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Exotic ladybirds for biological control of herbivorous insects – a review

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Abstract

Since the late 19th century, exotic ladybirds (Coleoptera: Coccinellidae) have been used extensively for suppressing herbivorous insects of economic importance. In recent decades, the introduction of non-native biological control (BC) agents has been greatly limited due to the awareness of the potential non-target effects of introductions. Nonetheless, recent episodes of biological invasions of economically important pests have raised the need to carefully consider whether the expected benefits of pest control go beyond the possible environmental risks of introduction. To better understand the factors that contributed to successful BC programs, here we review the literature behind classical and augmentative BC using exotic ladybirds. Additionally, by means of case studies, we discuss the BC efficacy of selected exotic species, e.g., *Coccinella septempunctata* L., *Harmonia axyridis* (Pallas), and *Hippodamia variegata* (Goeze), and their position within the communities of predators in the introduced areas of USA, Canada, and Chile. In Europe, much of the research on exotic ladybirds has been conducted on the undesired impact of *H. axyridis*. Therefore, we summarize the risk assessment data for this species and review the field research investigating the ecological impact on European aphidophagous predators. According to the BIOCAT database of classical BC programs, 212 ladybird species belonging to 68 genera have been released in about 130 years of BC activity, with 14.6% of introductions having resulted in partial, substantial, or complete control of the target pest. However, because post-release evaluation of establishment and BC success has not always been conducted, this rate could underestimate the successful cases. Among other factors, ladybird establishment and pest suppression mostly depend on (1) intrinsic factors, i.e., high voracity, synchronized predator-prey life cycle, and high dispersal ability, and (2) extrinsic factors, i.e., adaptability to the new environment and landscape composition. This review contributes to improved understanding of ladybirds as exotic BC agents.

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Introduction

The use of exotic – i.e., non-native – natural enemies of insect herbivores has been widely adopted in biological control (BC) (Van Driesche et al., 2008), to deal with the accidental introduction of plant pests into a new geographical area (classical BC) (Mason et al., 2008; Heimpel & Mills, 2017; Kenis et al., 2017b). The release of a predator having a coevolutionary history with the pest is advantageous, mostly due to the fact that the enemy is well synchronized with the life cycle of the prey (Hokkanen & Sailer, 1985; Dixon, 2000; Mason et al., 2008). Because non-native natural enemies used in classical BC have been selected based on favourable traits, such as voracity and reproductive investment, they have sometimes been used in addition against native (indigenous) pests (e.g., De Clercq, 2002; van Lenteren et al., 2003; Soares et al., 2004; Kenis et al., 2017b).

In recent years, tightened legislation for the export, import, and release of exotic agents in many countries around the world has resulted in decreased numbers of new agents (Barratt et al., 2010; van Lenteren, 2012). Firstly, awareness of potential negative environmental effects of biocontrol agents has prompted international organizations such as the Food and Agriculture Organization (FAO) and the Organisation for Economic Co-operation and Development (OECD) to ask for information for the risk assessment of new BC agents (OECD, 2004; IPPC, 2005). Often aided by regional plant protection organizations – e.g., North American Plant Protection Organization (NAPPO) and European and Mediterranean Plant Protection Organization (EPPO) – in many countries, national legislation for licensing of BC agents was then developed. The data requirements and the speed of the registration process thereby differ strongly between countries (Hunt et al., 2008; Mason et al., 2017). Today, all exotic ladybirds (Coleoptera: Coccinellidae) introduced into Canada, USA, most European countries, and Chile would have to pass through a risk assessment.

Secondly, the aim to foster fair and equitable sharing of benefits from genetic resources as stated in the Nagoya Protocol (https://www.cbd.int/abs/) is now being implemented in national legislations, putting different mechanisms on access and benefit sharing in place (Silvestri et al., 2020). During recent years this has impeded the development of exotic BC agents because national competent authorities are not always clearly designated, processes are often not established yet, and additional bureaucracy is being created (Barratt et al., 2018; Smith et al., 2018). Hopefully, experience with access and benefit sharing will accumulate to widen again this bottleneck of biological control (Mason et al., 2018; Smith et al., 2018). As of 2020, among 124 parties nearly half of the European countries have ratified the protocol, whereas Canada, USA, and Chile have not (updated list at https://www.cbd.int/abs/).

