

Patterns of the introduction, spread, and impact of the brown widow spider, *Latrodectus geometricus* (Araneae: Theridiidae), in the Americas

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Abstract. Introductions of non-native species to novel environments happen often, but a species must overcome multiple biotic and abiotic filters to establish and eventually spread. Focusing on patterns of introductions can provide insights as to underlying mechanisms that facilitate establishment, and in turn, their potential effects on native communities. The brown widow spider, *Latrodectus geometricus* C. L. Koch, 1841, is likely native to Africa, but now has a cosmopolitan distribution due to introductions via international trade. We reviewed the patterns of brown widow introductions in the Americas to determine if there are any large-scale inferences regarding their patterns, and potential impacts, of their introduction. A total of 5,004 records from 30 countries were synthesized and demonstrate their spread to higher latitudes across time with the majority of those records ($n = 4,923$; 98%) occurring in the past two decades. Brown widows are now documented in 30 of the 35 countries in North, Central, and South America, with one-third of those introductions detected in the last 30 years. Citizen-science databases (e.g., iNaturalist) have been instrumental in documenting the expansion of the brown widow, as more than 90% of the records synthesized came from these sources. Brown widows have proven to be successful invaders worldwide, and this review synthesizes expansion reports of their invasion in the Americas in hopes of spurring additional research in locations where they have become established.

Keywords: Non-native species, introduced species, invasive arthropods, citizen science, geographic distribution, range expansion

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Globally, an estimated 480,000 non-native species have been introduced to new ecosystems and that number is expected to rise by 35% by 2050 (Pimentel et al. 2001; Anton 2020). Though natural introductions of species do occur due to shifts in ranges from climatic changes and the removal of geographic barriers, humans cause the majority of introductions (Williamson 1996). Humans move species from their native range to non-native ranges intentionally (e.g., for food, biocontrol agents, etc.), but many of the introductions of species are accidental and are attributed to transport vessels used in international trade (Westphal et al. 2008). Globalization and environmental changes have led to over one-sixth of Earth's land surface being highly vulnerable to invasion (Early et al. 2016). Over the next ten years, international trade is expected to increase 1.8–2% annually, and as a result, the introductions of non-native species will likely continue to rise (Khotamov & Ismoilov 2020). Therefore, understanding the patterns of introduction and spread of previously introduced species is valuable for making future predictions for present-day invasions.

Non-native species can have direct detrimental effects on native species through novel interspecific interactions (e.g., predation, competition, and hybridization), which in turn can cause local extinction of native species (Wilcove et al. 1998; Mooney & Cleland 2001). For example, more than half of all emerging plant diseases were spread by introduction (Bebber et al. 2013), potentially causing direct and indirect effects on native organisms and humans. Humans can also be negatively affected by invasive species through cultural, climatic, and economic impacts (Vitousek et al. 1997; Pejchar & Mooney 2009). For example, a recent study highlighted that more than

half of crop pests (e.g., insects, fungus, bacteria) had a global distribution and were responsible for up to 16% of lost crop production due to plant damage and spreading pathogens (Bebber et al. 2013). In terms of financial losses, there is an estimated US\$248 billion in damage done annually to the world's agriculture industry from non-native organisms (Fried et al. 2017). As human populations grow and international trade increases, more regions of the Earth will be vulnerable to introductions by non-native species and will face the consequences that come from those introductions.

Outside their native range, terrestrial invertebrates can cause extensive economic and ecological impacts. A meta-analysis found that, on average, non-native terrestrial invertebrates reduced plant fitness by 52% (i.e., herbivore damage, reduction of seedling establishment, flowering, and fruiting), reduced animal diversity by 33%, and reduced animal abundance by 29% (Cameron et al. 2016). Europe has more than 1,300 non-native terrestrial invertebrate species, and an additional 964 species introduced outside their native range within Europe (Roques et al. 2009). Not only can damage caused by these non-native species be costly, but attempting to eradicate non-native species before they cause detrimental impacts can be just as expensive. For example, an attempt was made to eradicate an invasive beetle in Italy by removing over 2,000 trees at a cost of \$1.25 million and incalculable environmental costs, yet the operation was not successful and the beetle persisted (Vilá et al. 2010). The least-damaging course of action is to prevent the introduction of species to novel locations, but the inconspicuousness of many invertebrates makes this difficult to accomplish.

Hundreds of spider species have been transported all around the world in recent decades via human assistance (Kobelt & Nentwig 2008). From a detailed study conducted in Europe, it was found that more than 90% of all spider introductions came from three pathways: fruit shipments, potted plants, or packaging material (Nentwig 2015). Non-native spiders can cause economic impacts to the horticultural industry through web spinning activity, ecological impacts to native spiders by replacing them in the environment or by predation, and human health impacts through medically significant bites (Nentwig 2015). One of the most common families of spiders to be transported outside of its native range is the cobweb spiders, family Theridiidae (Vink et al. 2010; Vetter et al. 2012b; Nentwig 2015). Members of this family are easily transported around the world because of their affinity for anthropogenic structures, like vehicles and shipping containers.

The family Theridiidae includes 124 genera, with the genus *Latrodectus* Walckenaer, 1805 receiving widespread attention due to their medical significance and global distribution (WSC 2020). Members of the genus *Latrodectus* possess a neurotoxic venom component, α -latrotoxin, which is a protein that targets vertebrates and can cause symptoms such as nausea, vomiting, extreme pain, and in rare cases, death (McCrone 1964; Timms & Gibbons 1986; Hauke & Herzig 2017). The brown widow spider, *Latrodectus geometricus* C. L. Koch, 1841, was first described from a specimen collected in Colombia, though some believe the native range to be Africa (Levi 1959). Brown widows are urban exploiters most commonly found near humans, and because of their affinity for human structures, they are easily transported around the world (Brown et al. 2008; Sadir & Marske 2021). Spider webs are usually found on buildings, outdoor furniture, vehicles, and other anthropogenic structures (Lamoral 1968; Marie & Vetter 2015). They are occasionally found on more natural substrate, such as vegetation, but in the majority of these cases the vegetation is a microhabitat associated with urban environments (Brown et al. 2008; Vetter et al. 2012b). They are generalist predators and consume a wide variety of insects, arachnids, and occasionally much larger prey such as reptiles, amphibians, and small mammals (Lira & Costa 2014; Taucare-Ríos & Canals 2015; Vasava et al. 2015; Rocha et al. 2017; Luna et al. 2020). The venom of brown widow spiders is more toxic in mice, compared to the venom of most congeners, but on average they deliver a smaller amount of venom in their bite, posing a lower risk for human health (McCrone 1964). Furthermore, brown widow bites are uncommon because they often exhibit thanatosis when disturbed (Brown et al. 2008). In the rare instance where a brown widow bite requires medical attention, anti-venom is rarely needed and supportive care for pain and swelling is administered (Almeida et al. 2009). Due to brown widows' affinity for human structures, they have quickly expanded their range and are now a cosmopolitan species (Garb et al. 2004). Despite their widespread introductions, the majority of published information on brown widows only contains single occurrence records and does not include large-scale introduction patterns.

