins 1983). The main function of the larval stage is to eat and grow while avoiding predation (Bernays 1998). The larval stage of *Lonomia* spp. is the only one involved in human envenoming, which commonly occurs when a person accidentally come in contact with clusters of caterpillars (Favalesso et al. 2023).

Deforestation is considered one of the factors that directly affects the natural habitat of venomous animals, including *Lonomia* species. Tree felling and the destruction of forests for activities such as agriculture, livestock farming, and urbanization can create new environments that are more favorable for the development of caterpillars (García 2013). It is hypothesized that the loss of native host plants would lead to an adaptation of the caterpillars to non-native species in the South American continent, causing them to occupy new types of environments (Favalesso et al. 2019, García 2013, Lorini 1999). To validate these hypotheses, this study conducted a bibliographic and documentary review on the host plants of *Lonomia achelous* Crammer 1777 and *Lonomia obliqua* Walker 1855 – the only two species reported to cause human envenoming up to now (Favalesso et al. 2023) – to characterize them in terms of their evolutionary origin (native or non-native), their human uses, as well as the biological properties and distributional characteristics of native host plants that may be related to the presence and distribution of both caterpillar species. By understanding these interactions, public health officials can develop more effective prevention strategies for *Lonomia* spp. accidents in South America.

MATERIALS AND METHODS

Bibliographical survey

A review of the scientific literature was conducted to identify the host plants of *L. achelous* and *L. obliqua*. Scientific manuscripts, books, online databases, literature reports, as well as specialists/experts in Saturniidae were consulted, and the individual datasets were provided in the Supplementary Information (available online at https://github.com/mmfava/lonomia-host-plants-2024). The information from host plants identified at the species level was considered, and their scientific names were standardized using the "Taxonomic Name Resolution Service API" (TNRS version 5.0), as described in Boyle et al. (2013). To ensure data integrity, accuracy, and uniformity, the scientific name of the host species, the year of data compilation (or an approximation based on the publication date), whether the species is "native" (occurring naturally in South America) or "non-native", the reference type, and the names of the authors were recorded.

Characterization of host plants based on factors related to human accidents

To identify possible factors that lead to a possible association between *L. achelous*/*L. obliqua* host plants and the occurrence of human accidental contact, data were collected regarding the presence of tannins, human uses of host plants, and the biological and distributional characteristics of native species (Table 1). Information on these factors was obtained through a comprehensive review of the scientific literature, including scientific articles, books, and specialized websites. Interactions between the host plants and factors were recorded in a logical table, with a "true" entry when at least one author documented the presence or characteristic of the host plant in relation to a specific factor. The conservation status of native species was determined based on the International

Table 1. Factors that characterize the host plants of *L. achelous* and/or *L. obliqua* and may be related to the occurrence of accidents.

Cluster	Factor	Factor description	Applicable for
Tannin	Tannins in host leaves	They are organic compounds found in a variety of plant species, including trees, shrubs, and grasses. They are well known for their astringent properties and are frequently used in leather production, and for medicinal and culinary purposes.	Native Non-native
Anthropogenic use	Traditional medicine	Traditional, indigenous, or local medical practices that are often passed down from generation to generation. These practices may include the use of plants and other natural resources to treat various diseases or conditions.	Native Non-native
	Consumable fruits	Plants that produce fruits suitable for human consumption. These fruits can be eaten fresh or processed into other products such as jams, juices, or baked goods.	Native Non-native
	Marketable fruits	Plants that produce fruits suitable for commercial sale. These fruits can be sold fresh or processed into other products and are often farmed for their high demand and profitability.	Native Non-native
	Energy generation	It refers to the process of generating forms of energy from firewood or charcoal.	Native Non-native
	Use of wood	It refers to the use of wood products in various applications, such as construction and furniture.	Native Non-native
	Urban afforestation	Refers to the planting of trees and other vegetation in urban areas to provide a variety of benefits, such as shade, aesthetic value, biodiversity, and carbon sequestration.	Native Non-native
Distribution	Endemic to South America	It refers to the fact that the species is native and found only in South America. It is not found naturally anywhere else in the world.	Native
	Endemic to a country or biome	Refers to the species being native and found only within a specific country or biome (a large area of land characterized by a particular type of ecosystem, such as a tropical rainforest). It is not found naturally outside of this specific area.	Native
	Heliophile	Refers to plants that prefer full sun or partial sun conditions and may have difficulty growing in low light or shade.	Native

Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN, 2022).

Occurrence data of **L. achelous** *and* **L. obliqua**

Searches were conducted in various databases, including PubMed, Scielo, Scopus, Integrated Digitized Biocolections (iDigBio), SpeciesLink, Global Biodiversity Information Facility (GBIF), Brazilian Biodiversity Information System (SiBBR), Paraguay Biodiversity (PyBio), and Chico Mendes Institute for Biodiversity Conservation (ICMBio), to obtain the geographic coordinates of *L. achelous* and *L. obliqua* occurrences in South America. For some occurrences, latitude and longitude information was not available, but information about the location where individuals were sampled and/or the municipality with the respective state/province and country was provided. These occurrences were represented by a coordinate obtained through the geocoding from OpenStreetMap Nominatim API. The records of each species were cleaned by removing occurrences that took place outside the continent, had repeated coordinates, or had missing values.