Additionally, the Invasive Alien Species Regulation (EU 1143/2014) and the new Plant Health Regulation (EU 2016/2031) provide a set of measures to prevent the spread of invasive species across the EU and are expected to stimulate the use of exotic BC agents in the European member states in the near future. Increasing numbers of accidental introductions of herbivorous insects to new geographical areas prioritize the need for effective but ecologically safe BC agents (Naranjo et al., 2015; Harvey et al., 2020). Countries should therefore carefully evaluate whether the expected benefits of pest control outweigh the possible environmental risks of introduction (Heimpel and Cock, 2018; Charles et al., 2019). In this context, it is timely to assess the factors that have contributed to successful BC programs.

Here, we review some of the literature behind classical and augmentative BC using exotic ladybird species. We first present an overview of the historical use of ladybirds for classical BC targeting insect herbivores (mainly aphids, coccids, mealybugs, whiteflies, and psyllids). We extracted records of the use of Coccinellidae in classical BC from the BIOCAT database and compiled information about establishment and success. This database is managed by CABI (www.cabi.org) and documents all the planned classical BC programs targeting insect pests that have been conducted since the 1890s based on published literature up to the end of 2010 (details in Cock et al., 2016). Differences of establishment rate and BC success among ladybirds or pest groups are analysed by Fisher's Exact test using R (R Core Team, 2020). Additionally, Spearman's rank test is used to test the correlation between the number of introductions of the ladybird species, their establishment rate and BC success. We also review cases of exotic ladybird species obtained from commercial suppliers and used for augmentative BC. We present five regional case studies to better understand the diverse role of exotic ladybirds in BC. When data are available (for the USA, Canada, and Chile), we compare the BC efficacy of exotic species with that of natives in various habitats, as well as the ecological consequences of the introduction. Information on exotic species that have been used for BC in Europe mostly relies on *Harmonia axyridis* (Pallas). Because of its invasive tendency, this ladybird in particular contributed to an increased awareness of the possible environmental risks connected with the importation and release of exotic BC agents. Hence, we provide a summary of the risk assessment for this species and review the recent literature that assesses the ecological impact in open field settings.

Use of ladybirds in classical biological control

The first documented introduction of an exotic ladybird dates back to 1874, when *Coccinella undecimpunctata* L. was released in New Zealand for control of aphids and mealybugs (reviewed by Michaud, 2012). Another species, *Rodolia cardinalis* (Mulsant), was then successfully introduced in the USA (California citrus groves since 1888-1889) and in Europe (Portugal since 1898), for controlling the cottony cushion scale *Icerya purchasi* (Maskell) (Hemiptera: Monophlebidae) (Caltagirone & Doutt, 1989; Amaro, 1994). Since then, exotic ladybirds have been released in new areas to control insect pests, such as coccids, aphids, psyllids, and whiteflies (Obrycki & Kring, 1998; Roy & Migeon, 2010; Gerber & Schaffner, 2016; Soares et al., 2018). During the past century, their use became very frequent, with *Cryptolaemus montrouzieri* Mulsant and *R. cardinalis* released as classical BC agents in the largest number of countries (Cock et al., 2010). Some introduced ladybirds did not establish, whereas others successfully reproduced and spread (Dixon, 2000; Roy & Migeon, 2010). Besides the direct introductions, some species dispersed on their own into new geographical areas (secondary introduction), somewhat contributing to the fortuitous suppression of a given pest (Evans et al., 2011; Soares et al., 2018).

