

# Jewels on the go: exotic buprestids around the world (Coleoptera, Buprestidae)

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## Abstract

Buprestidae (Coleoptera: Buprestoidea) is one of the three wood-borer beetle groups of major phytosanitary interest worldwide, together with Cerambycidae and Scolytinae (Curculionidae). As in other beetle families, some buprestid species have been unintentionally or intentionally introduced around the world, in some cases causing significant environmental and economic damage in the invaded territories. Despite the phytosanitary relevance of the Buprestidae, information regarding the identity of exotic buprestids, their biogeographic areas of origin, introduction pathways, and larval host plants, have remained scattered in the literature. Our objective was to summarize much of the existing knowledge on these topics in the present paper. Our analysis resulted in a list of 115 exotic buprestids worldwide, representing introductions both within and between biogeographic realms and corresponding to less than 1% of the known buprestid species worldwide. Invasiveness does not seem to be linked to their larval host plant preferences, as introduced species utilize 158 plant genera in 70 plant families and are equally represented in all feeding guilds (monophagous, oligophagous, and polyphagous). As trade of plants or plant parts can serve as a pathway for future introductions, the information reported in this review can help in pest risk assessment.

## Keywords

Biodiversity, exotic species, invasive alien species, jewel beetles

## Introduction

Buprestidae Leach, 1815 (Coleoptera: Buprestoidea), commonly known as jewel beetles, include more than 15,000 described species distributed in all continents except Antarctica (Bellamy 2008). The family includes six subfamilies, namely Agrilinae, Buprestinae, Chrysochroinae, Galbellinae, Julodinae, and Polycestinae, (Bellamy 2003).

All Buprestidae are phytophagous and generally oligophagous (i.e., associated with a single plant family) as both adults and larvae (Curletti 1994). Buprestid larvae develop in both living and dead plant tissues; most species are internal feeders, boring or mining in roots, stems, branches, and leaves of both woody plants and herbaceous plants (Bellamy and Volkovitsh 2005), while only Julodinae possess soil-dwelling larvae that feed externally on roots (Kolibáč 2000).

Many buprestids, especially the wood-boring species, select dead, dying, or stressed plants for oviposition (Chamorro et al. 2015); however, some species are capable of infesting or even prefer healthy living hosts (Carlson and Knight 1969). This last group can have an important economic impact on human activities because it includes pests in orchards and tree plantations (Bonsignore et al. 2008; Hashim et al. 2018; Dawadi et al. 2019). Furthermore, buprestids can have substantial negative impacts on the natural ecosystems during outbreaks (Coleman et al. 2012; Muilenburg and Herms 2012; Sallé et al. 2014; Vuts et al. 2016; Haack and Petrice 2019).

The cryptic nature of most buprestid larvae, being hidden in woody tissues and, for some species, their slow larval development due to feeding in nutrient-poor xylem (Haack and Slansky 1987), has allowed multiple species to be transported in wood products and introduced to areas far from their place of origin. Much of this dispersal has been human-mediated and related to trade (Wu et al. 2017). One of the earliest accounts deals with the introduction of *Chalcophora detrita detrita* (Klug, 1829) from the Middle East to Southern Italy by the Etruscans or the Maritime Republics (from 1000 to 2000 years ago; Biagioni et al. 2015). However, since the end of the nineteenth century the introduction rate of exotic buprestids worldwide has substantially increased in similar fashion to many other invasive forest insects (Aukema et al. 2010; Chamorro et al. 2015; Hoebeke et al. 2017; Bozorov et al. 2018; Jendek et al. 2018; Roques et al. 2020; Volkovitsh et al. 2020).

Buprestidae have taken advantage of globalization with the opening of new trade routes and the increase in the number and speed of movement of goods and people (Pyšek and Richardson 2010). In some cases, species such as *Agrilus planipennis* Fairmaire, 1888 (hosts: *Chionanthus* and *Fraxinus* [main host]), *A. mali* Matsumura, 1924 (hosts: *Cydonia*, *Emmenopterys*, *Malus* [main], *Prunus*, *Pyrus*, *Sorbus*), and *Aphanisticus cochinchinae seminulum* Obenberger, 1929 (hosts: *Saccharum*, *Tripsacum*) have become invasive, causing significant damage in urban and natural forests and agriculture, and often requiring significant investments for monitoring and control (Hespenheide 2007; Bauer et al. 2008; Jones et al. 2013; Volkovitsh et al. 2020). Consequently, Buprestidae is one of the Coleoptera families of major silvicultural interest worldwide (Maynard et al. 2004; Inghilesi et al. 2013; Haack et al. 2014; MacQuarrie et al. 2020).

Given this condition, great efforts have been made in the last few decades to identify the main entry pathways, and to develop and implement early detection programs, effective monitoring strategies, and new tools for species identification (Meurisse et al. 2019; Poland and Rassati 2019). To date, however, little has been summarized about the main patterns of buprestid introductions worldwide, their taxonomic affinities, and their biogeographic origins.

The purpose of this article is to provide a comprehensive review of natural and human-assisted translocation of buprestid species among and within various biogeographic realms, describe the contribution of each realm and buprestid subfamily to this exchange of species, and provide the first comprehensive list of all introduced Buprestidae worldwide from the mid-1800s to present. Furthermore, a list of host plant associations at the genus and family level is provided, with an indication of the host range of each buprestid species. Our general aim is to provide information that can be used in pest risk assessment and invasion ecology.

## Methods

In order to compile and then review the literature on exotic Buprestidae, we performed reiterated research in Google Scholar through the use of keywords such as “Buprestidae,” “introduced,” “exotic,” and “alien” and then integrated with the Boolean operators AND, OR, NOT and the use of “ ” for specific word combinations. We also obtained a considerable amount of literature that was not available in Google Scholar thanks to the support of many colleagues and buprestid specialists. Screening of the literature collected was done following the PRISMA approach and only the papers retained are cited in the Suppl. material 1 and were used for the analysis (Moher et al. 2009). The resulting reference library included papers in Chinese, English, French, German, and Italian.

In the analysis, we considered only those publications where buprestids were identified to species or subspecies level, and for those records published between 1850 and December 2020. In the taxonomic discussion, we did not consider the rank of subgenus. In particular, the non-native status of a given species was evaluated for its consistency throughout the reviewed literature; in case there was only a single reference publication and in the absence of any further information, the non-native status of a species was considered as valid. For each species included in the present research, we considered the most recent and comprehensive publication highlighting and explaining the non-native status as a key reference. For those buprestid species for which the literature was limited, we referred to the original faunistic record published. A full list of the Buprestidae species, associated with the reference literature, is provided in Suppl. material 1.

Where the origin of a given taxon could not be assigned to a single biogeographic region, every possible area of origin was considered. The world’s biogeographic areas considered in this paper generally follow the interpretation and categorization provided by Löbl and Löbl (2016).

At times it was difficult to know if an insect was firmly established in a new area or was simply intercepted at a port of entry, because papers varied in terminology and detail. In our dataset, when considering the species status, we have generally adopted the following categorization: A) Neonative: species native to a continent but introduced into regions other than the native ones either through natural spread indirectly favored by human activities (climate change, habitat change) or through accidental human-mediated introductions; B) Established: non-native species that sustain self-replacing populations over several life cycles (inclusive of single specimens collected in the wild away from potential entry points); C) Invasive: a non-native species established in natural or semi-natural ecosystems or habitat, which has impact and threatens native biological diversity; D) Intercepted: insects detected during inspection procedures or similar situations where no reproducing population is known to occur; E) Intentionally introduced: species that have been actively introduced in areas other than their native range with a specific purpose, such as biological control of invasive plants; F) Unclear: all species for which the status is unclear (e.g., apparently extinct adventive populations, species described in areas where that specific genus does not occur, species record vague without any specific detail, mislabeling and misidentification).

Data collected were organized in an Excel spreadsheet including the following information, organized by columns: subfamily, tribe, genus, species (full name plus author), biogeographic region of origin, biogeographic region of detection, status, and host plants. Detection region and host plant were associated with a specific column called references, which included all relevant information used to recover the data. Each species could have multiple entries (rows) in cases of multiple introduction events in different biogeographic areas, or in situations where the origin of the species was not reducible to a single biogeographic region. In the case of single introductions of widely distributed species in which it was clear the biogeographic region of origin of the insects, we considered only the record for that specific region. The taxonomy of plant genera and families used in the paper is based on the information available on the “Plants of The World Online” database (<https://powo.science.kew.org/>). Analyses and graphics were realized using the R software (version 4.1.2).

Host plant preference was defined in the categories: monophagous (for buprestids feeding only on plant species of the same genus), oligophagous (buprestids feeding on different plant genera within the same host family), polyphagous (buprestids feeding on plant species from different host families).