Occurrence of native hosts

To carry out the search for *L. achelous* and *L. obliqua* native hosts, four databases were used:

1) Botanical Information and Ecology Network (BIEN)
2) The Global Biodiversity Information Facility (GBIF)
3) Integrated Digitized Biocollections (iDigBio)
4) SpeciesLink

Due to the large volume of data, the downloading process was automated using an R script. The data were accessed through the API of each database, utilizing the following packages: bien (Maitner 2018), rgbif (Chamberlain et al. 2023), ridigbio (Michonneau & Collins 2022), and rocc (Lauss 2019). The records of each species were then cleaned by removing occurrences outside the continent, as well as those with repeated coordinates, identical latitude and longitude values, or missing values.

Area buffer with accident records

A multilingual search was conducted using the keyword "*Lonomia*" in Lilacs, PubMed, ScienceDirect, and Scielo. Citations from articles were used to obtain additional data sources. Sources containing duplicate or unrelated information to human accidents were eliminated. The sources reviewed include academic articles, case reports, book chapters, epidemiological bulletins, and government databases. Accidents that occurred after 2020 were excluded to ensure methodological consistency. A 0.5-degree buffer was calculated based on occurrence data, resulting in a simple geometry representing accident locations in South America.

Data analysis

The absolute frequency of newly identified species as hosts of *L. achelous* and *L. obliqua* over time was plotted for both native and non-native species in South America. This allowed examining the evolution of knowledge about host species for both *Lonomia* species and determining whether the number of hosts has increased or decreased over time.

The factors listed in Table 1 were analyzed using descriptive statistics (n and %). The chi-square goodness-of-fit test was used to compare frequencies, considering only valid categories and excluding indeterminate categories from the analysis. In cases where restrictions related to category frequencies occurred during the statistical test, a Monte Carlo test (Hope 1968) with 2000 repetitions was employed. The proportions of non-native species were compared between the two species using the chi-square test for k proportions.

A Gaussian kernel was applied to the two-dimensional occurrence data of hosts to produce a density map of native species. The Gaussian kernel is a bell-shaped curve determined by the mean and standard deviation of the data, resulting in a map with redder shades representing higher densities and bluer shades representing lower densities (Duong 2007, 2022).

For additional data analysis, known occurrences of *L. achelous* and *L. obliqua*, as well as the locations of recorded accidents, were overlaid on the density map. By examining the intersections between these datasets, an attempt was made to determine if the distribution of *Lonomia* spp. is related to the distribution of native hosts and if both are correlated with the areas where accidents occur. This analysis aimed to understand the potential factors driving the distribution of these caterpillars in relation to their native hosts.

Programming Language

All analyses were conducted in R (version 4.2.2) using the following packages: CoordinateCleaner v2.0-20 (Zizka *et al*. 2019), eks v1.0.1 (Duong 2022), gtsummary v1.6.2 (Sjoberg *et al*. 2021), sf v1.0-9 (Pebesma 2018), sp 1.5-1 (Pebesma & Bivand 2005), and tidyverse v1.3.2 (Wickham *et al*. 2019).

RESULTS

Identification of host plants for L. achelous *and* L. obliqua

From the database analysis, we found that *L. achelous* biologically interacts with nine species belonging to nine genera distributed across nine families of plants. On the other hand, *L. obliqua* interacts with fifty-five species distributed across forty-five genera from thirty-one families of eudicotyledonous plants (Table 2), most of which are not closely related phylogenetically (APG IV 2016). The families with the largest number of species are Fabaceae (7 spp.), Rosaceae (7 spp.), Moraceae (6 spp.), Anacardiaceae (5 spp.) and Lauraceae (4 spp. (Table 2). The majority of the host species of *Lonomia* spp. – specifically 100% in the case of *L. achelous* hosts and 82% in the case of *L. obliqua* hosts – contain tannins in their chemical composition.

Socioeconomic aspects attributed to host plants and their characteristics as key mediators of Lonomia *envenomation*

The hosts of *L. achelous* and *L. obliqua* show a wide range of human uses, with all of the species listed in Table 2 being used for at least one anthropic use as shown in Table 3. It is worth noting that 76% and 56% of *L. achelous* and *L. obliqua* host species, respectively, are used in timber extraction, primarily native species. Around 75% of *L. obliqua* host species are used for urban afforestation, while for *L. achelous* it corresponds to 67%. On the other hand, only a small proportion of hosts produce fruits that are consumed and/or commercially used for humans (Table 3). It should be noted that the information provided in this table refers to the number of species and not the quantity of individuals available for caterpillar colonization.

Table 2. Host plants of *Lonomia achelous* and *Lonomia obliqua*.

[1]Year of first record. If the documentation did not include the sampling year, the year of the document was used instead.

Family	Species	Human use	Native	Lonomia achelous[1]	Lonomia obliqua[1]
Anacardiaceae	*Lithraea brasiliensis*	wood	yes	-	2005
	Lithraea molleoides	Medicinal and wood	yes	-	2001
	Mangifera indica	Medicinal and food	no	-	2017
	Schinus terebinthifolia	Medicinal	yes	2010	-
	Tapirira guianensis	Medicinal and wood	yes	1978	-
Annonaceae	*Annona emarginata*	Medicinal	yes	2020	1989
Apocynaceae	*Aspidosperma camporum*	Wood	yes	-	2005
Aquifoliaceae	*Ilex taubertiana*	Ornamental and medicinal	yes	-	1997
Araliaceae	*Didymopanax morototoni*	Medicinal, wood and ornamental	yes	-	2016

Table 2. continues in next page...

... **Table 2.** continued.

