Invasion history of *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae) in Ecuador

Diego F. Cisneros-Heredia, Emilia Peñaherrera-Romero

Universidad San Francisco de Quito USFQ, Colegio de Ciencias Biológicas y Ambientales COCIBA, ~~Laboratorio de Zoología Terrestre y Museo de Zoología, Casilla Postal 17-1200-841,~~ Quito 170901, Ecuador
Universidad San Francisco de Quito USFQ, Instituto de Diversidad Biológica Tropical iBIOTROP, Museo de Zoología & Laboratorio de Zoología Terrestre, Quito, Ecuador

Corresponding author:
Diego F. Cisneros-Heredia.
Universidad San Francisco de Quito USFQ, Colegio de Ciencias Biológicas y Ambientales COCIBA, ~~Laboratorio de Zoología Terrestre, Casilla Postal 17-1200-841,~~ Quito 170901, Ecuador

E-mail address: diego.cisnerosheredia@gmail.com
~~diego.cisnerosheredia@gmail.com~~

Abstract

Harmonia axyridis is a ladybird extensively used around the world for biological control of agricultural pests. However, it has become invasive in several countries, producing negative ecological and socio-economic~~economical~~ impacts. Herein, we review the invasion history of the Harlequin Ladybird, *Harmonia axyridis* (Pallas, 1773), in Ecuador. Although first reported in Ecuador in 2012, museum specimens date back to 2004~~2001~~ and it is currently established across the country, especially along the Andean region. Due to its invasive nature, further studies are urgently needed to evaluate possible impacts of *H. axyridis* on ~~the~~ Ecuadorian biodiversity and in agroindustry.

Key words: Andes; Coccinellinae; distribution; elevation; introduced species; ladybird; natural history; new records; range extension.

INTRODUCTION

Numerous species~~Humans~~ have ~~aided other species' extra-range dispersals either by deliberate translocations or by ecological facilitation (Boivin et al., 2016).~~ arrived ~~at~~in regions~~Unintentionally or deliberately, thousands of non-native species have been translocated to places~~ they would have never ~~have~~ reached on their own ~~thanks~~due to human-mediated processes~~and beyond the biogeographic barriers that typically prevented their spread in such a timeframe~~ (Ricciardi, 2007~~;). Non-native~~Boivin et al., 2016). Although many non-native species are unable to thrive in new environments, some are successful and become invasive by establishing fast-growing, spreading populations. Invasive species have been described as major drivers of current biodiversity changes due to their contribution to~~contribute to Earth's~~ biota homogenization, alteration of~~may modify~~ biological communities and ecosystem functions, and socio-~~may have~~ economic~~, social, cultural and health~~ impacts on humans (Chapin III et al., 2000; ~~human populations (~~Daszak et al., 2000; Crooks, 2002; O'Dowd et al., 2003; Clavero & García-Berthou, 2005; Mace et al., 2005; ~~2003;~~ Doody et al., 2009; Pejchar & Mooney, 2009; Ricciardi et al., 2013; Simberloff et al., 2013; ~~Cisneros-Heredia, 2018). Non-native species that are successful and spread in their new areas become invasive and have been described as major anthropogenic drivers of current changes in biodiversity (Chapin III et al., 2000; Clavero &~~

García-Berthou, 2005; Mace et al., 2005; Bellard et al., 2016; Doherty et al., 2016; Cisneros-Heredia, 2018).

Harmonia axyridis (Pallas, 1773), commonly referred to as the Harlequin Ladybird or Asian Multicolored Ladybeetle, is a member of the family Coccinellidae native to East Asia (Orlova-Bienkowskaja, Ukrainsky & Brown, 2015). It has been deliberately translocated as a control agent in America, Europe and Africa since the beginning of the 20th century, establishing naturalized and expanding populations in the three continents, becoming invasive (Lombaert et al., It 2010; Brown et al., 2011). It is a successful invader due to its wide dietary range, ability to establish and disperse, and robustness and flexibility of its immune system (Roy, Brown & Majerus, 2006; Vilcinskas, Mukherjee & Vogel, 2013). *Harmonia axyridis* is considered to beas the most invasive ladybird on Earth (Roy, Brown & Majerus, 2006).

Harmonia axyridis is a voracious predator of agricultural pests, consuming soft-bodied Sternorrhyncha hemipterans as essential preys, i.e. aphids, coccids, psyllids, and adelgids (Roy, Brown & Majerus, 2006). However, *H. axyridis* has a wider dietary range and is an interguild and intraguild polyphagous predator, being able to consume immature stages of coccinellids and other coleopterans, lepidopterans, neuropterans, dipterans, tetranychid mites, and plant material such as fruits, pollen, nectar, leaves, and seeds (Koch 2003; Koch et al., 2004; Berkvens et al. Roy & Wajnberg, 2008; Koch & Galvan, 2008; Moser, Harwood & Obrycki, 2008; Roy & Wajnberg, 2008; Martins et al., 2009; Lucas, 2012; Michaud, 2012). In general, *H. axyridis* is considered one of the top predators in aphidophagous and coccidophagous guilds, largely free from predation pressure, and regulated more by bottom-up than top-down forces (Lucas, 2012). *Harmonia axyridis* seems to dominate confrontations with other coccinellid species, exerting a strong intraguild predation pressure (Pell et al., 2008; Ware & Majerus 2008; Lucas, 2012; Katsanis et al. 2013).). Due to its polyphagy and guild interactions, non-native populations of *H. axyridis* havehas adverse effects on native biodiversity and agroindustry by attacking non-target arthropods, modifying the structure and dynamics of invertebrate assemblages, replacing or marginalising native coccinellids by competition and predation, and feeding on commercial fruits or damaging agricultural products (Koch, 2003; Koch et al., 2004; Koch & Galvan, 2008; Honěk, 2012; Lucas, 2012).

Commented [MJD<1]: North and South?

~~*Harmonia axyridis* has been deliberately translocated as a biological control in America, Europe and Africa since the beginning of the 20th century, becoming invasive and establishing naturalized and expanding populations in the three continents (Lombaert et al., 2010; Brown et al., 2011). It is a successful invader due to its wide dietary range, ability to establish and disperse, and robustness and flexibility of its immune system (Roy, Brown & Majerus, 2006; Vilcinskas, Mukherjee & Vogel, 2013).~~ In North America, the first translocation of ~~It is considered as the most invasive ladybird on Earth (Roy, Brown & Majerus, 2006). In America,~~ *Harmonia axyridis* was to the USA in 1916, and recurrent introductions to USA and Canada occurred between 1964 and 1983 (Gordon, 1985; Hoebeke & Wheeler 1996). The first established feral populations in North America~~deliberately introduced as a biocontrol agent in several countries and has dispersed and established naturalized populations throughout the continent (~~ were recorded in 1988 in eastern USA (Chapin & Brou, 1991), in 1991 in western USA (LaMana & Miller, 1996), and in 1994 in Canada (Coderre et al., 1995). The two USA populations originated from independent introductions from the species' native range (Lombaert et al., 2010), and the Canadian population apparently spread from eastern USA (McCorquodale, 1998). All subsequent successful introductions of *H. axyridis* across North America have seemingly sourced from eastern USA (Lombaert et al., 2010). Mexican populations descend from eastern USA stocks deliberately released in northern ~~Mexico~~ (ca. 1997) and southeastern Mexico (1999–early 2000s) (Quiñones Pando & Tarango Rivero, 2005; Barrera & López-Arroyo, 2007). First translocations to Argentina (1986) and Chile (1998) used parental stocks from France but were unsuccessful in establishing populations (García, Becerra & Reising, 1999; Saini, 2004; Grez et al., 2010). Naturalised populations reported in Argentina in 2001, southern Brazil in 2002, and Chile in 2003 descend from at least two different eastern USA stocks (Almeida & Silva, 2002; Saini, 2004; Grez et al., 2010; Lombaert et al., 2010; Brown et al., 2011).