## Results

### Faunistic part

Our literature review identified 162 events of buprestid introductions among and within biogeographic regions that involved 115 distinct taxa (Suppl. material 1). The taxa included 44 species in the subfamily Agrilinae (tribes Agrilini, Aphanistini, Coraebini, and Tracheini) (Table 1), 51 species of Buprestinae (tribes Anthaxiini,

Buprestini, Chrysobothrini, Curidini, Melanophilini, and Nascionini) (Table 2), 16 species of Chrysochroinae (Chalchophorini, Chrysochroini, Dicerini, Sphenopterini, Paraleptodemini, and Poecilonotini) (Table 3), and 6 species of Polycestinae (tribes Acmaeoderini, Polycestini, Prospherini and Ptosimini) (Table 4). No species of the subfamilies Galbellinae and Julodinae were recorded as introduced. The revision of all published records revealed that the buprestid species involved in introductions either within or between biogeographical realms constitute only 0.76% of all known buprestid species worldwide.

The analysis showed that the introduction of exotic Buprestidae included all biogeographic realms (with the obvious exclusion of the Antarctic realm), including introductions both among and within the realms (Fig. 1). In addition, our analysis revealed that the Nearctic and Palearctic bioregions contributed the greatest number of introduced species (90 in total) and also the most distinct introduction events (72.4% combined). The realm that was the source for the highest number of buprestids introduced elsewhere was the Palearctic, with 52 out of approximately 2,500 native species (2.1%), followed by the Nearctic (38 out of ~800; 4.8%), the Indomalayan (13 out of ~2,800; 0.5%), the Neotropical (13 out of ~3,700; 0.4%), the Australasian (10 out of ~1,600; 0.6%), the Afrotropical (7 out of ~3,800; 0.2%), and the Oceanian (2 out of ~70; 2.9%). The analyses between the number of buprestid species per biogeographic realm and the number of species introduced elsewhere from each realm did not show any significant statistical relation ( $t = -0.10389$ ,  $df = 5$ ,  $p\text{-value} = 0.9213$ ).

Palearctic and Nearctic were the two regions with the highest number of introduced species (Fig. 1) but, despite somewhat similar environments, climate, and flora, there were substantial differences in the patterns of inter- and intra-biogeographic realm introductions (Table 5). In the case of intra-realm introductions, Palearctic and Nearctic showed a similar number of species (23 vs 20) despite the fact that the genera contributing to more than 50% of total introductions were, at least in part, different: *Agrilus* (9 species) and *Buprestis* (4 species) in the Palearctic, and *Chrysobothris* (9) and *Agrilus* (6) in the Nearctic.

By contrast, when considering introductions between the two realms, it was possible to observe a strong imbalance with 9 exotic species recorded in the Palearctic compared with 25 in the Nearctic. Furthermore, Agrilinae represented the majority of the exotic buprestids in the Nearctic, while Buprestinae were dominant in the Palearctic.

With respect to all buprestid species considered introduced worldwide, we found 41 cases where the species were considered established, 43 cases as interceptions at entry points, 32 cases where the status was unclear, and 22 cases of neonative species. We also classified 13 introductions where the species became invasive, and 6 cases where species were intentionally introduced.

For the 41 cases of establishment, Buprestinae was the most represented subfamily, with 23 records subdivided among the genera *Anthaxia* (1 species), *Buprestis* (8 species), *Belionota* (1 species), *Chrysobothris* (6 species), and *Trachypteris* (1 species). Agrilinae accounted for 14 establishments, represented by 10 species of *Agrilus*, 1 *Diphucrania*, and 2 *Trachys*. The subfamilies Chrysochroinae and Polycestinae were involved in only a limited number of establishments, i.e., 1 *Steraspis*, 1 *Prospheres* and 2 *Acmaeodera*.

**Table 1.** Subfamily Agrilinae: species list, biogeographic realms concerned, status, and larval host plants.  
\* species confused with *Agrilus coxalis* Waterhouse, 1889 in the literature.

| Species                                         | Biogeographic realm                   |                          | Status                   | Plant host genera                                                                                                                                                                                                                  |
|-------------------------------------------------|---------------------------------------|--------------------------|--------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                 | origin                                | introduction             |                          |                                                                                                                                                                                                                                    |
| <i>Agrilus angustulus</i> (Illiger, 1803)       | Palearctic                            | Palearctic               | Unclear                  | <i>Corylus</i> , <i>Ostrya</i> (Betulaceae); <i>Fagus</i> , <i>Castanea</i> , <i>Quercus</i> (Fagaceae)                                                                                                                            |
| <i>Agrilus anxius</i> Gory, 1841                | Nearctic                              | Nearctic                 | Neonative                | <i>Betula</i> (Betulaceae)                                                                                                                                                                                                         |
| <i>Agrilus auriventris</i> Saunders, 1873       | Australasian, Indomalayan             | Oceanian                 | Invasive                 | <i>Citrus</i> (Rutaceae)                                                                                                                                                                                                           |
| <i>Agrilus auroguttatus</i> Schaeffer, 1905*    | Nearctic                              | Nearctic                 | Invasive                 | <i>Quercus</i> (Fagaceae)                                                                                                                                                                                                          |
| <i>Agrilus bilineatus</i> (Weber, 1801)         | Nearctic                              | Palearctic               | Established              | <i>Castanea</i> , <i>Quercus</i> (Fagaceae)                                                                                                                                                                                        |
| <i>Agrilus biguttatus</i> (Fabricius, 1776)     | Palearctic                            | Australasian             | Intercepted              | <i>Fagus</i> , <i>Castanea</i> , <i>Quercus</i> (Fagaceae); <i>Tilia</i> (Malvaceae); <i>Populus</i> (Salicaceae); <i>Ulmus</i> (Ulmaceae)                                                                                         |
| <i>Agrilus cavatus</i> Chevrolat, 1838          | Nearctic                              | Neotropical              | Unclear                  | <i>Rhus</i> (Anacardiaceae); <i>Acaciella</i> (Fabaceae)                                                                                                                                                                           |
| <i>Agrilus convexicollis</i> Redtenbacher, 1849 | Palearctic                            | Palearctic               | Neonative                | <i>Euonymus</i> (Celastraceae); <i>Philadelphus</i> (Hydrangeaceae); <i>Fraxinus</i> , <i>Ligustrum</i> , <i>Olea</i> , <i>Syringa</i> (Oleaceae)                                                                                  |
| <i>Agrilus cuprescens</i> (Ménétriés, 1832)     | Palearctic                            | Nearctic                 | Established              | <i>Rosa</i> , <i>Rubus</i> (Rosaceae)                                                                                                                                                                                              |
| <i>Agrilus cyanenoniger</i> Saunders, 1873      | Palearctic                            | Palearctic               | Neonative                | <i>Croton</i> (Euphorbiaceae); <i>Quercus</i> (Fagaceae)                                                                                                                                                                           |
| <i>Agrilus cyanescens</i> (Ratzeburg, 1837)     | Palearctic                            | Palearctic, Nearctic     | Unclear, Established     | <i>Lonicera</i> , <i>Symphoricarpos</i> (Caprifoliaceae); <i>Rhamnus</i> (Rhamnaceae)                                                                                                                                              |
| <i>Agrilus derasofasciatus</i> Lacordaire, 1835 | Palearctic                            | Nearctic                 | Non-native               | <i>Vitis</i> (Vitaceae)                                                                                                                                                                                                            |
| <i>Agrilus difficilis</i> Gory, 1841            | Nearctic                              | Nearctic                 | Established              | <i>Gleditsia</i> (Fabaceae); <i>Zanthoxylum</i> (Rutaceae)                                                                                                                                                                         |
| <i>Agrilus extraneus</i> Fisher, 1933           | Oceanian                              | Oceanian                 | Established              | <i>Argemone</i> (Papaveraceae)                                                                                                                                                                                                     |
| <i>Agrilus fleischeri</i> Obenberger, 1925      | Palearctic                            | Nearctic                 | Intercepted              | <i>Populus</i> , <i>Salix</i> (Salicaceae)                                                                                                                                                                                         |
| <i>Agrilus fuscillatus</i> Chevrolat, 1835      | Nearctic, Neotropical                 | Nearctic                 | Intercepted              | <i>Pinus</i> (Pinaceae); <i>Zea</i> (Poaceae); <i>Coffea</i> (Rubiaceae); <i>Salix</i> (Salicaceae)                                                                                                                                |
| <i>Agrilus graminis</i> Kiesenwetter, 1857      | Palearctic                            | Palearctic               | Neonative                | <i>Alnus</i> , <i>Corylus</i> , <i>Ostrya</i> (Betulaceae); <i>Euonymus</i> (Celastraceae); <i>Castanea</i> , <i>Quercus</i> (Fagaceae); <i>Acer</i> (Sapindaceae); <i>Viburnum</i> (Viburnaceae)                                  |
| <i>Agrilus hyperici</i> (Creutzer, 1799)        | Palearctic                            | Australasian, Nearctic   | Intentionally introduced | <i>Hypericum</i> (Hypericaceae)                                                                                                                                                                                                    |
| <i>Agrilus kaluganus</i> Obenberger, 1940       | Palearctic                            | Palearctic               | Neonative                | <i>Corylus</i> (Betulaceae)                                                                                                                                                                                                        |
| <i>Agrilus livers</i> Kerremans, 1892           | Indomalayan                           | Palearctic               | Unclear                  | <i>Citrus</i> (Rutaceae)                                                                                                                                                                                                           |
| <i>Agrilus mali</i> Matsumura, 1924             | Palearctic                            | Palearctic               | Neonative                | <i>Cydonia</i> , <i>Malus</i> , <i>Prunus</i> , <i>Pyrus</i> , <i>Sorbus</i> (Rosaceae); <i>Emmenopterys</i> (Rubiaceae)                                                                                                           |
| <i>Agrilus nicolanus</i> Obenberger, 1924       | Palearctic                            | Palearctic               | Neonative                | <i>Quercus</i> (Fagaceae); <i>Ulmus</i> (Ulmaceae)                                                                                                                                                                                 |
| <i>Agrilus occipitalis</i> (Eschscholtz, 1822)  | Australasian, Indomalayan, Palearctic | Oceanian                 | Invasive                 | <i>Citrus</i> (Rutaceae)                                                                                                                                                                                                           |
| <i>Agrilus pilosovittatus</i> Saunders, 1873    | Palearctic                            | Nearctic                 | Established              | <i>Wisteria</i> (Fabaceae)                                                                                                                                                                                                         |
| <i>Agrilus planipennis</i> Fairmaire, 1888      | Palearctic                            | Nearctic, Palearctic     | Invasive, Neonative      | <i>Chionanthus</i> , <i>Fraxinus</i> (Oleaceae)                                                                                                                                                                                    |
| <i>Agrilus prionurus</i> Chevrolat, 1838        | Nearctic                              | Nearctic                 | Neonative                | <i>Chionanthus</i> (Oleaceae); <i>Sapindus</i> (Sapindaceae)                                                                                                                                                                       |
| <i>Agrilus pulchellus</i> Bland, 1865           | Nearctic                              | Nearctic                 | Intercepted              | <i>Chrysanthamus</i> sp., <i>Erigeron</i> (Asteraceae); <i>Amsinkia</i> (Boraginaceae); <i>Celtis</i> (Cannabaceae); <i>Quercus</i> (Fagaceae); <i>Sphaeralcea</i> (Malvaceae); <i>Allionia</i> , <i>Boerhavia</i> (Nyctaginaceae) |
| <i>Agrilus ribesi</i> Schaefer, 1946            | Palearctic                            | Nearctic                 | Invasive                 | <i>Ribes</i> (Grossulariaceae)                                                                                                                                                                                                     |
| <i>Agrilus sinuatus</i> (Olivier, 1790)         | Palearctic                            | Nearctic                 | Established              | <i>Crataegus</i> , <i>Malus</i> , <i>Prunus</i> , <i>Pyrus</i> , <i>Sorbus</i> (Rosaceae)                                                                                                                                          |
| <i>Agrilus smaragdiformis</i> Ganglbauer, 1890  | Palearctic                            | Nearctic                 | Established              | <i>Ailanthus</i> (Simaroubaceae)                                                                                                                                                                                                   |
| <i>Agrilus sulciollis</i> Lacordaire, 1835      | Palearctic                            | Nearctic                 | Established              | <i>Fagus</i> , <i>Castanea</i> , <i>Quercus</i> (Fagaceae)                                                                                                                                                                         |
| <i>Agrilus subrobustus</i> Saunders, 1873       | Indomalayan, Palearctic               | Nearctic                 | Established              | <i>Albizia</i> (Fabaceae)                                                                                                                                                                                                          |
| <i>Aphanisticus antennatus</i> Saunders, 1873   | Palearctic                            | Indomalayan, Neotropical | Unclear                  | Not available                                                                                                                                                                                                                      |