Family	Species	Human use	Native	Lonomia achelous[1]	Lonomia obliqua[1]
Bignoniaceae	*Handroanthus pulcherrimus*	Ornamental and wood	yes	-	1989
	Handroanthus umbellatus	Ornamental and wood	yes	-	2001
Euphorbiaceae	*Alchornea glandulosa*	Medicinal	yes	-	2015
	Hevea brasiliensis	Industrial and wood	yes	1979	-
	Sebastiania brasiliensis	Medicinal	yes	-	2014
Fabaceae	*Albizia niopoides*	Wood and ornamental	yes	-	2019
	Bauhinia forficata	Medicinal	yes	-	1996
	Dahlstedtia muehlbergiana	Wood	yes	-	2001
	Erythrina cristagalli	Ornamental and medicinal	yes	2010	1997
	Machaerium paraguariense	Wood	yes	2020	-
	Muellera campestris	Wood	yes	-	2018
	Sesbania virgata	Ornamental and ecological restauration	yes	-	1997
Lamiaceae	*Vitex megapotamica*	Medicinal	yes	-	1997
Lauraceae	*Nectandra grandiflora*	Wood and medicinal	yes	-	2014
	Nectandra lanceolata	Medicinal and wood	yes	-	1997
	Ocotea lancifolia	Medicinal and wood	yes	2020	-
	Persea americana	Medicinal and food	no	-	1992
Lythraceae	*Lagerstroemia indica*	Ornamental	no	-	2001
Malvaceae	*Luehea divaricata*	Medicinal and wood	yes	-	2005
Meliaceae	*Cedrela fissilis*	Wood	yes	2020	1968
	Melia azedarach	Ornamental and medicinal	no	-	1997
Moraceae	*Ficus carica*	Food and medicinal	no	-	2005
	Ficus elastica	Ornamental	no	-	1997
	Ficus luschnathiana	Medicinal and ecological restauration	yes	-	2001
	Ficus pallida	Medicinal and ecological restauration	yes	-	2020
	Ficus pertusa	Ecological restauration	yes	-	1989
	Morus nigra	Food and medicinal	no	-	1997
Myrtaceae	*Psidium guajava*	Food and medicinal	no	-	1997
Pittosporaceae	*Pittosporum tobira*	Ornamental	no	-	1997

Table 2. continues in next page...

... **Table 2.** continued.

Family	Species	Human use	Native	Lonomia achelous[1]	Lonomia obliqua[1]
Platanaceae	*Platanus acerifolia*	Ornamental	no	-	2001
Proteaceae	*Grevillea robusta*	Wood and ornamental	no	-	1997
Rhamnaceae	*Hovenia dulcis*	Food and medicinal	no	-	1997
	Eriobotrya japonica	Food and medicinal	no	-	2001
	Malus pumila	Food and medicinal	no	-	2001
	Mespilus germanica	Food and medicinal	no	-	2020
Rosaceae	*Prunus domestica*	Food and medicinal	no	-	2001
	Prunus persica	Food and medicinal	no	-	1992
	Pyrus communis	Food and medicinal	no	2010	2001
	Rubus ulmifolius	Food and medicinal	no	-	2015
	Citrus limon	Food and medicinal	no	-	2001
Rutaceae	*Citrus sinensis*	Food and medicinal	no	-	2001
	Helietta apiculata	Food and medicinal	yes	-	2016
	Banara tomentosa	Medicinal	yes	-	2017
Salicaceae	*Casearia decandra*	Medicinal	yes	-	2019
	Casearia sylvestris	Medicinal	yes	-	2017
Sapindaceae	*Matayba elaeagnoides*	Wood, ornamental and ecological restauration	yes	-	2016
Sapotaceae	*Pouteria salicifolia*	Wood and ecological restauration	yes	-	2018
Solanaceae	*Solanum pseudoquina*	Medicinal	yes	-	2013
Styracaceae	*Styrax leprosus*	Medicinal and wood	yes	-	2015
Urticaceae	*Urera aurantiaca*	Medicinal	yes	-	2005
Verbenaceae	*Duranta erecta*	Ornamental	yes	-	1997

In other words, although a small percentage of species produce fruits, they can be abundant, have a wide geographic distribution, and be preferred by *Lonomia* spp. caterpillars. Furthermore, among the hosts that produce edible and marketable fruits, 67% of the species are non-native to South America ($\chi2=6.52$; $p<0.001$).

Occurrence of native and non-native hosts

Upon analyzing the available data, it was evident that the frequency of new non-native host plants has remained nearly unchanged since the 2000's for *L. obliqua*, with only one non-native host reported in 2010 for *L. achelous* (Figure 1). Approximately 11% and 38% of the host species for *L. achelous* and *L. obliqua*, respectively, are considered non-native, with no statistically significant differences between the proportions ($\chi^2=2.51$; $p=0.113$).

Distribution of native host species

Figures 2A and 2B show that the occurrence points of *L. achelous* and *L. obliqua* overlap with the geographical range where native hosts are found. Most of these native hosts are only found in South America (75% for *L. achelous* and 71% for *L. obliqua*), while endemism is relatively uncommon (12% for *L. achelous* and 15% for *L. obliqua*) (Table 4).

Regarding host density, the occurrence of *L. achelous* is slightly disconnected from some of the areas with higher density of native hosts, as seen in Figure 2A. In the case of *L. obliqua*, the occurrences

Table 3. Human use of host plants of *L. achelous* and *L. obliqua*. *p<0,05; **p<0,01; ***p<0,001. The statistics were carried out only with the yes and no categories, without including the indeterminate category.