The current reports of brown widow introductions, as well as their local impacts in novel ecosystems, are scattered across

databases and peer-reviewed articles (Koch 1841; Bianchi 1945; Baerg 1954; Anderson 1972; Garb et al. 2004; Brown et al. 2008). For a globally distributed species that continues to expand its non-native range, it is important to synthesize these patterns of their introductions and spread to develop predictions on the pathways and vectors of their movement into new areas around the world. Also, this information can help to develop and test new hypotheses addressing the underlying mechanisms facilitating their establishment. This review was conducted to consolidate current knowledge regarding the invasion history, the spatiotemporal patterns of the introductions, and the ecological impacts of the brown widow spider in the Americas, with remarks for each region: North, Central, and South America as well as the Caribbean Islands. This study is overall descriptive, but the general hypothesis is that the range of the brown widow will increase in latitude over time, and coupled with the increasing latitudinal range is the increase in the number of records over time. To understand the consequences of their introduction in novel environments, we also included information regarding human and ecological impacts of brown widows from published literature.

METHODS

To synthesize reports of introductions of brown widow spiders across the Americas, we conducted a literature search in January 2022 using Google Scholar and Scopus with the following key words: ("*Latrodectus geometricus*" OR "*L. geometricus*" OR "brown widow") AND (geographic OR distribution OR invas* OR intro* OR record). After the initial search in each database, results were further narrowed down by discarding articles if they investigated other subjects of brown widows, i.e., molecular biology, venom biochemistry. We also used the Global Biodiversity Information Facility (GBIF) to access museum specimens and geotagged photos, which includes the expansive iNaturalist database. Only observations categorized as "research-grade" on iNaturalist were used, meaning at least one other person has confirmed the identity of the specimen. When available, we recorded the coordinates and month and year of collection for each record. When no date was provided, we assigned the record year as the year of publication ($n = 71$ records). When no coordinates were provided, we assigned coordinates from the center of the study area (e.g., city, state; $n = 100$). We manually verified identifications from photographs for a random subset of samples from citizen-science databases. To determine whether brown widows exhibited a latitudinal range expansion across time, we employed linear models for each hemisphere using the maximum latitude of the record of each year as dependent variable and the year as independent variable. We performed these analyses in R software (R Core Team 2017).

RESULTS

The initial Scopus search yielded 26 articles, furthered narrowed down to 11 articles by the criteria mentioned above. The Google Scholar search yielded a total of 552 results, narrowed down to 132 articles, also by the criteria mentioned above. Of those 143 articles, articles focusing on venom biochemistry were discarded, resulting in 67 articles for a full

review. When data were available, information was also included on impacts of brown widows on members of recipient communities. In total, 42 articles from Google Scholar and 11 articles from Scopus were found to be relevant to brown widow distribution in the Americas, and another six studies contained information regarding their impacts.

In addition to those articles, GBIF records for brown widows included 4,808 occurrences through the end of 2021 from 46 datasets such as iNaturalist research-grade observations (4,427 records, 92.1%), *Natural History Museum of Los Angeles County Entomology Collection* (217 records, 4.5%), *Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* (MACN; 42 records, 0.9%), International Barcode of Life project (iBOL; 38 records, 0.8%), *Apoyo para la infraestructura de la colección de artrópodos con y sin importancia médica del Laboratorio estatal de Salud Pública del estado de Guanajuato* (31 records, 0.6%), *Actualización de la Colección de Artrópodos con importancia médica* (CAIM; 26 records, 0.5%), and other datasets that contained fewer than 20 records each (Table 1).

Approximately 74% of the records were from the United States and Canada (Fig. 1A), 11% from Central America and the Caribbean Islands, including Mexico (Fig. 1B), and 15% were from South America (Fig. 1C). Brown widow records increased in latitude over time in the northern hemisphere ($F_{1,31} = 75.03$, P -value < 0.05 , $R^2_{\text{adj}} = 0.70$; Fig. 2), but not in the southern hemisphere ($F_{1,29} = 2.70$, P -value $= 0.11$, $R^2_{\text{adj}} = 0.05$; Fig. 2). The northern and southern extent of the range reached its maximum at 43- and 38-degrees latitude, respectively (Fig. 2). Southern hemisphere had consistent records throughout the year while Northern hemisphere had two noticeable spikes in the number of observations, one in April and the other August through October (Fig. 3). The number of observations by year did not reach 100 until 2015, and since then has risen each year with the most recent year, 2021, having more than 1,300 observations (Fig. 4). The earliest report of a brown widow was in 1841, when the species was first described, while the most recent reports from our search efforts were from December 2021.

Spatiotemporal patterns of brown widow introductions.

South America: Argentina—The brown widow was reported in Argentina as early as 1939 in the province of Córdoba (Mello-Leitão 1940). By 1965, brown widow specimens were reported from Salta, Formosa, Catamarca, Chaco, Misiones, Santiago del Estero, Corrientes, and Buenos Aires provinces (Gerschman & Schiapelli 1965). Since 1965, brown widows have been documented in the provinces of Jujuy, Tucumán, Entre Ríos, Santa Fe, La Rioja, San Juan, Mendoza, and San Luis (GBIF 2022).