| Species                                                        | Biogeographic realm        |                                       | Status                      | Plant host genera                                                                                            |
|----------------------------------------------------------------|----------------------------|---------------------------------------|-----------------------------|--------------------------------------------------------------------------------------------------------------|
|                                                                | origin                     | introduction                          |                             |                                                                                                              |
| <i>Aphanisticus cochinchinae</i> seminulum<br>Obenberger, 1929 | Indomalayan                | Nearctic,<br>Neotropical,<br>Oceanian | Invasive                    | <i>Saccharum</i> , <i>Tripsacum</i> (Poaceae)                                                                |
| <i>Coraeus andrewesi</i> Obenberger, 1922                      | Indomalayan,<br>Palearctic | Neotropical                           | Unclear                     | Not available                                                                                                |
| <i>Coraeus rubi</i> (Linnaeus, 1767)                           | Palearctic                 | Palearctic                            | Neonative                   | <i>Rosa</i> , <i>Rubus</i> (Rosaceae)                                                                        |
| <i>Coraeus undatus</i> (Fabricius, 1787)                       | Palearctic                 | Palearctic                            | Intercepted                 | <i>Diospyros</i> (Ebenaceae); <i>Castanea</i> , <i>Fagus</i> ,<br><i>Quercus</i> (Fagaceae)                  |
| <i>Diphucrania viridipurpurea</i> Carter, 1924                 | Australasian               | Palearctic                            | Established                 | Not available                                                                                                |
| <i>Hylaeogena jureceki</i> Obenberger, 1941                    | Neotropical                | Afrotropical,<br>Australasian         | Intentionally<br>introduced | <i>Dolichandra</i> (Bignoniaceae)                                                                            |
| <i>Leiopleura carbonata</i> (LeConte, 1860)                    | Neotropical                | Neotropical                           | Unclear                     | Not available                                                                                                |
| <i>Leiopleura otero</i> (Fisher, 1935)                         | Neotropical                | Neotropical                           | Unclear                     | Not available                                                                                                |
| <i>Lius poseidon</i> Napp, 1972                                | Neotropical                | Oceanian                              | Intentionally<br>introduced | <i>Miconia</i> , <i>Chaetogastrea</i> (Melastomataceae)                                                      |
| <i>Trachys minutus</i> (Linnaeus, 1758)                        | Palearctic                 | Nearctic                              | Established                 | <i>Corylus</i> (Betulaceae); <i>Sorbus</i> (Rosaceae);<br><i>Salix</i> (Salicaceae), <i>Ulmus</i> (Ulmaceae) |
| <i>Trachys troglodytiformis</i> Obenberger, 1918               | Palearctic                 | Nearctic                              | Established                 | <i>Althea</i> , <i>Hibiscus</i> , <i>Malva</i> (Malvaceae)                                                   |

**Table 2.** Subfamily Buprestinae: species list, biogeographic realms concerned, status, and larval host plants.

| Species                                          | Biogeographic realm |                                                                           | Status                                                              | Plant host genera                                                                                                             |
|--------------------------------------------------|---------------------|---------------------------------------------------------------------------|---------------------------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|
|                                                  | origin              | introduction                                                              |                                                                     |                                                                                                                               |
| <i>Anthaxia godeti</i> Gory & Laporte, 1839      | Palearctic          | Palearctic                                                                | Neonative                                                           | <i>Picea</i> , <i>Pinus</i> (Pinaceae)                                                                                        |
| <i>Anthaxia laticeps</i> Abeille de Perrin, 1900 | Palearctic          | Palearctic                                                                | Neonative                                                           | <i>Pinus</i> (Pinaceae)                                                                                                       |
| <i>Anthaxia proteus</i> Saunders, 1873           | Palearctic          | Palearctic                                                                | Unclear                                                             | <i>Pinus</i> (Pinaceae)                                                                                                       |
| <i>Anthaxia salicis</i> (Fabricius, 1776)        | Palearctic          | Nearctic                                                                  | Established                                                         | <i>Castanea</i> , <i>Quercus</i> (Fagaceae); <i>Salix</i><br>(Salicaceae); <i>Acer</i> (Sapindaceae)                          |
| <i>Cobosina willineri</i> (Cobos, 1972)          | Neotropical         | Neotropical                                                               | Neonative                                                           | Not available                                                                                                                 |
| <i>Buprestis apricans</i> Herbst, 1801           | Nearctic            | Neotropical                                                               | Established                                                         | <i>Pinus</i> (Pinaceae)                                                                                                       |
| <i>Buprestis aurulenta</i> Linnaeus, 1767        | Nearctic            | Australasian,<br>Neotropical,<br>Palearctic,<br>Oceanian                  | Intercepted,<br>Established,<br>Unclear,<br>Established             | <i>Thuja</i> , <i>Juniperus</i> (Cupressaceae); <i>Abies</i> ,<br><i>Picea</i> , <i>Pinus</i> , <i>Pseudotsuga</i> (Pinaceae) |
| <i>Buprestis dalmatina</i> Mannerheim, 1837      | Palearctic          | Nearctic,<br>Palearctic                                                   | Intercepted<br>Neonative                                            | <i>Pinus</i> (Pinaceae)                                                                                                       |
| <i>Buprestis decora</i> Fabricius, 1775          | Nearctic            | Neotropical,<br>Palearctic                                                | Established                                                         | <i>Pinus</i> (Pinaceae)                                                                                                       |
| <i>Buprestis haemorrhoidalis</i> Herbst, 1780    | Palearctic          | Afrotropical,<br>Australasian,<br>Nearctic,<br>Neotropical,<br>Palearctic | Unclear,<br>Intercepted,<br>Established,<br>Unclear,<br>Unclear     | <i>Callitris</i> (Cupressaceae); <i>Abies</i> , <i>Picea</i> ,<br><i>Pinus</i> (Pinaceae)                                     |
| <i>Bruprestis humeralis</i> Klug, 1829           | Palearctic          | Palearctic                                                                | Neonative                                                           | <i>Pinus</i> (Pinaceae)                                                                                                       |
| <i>Buprestis lineata</i> Fabricius, 1781         | Nearctic            | Australasian,<br>Nearctic,<br>Neotropical,<br>Palearctic                  | Intercepted,<br>Neonative,<br>Established,<br>Unclear               | <i>Pinus</i> (Pinaceae)                                                                                                       |
| <i>Buprestis maculativentris</i> Say, 1825       | Nearctic            | Australasian                                                              | Intercepted                                                         | <i>Abies</i> , <i>Picea</i> , <i>Pinus</i> (Pinaceae)                                                                         |
| <i>Buprestis maculipennis</i> Gory, 1841         | Nearctic            | Neotropical                                                               | Established                                                         | <i>Taxodium</i> (Cupressaceae); <i>Pinus</i> , <i>Tsuga</i><br>(Pinaceae)                                                     |
| <i>Buprestis novemmaculata</i> Linnaeus, 1767    | Palearctic          | Afrotropical,<br>Indomalayan,<br>Nearctic,<br>Neotropical,<br>Palearctic  | Unclear,<br>Unclear,<br>Intercepted,<br>Established,<br>Established | <i>Larix</i> , <i>Picea</i> , <i>Pinus</i> (Pinaceae)                                                                         |
| <i>Buprestis salisburyensis</i> Herbst, 1801     | Nearctic            | Nearctic                                                                  | Established                                                         | <i>Pinus</i> (Pinaceae)                                                                                                       |