Variables	*Lonomia achelous*		*Lonomia obliqua*	
	N = 9	**p-value**	N = 55	p-value
Traditional medicine		-		***
no	2 (22%)		11 (21%)	
yes	7 (78%)		42 (79%)	
indeterminate	0		3	
Consumable fruits		-		*
no	6 (67%)		34 (63%)	
yes	3 (33%)		20 (37%)	
indeterminate	0		1	
Marketable fruits		-		**
no	6 (67%)		37 (69%)	
yes	3 (33%)		17 (31%)	
indeterminate	0		1	
Energy generation (charcoal or firewood)		-		-
no	4 (44%)		25 (47%)	
yes	5 (56%)		28 (53%)	
indeterminate	0		2	
Use of wood		-		-
no	2 (22%)		23 (44%)	
yes	7 (78%)		29 (56%)	
indeterminate	0		3	
Urban afforestation		-		***
No	3 (33%)		13 (25%)	
yes	6 (67%)		40 (75%)	
indeterminate	0		2	

are visually associated with areas of higher host density (highlighted in red) (Figure 2B).

Our study also revealed that none of the native hosts of *L. obliqua* are threatened or at risk of extinction, only two are listed as “vulnerable”, *C. fissilis* and *U. aurantiaca* (Table 4). Additionally, all native host plants of *L. achelous* and 91% of native host plants of *L. obliqua* are heliophilous (they grow and are exposed to full sunlight) (Table 4).

DISCUSSION

Identification of host plants of **L. achelous** *and* **L. obliqua**

Despite their involvement in accidents with venomous caterpillars, these plant species had not been addressed until the present study. Herein we identified several unrelated phylogenetically species as hosts for both *Lonomia* species, highlighting that they also provide hosting for other species/genus of Saturniidae (Randrianandrasana et al. 2014). Therefore, we proposed the hypothesis that there may be a interspecific competition for hosts during the egg-larva period. It is important to consider that the phenotype, diet, and behavior of *Lonomia* spp. allow them to adapt to the phenological changes of their hosts. It is estimated that less than 10% of herbivorous arthropods consume plants from more than six families (Bernays & Graham 1988).

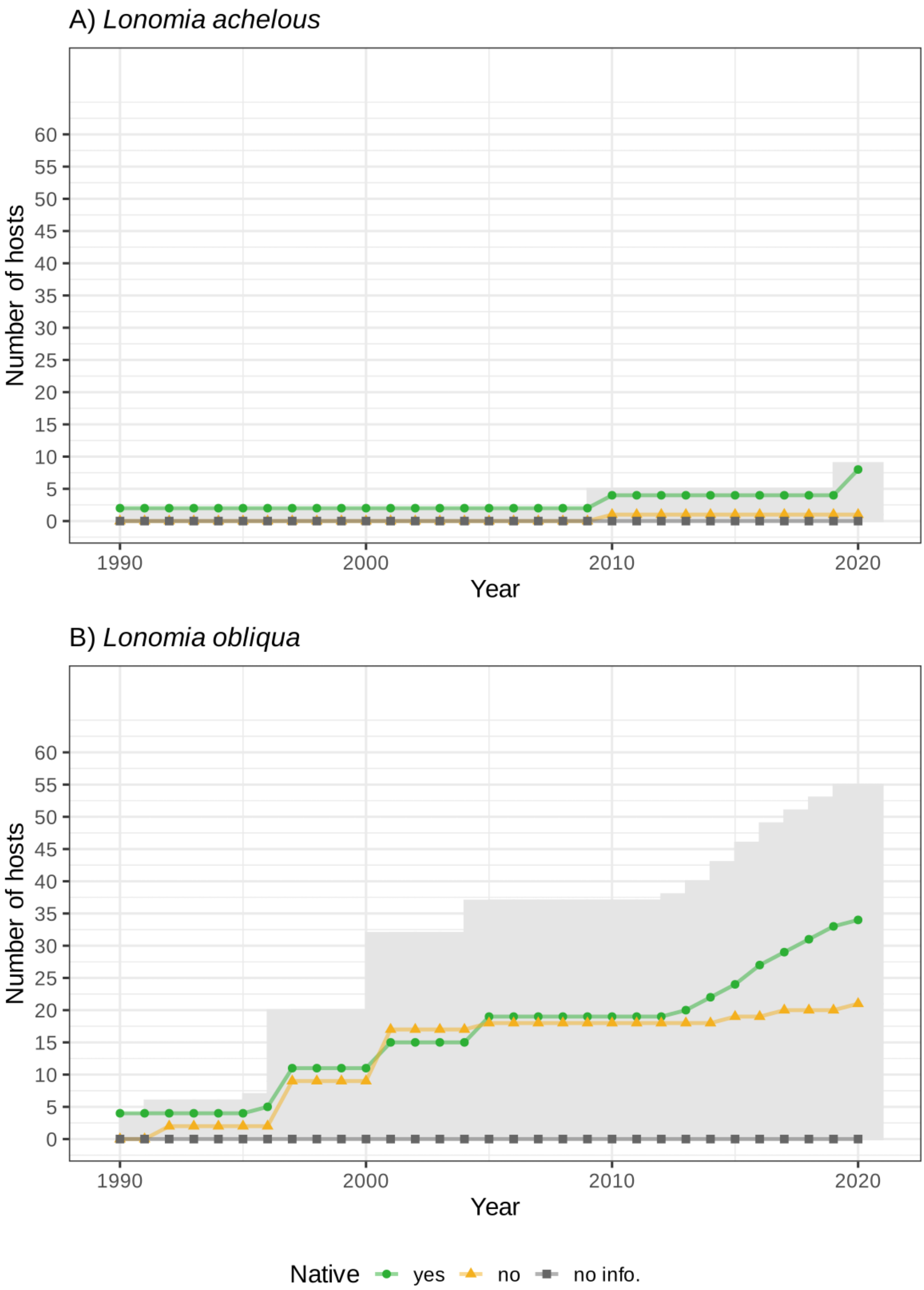

Figure 1. Cumulative frequency and status of species during the period 1990-2020.