The oldest known naturalised populations of *H. axiridis* in South America were established in Colombia, where it was first collected in 1989 (Kondo & González, 2013). Since *H. axyridis* was extensively raised and shipped in the USA in the 1980s and 1990s (Tedders & Schaefer, 1994), and based on available dates, Colombian populations may also descend from eastern USA stock. It is probable that unrecorded international shipments were sent to Colombia, Argentina, and

Formatted: English (United Kingdom)

Chile—possibly to private farmers, thus the absence of public records. Subsequent South American records come from Ecuador (2004, see below), Paraguay (2006, Silvie et al., 2007), Uruguay (2007, Nedvěd & Krejčík, 2011; Serra et al. 2013), Peru (ca. 2010, Grez et al., 2010), and Venezuela (ca. 2014, Solano & Arcaya, 2014). It has not been formally reported from Guyana, Suriname and Bolivia (Camacho-Cervantes, Ortega-Iturriaga & del-Val, 2017; Hiller & Haelewaters, 2019), but a recent citizen-science record ~~evidences~~ shows that it is already present in Bolivia (Maslowski, 2020). Reports of *H. axyridis* from Central America have only recently been published, but the oldest records date back to 1988 and 1996~~—~~ from Costa Rica. The species is currently established in most Central American countries, but is has not been reported from Belize, El Salvador and Nicaragua (Hiller & Haelewaters, 2019).

Harmonia axyridis was first recorded in Ecuador in 2012 by González & Kondo (2012) who reported~~; but geographic~~ 11 specimens collected in 2012 in deciduous forests on La Ceiba and Laipuna natural reserves (762 and 828 m elevation, respectively), province of Loja, in the extreme southwestern lowlands of Ecuador. Cornejo & González (2015) reported the species from mangroves on Santay ~~i~~Island (at sea level), province of Guayas, southwestern Ecuador. González (2015) reported *H. axyridis* from the provinces of Azuay, Guayas and Loja, but without referencing any voucher specimen from Azuay. Guamán Montaño (2017) presented photographs of *H. axyridis* from El Pangui (830 m elevation), province of Zamora-Chinchipe, providing the first reports on the south-eastern slopes of the Andes of Ecuador. Geographic and ecological data of *H. axiridis* in Ecuador are scarce. ~~and, to the best of our knowledge, only three localities on the southern Pacific lowlands of the country have been published in scientific literature (González & Kondo, 2012; Cornejo & González, 2015).~~ Herein, we discuss ~~about~~ the distribution, natural history, and introduction history of *Harmonia* ~~*axyridis*~~ in Ecuador, ~~evidencing~~ showing that it has been present at least since 2004 and is currently widespread across the country.

MATERIALS & METHODS

Coccinellid beetles were opportunistically collected since 2015 during field ~~We conducted~~ surveys of the Universidad San Francisco de Quito USFQ at 17~~different~~ localities across northern Ecuador, (Table S1, Figs. 1, 2). Field surveys were conducted by the authors, usually with 8-15 undergraduate students of the USFQ Biology program.~~Fig. 1).~~ All specimens were found by

searching vegetation to look for adults and larvae. Collected specimens were euthanized by immersion in 70% ethanol or by placing in a killing jar and stored. An Olympus Research Stereomicroscope System SZX16 outfitted with an Olympus DP73 digital colour camera was used to observe specimens. Voucher~~Collected~~ specimens collected during our surveys are deposited at the Museo de Zoología~~, Laboratorio de Zoología~~ (ZSFQ),~~Terrestre,~~ Universidad San Francisco de Quito USFQ, Ecuador~~ (ZUSFQ),~~ Research permits were issued by Ministerio de Ambiente del Ecuador, 001-16IC-FLO-FAU-DNB/MA, 018-2017-IC-FAU-DNB/MAE, 019-2018-IC-FAU-DNB/MAE, and 006-2015-FAU-DPAP-MA. ~~In addition, we reviewed the entomological collections of Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ), and Instituto Nacional de Biodiversidad INABIO, Quito (MECN).~~

We reviewed the entomological collections of Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ), and Instituto Nacional de Biodiversidad INABIO, Quito (MECN). Published information on *Harmonia axyridis* in Ecuador was synthesised based on a literature review using the library systems of King's College London and Universidad San Francisco de Quito USFQ, and Google Scholar™ scholarly text search (https://scholar.google.com). Relevant references were gathered using the search terms 'Coccinellidae', 'Harmonia', 'Harmonia axyridis', 'Mariquita', 'Ladybird', 'Ladybug', and 'Lady beetle', each one combined with 'Ecuador' by the Boolean operator 'AND'. Since *H.*~~Because *Harmonia*~~ *axyridis* has a diagnostic colouration pattern that allows its identification in photographs, we assembled data from photographic vouchers using the search engines of Flickr™ (https://www.flickr.com, by Yahoo!) and iNaturalist.org™ (http://www.inaturalist.org, by California Academy of Sciences and the National Geographic Society) through GeoCat (Bachman et al., 2011; http://geocat.kew.org/) using the same search terms used for text searches. All searches were run on 10 February 2019 using on-site search engines and were not limited by study type, study design, or language. iNaturalist searches were rerun on 09 August 2019 and on 01 April 2020.

All localities, based on field surveys, literature, museum and~~, or~~ photographic records, were georeferenced manually in Google Earth™ mapping service (7.3.1.5491 release by Google, Inc. on July 2018) based on direct information (coordinates and altitudinal data) when available, and

Formatted: English (United Kingdom)
Formatted: English (United Kingdom)
Formatted: English (United Kingdom)
Formatted: English (United Kingdom)
Formatted: English (United Kingdom)
Formatted: English (United Kingdom)
Formatted: English (United States)
Formatted: Font: Not Italic
Formatted: Font: Not Italic

additional data relevant to obtain an accurate and precise positioning, including catalogue and field notes, following recommendations by Wieczorek et al. (2004). All localities were reviewed and validated individually, and coordinates were amended when incorrectly georeferenced in the source (Table S1~~4~~). We determined the position most closely related with the locality description using toponymic information based on the Geographic Names Database, containing official standard names approved by the United States Board on Geographic Names and maintained by the National Geospatial-Intelligence Agency (http://geonames.nga.mil/gns/html/), OpenMapStreet data available under the Open Database Licence (http://www.openstreetmap.org), and gazetteers for Ecuador (Brown, 1941; Peters, 1955; Lynch & Duellman, 1997).

~~Specimens herein reported were identified as *Harmonia axyridis* by its characteristic morphology (Fig. 2), including: upper surfaces of elytra not hairy, distinct transverse fold at rear of elytra, underside of abdomen at least partially orange, brown to orange legs (Koch, 2003; Roy et al. 2016). One phenotypic form was found: f. *succinea*, with ground colour of pronotum white to light brown with M-shaped black marks, ground colour of elytra bright orange, usually with nine black elytral spots (2-3-3-1) and a scutellary spot (Dobzhansky, 1933; Tan & Li, 1934; Koch, 2003; Brown et al., 2008; Roy et al., 2013; Roy et al., 2016).~~

Formatted: English (United States)

RESULTS

In total, we collected information for 294~~183~~ records of *Harmonia axyridis* from 53~~56~~ localities in Ecuador (Table S1, Figs. 1, 2~~Fig. 1~~), including: 106 specimens collected during field surveys and deposited at ZSFQ, 11 individuals recorded during field surveys but uncollected, 37~~144~~ museum specimens (~~107 at ZSFQ,~~ 37 at QCAZ, none at MECN), 118 individuals recorded in iNaturalist, five photographic records from Flickr, and 17 ~~16 records in iNaturalist, four observations, and 14 specimens reported in the~~ literature records (González & Kondo, 2012; Cornejo & González, 2015; Guamán Montaño, 2017). Most records presented herein correspond to adult individuals, but larvae and pupa were recorded across the Andes (Table S1). Specimens were identified as *Harmonia axyridis* by its characteristic morphology (Fig. 3), including: upper surfaces of elytra not hairy, distinct transverse fold at rear of elytra, underside of abdomen at least partially orange, brown to orange legs (Koch, 2003; Roy et al. 2016). One

phenotypic colour form was found: f. *succinea*, with ground colour of pronotum white to light brown with M-shaped black marks, ground colour of elytra bright orange, usually with nine black elytral spots (2-3-3-1) on each elytra, and a scutellary spot (Dobzhansky, 1933; Tan & Li, 1934; Koch, 2003; Brown et al., 2008; Roy et al., 2013; Roy et al., 2016).