| Species                                                    | Biogeographic realm       |                                                               | Status                                                          | Plant host genera                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                        |
|------------------------------------------------------------|---------------------------|---------------------------------------------------------------|-----------------------------------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                            | origin                    | introduction                                                  |                                                                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                          |
| <i>Trachykele blondeli</i> Marseul, 1865                   | Nearctic                  | Australasian, Palearctic                                      | Intercepted, Non-native                                         | <i>Calocedrus</i> , <i>Chamaecyparis</i> , <i>Cupressus</i> , <i>Juniperus</i> , <i>Thuja</i> (Cupressaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| <i>Belionota prasina</i> (Thunberg, 1789)                  | Australasian, Indomalayan | Afrotropical, Australasian, Nearctic, Neotropical, Palearctic | Established, Intercepted, Established, Established, Intercepted | <i>Anacardium</i> , <i>Mangifera</i> (Anacardiaceae); <i>Delonix</i> , <i>Pithecellobium</i> (Fabaceae); <i>Casuarina</i> (Casuarinaceae); <i>Hopea</i> (Dipterocarpaceae); <i>Ceiba</i> (Malvaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| <i>Merimna atrata</i> (Gory & Laporte, 1837)               | Australasian              | Oceanian                                                      | Intercepted                                                     | <i>Eucalyptus</i> (Myrtaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| <i>Chrysobothris adelpha</i> Gemminger & Harold, 1869      | Nearctic                  | Oceanian                                                      | Intercepted                                                     | <i>Prosopis</i> (Fabaceae); <i>Carya</i> (Juglandaceae); <i>Amelanchier</i> (Rosaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| <i>Chrysobothris acutipennis</i> Chevrolat, 1835           | Nearctic, Neotropical     | Neotropical                                                   | Established                                                     | <i>Ebenopsis</i> , <i>Leucaena</i> (Fabaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| <i>Chrysobothris affinis</i> (Fabricius, 1794)             | Palearctic                | Australasian                                                  | Intercepted                                                     | <i>Pistacia</i> (Anacardiaceae); <i>Alnus</i> , <i>Betula</i> , <i>Carpinus</i> , <i>Corylus</i> , <i>Ostrya</i> (Betulaceae); <i>Cornus</i> (Cornaceae); <i>Arbutus</i> (Ericaceae); <i>Cercis</i> , <i>Gleditsia</i> , <i>Robinia</i> (Fabaceae); <i>Castanea</i> , <i>Fagus</i> , <i>Quercus</i> (Fagaceae); <i>Punica</i> (Lythraceae); <i>Juglans</i> (Juglandaceae); <i>Tilia</i> (Malvaceae); <i>Ficus</i> , <i>Morus</i> (Moraceae); <i>Eucalyptus</i> (Myrtaceae); <i>Fraxinus</i> (Oleaceae); <i>Cedrus</i> (Pinaceae); <i>Platanus</i> (Platanaceae); <i>Crataegus</i> , <i>Malus</i> , <i>Prunus</i> , <i>Pyrus</i> , <i>Rosa</i> , <i>Sorbus</i> (Rosaceae); <i>Populus</i> , <i>Salix</i> (Salicaceae); <i>Acer</i> (Sapindaceae); <i>Ulmus</i> (Ulmaceae) |
| <i>Chrysobothris analis</i> LeConte, 1860                  | Nearctic                  | Nearctic                                                      | Established                                                     | <i>Rhus</i> (Anacardiaceae); <i>Celtis</i> (Cannabaceae); <i>Diospyros</i> (Ebenaceae); <i>Cercis</i> , <i>Ebenopsis</i> , <i>Haematoxylum</i> , <i>Leucaena</i> , <i>Mimosa</i> , <i>Parkinsonia</i> , <i>Prosopis</i> (Fabaceae); <i>Carya</i> , <i>Juglans</i> (Juglandaceae); <i>Coccoloba</i> (Polygonaceae); <i>Prunus</i> (Rosaceae); <i>Citrus</i> (Rutaceae); <i>Sapindus</i> (Sapindaceae); <i>Ulmus</i> (Ulmaceae)                                                                                                                                                                                                                                                                                                                                            |
| <i>Chrysobothris cavifrons</i> Deyrolle, 1864              | Australasian              | Palearctic                                                    | Intercepted                                                     | Not available                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| <i>Chrysobothris cerceripraeda</i> Westcott & Thomas, 2015 | Nearctic                  | Nearctic                                                      | Unclear                                                         | Not available                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| <i>Chrysobothris chrysonota</i> Deyrolle, 1864             | Australasian              | Palearctic                                                    | Intercepted                                                     | Not available                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| <i>Chrysobothris costata</i> Kerremans, 1895               | Oceanian                  | Oceanian                                                      | Invasive                                                        | <i>Intsia</i> (Fabaceae); <i>Citrus</i> (Rutaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| <i>Chrysobothris costifrons</i> Waterhouse, 1887           | Nearctic                  | Nearctic                                                      | Neonative                                                       | <i>Quercus</i> (Fagaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| <i>Chrysobothris dorsata</i> (Fabricius, 1787)             | Afrotropical, Palearctic  | Palearctic                                                    | Unclear                                                         | <i>Acacia</i> , <i>Cenatonia</i> (Fabaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| <i>Chrysobothris ellyptica</i> Deyrolle, 1864              | Australasian              | Palearctic                                                    | Intercepted                                                     | Not available                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| <i>Chrysobothris femorata</i> (Olivier, 1790)              | Nearctic                  | Australasian, Oceanian, Palearctic                            | Intercepted                                                     | <i>Liquidambar</i> (Altingiaceae); <i>Carpinus</i> (Betulaceae); <i>Celtis</i> (Cannabaceae); <i>Diospyros</i> (Ebenaceae); <i>Cercis</i> (Fabaceae); <i>Castanea</i> , <i>Quercus</i> (Fagaceae); <i>Carya</i> , <i>Juglans</i> (Juglandaceae); <i>Tilia</i> (Malvaceae); <i>Fraxinus</i> (Oleaceae); <i>Platanus</i> (Platanaceae); <i>Amelanchier</i> , <i>Crataegus</i> , <i>Cydonia</i> , <i>Malus</i> , <i>Prunus</i> , <i>Sorbus</i> (Rosaceae); <i>Populus</i> , <i>Salix</i> (Salicaceae); <i>Acer</i> (Sapindaceae); <i>Ulmus</i> (Ulmaceae)                                                                                                                                                                                                                   |
| <i>Chrysobothris igniventris</i> Reitter, 1895             | Palearctic                | Nearctic                                                      | Intercepted                                                     | <i>Larix</i> , <i>Pinus</i> (Pinaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| <i>Chrysobothris indica</i> Castelnau & Gory, 1837         | Indomalayan               | Oceanian                                                      | Established                                                     | <i>Terminalia</i> (Combretaceae); <i>Shorea</i> (Dipterocarpaceae); <i>Acacia</i> (Fabaceae); <i>Myristica</i> (Myristicaceae); <i>Mimusops</i> (Sapotaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| <i>Chrysobothris knulli</i> Nelson, 1975                   | Nearctic                  | Nearctic                                                      | Established                                                     | <i>Acacia</i> (Fabaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                 |