Within the order Lepidoptera, approximately 85% of the species specialize on a small number of closely related plant species (Forister et al. 2015, Jaenike 1990). *Lonomia* spp. typically completes its life cycle using a single host plant. However, *Lonomia* spp. are considered generalists, as individuals can complete their life cycles on different host plants that are not necessarily phylogenetically related (Lorini 2008). This feeding strategy allows *Lonomia* larvae to thrive in diverse habitats and utilize a wide range of food sources, which could help them survive if their preferred host plants become scarce or unavailable. Furthermore, the measure of specialization can be useful in predicting which species are likely to thrive in landscapes degraded by human activities, indicating that generalist species are less likely to experience range loss due to deforestation (Devictor et al. 2008).

It may seem that generalists have an advantage over specialists due to their access to a greater variety of food. However, polyphagous insects – capable of consuming a wide range of plant species – may be disadvantaged due to their limited neuronal capacity. Specialist insects have developed specialized neural pathways and behaviors that allow them to efficiently locate and consume their preferred food sources, while generalists may have more diffuse neural pathways and behaviors that are less efficient in searching for a wide range of food types. Overall, the trade-off between the ability to exploit a broader range of food sources and the cost of a less specialized nervous system can vary depending on the ecological context and availability of food resources (Schoonhoven et al. 2005). Considering the lack of information and/or scarcity of knowledge on the neurobiological aspects of both lepidopteran species under study in this work, this should be explored in future research for a better ecological understanding of these entities.

Both *L. achelous* and *L. obliqua*, like other Saturniidae, have developed the ability to feed on older leaves, which are typically tougher and more fibrous than younger leaves. These older leaves are usually more resistant to herbivores due to their physical characteristics (Kursar & Coley 2003), but the large mandibles of *Lonomia* spp. caterpillars allow them to cut and consume these tough leaves. These caterpillars can obtain sufficient energy and nutrients from a diet of older leaves due to their lower

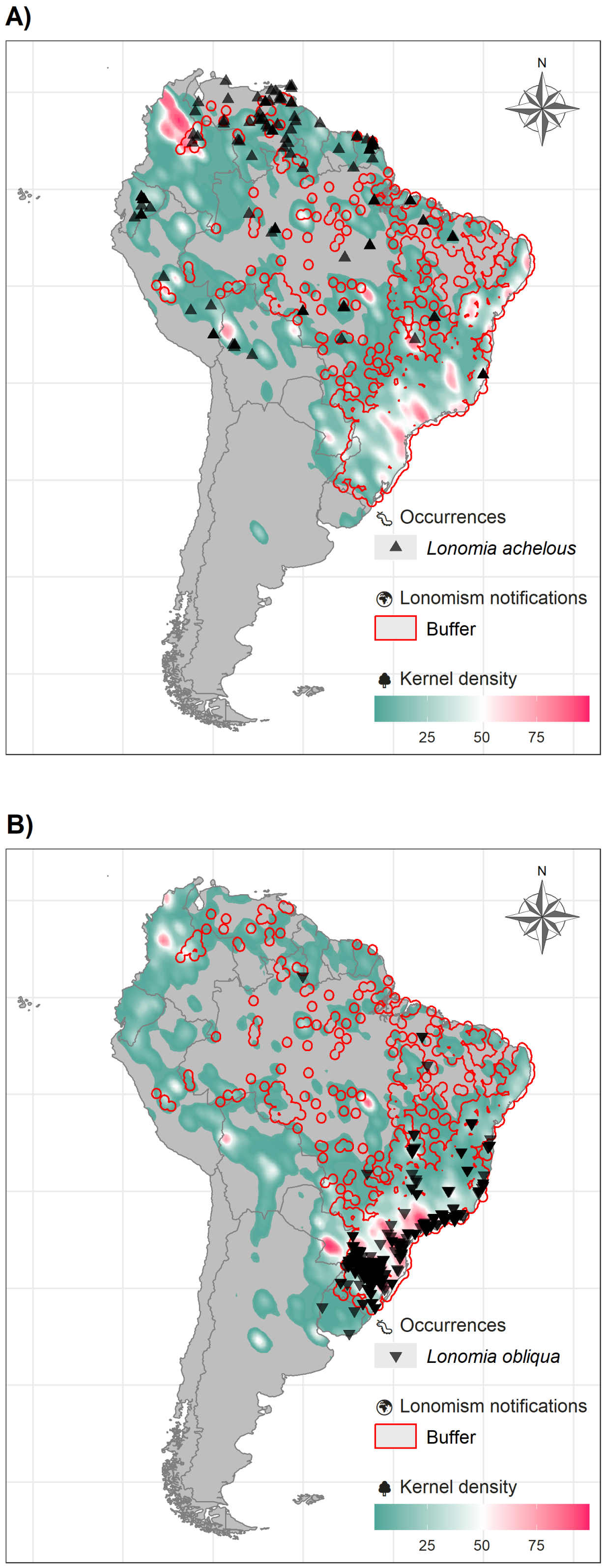

Figure 2. Kernel density map for host plants of *L. achelous* (A) and *L. obliqua* (B) in South America, with occurrence points of the species and locations with reported cases of accidents.

Table 4. Biological and distributional characteristics of native host plants. *p<0,05; **p<0,01; ***p<0,001. +Hosts not classified on the Red List or not classified as risk category were not included.