The first specimens of *H. axyridis* in Ecuador were collected on both geographical extremes of the country: in 2004 at Mindo, northwestern Ecuador, and in 2007 at Loja, in southwestern Ecuador (Table S1). Both localities are separated by about 450 km and nowadays have established populations. Our study reveals that *H.Harmonia axyridis* is nowadays established in all main biogeographic regionsareas of Ecuador, from sea level to at least 4020 m elevation, across 1613 provinces (administrative geopolitical divisions of Ecuador) (Table S114, Fig. 1). At least one record (at Estación Científica Yasuní) may correspond to a hitchhiking individual, since no established population in the Amazonian lowlands has been confirmed. 1). The only regions where we did not findfound records are the southern Amazonian lowlands and the Galapagos Archipelago. The first specimens found were collected on both geographical extremes of Ecuador: in 2004 at Mindo, northwestern Ecuador, and in 2007 at Loja, in southwestern Ecuador (Table 1). Both localities are separated by about 450 km.

Almost two-thirds of theAt least 33 localities where we found records of *H. axiridis* are anthropogenic habitats (51% are urban green spaces in mid-size towns and large cities, and 20% are agricultural lands; Table S1). Most of the records of *H. axyridis* in Ecuador come from the Andes, a region with significant agricultural and urban areas, including the capital city, Quito, and its metropolitan district. In urban green spaces, *H. axiridis* usually where *Harmonia axyridis* occupies gardens and parks urban and suburban green spaces dominated by non-native plants. *Harmonia axiridis* has been found also in 12 different ecosystems withOther localities correspond to agricultural areas or natural environments, including protected areas. In areas covered by native vegetation, usually*H. axyridis* was mainly collected alongon road borders and near human settlements. . At least one record, at Estación Científica Yasuní, may correspond to a hitchhiking individual, since no established population in the Amazonian lowlands has been confirmed.

During our surveys, *H. axyridis* was~~Since 2015, we surveyed periodically the population of *Harmonia axyridis* at Cumbayá, a suburban parish of Quito, capital city of Ecuador. *Harmonia axyridis* is well established in Cumbayá, with several subpopulations detected in gardens and small urban and suburban green areas. They are usually~~ associated with the following plants (local names and families in parentheses): *Ambrosia arborescens* (Marco, Asteraceae), *Baccharis latifolia* (Chilca, Asteraceae), *Citrus* × *limon* (Limonero, Rutaceae), *Chusquea* sp. (Suro, Poaceae), *Cupressus* sp. (Ciprés, Cupressaceae), *Delostoma integrifolium* (Yalomán, Bignoniaceae), *Erigeron* sp. (Asteraceae), *Ficus benjamina* (Ficus, Moraceae), *Hibiscus rosa-sinensis* (Cucarda, Malvaceae~~), *Senna multiglandulosa* (Chinchín), *Citrus* x *limon* (Limonero), *Prunus setorina* (Capulí), *Prunus persica* (Peach~~), *Lantana camara* (Tupirrosa or Supirrosa, Verbenaceae), *Ligustrum* sp. (Oleaceae), *Lilium* sp. (Lirio amarillo, Liliaceae), *Ocimum basilicum* (Albahaca, Lamiaceae), *Petroselinum crispum* (Perejil, Apiaceae), *Prunus persica* (Durazno, Rosaceae), *Prunus serotina capuli* (Capulí, Rosaceae), *Rosa* sp. (Rosa, Rosaceae), *Senna multiglandulosa* (Chinchín, Fabaceae), *Solanum nigrescens* (Yerbamora, Solanaceae), *Tecoma stans*, (Cholán, Bignoniaceae), *Trifolium repens* (Trébol blanco, Fabaceae), and *Verbesina sodiroi* (Asteraceae). The following coccinellids were found in sympatry with *H. axyridis* during our surveys at different localities: *Brachiacantha* sp. cf. *anita* (Mindo), *Cheilomenes sexmaculata* (Quito, Cumbayá, Tumbaco), *Cycloneda ecuadorica* (Guajalito, San Vicente), *C. emarginata* (Guajalito, Loja), *C. sanguinea* (Cumbayá, San Vicente), *Epilachna monovittata* (Guajalito), *E. flavofasciata* (Guajalito), *E. paenulata* (Quito, Mindo), *Hippodamia convergens* (Quito, Lumbisí, Cumbayá, Tumbaco, Yaruquí, Guajalito, San Vicente, Mindo, Loja), *Mulsantina mexicana* (Cumbayá, Yaruquí, Guajalito), *Neda norrisi* (San Antonio de Pichincha), and *Rodolia cardinalis* (San Antonio de Pichincha, Cumbayá). No parasitoids were detected.

Almost 30% of our field records of *H. axyridis* come from the Cumbayá-Tumbaco valley, an inter-Andean valley near Quito (Fig. 2), in northern Ecuador, where we had a higher sampling effort and were able to observe the coccinellid community in more detail.~~*Ficus benjamina* (Ficus).~~ We found six~~five~~ coccinellid species in sympatry in gardens, parks ~~urban/suburban green areas~~ and agricultural areas~~lands~~ of the Cumbayá-Tumbaco valley: *Harmonia axyridis*,

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Formatted: Spanish (Ecuador)

Cheilomenes sexmaculata, *Hippodamia convergens*, *Mulsantina mexicana*, ~~*Cheilomenes sexmaculata* and~~ *Rodolia cardinalis*, and *Cycloneda sanguinea*. *Harmonia axyridis* was the most common species in ~~gardens and urban/suburban~~ green urban areas, but is uncommon ~~it was not found~~ in agricultural areas, where *H. convergens* was dominant. *Rodolia*~~Only *R.*~~ *cardilanis* and *C. sexmaculata* were~~was~~ found in syntopy with *H. axyridis*. By 2017, *H. convergens* was~~is~~ almost absent in most ~~gardens and~~ urban green~~/surburban~~ areas of the Cumbayá-Tumbaco valley, remaining common only in agricultural areas. *Cheilomenes*~~*C.*~~ *sexmaculata*, an apparently recent arrival—first recorded in the area on 2017, is nowadays becoming the second most common coccinellid in urban~~/suburban~~ green areas of Quito-Cumbayá-Tumbaco, although still with a patchy distribution.

~~The following coccinellids have been found in sympatry with *Harmonia axyridis* at different localities: *Brachiacantha* sp. cf. *anita* (Mindo), *Cheilomenes sexmaculata* (Quito, Cumbayá), *Cycloneda ecuadorica* (Guajalito, San Vicente), *C. emarginata* (Guajalito, Loja), *C. sanguinea* (San Vicente), *Epilachna monovittata* (Guajalito), *E. flavofasciata* (Guajalito), *E. paenulata* (Quito, Mindo), *Hippodamia convergens* (Quito, Lumbisí, Cumbayá, Yaruquí, Guajalito, San Vicente, Mindo, Loja), *Mulsantina mexicana* (Cumbayá, Yaruquí, Guajalito), *Neda norrisi* (San Antonio de Pichincha), and *Rodolia cardinalis* (San Antonio de Pichincha, Cumbayá).~~

Formatted: English (United Kingdom)

Formatted: English (United States)

DISCUSSION

~~In America, the first translocation of *Harmonia axyridis* was to the USA in 1916, and recurrent introductions to that country occurred between 1964 and 1982 (Gordon, 1985). The first established feral populations were recorded in 1988 in eastern USA (Chapin & Brou, 1991), in 1991 in western USA (LaMana & Miller, 1996), and in 1994 in Canada (Coderre et al., 1995). The two USA populations originated from independent introductions from the species' native range (Lombaert et al., 2010), and the Canadian population apparently spread from eastern USA (McCorquodale, 1998). All subsequent successful introductions of *H. axyridis* across America have seemingly sourced from eastern USA (Lombaert et al., 2010). Mexican populations descend from eastern USA stocks deliberately released in northern Mexico (ca. 1997) and southeastern Mexico (1999–early 2000s) (Quiñones Pando & Tarango Rivero, 2005; Barrera & López-Arroyo, 2007). First translocations to Argentina (1986) and Chile (1998) used parental stocks from France~~