Bolivia—Patrick & Renée (2013) surveyed six departments in the country for *Latrodectus* spp. and only documented brown widows in the department of La Paz. A single female specimen was found in 2017, and in 2019–2020 female specimens and egg sacs were reported from the departments of Santa Cruz, Cochabamba, and Beni. There is also a female specimen in the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” collection from the department of Santa Cruz, though no date is given with the specimen (GBIF 2022).

Table 1.—Number and source of records by country for the brown widow spider (*Latrodectus geometricus*) in the Americas.

Country	Number of Observations by Source		
	All Records	Peer-reviewed	Citizen Science
United States	3672 (73%)	73 (2%)	3599 (98%)
Mexico	436 (8.7%)	21 (5%)	415 (95%)
Brazil	423 (8.5%)	27 (6%)	396 (94%)
Argentina	209 (4.2%)	13 (6%)	196 (94%)
Dominican Republic	37 (0.7%)	1 (3%)	36 (97%)
Colombia	32 (0.6%)	4 (12%)	28 (88%)
Costa Rica	26 (0.5%)		26 (100%)
Uruguay	20 (0.4%)	20 (100%)	
Ecuador	19 (0.4%)		19 (100%)
Puerto Rico	16 (0.3%)		16 (100%)
Bolivia	15 (0.3%)	1 (7%)	14 (93%)
Honduras	13 (0.3%)		13 (100%)
Paraguay	10 (0.2%)	4 (40%)	6 (60%)
Peru	9 (0.2%)		9 (100%)
Venezuela	9 (0.2%)	4 (44%)	5 (56%)
Jamaica	8 (0.2%)	5 (62%)	3 (38%)
Cuba	6 (0.1%)	2 (33%)	4 (67%)
Panama	6 (0.1%)	6 (100%)	
Chile	6 (0.1%)	5 (83%)	1 (17%)
Guatemala	6 (0.1%)		6 (100%)
El Salvador	6 (0.1%)		6 (100%)
Curacao	5 (0.1%)	3 (60%)	2 (40%)
Haiti	4 (0.1%)	2 (50%)	2 (50%)
Trinidad and Tobago	3 (0.1%)	1 (33%)	2 (67%)
Turks and Caicos	2 (<0.1%)		2 (100%)
Bahamas	2 (<0.1%)	1 (50%)	1 (50%)
Bermuda	1 (<0.1%)	1 (100%)	
French Guiana	1 (<0.1%)		1 (100%)
Guyana	1 (<0.1%)	1 (100%)	
Aruba	1 (<0.1%)	1 (100%)	
Total	5004	196 (4%)	4808 (96%)

Brazil—Pickard-Cambridge (1902) mentions examining specimens from several locations in Brazil including Rio de Janeiro, Minas Gerais, Amazonas, and Pará. Badcock (1932) found a female brown widow (reported as *Chacoca distincta*) in 1926 in the state of São Paulo, then six adult females were also collected from there in 1944 (De Biasi 1962). Levi (1959) reports brown widows occurring in the states of Paraíba, Pernambuco, Minas Gerais, and Rio de Janeiro. By 1969, records expanded to include the Brazilian states of Bahia and Espírito Santo (Bücherl 1964; Anderson 1972). More recently, brown widows have been reported in the Brazilian states of Rio Grande do Sul, Santa Catarina, Paraná, Mato Grosso, Rondônia, Rio Grande do Norte, Piauí, Alagoas, Goiás, and Tocantins (GBIF 2022).

Chile—Brown widows were reported during the early and mid-20th century in the provinces of San Pedro (Pickard-Cambridge 1902) and Santiago (Gerschman & Schiapelli 1965). More recent reports include adult females from the province of Iquique in 2003 and 2010 and the province of Arica in 2020 (GBIF 2022). Both Iquique and Arica have cities that commonly receive goods from Asia, Africa, and Europe. Due to the locations and infrequency of reports, it appears brown widows are being introduced multiple times in the