| Species                                                  | Biogeographic realm |                     | Status      | Plant host genera                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
|----------------------------------------------------------|---------------------|---------------------|-------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                          | origin              | introduction        |             |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                         |
| <i>Chrysobothris mali</i> Horn, 1886                     | Nearctic            | Nearctic            | Intercepted | <i>Alnus</i> , <i>Betula</i> , <i>Corylus</i> (Betulaceae); <i>Arbutus</i> , <i>Arctostaphylos</i> (Ericaceae); <i>Pickeringia</i> , <i>Prosopis</i> , <i>Wisteria</i> (Fabaceae); <i>Fagus</i> , <i>Quercus</i> (Fagaceae); <i>Ribes</i> (Grossulariaceae); <i>Juglans</i> (Juglandaceae); <i>Persea</i> (Lauraceae); <i>Liriodendron</i> (Magnoliaceae); <i>Ficus</i> (Moraceae); <i>Eucalyptus</i> (Myrtaceae); <i>Platanus</i> (Platanaceae); <i>Ceanothus</i> , <i>Rhamnus</i> (Rhamnaceae); <i>Adenostoma</i> , <i>Cercocarpus</i> , <i>Cotoneaster</i> , <i>Crataegus</i> , <i>Cydonia</i> , <i>Malus</i> , <i>Oemleria</i> , <i>Photinia</i> , <i>Prunus</i> , <i>Pyracantha</i> , <i>Pyrus</i> , <i>Rhaphiolepis</i> , <i>Rosa</i> , <i>Rubus</i> , <i>Sorbus</i> (Rosaceae); <i>Populus</i> , <i>Salix</i> (Salicaceae); <i>Acer</i> , <i>Aesculus</i> (Sapindaceae); <i>Ulmus</i> (Ulmaceae) |
| <i>Chrysobothris octocola</i> LeConte, 1858              | Nearctic            | Oceanian            | Established | <i>Acacia</i> , <i>Parkinsonia</i> , <i>Prosopis</i> (Fabaceae); <i>Prunus</i> (Rosaceae); <i>Salix</i> (Salicaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| <i>Chrysobothris pupureoplagiata</i> Scheaffer, 1904     | Nearctic            | Nearctic            | Intercepted | <i>Canotia</i> sp. (Celastraceae), <i>Psoralea</i> (Fabaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| <i>Chrysobothris quadriimpressa</i> Gory & Laporte, 1837 | Nearctic            | Nearctic            | Neonative   | <i>Liquidambar</i> (Altingiaceae); <i>Quercus</i> (Fagaceae); <i>Juglans</i> (Juglandaceae); <i>Sapindus</i> (Sapindaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| <i>Chrysobothris rotundicollis</i> Gory & Laporte, 1837  | Nearctic            | Neotropical         | Unclear     | <i>Ebenopsis</i> (Fabaceae); <i>Larix</i> , <i>Pinus</i> (Pinaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
| <i>Chrysobothris rugosiceps</i> Melsheimer, 1845         | Nearctic            | Nearctic            | Neonative   | <i>Castanea</i> , <i>Quercus</i> (Fagaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
| <i>Chrysobothris sexpunctata</i> , Fabricius 1801        | Neotropical         | Neotropical         | Established | Not available                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| <i>Chrysobothris superba</i> Deyrolle, 1864              | Australasian        | Paleartic           | Intercepted | Not available                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| <i>Chrysobothris tranquebarica</i> (Gmelin, 1790)        | Neotropical         | Nearctic            | Unclear     | <i>Casuarina</i> (Casuarinaceae); <i>Conocarpus</i> (Combretaceae); <i>Cassia</i> (Fabaceae); <i>Pinus</i> (Pinaceae); <i>Rhizophora</i> (Rhizophoraceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| <i>Chrysobothris trinervia</i> (Kirby, 1837)             | Nearctic            | Nearctic            | Intercepted | <i>Larix</i> , <i>Picea</i> , <i>Pinus</i> , <i>Pseudotsuga</i> (Pinaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| <i>Anilara hoschekei</i> Obenberger, 1916                | Australasian        | Paleartic           | Intercepted | Not available                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
| <i>Melanophila consupta</i> LeConte, 1857                | Nearctic            | Oceanian            | Non-native  | <i>Calocedrus</i> (Cupressaceae); <i>Eucalyptus</i> (Myrtaceae); <i>Pinus Pseudotsuga</i> (Pinaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| <i>Phaenops cyanea</i> (Fabricius, 1775)                 | Paleartic           | Nearctic            | Intercepted | <i>Abies</i> , <i>Larix</i> , <i>Pinus</i> (Pinaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                   |
| <i>Phaenops drummondi</i> (Kirby, 1837)                  | Nearctic            | Nearctic, Paleartic | Intercepted | <i>Abies</i> , <i>Cedrus</i> , <i>Larix</i> , <i>Picea</i> , <i>Pseudotsuga</i> (Pinaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| <i>Trachypteris picta decostigma</i> (Fabricius, 1787)   | Paleartic           | Neotropical         | Established | <i>Populus</i> , <i>Salix</i> (Salicaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                              |
| <i>Nasico vetusta</i> (Boisduval, 1835)                  | Australasian        | Australasian        | Intercepted | <i>Eucalyptus</i> , <i>Metrosideros</i> (Myrtaceae); <i>Xanthorrhoea</i> (Asphodelaceae)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |

With respect to the 43 cases where the buprestids were apparently only intercepted, the Buprestinae had the highest number of interceptions worldwide (28), which included 24 species. The most commonly intercepted genus was *Chrysobothris* (14 species), followed by *Buprestis* (6 species). There were 6 cases of intercepted Agrilinae, involving 4 species of *Agrilus* and 1 *Coraeus*. For both Chrysochroinae and Polycestinae there were multiple single species interceptions. For 28 species among Agrilinae, Buprestinae, Chrysochroinae and Polycestinae it was not possible to assign their status to any of the existing categories; therefore, they were classified as “unclear.” We recognize that many more species of Buprestidae have been intercepted at ports throughout the world, but in almost all cases these datasets are not available to the public and therefore could not be considered in our paper.

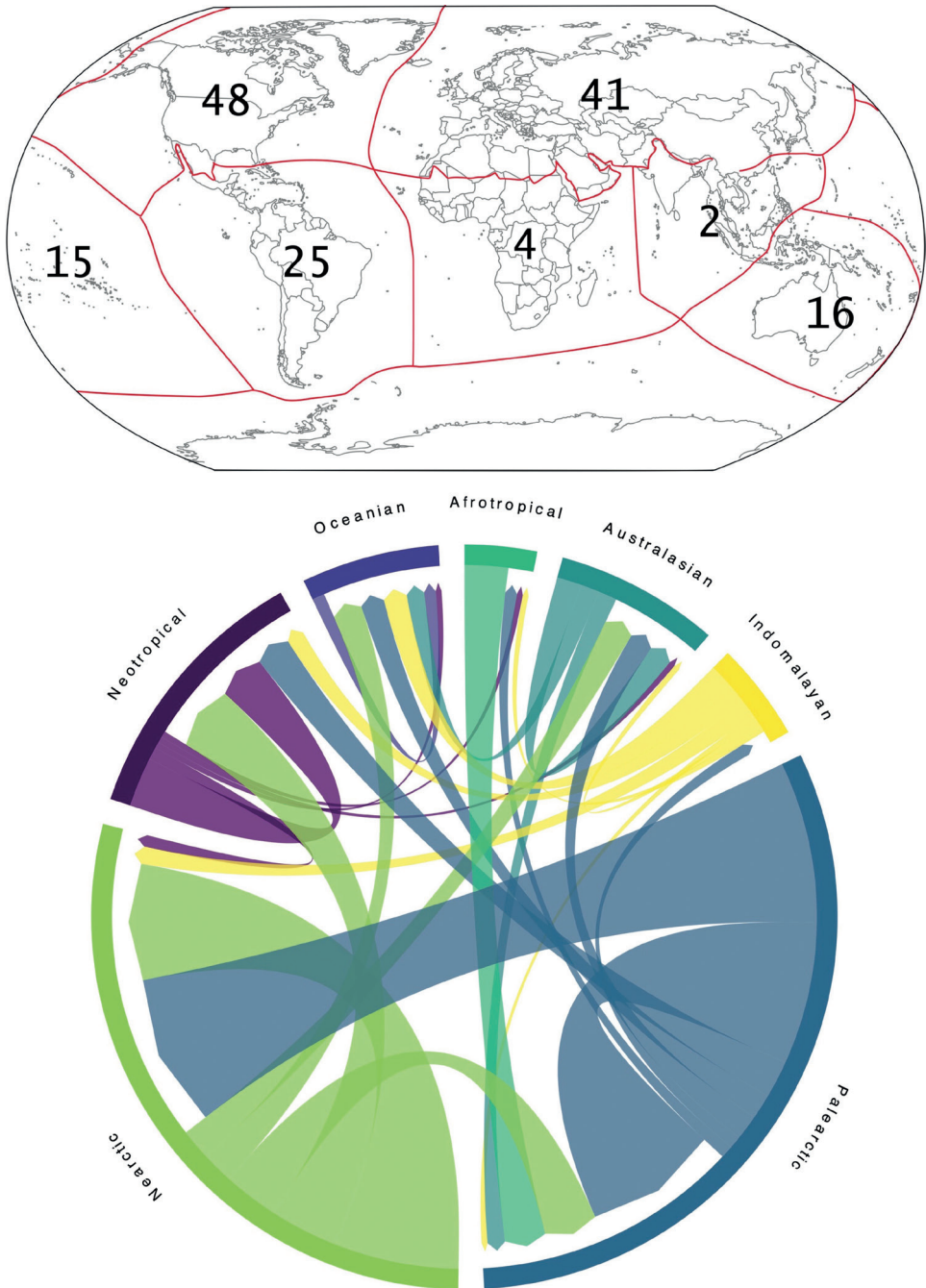
**Table 3.** Subfamily Chrysochroinae: species list, biogeographic realms concerned, status, and larval host plants.