~~but were unsuccessful in establishing populations (García, Becerra & Reising, 1999; Saini, 2004; Grez et al., 2010). Naturalised populations reported in Argentina in 2001, southern Brazil in 2002, and Chile in 2003 descend from at least two different eastern USA stocks (Almeida & Silva, 2002; Saini, 2004; Grez et al., 2010; Lombaert et al., 2010). The oldest known naturalised populations in South America were established in Colombia, where *H. axyridis* was first collected in 1989 (Kondo & González, 2013). Since *Harmonia axyridis* was extensively raised and shipped in the USA in the 1980s and 1990s (Tedders & Schaefer, 1994), and based on available dates, Colombian populations may also descend from eastern USA stock. It is probable that unrecorded international shipments were sent to Colombia, Argentina, and Chile — possibly to private farmers, thus the absence of public records. Subsequent South American records come from Ecuador (2004, this study), Paraguay (2006, Silvie et al., 2007), Uruguay (2009, Nedvěd & Krejčík, 2011), Peru (ca. 2010, Grez et al., 2010), and Venezuela (ca. 2014, Solano & Arcaya, 2014). It has not been formally recorded in Central America, Guyana, Suriname and Bolivia (Camacho-Cervantes, Ortega-Iturriaga & del-Val, 2017). However, established populations may occur at least in southern Mexico (Saenz-Garcia, 2015; Ramírez Marcial, 2016), Guatemala (Amador da Silva, 2017), and Costa Rica (Cralingworld, 2009; Spring,2011; Mclaren, 2015).~~

~~All published records of *Harmonia axyridis* in Ecuador were reported from southern Ecuador. González & Kondo (2012) presented the first reports of *H. axyridis* in the country, based on 11 specimens collected in 2012 in deciduous forests on La Ceiba and Laipuna natural reserves (762 and 828 m elevation, respectively), province of Loja, extreme southwestern lowlands of Ecuador. Cornejo & González (2015) reported the species from mangroves on Santay island (at sea level), province of Guayas, southwestern Ecuador. González (2015) reported *H. axyridis* from the provinces of Azuay, Guayas and Loja, but without referencing any voucher specimen from Azuay. Guamán Montaño (2017) presented photographs of *H. axyridis* from El Pangui (830 m elevation), province of Zamora-Chinchipe, providing the first reports on the south-eastern slopes of the Andes of Ecuador.~~

Extensive and intensive entomological studies conducted in northern Ecuador up to 2001 did not record~~recorded~~ *Harmonia axyridis* (e.g., Cardona et al., 2005; Carvajal et al., 2005). Thus, the first naturalised populations of *H. axyridis* in Ecuador probably ~~got~~ became established between

2001 and 2004, possibly as a result of intentional releases. ~~Intentional introduction of *H. axyridis* in Ecuador seems probable.~~ Introduction of ladybirds ~~in Ecuador~~ has a long history in Ecuador; ~~,~~ for example, in 1978, official national authorities released 24 million individuals of *Hippodamia convergens* in the city of Quito and surroundings, in ~~as~~ an attempt to control *Icerya purchasi* (Molineros Andrade, 1984). However, it is also possible ~~likely~~ that Ecuadorian populations spread from southern Colombia, since the oldest Colombian records ~~populations~~ occurred very close to the Ecuadorian border (Kondo & González, 2013). The presence of the earliest Ecuadorian localities on opposite sides of the country (Mindo and Loja) and the absence of geographically intermediate records could suggest that Ecuadorian populations had ~~have~~ two independent origins. However, museum records are biased due to limited collection efforts in the central provinces of Ecuador. Furthermore, spread rate of *H. axyridis* may be extremely fast and compensate for the distance between the localities (58–144.5 ~~100~~ km/year in the UK Brown et al. 2007, 200 km/year in Slovakia, Roy et al. 2016; 185 km/year in Chile, Grez et al., 2016; 442 km/year in USA-Canada, McCorquodale, 1998; 500 km/year in South Africa, Stals, 2010). If the southern Ecuadorian population ~~would be~~ is demonstrated to have an independent origin, they may have ~~given origin to~~ been the source of the northern Peruvian populations ~~— which~~, although these remained unrecorded during extensive surveys in 2006 (Miró-Agurto & Castillo-Carrillo, 2010) and became established around 2010 (Grez et al., 2010).

The highest record ~~Populations~~ of *H.* ~~*Harmonia*~~ *axyridis* in Ecuador, ~~are established~~ at the locality of Mojanda, is also ~~elevations between sea level and 4020 m,~~ the highest record worldwide, 500 m higher than the upper elevation ~~al~~ ranges reported by Grez et al. (2017) and González et al. (2018). Unfortunately, no ecological information was associated with that specimen. Lowland records mainly come from the Pacific lowlands and western Andean slopes, but also from the Amazonian foothills and lowlands. The Andean region was predicted as suitable for the expansion of *H. axyridis* by distribution models analysed by Koch et al. (2006) and Poutsma et al. (2007), ~~which~~ and although they predicted the expansion of *H. axyridis* across different habitats ~~habitat~~ of America, their models did not show ~~predict~~ lowland forest. Interestingly, Ecuadorian records come from a variety of habitats, including ~~cloud montane~~ forest and shrublands, evergreen ~~dry montane~~ and semideciduous vegetation ~~lowland forest~~, and across the

Commented [MJD<2]: Please state elevation

urban-agriculturalsuburban matrix. However, the most extensive and dense populations were found in urban and suburban areas.

It is likely that *H.Harmonia axyridis* will keep spreadingspread across most of Ecuador, especially in urban and agricultural environments, having effects on the diverse Ecuadorian. Establishment of *H. axyridis* may significantly impact predatory arthropods guilds (Lucas et al. 2002, Koch 2003, Ducatti et al. 2017, Koch & Galvan 2008); having varied impacts on the diverse South American fauna of coccinellids due to competition, exclusion, and intraguild predation. *Harmonia axyridis* may significantly impactChanges in the predatory arthropod guilds, interfering may interfere with invertebrate population dynamics, potentially producing impacts on native aphidophage groups and impacting agricultural pests (Lucas et al. 2002, Koch 2003, Pervez & Omkar 2006, Koch & Galvan 2008, Ducatti et al. 2017).). In particular, the arrival of *H. axyridis* to the Galapagos Archipelago could be problematic, due to the vulnerability of island ecosystrems to impacts on endemic and native invertebrates and profound irruptions on trophic interactions (Causton et al. 2006).

Harmonia axyridis has attained the status of agricultural pest in North America because addition, since it feeds opportunistically on damaged fruit when prey is scarce and acts as a wine contaminant (Koch et al. 2004, Koch & Galvan 2008). Grapes, apples, peaches, plums, pears, raspberries, among other fruits, have been reported to be consumed by *H. axyridis*, blemishing the fruits and reducing their value (Majerus, Strawson, Roy 2006, Koch & Galvan 2008, Guedes & Almeida 2013). All these fruits are produced in Ecuador, usually for local consumption but, in recent decades, have become important exportation products. Fruit crops occupy over 1600 km^2 in Ecuador (excluding bananas), are produced by more than 120 000 farmers, and represent a small but growing sector in non-traditional agricultural exports in the country—contributing to ca. 4.4% of all non-traditional exportations (Viera et al. 2016, Verdugo-Morales & Andrade Díaz 2018, BCE 2020). Most Ecuadorian fruit crops are located across the highlands and western lowlands of the country (Niegel 1992, Huttel, Zebrowski, Gondard 1999), coinciding with areas where *H. axyridis* is expanding. Research on the impacts of *H. axyridis* in Ecuadorian), *H. axyridis* may impact fruit production Ecuador is urgently needed.

Wine contamination has been described as the most important agricultural impact of *H. axyridis*. Adults aggregate on injured grapes and can be disturbed or crushed during harvesting or pressing, releasing haemolymph that affects wine quality by causing unpleasant odour and taste—i.e., ladybug taint (Pickering et al. 2004, 2008, Koch & Galvan 2008). ~~Despite~~Although table and wine grapes have been grow~~th~~n in Ecuador for local consumption since the 16th century (Popenoe 1924), commercial production has only been fostered in recent decades (El Comercio 2017; Revista Líderes 2012, 2013; Viera et al. 2016). Vineyards in Ecuador have increased from 0.6 km^2 in 1985 to more than 2 km^2 ~~nowa~~today~~s~~ —and is expected~~ing~~ to reach 10 km^2 in the near future (Niegel 1992, El Comercio 2017; Revista Líderes 2012, 2013). Established populations of *H. axyridis* have been reported in all areas where Ecuadorian wineries ~~have been developed~~are situated (i.e., provinces of Guayas, Pichincha, Azuay, and El Oro). Although Ecuadorian wine production is still modest, its presence in national and international markets is expanding (ProEcuador 2017) and ladybug taint could negatively impact this growing industry.