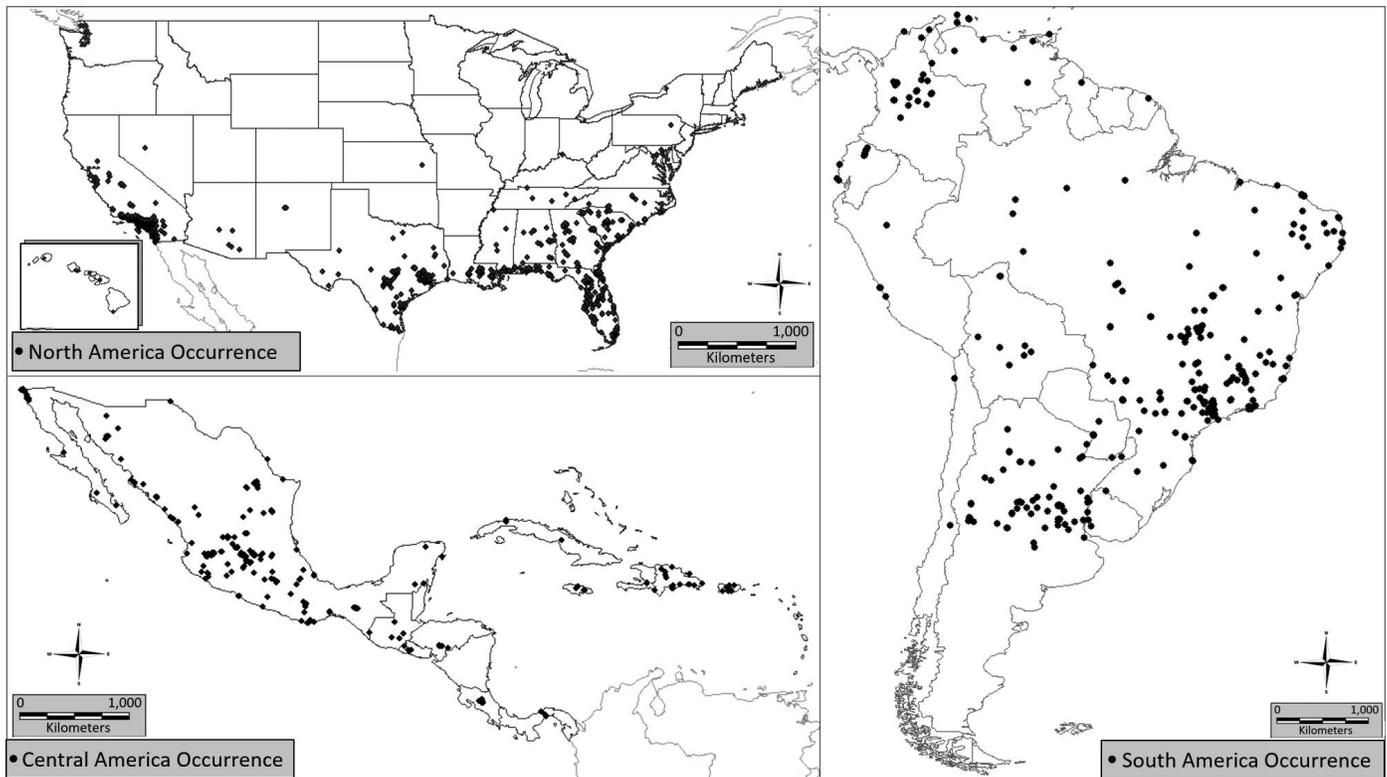


Figure 1.—Location of brown widow (*Latrodectus geometricus*) records in the United States of America and Canada (A), Mexico, Central America, and the Caribbean Islands (B), and South America (C).

country but have not established. Based on the climate in Chile, the likelihood of brown widows successfully establishing is low (Taucare-Ríos 2011).

Colombia.—Despite the holotype of the brown widow originating from Colombia, there are few reports of brown widows from the country. Pickard-Cambridge (1902) examined brown widow specimens from Rio Apia in the

department of Risaralda. More recently, brown widows have been reported from the departments of Antioquia, Bolívar, Boyacá, Caldas, Cundinamarca, Guajira, Huila, Meta, Nariño, Norte de Santander, Quindío, Santander, Tolima, Valle del Cauca, and Vichada, though collection dates were not always included (Noriega 2016; Urrego 2020; GBIF 2022).

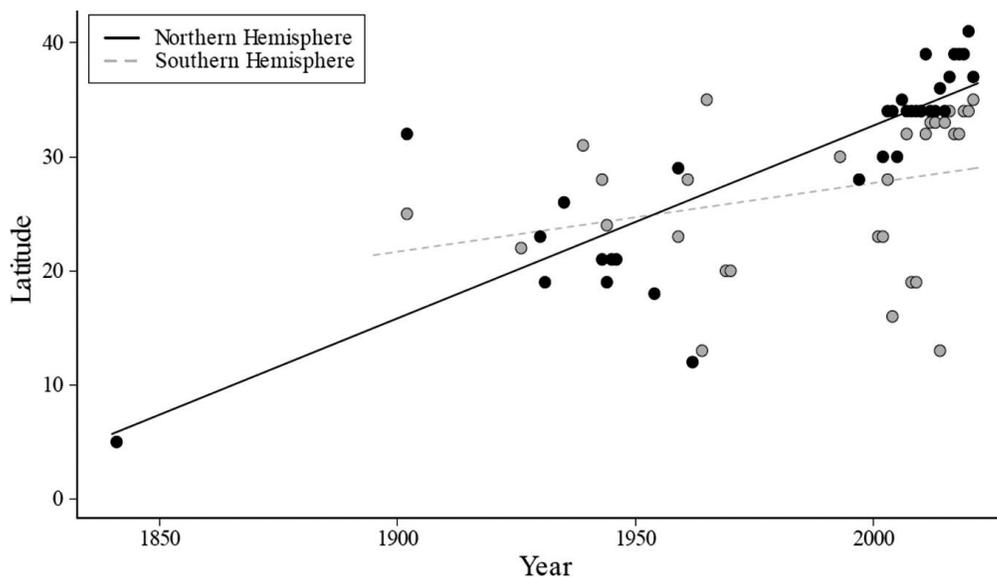


Figure 2.—Maximum latitude of brown widow (*Latrodectus geometricus*) records by year in the Americas for the northern hemisphere (black) and southern hemisphere (gray).

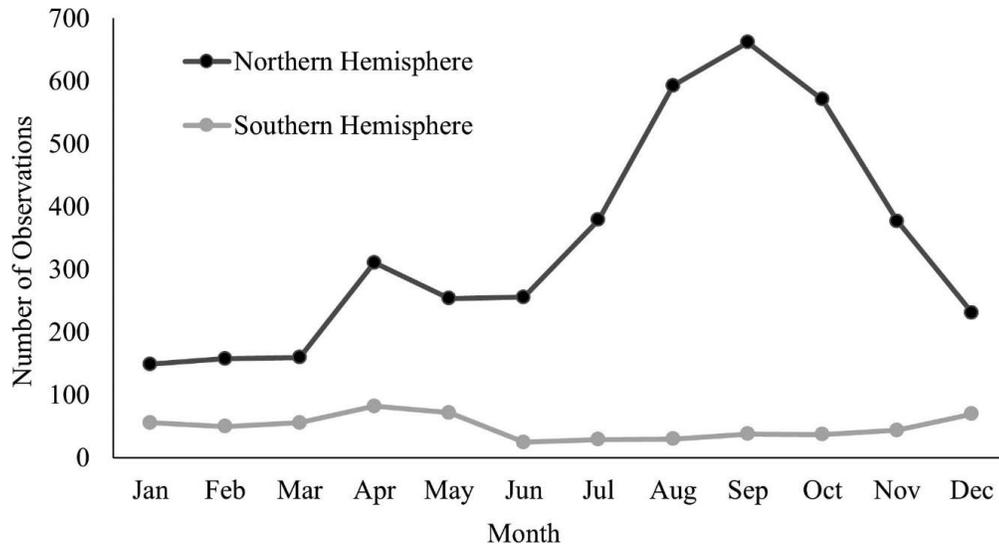


Figure 3.—Number of observations of the brown widow (*Latrodectus geometricus*) by month in the Americas for the northern hemisphere (black) and southern hemisphere (gray).

Paraguay.—Pickard-Cambridge (1902) mentioned examining brown widow specimens from Paraguay, but locale and collection date were not reported. Badcock (1932) reported brown widows in 1926 (see report from Brazil above) and Vellard (1936) reported them several years later, though specific locations were not reported for either record. There are four records from 2015 in the department of Central (GBIF 2022).