Variables	***Lonomia achelous***		***Lonomia obliqua***	
	N = 8	**p-value**	**N = 34**	**p-value**
Endemic to South America		-		*
no	2 (25%)		10 (29%)	
yes	6 (75%)		24 (71%)	
Endemic to a biome		-		***
no	7 (88%)		29 (85%)	
yes	1 (12%)		5 (15%)	
Status on the Red List+		-		***
Least concern	6 (86%)		21 (91%)	
Vulnerable	1 (14%)		2 (8.7%)	
Heliophile				***
no	-	-	3 (9.4%)	
yes	7 (100%)		29 (91%)	
indeterminate	1		2	

metabolic rates and greater digestive efficiency (Jaenike 1990, Tonelotto 2017). In relation to this, the work of Tonelotto (2017) has demonstrated that *L. obliqua* larvae alter their metabolic strategies, specifically the activity of digestive enzymes, when feeding on four different types of diets (one based on a native plant, *Alchornea* spp., and three based on non-native plants, *Eriobotrya japonica*, *Psidium guajava*, and *Mangifera indica*), in order to take advantage of their different type of food resources. It is also noteworthy that no variations in enzymatic activity in the hemolymph of these caterpillars were observed with the change of diet in that study, suggesting that the production/characteristics of their venom are also likely unaffected.

On the other hand, tannins are chemical compounds characterized by an astringent taste and the ability to bind to proteins (Soares et al. 2020). These compounds are produced by plants as a defense mechanism against herbivores, making plant tissues less appealing or even toxic (Barbehenn & Peter Constabel 2011). Despite this, the majority of hosts of *L. achelous* and *L. obliqua* contain tannins in their chemical composition, suggesting that both species of *Lonomia* caterpillars have developed the ability to feed on plants that have these polyphenolic compounds (Chapman 1998). Consuming tannin-rich plants can offer benefits, such as making the caterpillar less palatable, providing antimicrobial defense against infections and parasites, and offering antioxidant protection against oxidative stress (Barbehenn et al. 2003; Barbehenn & Peter Constabel 2011; Bernays 1981).

According to the hypothesis proposed by Endara et al. (2022), the protective characteristics found in lepidopteran caterpillars, such as spines and gregarious behavior, may have evolved as a result of feeding on older, less nutritious leaves that contain astringent/unpleasant compounds like tannins. By feeding on and sheltering in host plants with these characteristics, *Lonomia* spp. caterpillars may experience less competition for this resource since most other lepidopterans prefer younger and more nutritious leaves. The low nutritional quality of older leaves and the resulting slower larval growth should lead the larvae to greater exposure to predators and investment of energy in protective characteristics.

Socioeconomic aspects attributed to host plants and their characteristics as mediators of **Lonomia** *envenomation*

This study found evidence that human interactions with host plants of *Lonomia* spp. are common and occur for personal consumption, local use, and/or economic purposes. Tree logging is a common activity in South America, as wood is valued as a material for construction, carpentry, and other products. Between 2010 and 2020, South America lost approximately 2.6 million hectares of forest, reducing drastically the vegetation cover and fragments natural habitats (FAO 2021). Illegal logging is particularly detrimental as it does not comply with environmental regulations or respect the rights of indigenous people who inhabit forests. Considering that most of the host plants of *L. achelous* and *L. obliqua* are used in timber extraction, primarily native species, it can be considered that this activity/resource exploitation exposes workers, loggers, or civilians to the risk of accidents with such venomous caterpillars.

Wood is also an important source of energy in the form of coal and firewood (Simioni et al. 2017). In indigenous communities, firewood is a common way of cooking and heating homes, often obtained through active searching for branches or other parts of trees in forests (Dario 2018). Wood is also used in the production of charcoal, a solid fuel used in industry and energy generation (Simioni et al. 2017). While there are many reports of accidents occurring during tree felling, none have been found in which it is mentioned that such felling was being carried out for this specific purpose.

Accident records typically present generic reports, such as the example in Misiones, Argentina, where an adult woman was felling a tree in the jungle in search of firewood and, while handling *M. elaeagnoides*, inadvertently touched a cluster of *Lonomia* sp. larvae and was envenomed (unpublished record from this research group). There are also accounts of cases in the same region where farmers suffered envenoming while clearing land by felling trees and brush (Casafús et al. 2021, Stetson 1998).

Urban reforestation has become an increasingly popular environmental initiative, offering numerous benefits such as improved air quality and thermal sensation, positive psychological impacts, enhanced habitats for wildlife, more green spaces in densely populated areas, and improved aesthetics of cities. Various native tree species are frequently cultivated in parks, public gardens, squares, etc., which are not intended for manipulation or exploitation for commercial purposes (Perkins et al. 2004, Soares et al. 2021), but they provide opportunities for the presence of *Lonomia* spp., which benefit from the host plants found in these locations. In fact, accidents involving caterpillars of this lepidopteran have been reported in orchards, parks, squares, and areas near residential homes (Casafús et al. 2021, Favalesso et al. 2021, Malaque et al. 2006, Medeiros et al. 2014). Around 75% of the host species of *L. obliqua* can be found in these areas, which could explain the high rate of accidents in urban zones (Favalesso et al. 2021).

However, it is important to note that, despite being venomous animals, species of this genus are part of the native South American fauna. Consequently, urban forested areas must plan how to distribute their tree individuals, avoiding the proximity of *Lonomia* spp. host plants to areas where people circulate, in order to protect both humans and caterpillars. When involved in accidents, caterpillars are often sacrificed in various ways, either by the victim themselves or by their relatives. Therefore, when clusters are identified on trees, necessary measures should be taken to isolate the surrounding area of the host plant to protect caterpillars and prevent accidents.