Information ~~. Unfortunately, information~~ on the coccinellids of Ecuador is limited and fragmentary. It is important to increase research on the diversity, distribution, natural history, ~~and population~~ ecology and socio-economic effects of coccinellids in the country. Especially, information is needed~~of Ecuador, including ecological relationships between native and non-native arthropod species~~ across urban-agricultural-natural matrices, in order to evaluate the impacts of *H. axyridis* and other non-native species ~~in the country~~.

Acknowledgements

~~We thank anonymous reviewers for their comments.~~ We express our gratitude to Ana Nicole Acosta-Vásconez, Mateo Dávila-Játiva and Izan Chalen for their assistance, and to the students of the USFQ courses~~course~~ of Introduction to Biology and Zoology (years ~~(~~2015, 2016, 2017, 2018, 2019) ~~) of Universidad San Francisco de Quito USFQ~~ for their help in finding some of the populations of *Harmonia axyridis* herein reported. We thank the following people for provision of support and working space in their respective institutions or for the loan of specimens under their care: Santiago Villamarín (INABIO), Alvaro Barragán and Clifford Keil (QCAZ), and Giovani Ramón (ZSFQ). We are grateful to Carlos Ruales for helping us to find some key literature about the first introductions of ladybirds in Ecuador and to all citizens scientists that

continuously contribute to iNaturalist. We thank anonymous reviewers for their comments ~~to~~on a previous version~~s~~ of this paper, and Ministerio de Ambiente del Ecuador for issuing research permits. This study was supported by Universidad San Francisco de Quito USFQ (projects HUBI ID 35 “Estudio de la biodiversidad en áreas urbanas y rurales”, ID 1057 “Impact of hábitat changes on the biological diverity of the northern Andes”), and operative funds assigned to Instituto de Diversidad Biológica Tropical iBIOTROP, Museo de Zoología & Laboratorio de Zoología Terrestre; and by Programa “Becas de Excelencia” of Secretaría de Educación Superior, Ciencia, Tecnología e Innovación SENESCYT, Ecuador.

References

Aldana A. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/18904677 Access date: 09/01/2019

Aldana A~~. 2018. *Harmonia axyridis*. iNaturalist.~~ https://www.inaturalist.org/observations/18948118 Access date: 09/01/2019

Almeida~~-~~ LD, Silva VD. 2002. Primeiro registro de *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae): um coccinelídeo originário da região Paleártica. *Revista Brasileira de Zoologia* 19(3): 941-944. DOI~~Doi~~: http://dx.doi.org/10.1590/S0101-81752002000300031

Alyokhin, A. & Sewell, G. Biological Invasions (2004) 6: 463. doi: https://doi.org/10.1023/B:BINV.0000041554.14539.74

Amador da Silva, C. (2017) *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/9059067. Access date: 22/02/2019

Amat-García G, Amat-García E, Ariza-Marín E. 2011. Insectos invasores en los tiempos de cambio climático. Innovación y Ciencia 18: 45–53.

andrew-av97. 2018. ~~*Harmonia axyridis*.~~ iNaturalist. https://www.inaturalist.org/observations/18401263 Access date: 09/01/2019

Bachman S, Moat J, Hill A~~AW~~, de la Torre J, Scott B. 2011. Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. ~~In: Smith V, Penev L (eds). e-Infrastructures for data publishing in biodiversity science.~~ ZooKeys 150: 117–126. DOI: https://doi.org/10.3897/zookeys.150.2109 Available at http://geocat.kew.org~~*http://geocat.kew.org*~~

Formatted: English (United States)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Field Code Changed
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: English (United States)
Formatted: English (United States)
Formatted: English (United States)
Formatted: Font: Not Italic
Formatted: Font: Not Italic

Barrera JF, López-Arroyo JI. 2007. Control biológico de insectos plaga en el sureste de México; pp. 201–233, in: L.A. Rodríguez-del-Bosque and H.C. Arredondo- Bernal (eds.). Teoría y Aplicación del Control Biológico. México: Sociedad Mexicana de Control Biológico.

BCE. 2020. Exportaciones no tradicionales. Información Estadística Mensual 2017 – Marzo 2020. Available at https://contenido.bce.fin.ec/home1/estadisticas/bolmensual/IEMensual.jsp (accessed 02 May 2020).

Bellard C, Cassey P, & Blackburn TM. 2016. Alien species as a driver of recent extinctions. Biology letters, 12(2), 20150623. DOI: https://doi.org/10.1098/rsbl.2015.0623~~DOI: 10.1098/rsbl.2015.0623~~

Berkvens N, Bonte J, Berkvens D, Deforce K, Tirry L, De Clercq P. 2008. Pollen as an alternative food for *Harmonia axyridis*. BioControl 53: 201–210. DOI: https://doi.org/10.1007/s10526-007-9128-7

Boivin NL, Zeder MA, Fuller DQ, Crowther A, Larson G, Erlandson JM, Denham T, Petraglia MD. 2016. Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. Proceedings of the National Academy of Sciences, 113(23):6388-6396. DOI: http://doi.org/10.1073/pnas.1525200113~~DOI: 10.1073/pnas.1525200113~~

Brown FM. 1941. A Gazetteer of Entomological Stations in Ecuador. Annals of the Entomological Society of America~~,~~ 34(4): 809-851. DOI: https://doi.org/10.1093/aesa/34.4.809~~https://doi.org/10.1093/aesa/34.4.809~~

Brown MJP, Thomas CE, Lombaert E, Jeffries DL, Estoup A, Lawson Handley LJ. 2011. The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion. BioControl 56: 623-641. DOI~~doi~~: http://dx.doi.org/10.1007/s10526-011-9379-1

Brown P, Roy H, Rothery P, Roy D, Ware R, Majerus M. 2007. *Harmonia axyridis* in Great Britain: analysis of the spread and distribution of a non-native cocinellid. BioControl. DOI~~Doi~~: http://dx.doi.org/10.1007/s10526-007-9124-y

Brown PMJ, Adriaens T, Bathon H, Cuppen J, Goldarazena A, Hägg T, Kenis M, Klausnitzet BEM, Kovář I, Loomans~~,~~ AJM, Majerus~~,~~ MEN. 2008. *Harmonia axyridis* in Europe: spread and distribution of a non-native coccinellid. BioControl, 53(1), 5-21. DOI~~Doi~~: https://doi.org/10.1007/s10526-007-9132-y

Formatted: Spanish (Spain)

Formatted: Font: Not Italic

Formatted: Font: Not Italic

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Field Code Changed

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Cadena E. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/17824845 Access date: 09/01/2019

Camacho-Cervantes M, Ortega-Iturriaga A, del-Val E. 2017. From effective biocontrol agent to successful invader: the harlequin ladybird (*Harmonia axyridis*) as an example of good ideas that could go wrong. PeerJ, 5, e3296. DOI: https://doi.org/10.7717/peerj.3296DOI: 10.7717/peerj.3296

Campoverde JA. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/18283725 Access date: 09/01/2019

Cardona C, López-Avila A, Valarezo O. 2005. Chapter 4.2 Colombia and Ecuador; pp. 274–284, in: Anderson, P. K. & Morales, F. J. (eds.), Whitefly and whitefly-borne viruses in the Tropics: Building a knowledge base for global action. Cali: Centro Internacional de Agricultura Tropical CIAT (no. 341). Available at https://books.google.com.ec/books?id=F0FgBQAAQBAJ

Carvajal L. 2005. Lista preliminar de artrópodos del Bosque Protector Pichincha y sus alrededores. Revista Politécnica 26(1) Biología 6: 141–160. Available at: http://bibdigital.epn.edu.ec/handle/15000/6356

Causton CE, Peck SB, Sinclair BJ, Roque-Albelo L, Hodgson CJ, Landry B (2006). Alien Insects: Threats and Implications for Conservation of Galápagos Islands. Annals of the Entomological Society of America, 99(1), 121–143. DOI: https://doi.org/10.1603/0013-8746(2006)099[0121:AITAIF]2.0.CO;2

Celorio L. (2018). *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/18135386 Access date: 09/01/2019

Chapin FS III, Zavaleta ES, Eviner VT, Naylor RL, Vitousek PM, Reynolds HL, Hooper DU, Lavorel S, Sala OE, Hobbie SE, Mack MC, Díaz S. 2000. Consequences of changing biodiversity. *Nature*, 405(6783): 234-242. DOI: https://doi.org/10.1038/35012241DOI: 10.1038/35012241

Chapin JB, Brou VA. 1991. *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). Proc Entomol Soc Wash 93:630–635.