Uruguay.—Simo et al. (2013) revisited specimens deposited in the arachnological collections at two museums in addition to sampling field trips throughout the country during 2009–2011. The oldest specimen found in the collections was a female collected in 1993 from the Department of Artigas in

northwestern Uruguay (Simo et al. 2013). Other specimens were collected from the departments of Paysandú, Río Negro, Salto, and Soriano (Simo et al. 2013). Despite surveys conducted in other parts of the country, brown widows were only found along the western border of the country. Their location within Uruguay is consistent with transport via humans along the Uruguay River, which borders the country to the west (Simo et al. 2013).

Countries with minimal records.—A female was found in the province of Pichincha, **Ecuador** in 2013, then another found in the province of Santa Elena in 2020 (GBIF 2022). A male specimen was collected in 1974 from the state of Mérida, **Venezuela** and a female specimen was found in 2018 in the

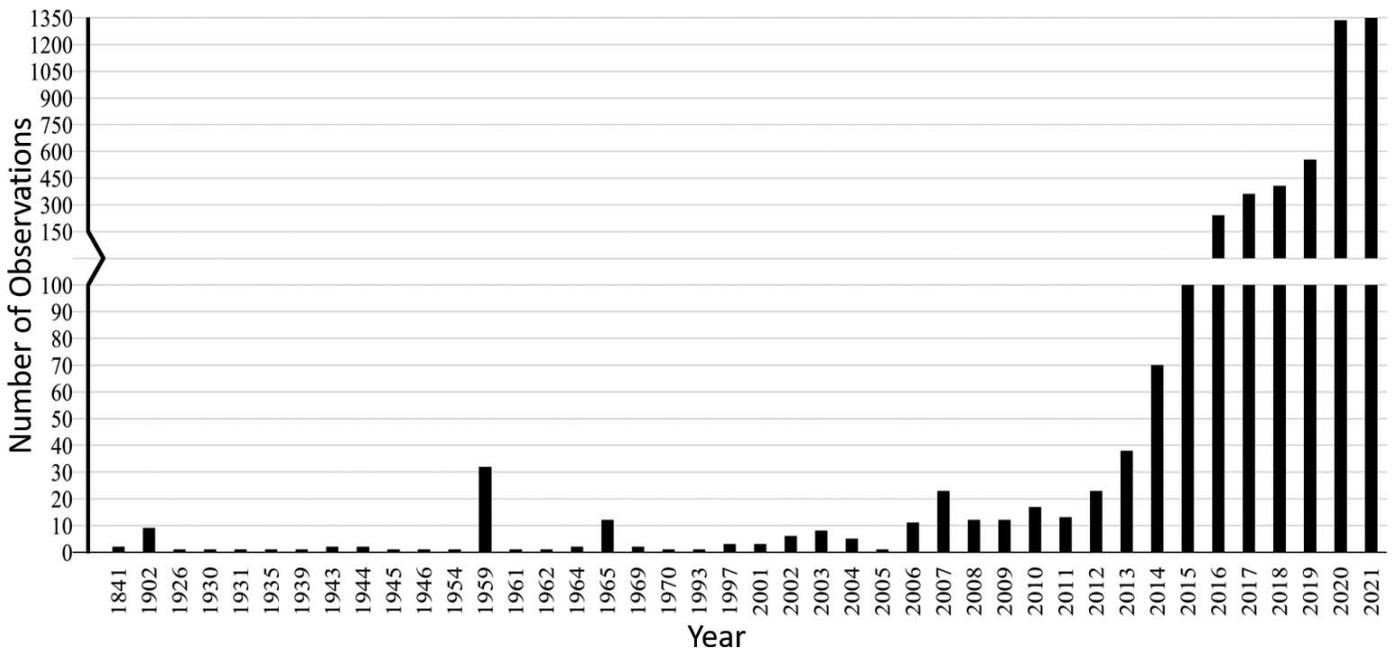


Figure 4.—Number of observations by year of the brown widow (*Latrodectus geometricus*) in the Americas.

state of Aragua (GBIF 2022). A single record comes from **Suriname** in the district of Sipaliwini in 2019, and a single record was also found for **French Guiana** in the capital city of Cayenne in 2020 (GBIF 2022). Levi (1959) reported brown widows from **Guyana** and **Peru** but did not provide additional details.

Mexico, Central America, and the Caribbean Islands: Costa Rica.—Female specimens were collected in 1995 and 1997 from the state of Heredia (GBIF 2022). Four additional records since then have all come from Heredia, except one from the state of San Jose. Photos of one female taken in Costa Rica shows more than eight egg sacs, several appearing to have already hatched (GBIF 2022).

Cuba.—Several female specimens were found in Havana in 1930 (Bryant 1940). De Armas (2012) stated that brown widows were widespread in Cuban cities and farms but did not elucidate further. Since 2015, there have been several records of females with egg sacs from Guantánamo (GBIF 2022).

Curaçao.—Pickard-Cambridge (1902) mentioned brown widows are found in Curaçao, though there is no collection date provided. McCrone & Levi (1964) discuss brown widows being abundant near Willemstad in late 1962 but did not provide specific records. There is also a specimen from 2004 and a single report from 2018 (GBIF 2022).

Dominican Republic and Haiti.—Pickard-Cambridge (1902) mentioned brown widows occur in San Domingo, which might refer to Santo Domingo, and if so, then this is the first record for the island. A female brown widow was collected from Ouest, Haiti, likely between 1927–1931 (Bryant 1948). In the Dominican Republic, brown widows have been found in the provinces of La Altagracia, La Romana, Santo Domingo, San Pedro de Macorís, and Santiago (GBIF 2022).

Mexico.—An adult female specimen is known from Yucatán in 1940 (GBIF 2022). There are three records from Jalisco in 1997, though there are no photos and no specimens provided for any of these records (GBIF 2022). Reports to date also include the states of: Baja California, Baja California Sur, Sonora, Chihuahua, Tamaulipas, Sinaloa, Coahuila, San Luis Potosí, Durango, Chiapas, Yucatán, Quintana Roo, Oaxaca, Guerrero, Morelos, Puebla, Guanajuato, Veracruz, Querétaro, Hidalgo, Michoacán, Aguascalientes, Tlaxcala, and Nuevo León (Salceda-Sánchez et al. 2017; Castañeda-Gómez et al. 2020; GBIF 2022).