| Species                                           | Biogeographic realm      |                         | Status                   | Plant host genera                                                                                                                                                                                                  |
|---------------------------------------------------|--------------------------|-------------------------|--------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                   | origin                   | introduction            |                          |                                                                                                                                                                                                                    |
| <i>Chalcophora angulicollis</i> (LeConte, 1857)   | Nearctic                 | Nearctic, Palearctic    | Unclear                  | <i>Abies</i> , <i>Pinus</i> , <i>Pseudotsuga</i> (Pinaceae)                                                                                                                                                        |
| <i>Chalcophora japonica</i> (Gory, 1840)          | Palearctic               | Nearctic                | Intercepted              | <i>Pinus</i> (Pinaceae)                                                                                                                                                                                            |
| <i>Chalcophora virginienis</i> (Drury, 1770)      | Nearctic                 | Neotropical, Palearctic | Unclear                  | <i>Taxodium</i> (Cupressaceae); <i>Pinus</i> (Pinaceae)                                                                                                                                                            |
| <i>Cyphogastra foveicollis</i> (Boisduval, 1835)  | Australasian             | Palearctic              | Intercepted              | Not available                                                                                                                                                                                                      |
| <i>Dicerca moesta</i> (Fabricius, 1794)           | Palearctic               | Nearctic, Palearctic    | Intercepted, Unclear     | <i>Abies</i> , <i>Pinus</i> , <i>Picea</i> (Pinaceae)                                                                                                                                                              |
| <i>Dicerca furcata</i> (Thunberg, 1787)           | Palearctic               | Australasian            | Intercepted              | <i>Betula</i> (Betulaceae)                                                                                                                                                                                         |
| <i>Dicerca tuberculata</i> (Laporte & Gory, 1837) | Nearctic                 | Neotropical             | Non-native               | <i>Tsuga</i> (Pinaceae)                                                                                                                                                                                            |
| <i>Euchroma gigantea</i> (Linnaeus, 1758)         | Neotropical              | Neotropical             | Unclear                  | <i>Ceiba</i> , <i>Pachira</i> , <i>Pseudobombax</i> (Malvaceae)                                                                                                                                                    |
| <i>Lampetis bahamica</i> Fisher, 1925             | Neotropical              | Neotropical             | Intercepted              | Not available                                                                                                                                                                                                      |
| <i>Lampetis corruscans</i> (Carter, 1924)         | Australasian             | Australasian            | Unclear                  | Not available                                                                                                                                                                                                      |
| <i>Lampetis fastuosa</i> (Fabricius, 1775)        | Australasian             | Australasian            | Unclear                  | <i>Areca</i> (Arecaceae); <i>Acacia</i> (Fabaceae); <i>Eucalyptus</i> (Myrtaceae); <i>Tectona</i> (Lamiaceae)                                                                                                      |
| <i>Lamprodila festiva</i> (Linnaeus, 1767)        | Palearctic               | Palearctic              | Neonative                | <i>Callitris</i> , <i>Chamaecyparis</i> , <i>Cupressus</i> , <i>Juniperus</i> , <i>Platyclusus</i> , <i>Tetraclinis</i> , <i>Thuja</i> (Cupressaceae); <i>Ziziphus</i> (Rhamnaceae); <i>Tamarix</i> (Tamaricaceae) |
| <i>Lamprodila vivata</i> (Lewis, 1893)            | Palearctic               | Nearctic                | Intercepted              | <i>Cryptomeria</i> , <i>Chamaecyparis</i> , <i>Juniperus</i> (Cupressaceae)                                                                                                                                        |
| <i>Sphenoptera jugoslavica</i> Obenberger, 1926   | Palearctic               | Nearctic                | Intentionally introduced | <i>Centaurea</i> (Asteraceae)                                                                                                                                                                                      |
| <i>Steraspis squamosa</i> (Klug, 1829)            | Afrotropical, Palearctic | Palearctic              | Established, Neonative   | <i>Tamarix</i> (Tamaricaceae)                                                                                                                                                                                      |

**Table 4.** Subfamily Polycestinae: species list, biogeographic realms concerned, status, and larval host plants.

| Species                                                 | Biogeographic realm   |              | Status      | Plant host genera                                                                                                                                                                           |
|---------------------------------------------------------|-----------------------|--------------|-------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                                         | origin                | introduction |             |                                                                                                                                                                                             |
| <i>Acmaeodera bipunctata</i> (Olivier, 1790)            | Palearctic            | Palearctic   | Neonative   | <i>Euphorbia</i> (Euphorbiaceae); <i>Juniperus</i> , <i>Thuja</i> (Cupressaceae); <i>Ficus</i> (Moraceae); <i>Abies</i> , <i>Cedrus</i> , <i>Larix</i> , <i>Pinus</i> (Pinaceae)            |
| <i>Acmaeodera flavomarginata</i> (Gray, 1832)           | Nearctic, Neotropical | Neotropical  | Established | <i>Acacia</i> , <i>Prosopis</i> (Fabaceae); <i>Diospyros</i> (Ebenaceae)                                                                                                                    |
| <i>Acmaeodera neoneglecta</i> Fisher, 1949              | Nearctic              | Nearctic     | Intercepted | <i>Acacia</i> , <i>Ebenopsis</i> , <i>Leucaena</i> , <i>Prosopis</i> , <i>Sophora</i> (Fabaceae); <i>Carya</i> (Juglandaceae); <i>Ulmus</i> (Ulmaceae)                                      |
| <i>Prospheres aurantiopictus</i> (Laporte & Gory, 1837) | Australasian          | Australasian | Established | <i>Anacardia</i> (Araucariaceae); <i>Pinus</i> (Pinaceae)                                                                                                                                   |
| <i>Prosimia undecimmaculata</i> (Herbst, 1784)          | Palearctic            | Nearctic     | Intercepted | <i>Mangifera</i> (Anacardiaceae); <i>Cenotonia</i> (Fabaceae), <i>Crataegus</i> , <i>Malus</i> , <i>Prunus</i> , <i>Pyrus</i> (Rosaceae); <i>Citrus</i> (Rutaceae); <i>Vitis</i> (Vitaceae) |

Among all the taxa investigated, 22 species were considered as neonatives. There were 10 Agrilinae (9 *Agrilus* and 1 *Coraeus*); 9 Buprestinae (2 *Anthaxia*, 1 *Cobosina*, 3 *Buprestis*, and 3 *Chrysobothris*); 2 Chrysochroinae (1 *Steraspis* and 1 *Lamprodila*), and 1 Polycestinae (1 *Acmaeodera*). Neonative species were recorded almost exclusively in the Northern Hemisphere, with 15 species in the Palearctic and 6 in the



**Figure 1.** World map illustrating the number of introduced species of Buprestidae within and between biogeographic realms (above) and graphical representation of the exchanges (below), with the thickness of the arrows directly proportional to the number of introduction events. The length of the colored arc of each realm corresponds to the total number of introduced species, either in or out.

**Table 5.** Comparison between buprestid introductions within and between the Nearctic and Palearctic realms, with details on the number of species within each genus.

| within Palearctic      | within Nearctic        | Palearctic to Nearctic                                   | Nearctic to Palearctic |
|------------------------|------------------------|----------------------------------------------------------|------------------------|
| 9 <i>Agrilus</i>       | 9 <i>Chrysobothris</i> | 12 <i>Agrilus</i> (one species intentionally introduced) | 3 <i>Buprestis</i>     |
| 4 <i>Buprestis</i>     | 6 <i>Agrilus</i>       |                                                          | 2 <i>Chalcophora</i>   |
| 3 <i>Anthaxia</i>      | 2 <i>Buprestis</i>     | 3 <i>Buprestis</i>                                       | 1 <i>Agrilus</i>       |
| 2 <i>Coraeobus</i>     | 1 <i>Acmaeodera</i>    | 2 <i>Trachys</i>                                         | 1 <i>Chrysobothris</i> |
| 1 <i>Acmaeodera</i>    | 1 <i>Chalcophora</i>   | 1 <i>Anthaxia</i>                                        | 1 <i>Phaenops</i>      |
| 1 <i>Chrysobothris</i> | 1 <i>Phaenops</i>      | 1 <i>Chalcophora</i>                                     | 1 <i>Trachykele</i>    |
| 1 <i>Dicerca</i>       |                        | 1 <i>Chrysobothris</i>                                   |                        |
| 1 <i>Steraspis</i>     |                        | 1 <i>Dicerca</i>                                         |                        |
| 1 <i>Lamprodila</i>    |                        | 1 <i>Lamprodila</i>                                      |                        |
|                        |                        | 1 <i>Phaenops</i>                                        |                        |
|                        |                        | 1 <i>Prosimia</i>                                        |                        |
|                        |                        | 1 <i>Sphenoptera</i>                                     |                        |
|                        |                        | (intentionally introduced)                               |                        |

Nearctic realm. *Agrilus* was the most represented genus in the Palearctic with 7 species, while *Chrysobothris* was the most represented genus in the Nearctic with 3 species. A single species of *Cobosina* was the only example of a neonative taxon in the Neotropical realm.