Cisneros-Heredia D.F. 2018. The Hitchhiker Wave: Non-native Small Terrestrial Vertebrates in the Galapagos. In: Torres M., Mena C. (eds) Understanding Invasive Species in the Galapagos

Formatted: English (United States)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Field Code Changed
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Field Code Changed
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)

Islands. Social and Ecological Interactions in the Galapagos Islands. Cham: Springer. DOI: https://doi.org/10.1007/978-3-319-67177-2_7

Clavero M, García-Berthou E. 2005. Invasive species are a leading cause of animal extinctions. Trends in Evology and Evolution, 20(3): 110. DOI: https://doi.org/10.1016/j.tree.2005.01.003~~10.1016/j.tree.2005.01.003~~

Coderre D, Lucas É, Gagné I. 1995. The occurrence of *Harmonia axyridis* (Pallas)(Coleoptera: Coccinellidae) in Canada. *The Canadian Entomologist*, 127(4): 609-611.

Cornejo X, González G. 2015. Contribución al conocimiento de la fauna entomológica de los manglares: *Olla roatanensis* Vandenberg y *Cheilomenes sexmaculata* Fabricius, dos nuevos registros de Coleoptera: Coccinellidae para Ecuador y Perú. Revista Científica de Ciencias Naturales y Ambientales (Ecuador), 8(2): 76–80.

Crawlingworld (2009) *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/19065175. Access date: 22/02/2019

Crespa L. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/19253648 Access date: 09/01/2019

Crooks JA. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos*, 97(2): 153-166- DOI: https://doi.org/10.1034/j.1600-0706.2002.970201.x~~https://doi.org/10.1034/j.1600-0706.2002.970201.x~~

Daszak P, Cunningham AA, Hyatt AD. 2000. Emerging infectious diseases of wildlife--threats to biodiversity and human health. Science, 287(5452): 443–449. DOI: https://doi.org/10.1126/science.287.5452.443

Del Hierro Calvachi AG. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/19215262 Access date: 09/01/2019

Del Hierro Calvachi AG. 2019. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/19375805 Access date: 09/01/2019

Dobzhansky T. 1933. Geographical variation in lady-beetles. The American Naturalist, 67(709), 97-126.

Doherty TS, Glen AS, Nimmo DG, Ritchie EG, Dickman CR. 2016. Invasive predators and global biodiversity loss. Proceedings of the National Academy of Sciences, 113(40): 11261-11265. DOI: https://doi.org/10.1073/pnas.160248011310.1073/pnas.1602480113

Formatted: English (United States)
Formatted: Font: Not Italic
Formatted: Font: Not Italic
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Spanish (Spain)
Formatted: Font: Not Italic
Formatted: Font: Not Italic
Formatted: Font: Not Italic

Doody JS, Green B, Rhind D, Castellano CM, Sims R, Robinson T. 2009. Population-level declines in Australian predators caused by an invasive species. Animal Conservation~~,~~ 12: 46-53. DOI: https://doi.org/10.1111/j.1469-1795.2008.00219.x~~10.1111/j.1469-1795.2008.00219.x~~

Ducatti RDB, Ugine TA, Losey J. 2017. Interactions of the Asian lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae), and the North American Native Lady Beetle, *Coccinella novemnotata* (Coleoptera: Coccinellidae): prospects for recovery post-decline. Environmental Entomology 46: 21–29.

El Comercio. 2017. La siembra de uva crece en las tierras de Santa Elena; la producción el 2016 llegó a 3,93 millones de kilos. El Comercio 26/11/2017. Available at https://www.elcomercio.com/actualidad/siembra-uva-santaelena-cultivo-produccion.html (accessed 2 May 2020).

~~Galárraga D. 2011. Lady Bug. Flickr https://www.flickr.com/photos/podolsky86/5442785577~~

García~~,~~ MF, Becerra VC, Reising CE. 1999. *Harmonia axyridis* Pallas (Col.: Coccinellidae). Estudio biológico. Revista de la Facultad de Ciencias Agrarias 31: 85–91.

Gelis R. 2019. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/19483599 Access date: 09/01/2019

González G, Bustamante A, Grez AA. 2018. Touching the Sky: Coccinellids (Coleoptera: Coccinellidae) at High Altitudes in South America. Neotropical Entomology. DOI~~doi~~: https://doi.org/10.1007/s13744-018-0644-1

González G, Kondo T. 2012. Primer registro de la especie invasora *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) en Ecuador. Boletín de la Sociedad Entomológica Aragonesa, 51, 310.

González G. 2015. Los Coccinellidae de Ecuador *Available at:* http://www.coccinellidae.cl/paginasWebEcu/Paginas/InicioEcu.php

Gordon~~,~~ RD. 1985. The Coccinellidae (Coleoptera) of America north of Mexico. Journal of New York Entomology Society 93(1): 1–912.

Grez AA, Zaviezo T, González G, Rothmann S. 2010. *Harmonia axyridis* in Chile: a new threat. Ciencia e Investigación Agraria 37(3): 145–149. DOI: http://dx.doi.org/10.4067/rcia.v37i3.157

Formatted: Font: Not Italic

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Formatted: Spanish (Ecuador)

Field Code Changed

Formatted: Spanish (Spain)

Grez AA, Zaviezo T, Roy HE, Brown PM, Bizama G. 2016. Rapid spread of *Harmonia axyridis* in Chile and its effects on local coccinellid biodiversity. Diversity and Distributions, 22(9), 982-994. DOI: https://doi.org/10.1111/ddi.12455~~DOI: https://doi.org/10.1111/ddi.12455~~

Grez AA., Zaviezo T, Roy HE, Brown PMJ, Segura B. 2017. In the shadow of the condor: invasive *Harmonia axyridis* found at very high altitude in the Chilean Andes. Insect Conservation and Diversity 10: 483–487. DOI~~doi~~: http://doi.org/10.1111/icad.12258

~~Grez, AA, Zaviezo T, González G, Rothmann S. 2010. *Harmonia axyridis* in Chile: a new threat. Ciencia e Investigación Agraria 37(3): 145–149.~~ doi: http://dx.doi.org/10.4067/rcia.v37i3.157

Guamán Montaño~~,~~ DR. 2017. Inventario de las plagas y los insectos benéficos del cacao Theobroma cacao L. en el cantón El Pangui, provincia de Zamora Chinchipe (Bachelor's thesis, Loja: Universidad Nacional de Loja).

Guedes CFDC, Almeida LMD. 2013. The potential of different fruit species as food for *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae). Revista Brasileira de Fruticultura 35(4): 1025–1031. DOI: https://doi.org/10.1590/S0100-29452013000400013

Hiller T, Haelewaters D. 2019. A case of silent invasion: Citizen science confirms the presence of *Harmonia axyridis* (Coleoptera, Coccinellidae) in Central America. PLoS ONE 14(7): e0220082. DOI: https://doi.org/10.1371/journal.pone.0220082

Hoebeke ER, Wheeler Jr AG. 1996. Adventive lady beetles (Coleoptera: Coccinellidae) in the Canadian Maritime Provinces, with new eastern US records of *Harmonia quadripunctata*. Entomological News 107(5): 281-290.

Honěk A. 2012. Distribution and habitats; pp. 110–140, in: I. Hodex, H.F. van Emden and A. Honěk (eds.). Ecology and behaviour of the ladybird beetles (Coccinellidae). Chichester: Blackwell Publishing. DOI~~doi~~: http://dx.doi.org/10.1002/9781118223208.ch4

Huttel C, Zebrowski C, Gondard P. 1999. Paisajes Agrarios del Ecuador. Geografía Básica del Ecuador, Tomo V Geografía Agraria, Vol. 2. Quito: IRD, IPGH, IFEA, IGM, PUCE. 285 pp.