Puerto Rico, United States.—Early reports mention brown widows occur in the municipalities of Salinas and San Juan (Levi 1959). Gutiérrez-Fonseca & Ortiz-Rivas (2014) observed brown widows in the dry regions of the island, mostly Central and South. Records also came from the municipalities of Yauco and Vega Baja since 2016 (GBIF 2022).

Countries with minimal records.—Brown widows are known from Kingston, Saint Andrew, and Saint Ann Parishes in **Jamaica** (Levi 1959). Since then, there has only been a report of a female and egg sacs from Saint Ann Parish in 2019 (GBIF 2022). Levi (1959) reported brown widows occurring on the islands of **Aruba**, **Bermuda**, **British West Indies**, and **Navassa Island** and lists records from locations in **Panama**: Panama City, Ancon, Colon, Fort Amador, Fort Randolph, and Quarry Heights. Two specimens were collected from San Augustine province, **Trinidad and Tobago**, during the summer of 1999 (GBIF 2022). Four specimens were collected from the

island of **Sint Maarten** in 2013 (GBIF 2022). **Guatemala** has two records since 2019 from the departments of Jalapa and Zacapa, both of which are females with many egg sacs (GBIF 2022). In **Honduras** there are four records from the departments of Francisco, Morazán, and El Paraíso dating back to 2018 (GBIF 2022). There is a single record of a female in **El Salvador** from 2020 in the department of San Salvador (GBIF 2022).

States within the United States: Arizona.—There is a museum specimen from Maricopa County from August 1970, then a second from July 1996 in Pima County (GBIF 2022) From 2019–present there are about a dozen records from the southern half of the state (iNaturalist 2022).

California.—The first specimen was accessioned at the Los Angeles County Natural History Museum in 2003 (Vincent et al. 2008). Shortly after, brown widows could be found in various cities in southern California in large numbers (Vetter et al. 2012a). Vetter et al. (2012a) placed an ad in the newspaper and contacted the local news asking residents to mail in brown widow egg sacs and they were sent specimens from over 100 people. California quickly became a hot spot for brown widows in the United States and they can easily be found established all over the southern portion of the state today (Vetter et al. 2012a; GBIF 2022). Though mostly restricted to southern California, records have been made from as far north as Sacramento (GBIF 2022).

Florida.—In September 1935, students working on a building at the University of Miami collected specimens and sent them to the American Museum of Natural History (Pearson 1936). They were confirmed to be brown widows, this being the first record of this species in the United States (Pearson 1936). Restricted to southern Florida for decades, by the mid-1980s the brown widow had become established in northern Florida (Brown et al. 2008).

Georgia.—By the late 1990s, brown widows had expanded northward from Florida and were being found in the southern portion of Georgia (Brown et al. 2008). They can now be found throughout the state, even during winter months (iNaturalist 2022).

Hawaii.—Krauss (1943) reports finding brown widows on the island of Molokai in May of 1943. In 1944, the Morse Field Air Force base on the island of Hawaii was surveyed and brown widows occurred in high abundance (Bianchi 1945). Records today are known from the islands of Kauai, Oahu, Maui, and Hawaii (GBIF 2022).

Louisiana.—The first known record in this state was in the city of Harvey, Louisiana in July 2002 (Brown et al. 2008). Over the next few years, reports of brown widows became increasingly common throughout New Orleans and other cities in southern Louisiana where it is common to find dozens on buildings in town (Brown et al. 2008; GBIF 2022). Reports today continue to come from the southern portion of the state (GBIF 2022).

Mississippi.—The first known collection of the brown widow in the state was made by a state agriculture inspector in January 2005 in Biloxi (Brown et al. 2008). Soon after, established populations were discovered along the Gulf Coast of the state (Brown et al. 2008; GBIF 2022). The following year populations were found on the northern side of the state in DeSoto County, which borders the Tennessee state line,

though they are not seen regularly that far north (Brown et al. 2008, GBIF 2022).

Texas.—Jackman (1997) reported brown widows had recently been found in the state, but does not give specific locales. By 2007, there were established populations along the coast (Brown et al. 2008). Dean (2016) reported brown widows from only five counties in Texas, and now they are reported from more than 22 counties in Texas just four years later (GBIF 2022).

States with minimal records.—**South Carolina** had its first record in the early 2000s and they can now be found throughout the state (Brown et al. 2008; GBIF 2022). **Alabama** had its first record of a female from August 2009, and now brown widows can be found all the way north near the Tennessee border (GBIF 2022). **Tennessee** has a record from 2014 of a female found dead on a car from Louisiana, so it is likely the spider was a stowaway on the vehicle and few records from the state have been reported since that initial report (GBIF 2022). **Indiana** and **Maryland** have records from 2017, **North Carolina** and **New York** have records starting in 2018, **New Mexico**, **Connecticut**, and **Kansas** have records from 2019, and **Arkansas**, **Pennsylvania**, **Nevada**, **Oregon**, and **Virginia** have records from 2020 (GBIF 2022; Williams & Trumbule 2021). In 2021, **Illinois**, **Michigan**, **Ohio**, and **Delaware** also had minimal observations (GBIF 2022; iNaturalist 2022).

Territories of the United States.—Kerr (2013) says brown widows are established on a military base in **Guam** but does not indicate when they were first detected.

Human and ecological impacts.—Brown widows are generalist predators that prey mostly upon other arthropods, though they have been recorded preying upon vertebrates many times their size. Most of their diet consists of insects from the orders Coleoptera, Isopoda, and Diptera (Rossi & Godoy 2005; Taucare-Ríos & Canals 2015). A study in Chile found the diet of brown widows to consist of nine arthropod orders, with Coleoptera and Isopoda representing 22.2% and 25.4%, respectively (Taucare-Ríos & Canals 2015). In Brazil, the diet of the brown widow consisted of six arthropod orders with Coleoptera representing 48% and Diptera representing 34% of their prey (Rossi & Godoy 2005). Though not a main portion of their diet, brown widows are also regularly seen feeding upon other arachnids (Vellard 1936). In Brazil, a brown widow was observed preying upon a native black-headed snake (*Tantilla melanocephala*) that was more than 18 times larger than the spider (Rocha et al. 2017), and in Mexico a brown widow was observed feeding on a non-native house gecko (*Hemidactylus frenatus*) (Luna et al. 2020). Rarely, brown widows have been observed preying upon small mammals such as a deer mouse (*Peromyscus maniculatus*) and a young rat (*Rattus* sp.) in the United States (Nyffeler & Vetter 2018).