All 13 cases of invasive buprestids are species of Agrilinae and Buprestinae. These species became invasive once introduced to the Nearctic, Oceanian and Neotropical realms. There were 6 species of invasive Agrilinae (5 *Agrilus* and 1 *Aphanistichus*), and only two invasive Buprestinae in the genera *Belionota* and *Chrysobothris*.

Six cases of intentionally introduced taxa were found, representing 4 species in the genera *Agrilus* (Agrilini), *Sphenoptera* (Sphenopterini), *Hylaeogena* and *Liua* (Tracheini). These species were introduced into the Nearctic, Afrotropical, and Australasian realms.

Larval host plants

The analysis of larval host plants for all Buprestidae introduced worldwide identified 158 different plant genera within 70 families (3 Gymnosperms and 67 Angiosperms), with only a few introduced buprestids without host information (Tables 1–4). The exotic Buprestidae included sets of species with wide variation in the range of their larval hosts, varying from highly polyphagous on non-phylogenetically related plant families to monophagous on a single plant genus. Larval host specificity (i.e., monophagous, oligophagous and polyphagous) of introduced Buprestidae is equally distributed among the subfamilies (Kruskal-Wallis chi-squared = 1.2007, df = 2, *p*-value = 0.5486) (Table 6).

The larval host families most represented were Pinaceae (60 host records), Rosaceae (52), Fabaceae (49), Fagaceae (36), and Cupressaceae (24), which together accounted for 52% of all host records (Table 7). Considering introductions within and between biogeographic realms, it emerged that the most common genera of host plants varied greatly among world biogeographic realms, both in abundance and diversity (Table 8).

**Table 6.** Number of introduced species with different levels of larval host-use specialization by buprestid subfamilies.

|                | Monophagous | Oligophagous | Polyphagous | Unknown |
|----------------|-------------|--------------|-------------|---------|
| Agrilinae      | 13          | 9            | 17          | 5       |
| Buprestinae    | 11          | 11           | 20          | 8       |
| Chrysochroinae | 5           | 4            | 3           | 3       |
| Polycestinae   | 0           | 0            | 6           | 0       |
| Total          | 29          | 24           | 46          | 16      |

**Table 7.** Summary table of the main plant families and genera exploited as larval host plants by introduced Buprestidae by subfamily. Numbers between parenthesis refers to the number of records, not distinct species.

| Plant Families    | Plant Genera                                                                         | Buprestid subfamilies                                                    | Buprestid genera                                                                                  |
|-------------------|--------------------------------------------------------------------------------------|--------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------|
| Pinaceae (60)     | <i>Pinus</i> (27), <i>Abies</i> (8), <i>Picea</i> (8),<br><i>Larix</i> (7)           | Buprestinae (45), Chrysochroinae (9),<br>Polycestinae (4), Agrilinae (1) | <i>Buprestis</i> (21), <i>Chrysobothris</i> (10),<br><i>Phaenops</i> (8), <i>Chalcophora</i> (5)  |
| Rosaceae (52)     | <i>Prunus</i> (9), <i>Malus</i> (7), <i>Sorbus</i> (7),<br><i>Pyrus</i> (5)          | Buprestinae (30), Agrilinae (15),<br>Polycestinae (7)                    | <i>Chrysobothris</i> (30), <i>Agrilus</i> (10),<br><i>Ptosima</i> (4), <i>Acmaeoderella</i> (3)   |
| Fabaceae (49)     | <i>Acacia</i> (9), <i>Prosopis</i> (6),<br><i>Ebenopsis</i> (4), <i>Leucaena</i> (3) | Buprestinae (31), Polycestinae (14),                                     | <i>Chrysobothris</i> (29), <i>Acmaeodera</i> (7),<br><i>Acmaeoderella</i> (6), <i>Agrilus</i> (3) |
| Fagaceae (35)     | <i>Quercus</i> (18), <i>Castanea</i> (11),<br><i>Fagus</i> (6)                       | Agrilinae (20), Buprestinae (13),<br>Polycestinae (2)                    | <i>Agrilus</i> (17), <i>Chrysobothris</i> (11),<br><i>Coraebus</i> (3)                            |
| Cupressaceae (23) | <i>Juniperus</i> (5), <i>Thuja</i> (4)                                               | Chrysochroinae (11), Buprestinae<br>(10), Polycestinae (2)               | <i>Lamprodila</i> (10), <i>Trachykele</i> (5),<br><i>Buprestis</i> (2), <i>Acmaeodera</i> (2)     |
| Betulaceae (18)   | <i>Corylus</i> (6), <i>Betula</i> (4), <i>Alnus</i> (3)                              | Buprestinae (9), Agrilinae (8),<br>Chrysochroinae (1)                    | <i>Chrysobothris</i> (9), <i>Agrilus</i> (7)                                                      |
| Salicaceae (16)   | <i>Salix</i> (9), <i>Populus</i> (7)                                                 | Buprestinae (10), Agrilinae (5),<br>Polycestinae (1)                     | <i>Chrysobothris</i> (7), <i>Agrilus</i> (4),<br><i>Trachypterus</i> (2)                          |

## Discussion

The low introduction rate, 0.76% compared for example to the 2.17% out of ~ 6000 taxa of Curculionidae Scolytinae (Lantschner et al. 2020), indicates a general low propensity for Buprestidae to be introduced by humans, either directly or indirectly. In support of this contention is the high number of single buprestid introductions (i.e., one species introduced only once and only in a single biogeographic realm), with respect to the total number of introduction events. In addition, the invasiveness does not seem to be linked to larval host plant preferences, as introduced species are included in all feeding guilds (monophagous, oligophagous, and polyphagous).

The genera *Agrilus* (Agrilinae: Agrilini), *Buprestis* (Buprestinae: Buprestini), and *Chrysobothris* (Buprestinae: Chrysobothrini) would seem to be more predisposed to introduction events than other genera, possibly owing to both their morphological and biological traits. *Agrilus* are generally small in size and univoltine (Solomon 1995; Chamorro et al. 2015). They infest mostly live plants and signs of their presence are difficult to detect prior to adult emergence and host dieback. Therefore, several *Agrilus* species have likely been moved over time through trade of live plants, such as ornamentals or nursery stock, as well as through domestic and international movements

**Table 8.** Summary table of the most common plant genera exploited as larval host plants by buprestid species introduced either within or between biogeographic realms.