Katsanis A, Babendreier~~Iannacone J, Perla~~ D, Nentwig W, Kenis M. 2013. Intraguild predation between the invasive ladybird~~. 2011. Invasion of predator~~ *Harmonia axyridis* and non-target European coccinellid species. BioControl 58: 73. DOI: https://doi.org/10.1007/s10526-012-9470-2

Formatted: Spanish (Spain)

Formatted: English (United States)

Formatted: English (United States)

Formatted: English (United States)

Formatted: English (United States)

Koch RL. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. Journal of Insect Science 3: 1–16. DOI: http://dx.doi.org/10.1093/jis/3.1.32

Koch RL, Galvan TL. 2008. Bad side of a good beetle: the North American experience with *Harmonia axyridis*. Biocontrol 53: 23–35. DOI: http://dx.doi.org/10.1007/s10526-007-9121-1

Koch RL, Venette RC, Hutchison WD. 2006. Invasions by *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in the Western Hemisphere: implications for South America, Neotropical Entomology 35: 421–434. DOI: http://doi.org/10.1590/S1519-566X2006000400001~~and an evaluation of the environmental risk in Peru. The Biologist (Lima). 9(2): 213-233.~~

~~Inclan D. 2018. *Harmonia axyridis*,~~ iNaturalist. https://www.inaturalist.org/observations/18699219 Access date: 09/01/2019

Koch RL, Burkness EC, Wold Burkness SJ, Hutchinson WD. 2004. Phytophagous preferences of the multicolored Asian lady beetle (Coleoptera: Coccinellidae) for autumn-ripening fruit. Journal of Economic Entomology 97(2): 539–544. DOI~~doi~~: http://dx.doi.org/10.1603/0022-0493-97.2.539

~~Koch RL, Galvan TL. 2008. Bad side of a good beetle: the North American experience with *Harmonia axyridis*. Biocontrol 53: 23–35. DOI: http://dx.doi.org/10.1007/s10526-007-9121-1~~

~~Koch RL, Venette RC, Hutchison WD. 2006. Invasions by *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) in the Western Hemisphere: implications for South America, Neotropical Entomology 35: 421–434. DOI: http://dx.doi.org/10.1590/S1519-566X2006000400001~~

~~Koch RL. 2003. The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. Journal of Insect Science 3: 1–16. DOI: http://dx.doi.org/10.1093/jis/3.1.32~~

Kondo T, González G. 2013. The multicolored Asian lady beetle, *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae), a not so new invasive insect in Colombia and South America. Insecta Mundi, 0283, 1-7.

LaMana ML, Miller JC. 1996. Field observations on *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) in Oregon. *Biological Control*, 6: 232-237

Formatted: Font: Italic

Lombaert E, Guillemaud T, Cornuet JM, Malausa T, Facon B, Estoup A. 2010. Bridgehead effect in the worldwide invasion of the biocontrol Harlequin Ladybird. PLoS ONE 5(3): e9743. DOI~~doi~~: http://dx.doi.org/10.1371/journal.pone.0009743

Lucas E. 2012. Intraguild interactions; pp. 343–374, in: I. Hodex, H.F. van Emden and A. Honěk (eds.). Ecology and behaviour of the ladybird beetles (Coccinellidae). Chichester: Blackwell Publishing. DOI~~doi~~: http://dx.doi.org/10.1002/9781118223208.ch7

Lucas E, Gagné I, Coderre D. 2002. Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology*, 99, 457–463.

Lynch JD, Duellman WE. 1997. Frogs of the genus *Eleutherodactylus* (Leptodactylidae) in western Ecuador: systematic, ecology, and biogeography. University of Kansas: Natural History Museum.

Mace GM, Masundire H, Baillie J, Ricketts T, Brooks T, Hoffmann M, Stuart S, Balmford A, Purvis A, Reyers B, Wang J, Revenga C, Kennedy E, Naeem S, Alkemade R, Allnutt T, Bakarr M, Bond W, Chanson J, Cox N, Fonseca G, Hilton-Taylor C, Loucks C, Rodrigues A, Sechrest W, Stattersfield A, Janse van Rensburg B, Whiteman C, Abell R, Cokeliss Z, Lamoreux J, Pereira HM, Thönell J, Williams P. 2005. Biodiversity. In Rashid M. Hassan et al. (eds.) Ecosystems and human well-being: current state and trends: findings of the Condition and Trends Working Group of the Millennium Ecosystem Assessment. The millennium ecosystem assessment series. Washington, DC: Island Press. p. 77–122.

Majerus M, Strawson V, Roy H. 2006. The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), in Britain. Ecological Entomology 31: 207–215.

Martins C., Almeida LM, Zonta-de-Carvalho RC, Castro CF & Pereira RA. 2009. *Harmonia axyridis*: a threat to Brazilian Coccinellidae? Revista Brasileira de Entomologia 53(4): 663–671. DOI: http://dx.doi.org/10.1590/S0085-56262009000400018

Maslowski J. 2020~~Majka CG, McCorquodale DB. 2018. The Coccinellidae (Coleoptera) of the maritime provinces of Canada: new records, biogeographic notes, and conservation concerns, Zootaxa, 1154, 49–68.~~

~~Maldonado I. 2014. Ladybug. Flickr~~ ~~https://www.flickr.com/photos/mali_mf/14793117493~~

Formatted: Spanish (Ecuador)

Formatted: Spanish (Ecuador)

Field Code Changed

Formatted: Spanish (Ecuador)

Formatted: Spanish (Ecuador)

, *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/43139216. Access date: 02/05/2020

McCorquodale DB. 1998. Adventive lady beetles (Coleoptera: Coccinellidae) in eastern Nova Scotia, Canada. Entomological News, 109(1), 15-20.

~~Mclaren D. 2015. Chinese Ladybug (*Harmonia axyridis*). Flickr 391https://www.flickr.com/photos/57132069@N00/21228927693/~~

Michaud JP. 2012. Coccinellids in biological control; pp. 488–519, in: I. Hodex, H.F. van Emden and A. Honěk (eds.). Ecology and behaviour of the ladybird beetles (Coccinellidae). Chichester: Blackwell Publishing. DOI~~doi~~: http://dx.doi.org/10.1002/9781118223208.ch11

Miró-Agurto JJ, Castillo-Carrillo PS. 2010. Especies de "mariquitas" (Coleoptera: Coccinellidae) en los frutales de Tumbes. *Revista Peruana de Entomología*. 46(1): 21 - 29.

Molineros Andrade J. 1984. Control de la Escama Algodonosa *Icerya purchasi* Maskell en Quito y sus alrededores 1977–1979. Memorias del Encuentro Entomológico Ecuatoriano. Publicaciones del Museo Ecuatoriano de Ciencias Naturales, Serie Miscelánea 3. Quito: Museo Ecuatoriano de Ciencias Naturales.

Mora E. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/18284163 Access date: 09/01/2019

Moser SE, Harwood JD, Obrycki JJ. 2008. Larval feeding on Bt-hybrid and non-Bt corn seedlings by *Harmonia axyridis* (Coleoptera, Coccinellidae) and *Coleomegilla maculata* (Coleoptera, Cocinellidae). Environmental Entomology 37(2): 525–533. DOI: https://doi.org/10.1093/ee/37.2.525~~DOI: https://doi.org/10.1093/ee/37.2.525~~

Nedvěd O, Krejčík S. 2010. Record of the ladybird *Harmonia axyridis* (-Coleoptera: Coccinellidae) from Uruguay. Klapalekiana 46:203-204.

Niegel W. 1992. La fruticulture de hoja caduca en Ecuador. Acta Horticulturae 310: 23–33.

O'Dowd DJ, Green PT, Lake PS. 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters*, 6:812-817. DOI: https://doi.org/10.1046/j.1461-0248.2003.00512.x~~DOI: 10.1046/j.1461-0248.2003.00512.x~~

Orlova-Bienkowskaja MJ, Ukrainsky A, Brown PMJ. 2015. *Harmonia axyridis* (Coleoptera: Coccinellidae) in Asia: a re-examination of the native range and invasion to southeastern Kazakhstan and Kyrgyzstan. Biological Invasions 17: 1941–1948. DOI~~doi~~: http://dx.doi.org/10.1007/s10530-015-0848-9

Formatted: English (United States)