McCrone & Levi (1964) suggested that introduced brown widows might have displaced the native South American widow (*L. curacaviensis* Müller, 1776) on the island of Curaçao due to their extirpation after brown widows had been introduced. However, a formal study was not explicitly conducted. In Louisiana, the native southern black widow was previously rarely collected within large cities in the area, and it is hypothesized that the now common brown widows are exploiting an open niche in these areas (Brown et al. 2008).

Brown widows are also tolerant of disturbance and can be found in very high densities. A beach in São Paulo, Brazil, with a large population of brown widows was burned with subsequent surveys not reporting any brown widows immediately following the fire. However, three months later, the vegetation had reestablished and brown widow abundance matched the pre-burn numbers (Anderson 1972).

Many parasites and parasitoids have been documented emerging from egg sacs of the brown widow, most commonly *Philoletia latroducti* (Hymenoptera: Eurytomidae) and *Pseudogaurax signatus* (Diptera: Chloropidae) that can parasitize upwards of 31% of brown widow egg sacs (Bianchi 1945; Vetter et al. 2012a; Marie & Vetter 2015). These parasites have been suggested as biocontrol agents for brown widows in their non-native range, though there is little evidence of their effectiveness (Bianchi 1945). In 1939, a military base in Hawaii was found to have an exceptionally high number of southern black widows, *Latrodectus mactans* (Fabricius, 1775), and in an attempt to eradicate them a large number of a known widow parasitoid, *Baeus californicus* (Hymenoptera: Scelionidae), was released (Bianchi 1945). When the military base was surveyed again in 1944, a high number of *L. geometricus* were found in the same locations previously occupied by *L. mactans*, and very few *L. mactans* or the released parasitoids could be found (Bianchi 1945). It is likely several species of egg sac parasites and parasitoids have been introduced to new countries through brown widow introductions. The type specimen for a parasitic wasp (*Eurytoma abalosi*) (Hymenoptera: Eurytomidae) hatched out of a brown widow egg sac collected in Santiago del Estero, Argentina, in 1960 (Loiácono et al. 2006). The type specimen for another parasitic wasp (*Philoletia latroducti*) (Hymenoptera: Eurytomidae) also hatched out of a brown widow sac in Hawaii in the mid-1940s (Fullaway 1953). The native ranges of many of the parasitoids associated with brown widow egg sacs are not known because the first time they were observed was in a location where brown widows had recently been introduced.

From 1987–1992, 15 brown widow bites showed symptoms including burning sensation at the bite site, abdominal pain, and regional lymph node pain (Müller 1993). In 2006, a 31-year-old female from Anzoátegui, Venezuela went to the hospital with pain and redness from a brown widow bite (Kiriakos et al. 2008). A 19-year-old woman in São Paulo state, Brazil, was bitten by a brown widow while in her bed and discharged after two days (Almeida et al. 2009). Of four brown widow bites reported in the United States (three in Florida and one in California) only one individual exhibited severe symptoms (Brown et al. 2008). As their range expands, especially in urban environments, more bites to humans are likely.

DISCUSSION

Since its initial description, brown widow distribution has greatly expanded, and they are now found on every continent except Antarctica (Levi 1959; GBIF 2022). Since the 1950s, the geographic distribution of brown widows increased substantially; the number of countries in Northern and Southern hemispheres with records has almost tripled. Brown widows have been recorded from about one-third of the countries in Northern and Southern hemispheres, and the introduction has happened in the last 30 years. During this same time frame,

there has been an upward trend in the maximum latitude at which brown widows have been documented. This trend in latitude could either be a consequence of climate change (Pauchard et al. 2016), urbanization, an artifact of more reports from citizen scientists, or a combination of these factors (Sadir & Marske 2021). Citizen science proved to be a useful tool to understand the patterns of the expansion of the brown widow, especially in the United States.

Most records of brown widows in the Americas come from tropical and subtropical regions, which coincides with their physiological tolerances (Barnes et al. 2019). We observed that records of brown widows came from sites located at less than 45 degrees latitude; however, we were not able to determine if those records are the result of new introductions or new detections. Brown widows are unlikely to successfully establish in Canada, the northern half of the United States, or high elevations in Central and South America due to their physiological constraints at lower temperatures (Taucare-Ríos et al. 2016). Based on the small number of records in some of those localities, we speculate that brown widows have not been able to successfully establish viable populations in those areas. Many northern states in the United States have very few records and only during warm summer months, suggesting that while individuals are being introduced in these areas, they are not able to survive with the onset of colder winter months (GBIF 2022). According to Taucare-Ríos et al. (2016), the southeastern United States, southeast Brazil, eastern Paraguay, eastern Argentina, and Uruguay have the highest probability of occurrence based on global climate niche in the Americas. These locations are consistent with where the majority of records are currently reported, in addition to southern California in the United States (GBIF 2022).

The surge in records during the past decade can represent either new introductions or new detections (i.e., already present but the internet has made documenting them easier in recent times). However, citizen science databases are a useful tool to look for trends over the upcoming decades, especially in areas with many users (i.e., the United States). Most records from iNaturalist were uploaded by users in the United States, allowing more reliable conclusions about introduction history and geographic distribution. On the other hand, there was a lack of records in other parts of the Americas (e.g., Peru and the Brazilian Amazon) which is probably related to these regions having a lower human population density and fewer citizen science participants. Nevertheless, about 30% of the countries throughout the Americas only contain brown widow records from citizen science databases, and none from peer-reviewed journals. iNaturalist was founded in 2008, and just a few years after it was created, the number of brown widow observations per year increased substantially, with over 90% of the total observations originating from iNaturalist and being reported in the past decade. Citizen science databases have contributed greatly to large-scale studies and tracking range extensions of non-native species throughout the world (Delaney et al. 2008; Middleton et al. 2021). Many databases have measures in place to ensure proper identifications are made, as in iNaturalist that requires confirmation by others of the identity through photos or videos for an observation to be considered “research-grade.” In general, researchers using data from iNaturalist will only use the research grade observations,

thus increasing the likelihood of an accurate identification. These databases can still be limited by biased sampling (e.g., residential and other public areas) and species misidentifications, but as long as they are always used with caution and on conspicuous species, citizen science databases should be encouraged for the general public to use. These data provide researchers with valuable information that can be used to track population trends and range expansions on a large-scale basis.