The presence of host plants in urban or rural areas can be found in gardens/yards of residences, on streets, or other locations close to humans. Accidental contact with *Lonomia* spp. caterpillars can occur when leaning against a tree in human-inhabited areas. For instance, there have been cases of children accidentally touching a tree harboring a cluster of *Lonomia* spp. while playing in their backyard or garden (Duarte et al. 1997, Medeiros et al. 2014, Sánchez et al. 2015). Other reports include accidents that occurred while adults were engaging in domestic or recreational activities in their gardens (Corrêa et al. 2004, Fan 1998, Sandoval et al. 2008).

In many agricultural and urban areas, humans cultivate fruit species in their yards or gardens to obtain fresh food and/or an additional source of income. In this regard, it should be noted that the cultivation of mango (*M. indica*) and avocado (*P. americana*) is quite common in South American yards and gardens (Altendorf, 2019), and these trees serve as hosts for *Lonomia* spp. caterpillars, as evidenced in the scientific literature reviewed for this work. Thus, when attempting to collect these fruits, accidental contact can occur. In fact, the Ministry of Health of Peru (2007) reported the case of a 12-year-old girl who had an accident while touching a cluster of such caterpillars while searching for fruits on a tree.

There are also plantations of popular fruit species in the continent (and in the world), such as plum (*Prunus domestica*), avocado (*Persea americana*), guava (*Psidium guajava*), pear (*Pyrus communis*), fig (*Ficus* spp.), apple (*Malus pumila*), mango (*Mangifera indica*), peach (*Prunus persica*), lemon (*Citrus limon*), and orange (*Citrus sinensis*). It is estimated that the area harvested with these fruit species in South America increased five-fold between the 1960s and 2000, reaching 1,690,765 hectares (FAO 2022). Fruit cultivation often occupies regions that were previously occupied by natural forests, which are often deforested for this purpose.

The replacement of previously native regions with homogeneous plantations of trees, such as fruit orchards or forestry, reduces vegetation diversity and consequently makes the environment less stable and capable of absorbing disturbances (Risch et al. 1983), thereby increasing entomological problems. Just as many genera of lepidopterans are considered pests of various crops (Gallo et al. 1988), defoliation caused by *Lonomia* spp. caterpillars is becoming more frequent. There are reports of *L. obliqua* as a defoliating pest in eucalyptus plantations (Bernardi et al. 2011), *L. circumstans* as a secondary pest of coffee plants (Gallo et al. 1978), and more recently, two reports involving *Lonomia* sp. in the attack on rubber tree plantations in Brazil (Santos et al. 2015, Souza-Santos & Gonçalves 2015). This indicates not only the involvement of *Lonomia* spp. in economic damage but also potential cases of envenoming in agricultural workers.

Native hosts and the consequence of adaptation to non-native hosts

Some researchers investigating the Saturniidae family have raised the hypothesis that the destruction of natural habitats has forced *Lonomia* spp. to find new non-native hosts to sustain their populations (García 2013, Lorini 1999, Moraes 2002). However, this is not supported by the results obtained in this study. It is possible that this relationship may have occurred in the mid-20th century as a consequence of deforestation in South America (Armenteras et al. 2017, Davidson et al. 2012) or may be even occurring currently, but there is limited information on the host range of *Lonomia* spp., particularly *L. achelous*, to definitively affirm this.

It is known that the introduction of non-native species into new environments alters the dynamics of native communities, including lepidopterans (Graves & Shapiro 2003). According to Britton and New (2004), this relationship may be part of a long-term decline rather than simply an increase in the list of species switching to non-native hosts. As a result, this could be influencing the biology and interactions of this lepidopteran with its respective communities.

Moth larvae, including those of the genus *Lonomia*, can adapt to new host plants through genetic variation within the population, environmental pressures such as land-use and climate changes, and other factors such as nutrient and water availability in the new host, the presence of predators and parasites, and social interactions within the population (Abella et al. 1999). Epigenetic changes, involving changes in gene expression without altering the DNA sequence, may also play a role in adaptation (Futuyma 2000).

It is important to note that the fact that female moths lay eggs on plants that are non-native to the moth's natural habitat, or oviposition on non-native hosts, may be due to non-adaptive errors rather than an adaptive choice by the female (Futuyma 2000). In other words, the female moth may deposit eggs on a non-native plant because it is chemically similar to a native plant and therefore triggers the same oviposition signals, rather than the non-native plant being a preferred host for larvae. This differs from an adaptive choice, which would be based on the female moth's innate preference for the non-native plant as a host for her offspring.

The adaptation of *L. achelous* and *L. obliqua* larvae to non-native hosts can have important implications for public health, as it may increase the likelihood of accidents involving them. If the larvae can adapt to non-native trees that are more commonly found in areas with human activity (García 2003, Lorini 1999), there may be a higher risk of accidental contact with their venomous setae/spines. Furthermore, if the larvae can thrive on these non-native trees, their population size may increase, further escalating the risk of accidents.

With the large number of native and non-native host species of *Lonomia* spp., the challenge of mitigating envenomation caused by caterpillars of this genus arises since it cannot be restricted to specific hosts as it happens with the caterpillar of *Premolis semirufa* Walker, 1856; family Erebidae.