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Field Code Changed

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

690 Pejchar L, Mooney HA. 2009. Invasive species, ecosystem services and human well-being.
691 *Trends in ecology and evolution*, 24(9): 497-504. DOI:
692 https:/doi.org/10.1016/j.tree.2009.03.016
693 Pell JK, Baverstock J, Roy HE, Ware RL, Majerus MEN. 2008. Intraguild predation involving
694 *Harmonia axyridis*: a review of current knowledge and future perspectives. BioControl 53:
695 147. DOI: https://doi.org/10.1007/s10526-007-9125-x
696 Pervez A, Omkar. 2006. Ecology and biological control application of multicoloured Asian
697 ladybird, *Harmonia axyridis*: a review. Biocontrol Science and Technology 16(2), 111–128.
698 Peters JA. 1955. Herpetological type localities in Ecuador. *Revista Ecuatoriana de Entomología*
699 *y Parasitología*, 2(3-4): 335-352.
700 Pickering GJ, Lin J, Riesen R, Reynolds A, Brindle I & Soleas G. 2004. Influence of *Harmonia*
701 *axyridis* on the sensory properties of white and red wine. American Journal of Enology and
702 Viticulture 55: 153–159. DOI: https://doi.org/10.5073/vitis.2008.47.227-230
703 Pickering GJ, Spink M, Kotseridis Y, Brindle ID, Sears M, Inglis D. 2008. The influence of
704 *Harmonia axyridis* morbidity on 2-Isopropyl-3-methoxypyrazine in 'Cabernet Sauvignon'
705 wine. Vitis 47(4): 227–230.
706 Popenoe W. 1924. Economic fruit-bearing plants of Ecuador. Contributions from the United
707 States National Herbarium 24: 101–134.
708 ~~Phillipsen S. (2013) LadyBug2. https://www.flickr.com/photos/planet_irony/10674523115/~~
709 Poutsma J, Loomans AJM, Aukema B, Heijerman T. (2007). Predicting the potential
710 geographical distribution of the harlequin ladybird, *Harmonia axyridis*, using the CLIMEX
711 model. BioControl 53: 103–125. DOI: https://doi.org/-10.1007/s10526-007-9140-y
712 ProEcuador. 2017. Vinos y licores ecuatorianos conquistan paladares en el mundo. Available at
713 https://www.proecuador.gob.ec/vinos-y-licores-ecuatorianos-conquistan-paladares-en-el-
714 mundo/ (accessed May 27, 2020).
715 Quiñonez Pando FJ, Tarango Rivero SH. 2005. Desarrollo y supervivencia de *Harmonia axyridis*
716 Pallas (Coleoptera: Coccinellidae) en función de la especie presa. Agricultura Técnica en
717 México 31(1): 3–9.
718 Revista Líderes. 2012. De playas para finos paladares de vino. Revista Líderes 18/12/2012.
719 Available at https://www.revistalideres.ec/lideres/playas-finos-paladares-vino.html (accessed
720 2 May 2020).

Revista Líderes. 2013. El vino de Yaruquí cosecha paladares en el país. Revista Líderes 18/11/2013. Available at https://www.revistalideres.ec/lideres/vino-yaruqui-cosecha-paladares-pais.html (accessed 2 May 2020).

~~Ramírez Marcial, N. (2016). *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/4371281. Access date: 22/02/2019~~

~~Realpe P. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/18463677 Access date: 09/01/2019~~

Ricciardi A. 2007. Are Modern Biological Invasions an Unprecedented Form of Global Change? Conservation Biology, 21(2): 329-336. DOI: https://doi.org/10.1111/j.1523-1739.2006.00615.x

Ricciardi A, Hoopes MF, Marchetti MP, Lockwood JL. 2013. Progress toward understanding the ecological impacts of nonnative species. Ecological Monographs~~,~~ 83(3):263-282. DOI: https://doi.org/10.1890/13-0183.1

~~Ricciardi A. 2007. Are Modern Biological Invasions an Unprecedented Form of Global Change?. Conservation Biology, 21(2): 329-336.~~ DOI: 10.1111/j.1523-1739.2006.00615.x

Rojas H. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/17824493 Access date: 09/01/2019

Roy H, Brown P, Majerus M. 2006. *Harmonia axyridis*: A successful biocontrol agent or an invasive threat?; pp. 295–309, in: J. Eilenberg and H.M.T. Hokkanen (eds.). An ecological and societal approach to biological control. Amsterdam: Springer. DOI~~doi~~: http://dx.doi.org/10.1007/978-1-4020-4401-4_15

Roy H, Wajnberg E. 2008. From biological control to invasion: the ladybird *Harmonia axyriris* as a model species. *BioControl*, 53:1-4. DOI: https://doi.org/10.1007/s10526-007-9127-8

Roy HE, Brown, PMJ, Comont RF, Poland RL, Sloggett, JJ. 2013. Ladybirds. 2nd Edition. Naturalist's Handbooks 10. Exeter: Pelagic Publishing.

Roy, HE, Brown PM, Adriaens T, Berkvens N, Borges I, Clusella-Trullas S, Comont RF, De Clercq P, Eschen R, Estoup A, Evans EW. 2016. The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. Biological Invasions, 18(4), 997-1044. DOI: https://doi.org/10.1007/s10530-016-1077-6

Saenz García, E. (2015) *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/6010433 . Access date: 22/02/2019

Formatted: Font: Not Italic

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

Saini ED. 2004. Presencia de *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) en la provincia de Buenos Aires: aspectos biológicos y morfológicos, RIA 33: 151–160.

Serra WS, González G, Greco-Spíngola S. 2013. Lista sistemática y distribución geográfica de las especies de Coccinellidae (Insecta: Coleoptera) presentes en Uruguay. Boletín de la Sociedad Entomológica Aragonesa (S.E.A.) 53: 229–242.

~~Serrano J. (2010). Camino a casa. Flickr https://www.flickr.com/photos/jaimeserrano/6214579597~~

~~Sierra Herrera N. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/18283781 Access date: 09/01/2019~~

Silvie P, Aberlenc HP, Duverger C, Bérenger JM, Cardozo R, Gómez V. 2007. *Harmonia axyridis* no Paraguai e novos predadores identificados no cultivo do algodoeiro. In : X Simposio de Controle Biológico, 30 June - 4 July 2007, Brasilia, Brasil, s.n., 1 p. http://agritrop.cirad.fr/542623/

Simberloff D, Martin JL, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M.2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution*, 28(1):58-66. DOI: http://doi.org/10.1016/j.tree.2012.07.013~~DOI: 10.1016/j.tree.2012.07.013~~

Solano Y, Arcaya E. 2014. Primer registro de *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae) en Venezuela. Entomotropica 29(1): 57–61.

Spring, M. (2011) *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/8334546. Access date: 22/02/2019

Stals R. 2010. The establishment and rapid spread of an alien invasive lady beetle: *Harmonia axyridis* (Coleoptera: Coccinellidae) in southern Africa, 2001–2009. IOBC/wprs Bulletin, 58, 125–132.

Tan CC, Li JC. 1934. Inheritance of the elytral color patterns of the lady-bird beetle, *Harmonia axyridis* Pallas. The American Naturalist, 68(716), 252-265.

Tedders WL, Schaefer PW. 1994. Release and establishment of *Harmonia axyridis* (Coleoptera: Coccinellidae) in the southeastern United States. Entomological News, 105(4), 228-243.

Verdugo-Morales N, Andrade-Díaz V~~Tovar B. 2015. Mariquita. Flickr https://www.flickr.com/photos/blasfelipe/18784093131~~

Formatted: Spanish (Spain)

Field Code Changed

Formatted: English (United States)

Formatted: Spanish (Spain)

Formatted: Spanish (Spain)

, 2018. Productos tradicionales y no tradicionales del Ecuador: Posicionamiento y eficiencia en el mercado internacional para el período 2013 –2017. X-Pedientes Económicos 2(3): 84–102.

Viera W, Moreira R, Vargas Y, Martínez A, Álvarez H, Castro J, Zambrano J. 2016. Current status of fruit production in Ecuador. International Journal of Clinical and Biological Science 1(Suppl. 1): S1.

Vilcinskas A, Mukherjee K, Vogel H. 2013. Expansion of the antimicrobial peptide repertoire in the invasive ladybird *Harmonia axyridis*. Proceedings of the Royal Sociey B 280(1750): 20122113. http://dx.doi.org/10.1098/rspb.2012.2113

Ware RL, Majerus MEN. 2008. Intraguild predation of immature stages of British and Japanese coccinellids by the invasive ladybird~~Vivar Ayora L. 2018. *Harmonia axyridis*. iNaturalist. https://www.inaturalist.org/observations/10752850. Access date: 09/01/2019~~

Harmonia axyridis, BioControl 53:169. DOI: https://doi.org/10.1007/s10526-007-9135-8

Wieczorek J, Guo Q, Hijmans RJ. 2004. The point-radius method for georeferencing locality descriptions and calculating associated uncertainty. International Journal of Geographical Information Science, 18(8): 745-767. DOI: https://doi.org/10.1080/13658810412331280211

Formatted: Spanish (Spain)

Formatted: Font: Italic