We found that the latitude of brown widow records is increasing over time, which was observed due to the majority of observations on iNaturalist. This is an interesting observation that can be related to new detections as stated above, or with expansions of their range to novel regions. As there is an expansion of urban areas worldwide in which anthropogenic structures can buffer extreme temperatures, combined with increasing temperatures due to climate change (Cadotte et al. 2017), the expansion of the brown widows should continue to be monitored to assess if the increasing latitude trend continues. It is vital to investigate populations on the edge of the geographic range (nearly 45 degrees latitude for North and South America) to determine if their occurrences in these sites represent established introductions or if they are individuals from repeated new colonization events.

Temporal changes in occurrence of brown widows vary between Northern and Southern hemispheres. Seasonally, brown widow records from Southern hemisphere are consistent throughout the year while records from Northern hemisphere show a moderate increase in the spring and a larger increase in the fall. Most Southern hemisphere records of brown widows are located in tropical or subtropical climates. Compared to temperate regions, the tropics and subtropics have less pronounced seasonal fluctuations in temperature (Heckman 1998; Bellprat et al. 2015), which might affect the establishment of brown widows. Tropical regions tend to have more varied precipitation patterns with a defined rainy season and a dry season (Bellprat et al. 2015). Though these precipitation changes can alter their invertebrate prey populations (Heckman 1998) and spiders are well adapted to going long periods of time with little to no food available, we argue that their consistent records in South America throughout the year are as expected (Forster & Kavale 1989). However, most of North America experiences a temperate climate and temperature fluctuations do occur throughout the year, and we see a noticeable cycle in brown widow detections. Peak widow breeding season occurs during late summer to early fall in North America (Trubl et al. 2012), and this coincides with a higher number of records as individuals move more to look for mates, which can potentially increase the records documented through citizen science. Females lay egg sacs shortly after mating, and spiderlings either emerge in the fall or overwinter in the egg sac and emerge in the spring (Mohafez 2015). As temperatures increase in the spring, juveniles become more active and increase in size, likely facilitating their detection during spring in North America. Tracking brown widow records from fall to the following spring can give insight into their pending establishment in an area if they are able to overwinter. Based on climatic variables from about 200 occurrences, the top variables associated with brown widows were annual temperature, annual precipitation, monthly temperature range, and

seasonal precipitation (Taucare-Ríos et al. 2016). As suitable temperatures are related with the establishment of brown widows (Taucare-Ríos et al. 2016), we can expect the expansion in their distribution under climate change scenarios in regions with increasingly amenable temperatures. In addition, it is known that brown widows establish consistently in urban environments (Sadir & Marske 2021). Thus, the combination of climate change and urbanization can lead brown widows to further expand their distribution, which may have cascading impacts on native fauna as well as humans.

Throughout the introduced range of the brown widow, future studies should be conducted on a local level to determine the impacts brown widows have on recipient communities. Impacts by this non-native species should not be assumed to be ubiquitous across all novel ecosystems, especially given their cosmopolitan distribution. Multiple factors lead to the establishment of a non-native species in an area, and all aspects of their establishment and its potential consequences should be analyzed. Any impacts to native species are most likely to affect their congeners and other closely related species in the Theridiidae because of their similar resource requirements. One aspect that can facilitate the establishment of a non-native species is the lack of reproductive pressures from parasites and parasitoids, especially when compared to a native congener. In California, Vetter et al. (2012a) found that non-native brown widows have an egg sac infestation rate of 2.38% compared to the native western black widows' 6.1%. In Costa Rica, Triana et al. (2012) found brown widow egg sacs to be parasitized only 2.12% of the time, whereas egg sacs of other members of the Theridiidae were parasitized at least 12% of the time. These studies also show that native congeners are susceptible to a wider range of parasitoid species than the non-native brown widows (Triana et al. 2012; Vetter et al. 2012a).

Another major aspect that can facilitate the establishment of non-native species is the rate of reproduction. Adult female brown widows can produce an egg sac every 5–10 days with an average of 129 eggs per egg sac, and up to 30 egg sacs in her lifetime (Baerg 1954; Vetter et al. 2012a; Danielson et al. 2014). This reproductive rate is higher than most congeners and is believed to be a main reason brown widows are seemingly outcompeting the native *Latrodectus* species in some locations (Lewis 2013; Jones 2020). A third aspect that should be studied on a local level where brown widows have established is their resource use, such as prey and microhabitat use. In Chile, Taucare-Ríos and Canals (2015) found the diet of the brown widow to be dominated by Isopoda (25.4%), Coleoptera (22.2%), and Hymenoptera (17.5%). In California, Vetter et al. (2012b) found non-native brown widows to occur higher from the ground, occur in more urbanized locations while being absent from rural locations, and found in a much higher frequency than the native western black widows. A multidimensional approach to the resource use of brown widows at the local scale throughout their introduced range can help elucidate their effect on recipient spider communities and the broader ecosystem.

CONCLUSIONS

The brown widow has proven to be a successful invader worldwide, and this review synthesizes expansion reports of their invasion in the Americas in hopes of spurring additional research in locations where they have become established. We

found that in recent decades the maximum latitude at which brown widows are found has increased along with an increase in the number of observations reported each year. In their introduced range, most of our knowledge comes from isolated observations not conducted as part of any systematic survey of establishment and local impacts. Studies should be done on a local scale to determine how brown widows are fitting into the recipient spider communities and whether action needs to be taken to control their future expansion. In addition, citizen science should be recommended to complement the information gathered by researchers regarding species of interest, such as the brown widow.

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