| Origin – Introduction realm | Most common larval host plant genera exploited by those species with a narrow host range                                                                                                           |
|-----------------------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Afrotropical – Palearctic   | Angiosperms: <i>Acacia</i> , <i>Ceratonia</i> , <i>Tamarix</i>                                                                                                                                     |
| Australasian – Australasian | Angiosperms: <i>Eucalyptus</i>                                                                                                                                                                     |
| Australasian – Oceanian     | Angiosperms: <i>Citrus</i>                                                                                                                                                                         |
| Australasian – Palearctic   | Angiosperms: <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i>                                                        |
| Indomalayan – Afrotropical  | Angiosperms: <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i>                                                        |
| Indomalayan – Australasian  | Angiosperms: <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i>                                                        |
| Indomalayan – Palearctic    | Angiosperms: <i>Citrus</i>                                                                                                                                                                         |
| Indomalayan – Nearctic      | Angiosperms: <i>Albizia</i> , <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i> , <i>Saccharum</i> , <i>Tripsacum</i> |
| Indomalayan – Neotropical   | Angiosperms: <i>Anacardium</i> , <i>Casuarina</i> , <i>Ceiba</i> , <i>Delonix</i> , <i>Hopea</i> , <i>Mangifera</i> , <i>Pithecellobium</i> , <i>Saccharum</i> , <i>Tripsacum</i>                  |
| Indomalayan – Oceanian      | Angiosperms: <i>Citrus</i>                                                                                                                                                                         |
| Nearctic – Australasian     | Gymnosperms: <i>Pinus</i>                                                                                                                                                                          |
| Nearctic – Nearctic         | Angiosperms: <i>Acacia</i> , <i>Juglans</i> , <i>Prosopis</i> , <i>Sapindus</i> , <i>Ulmus</i><br>Gymnosperms: <i>Pinus</i> , <i>Pseudotsuga</i>                                                   |
| Nearctic – Oceanian         | Angiosperms: <i>Amelanchier</i> , <i>Carya</i> , <i>Prosopis</i> , <i>Prunus</i> , <i>Salix</i><br>Gymnosperms: <i>Pinus</i> , <i>Pseudotsuga</i>                                                  |
| Nearctic – Palearctic       | Gymnosperms: <i>Abies</i> , <i>Pinus</i> , <i>Pseudotsuga</i>                                                                                                                                      |
| Nearctic – Neotropical      | Gymnosperms: <i>Pinus</i>                                                                                                                                                                          |
| Neotropical – Afrotropical  | Angiosperms: <i>Dolichandra</i>                                                                                                                                                                    |
| Neotropical – Australasian  | Angiosperms: <i>Dolichandra</i>                                                                                                                                                                    |
| Neotropical – Nearctic      | Gymnosperms: <i>Pinus</i>                                                                                                                                                                          |
| Neotropical – Neotropical   | Angiosperms: <i>Acacia</i> , <i>Ceiba</i> , <i>Diospyros</i> , <i>Ebenopsis</i> , <i>Leucaena</i> , <i>Pachira</i> , <i>Prosopis</i> , <i>Pseudobombax</i>                                         |
| Neotropical – Oceanian      | Angiosperms: <i>Miconia</i> , <i>Tibouchina</i>                                                                                                                                                    |
| Palearctic – Afrotropical   | Gymnosperms: <i>Picea</i> , <i>Pinus</i>                                                                                                                                                           |
| Palearctic – Australasian   | Angiosperms: <i>Castanea</i> , <i>Fagus</i> , <i>Populus</i> , <i>Quercus</i> , <i>Tilia</i> <i>Ulmus</i>                                                                                          |
| Palearctic – Indomalayan    | Gymnosperms: <i>Larix</i> , <i>Picea</i> , <i>Pinus</i>                                                                                                                                            |
| Palearctic – Nearctic       | Angiosperms: <i>Salix</i> Gymnosperms: <i>Abies</i> , <i>Larix</i> , <i>Picea</i> , <i>Pinus</i>                                                                                                   |
| Palearctic – Neotropical    | Gymnosperms: <i>Picea</i> , <i>Pinus</i>                                                                                                                                                           |
| Palearctic – Oceanian       | Angiosperms: <i>Citrus</i>                                                                                                                                                                         |
| Palearctic – Palearctic     | Angiosperms: <i>Castanea</i> , <i>Quercus</i><br>Gymnosperms: <i>Abies</i> , <i>Picea</i> , <i>Pinus</i>                                                                                           |
| Oceanian – Oceanian         | Angiosperms: <i>Argemone</i> , <i>Citrus</i> , <i>Intsia</i>                                                                                                                                       |

of recently cut logs and manufactured wood products, especially when not debarked. The example of the emerald ash borer, *A. planipennis*, is remarkable in the number of pathways (e.g., logs, firewood, nursery stock) by which it has moved in North America (Herms and McCullough 2014; Haack et al. 2015).

By contrast to *Agrilus*, most *Buprestis* and *Chrysobothris* species have longer larval developmental periods; they can infest both living, stressed, and dead plants; and they typically tunnel in host xylem, including both sapwood and heartwood (Solomon 1995; Evans et al. 2004). As a consequence of this multi-year developmental period deep inside wood, infestations are generally difficult to detect until adult emergence. Although most species oviposit in bark cracks or under the bark, a few species can oviposit directly on exposed wood (xylem). Moreover, once larvae have entered the xylem, the presence of bark is no longer required. Therefore,



introductions of these species can result from movement of logs and milled wood products either with or without bark.

Given the relatively low number of exotic buprestids investigated and the heterogeneity of the sources consulted, it has not been possible to delineate an exact temporal trend for worldwide buprestid introductions, although it seems evident that most species were likely introduced before the 1970s, with very few ever intercepted during port surveys. This condition likely reflects the lack of strict phytosanitary regulations in the early 1900s (Eschen et al. 2015). In addition, international trade among European countries and their overseas colonies likely facilitated the movement of some species early on, as well as later during the two world wars. Examples come from *Buprestis aurulenta* Linnaeus, 1767 and *Buprestis novemmaculata* Linnaeus, 1767, two species introduced in all biogeographic realms edging the Atlantic Ocean, including Azores and Canary Islands, two important bridgeheads in the trade routes between Europe and the Americas (Steckley 1972; Crosby 1984; de Avilez Rocha 2019). Similarly, sugar cane cultivation is associated with the worldwide spread of *Aphanisticus cochinchinae seminulum* Obenberger, 1929 (Zack et al. 2009).

In more recent times, many examples of intracontinental spread of buprestids have been reported, especially for certain species of *Agrilus*, *Anthaxia*, and *Chrysobothris* (Westcott 2005; Fägerström et al. 2009; Izzillo 2013; Orlova-Bienkowskaja and Volkovitsh 2015; Westcott et al. 2018; Curletti and Ranghino 2020). Rapid intracontinental spread probably reflects greater connectivity among trading partners as well as increased speed of transport, especially in the European Union and North America. Range expansion of some neonative species has apparently resulted from human-caused climate and environmental changes, such as for *Agrilus graminis* Kiesenwetter, 1857; *Agrilus nicolanus* Obenberger, 1924; *Buprestis dalmatina* Mannerheim, 1837; *Lamprodila festiva* (Linnaeus, 1767). In the USA, the southward and westward spread of the native birch specialist *Agrilus anxius* Gory, 1841 has been attributed to the widespread planting of ornamental birch trees in many areas outside the native range of North American birch species (Muilenburg and Herms 2012).

It is interesting to note that most neonatives have caused little damage, although there are a few exceptions often associated with the inadvertent movement of infested live plants. For example, the introduction of *Agrilus planipennis* from Eastern Asia to the Moscow area resulted in severe mortality of ash (*Fraxinus*) trees in European Russia (Orlova-Bienkowskaja 2014); however, it is also plausible that *Agrilus planipennis* could have been introduced in Moscow on ash nursery stock imported from North America (Haack et al. 2015). Another example is *Lamprodila festiva* (Linnaeus, 1767), a southern European – circum-Mediterranean species, which has expanded its distribution northward and eastward, benefiting from extensive plantings of its host plants (Cupressaceae) as ornamental plants in private and public gardens (Nitzu et al. 2016; Rabl et al. 2017; Volkovitsh and Karpun 2017; Ruicănescu and Stoica 2019). Similarly, *Agrilus mali* Matsumura, 1924, an eastern Palearctic species, has taken advantage of expanding cultivation of Rosaceae fruit trees and patches of natural forest as a springboard to spread westward in the Palearctic (Volkovitsh et al. 2020; Zhang et al. 2021; Lu et al. 2022).



Only four buprestid species have been intentionally introduced as biological control agents against invasive weeds in North America, South Africa, and Australia. *Sphenoptera jugoslavica* Obenberger, 1926 has been intentionally introduced and successfully established in the western USA where it is used to control the invasive plant *Centaurea diffusa* Lam. (Asteraceae) (Lang et al. 1998); *Agrilus hyperici* (Creutzer, 1799) was introduced in the USA and Australia where it provides efficient control of invasive *Hypericum* species (Hypericaceae); while *Hylaeogena jureceki* Obenberger, 1941 was introduced and established with different rates of success in South Africa and Australia to control the invasive plant *Dolichandra unguis-cati* (L.) L.G.Lohmann (Bignoniaceae) (King et al. 2011; Snow and Dhileepan 2014). The Neotropical *Lius poseidon* Napp, 1972 was instead intentionally introduced to Hawai'i to control the invasive *Miconia crenata* (Vahl) Michelang (Melastomataceae); however, in Hawai'i the species naturally became a biocontrol agent of another invasive plant *Chaetogastra herbacea* (DC.) P.J.F.Guim. & Michelang. (Melastomataceae) (Culliney and Nagamine 2000; Conant and Hirayama 2001; Conant et al. 2013).

## Conclusion

The family Buprestidae is highly diverse with a global distribution defined by multiple abiotic and biotic factors, including human-mediated introductions. Although some biological and ecological traits, such as apparent obligate outbreeding and obligate maturation feeding for all buprestids, can serve as barriers to successful establishment, the opening of new continental and intercontinental trade routes as well as the ever-increasing volume and types of goods and plants traded increases the risk of future introductions or passive diffusion of more buprestid species. With respect to climate change and the widespread practice of introducing exotic plants for ornamental, agricultural, and forestry purposes around the world, it will be important to identify possible new introduction pathways for exotic Buprestidae along with pest risk assessments. In this regard, more research is needed on buprestid taxonomy and ecology, together with training and funding of more buprestid specialists. The development of new technologies for rapid species identification, either morphological or molecular, would be very useful for the management of this important group of plant pests, which are becoming of increasing economic importance worldwide.

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## Supplementary material I

### Systematic list of all Coleoptera Buprestidae introduced around the world between 1850 and 2020

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Data type: table (excel document)

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