This species inhabits the Amazon rainforest and in its larval stage feeds almost exclusively on the leaves of the rubber tree *Hevea brasiliensis*. These larvae cause a type of envenomation that is considered an occupational disease, affecting almost exclusively workers involved in the extraction of natural rubber. While accidents with this caterpillar were quite frequent during the 1970s, they later on decreased with the acquired knowledge about the species and the adoption of preventive measures, such as the use of gloves by the rubber workers (Monteiro-Costa 2009).

Distribution of native host species

As demonstrated in this study, the distributions of *L. achelous* and *L. obliqua* are determined by the availability of their native hosts. The presence of multiple hosts can allow the caterpillars to disperse and establish in a wide range of habitats, enhancing their ability to survive and reproduce. This is likely a crucial factor in the geographical range of both species on the continent. Additionally, the rarity of endemism also helps explain the distribution of both species within a relatively broad geographic range.

Regarding host density, in Venezuela and the Amazon region, there are some areas where the occurrence points of *L. achelous* do not overlap with areas of native host density, which could indicate a lack of understanding of specific host preferences in these regions or a deficit in finding occurrences. However, findings of *L. achelous* associated with *T. guianensis* trees have already been reported in Venezuela (Arocha-Piñango 1987, Lemaire 2002), as well as accidents in areas of the Amazon rainforest where occurrences of *L. achelous* are not known (Favalesso et al. 2023). This highlights the need for further research efforts on host preferences of *L. achelous* in these regions to aid in understanding the distribution of this species and its potential impacts.

With the loss of native hosts, *L. obliqua* may be adapting to new non-native hosts (García 2013), thus increasing its distribution range. However, the data obtained in this study suggest a different interpretation, as the findings of *L. obliqua* were closely associated with areas of higher abundance of native species, indicating that its distribution range has always been the same and have not changed on a macro scale as a consequence of anthropogenic actions. Furthermore, since none of the native hosts of *L. obliqua* are threatened or at risk of extinction, it could be considered that the species does not have an immediate need to adapt to new hosts.

Sometimes habitat alteration forces animals to move to human-inhabited areas in search of food, shelter, and mates for reproduction, increasing the likelihood of encounters with humans. In line with this, during her research in southern Brazil, Lorini (1999) found *L. obliqua* caterpillars primarily in human-altered and human-transition environments, such as parks, farms, and orchards. In addition, Arocha-Piñango (1987) described accidents with *L. achelous* mainly at the edges of deforested areas in Venezuela. This could be due to the greater availability of food sources or the introduction of non-native species near inhabited areas. It is important to keep in mind that, in any case, accidental contact with *Lonomia* spp. can be dangerous and, in some cases, fatal (Favalesso et al. 2021).

It has been observed that both *L. achelous* and *L. obliqua* caterpillars stay together in clusters on trunks of trees growing near houses in rural areas (Casafús et al. 2021, Lorini 1999), in plazas (Lorini 1999), at forest edges (Arocha-Piñango 1987, Riella et al. 2008), and in other regions where the trunk is exposed to high levels of direct sunlight. This is indeed related to our findings of most native hosts of both species being heliophilous. These plants are adapted to grow under full sunlight conditions and are characterized by their exposure to direct sunlight. In tropical forests, heliophytes are most commonly found in edge areas (at the interface between forested and non-forested ecosystems or between two forests of contrasting composition or structure) (Harper et al. 2005, Eldegard et al. 2015).

In plants exposed to excessive light, the production of phenolic compounds, including tannins, can be useful in reducing the harmful effects generated by free radicals and other reactive species due to radiation (Zhang et al. 2022). Thus, the preference for tannin-rich species may be related to the greater presence of *Lonomia* spp. in heliophilous plants. Additionally, exposure to solar radiation can have a significant impact on the temperature of larval aggregations due to heat accumulation (Klok & Chown 1999), potentially aiding them in maintaining optimal physiological processes (Reader & Hochuli 2003).

The quality of host plants can also play a role in diapause induction. The diapause period allows individuals to survive in unfavorable environmental conditions and resume development when conditions become more favorable (Lorini et al. 2007, Favalesso et al. 2019). In a study conducted by Hunter and Mcneil (1997), it was found that the proportion of *Choristoneura rosaceana* larvae (Lepidoptera: Tortricidae) entering diapause varied depending on the host plant species. Larvae feeding on common chokecherry (*Prunus virginiana*) were more likely to continue their development and produce a second generation, while those feeding on red maple (*Acer rubrum*) or black ash (*Fraxinus nigra*) were more likely to enter diapause. An intermediate response in diapause induction was obtained with paper birch (*Betula papyrifera*). Similarly, Sayed et al. (2021) found that a low-quality diet induced diapause in the cotton leafworm, *Spodoptera littoralis* (Lepidoptera: Noctuidae).

CONCLUSION

This research supports the idea that *L. achelous* and *L. obliqua* caterpillars are polyphagous, with a possible preference for plants that produce tannins as secondary metabolites. Most host plants have at least one human use, which increases the risk of accidental contact with both species. On the other hand, our results do not support the hypothesis that deforestation and land occupation expand the occurrence area of *Lonomia* spp. since more native host species have been identified in recent years, with few non-native species reported since 2000. The distribution of *L. obliqua* is associated with areas of higher abundance of native species, suggesting stability in its global distribution range. This work also shows that most host plants of both species are heliophilous, growing in full sunlight. Therefore, *L. achelous* and *L. obliqua* caterpillars are more likely to be found in open environments. Thus, we revealed herein features of *Lonomia* host plants that had been overlooked until now, but they appear to play as key drivers for accidental contact with these venomous caterpillars. These findings could be used to help in designing effective prevention and risk management strategies for addressing *Lonomia* accidents in South America.

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