The current version of the BIOCAT database for ladybirds (here designated BIOCAT 2010.4; Figure 1; Table S1; ladybird tribes updated according to Nedvěd & Kovář, 2012) reports 822 cases where fully identified species were introduced (i.e., imported and released) for classical BC of herbivorous insects through the early 2000s. Each case represents one or more introductions of a species in a target country/area within a decade (more details in Cock et al., 2010, 2016). In our review, we do not include 102 introductions, because the ladybird was not documented to species level and should be further revised. Full details of these introductions with partially identified species and suggestions for future nomenclature revision are given in Cock (2019). The BIOCAT database does not include information about the use of ladybirds in classical BC of mites; this aspect has been reviewed elsewhere (Biddinger et al., 2009). Lastly, information on the recent importation and release of a few additional exotic ladybirds in the USA (*Eriopis connexa* Germar against aphids and three *Scymnus* spp. against the hemlock woolly adelgid, *Adelges tsugae* Annand) can be found in Van Driesche et al. (2018).

The 822 introductions of fully identified Coccinellidae comprise 212 species of 68 genera. Of these, 270 (32.8%) introductions led to a permanent establishment (79 species of 37 genera), of which 120 (14.6%; 34 species of 20

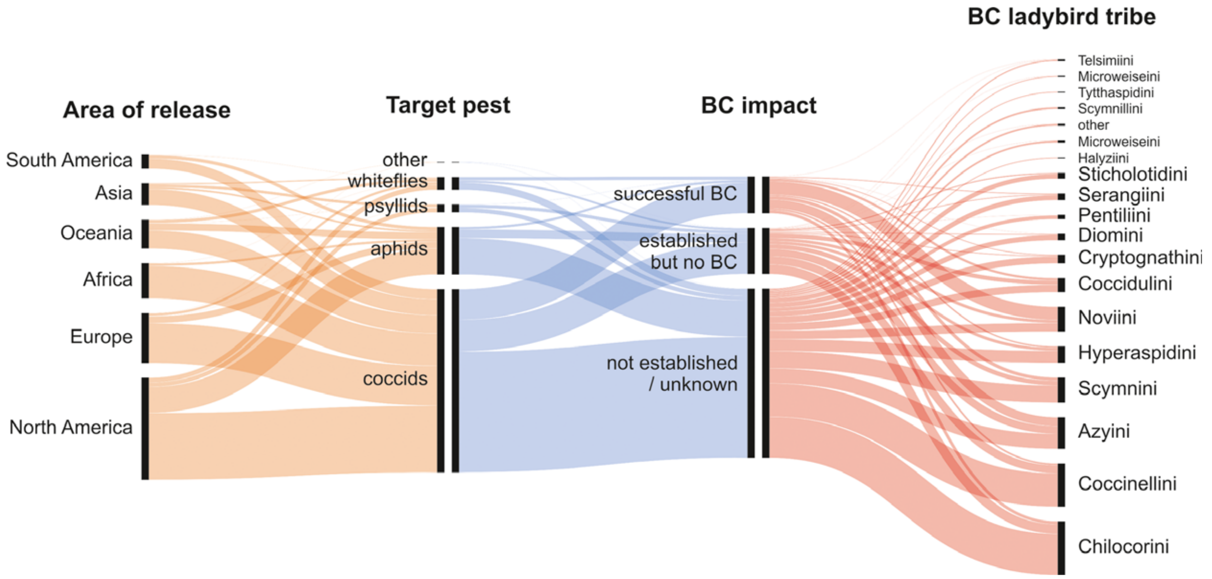

Figure 1 Flow diagram illustrating the connection between the area of release of the exotic ladybirds, the target pest group, the impact on biological control (BC) of the introduced species, and the ladybird tribe. The width of each line is proportional to the relative percentage of introduction events. One event represents an introduction of a biological control ladybird that was released in one country/area to control a target pest within a decade (details in Table S1 for the data used to create the figure). [Colour figure can be viewed at wileyonlinelibrary.com]

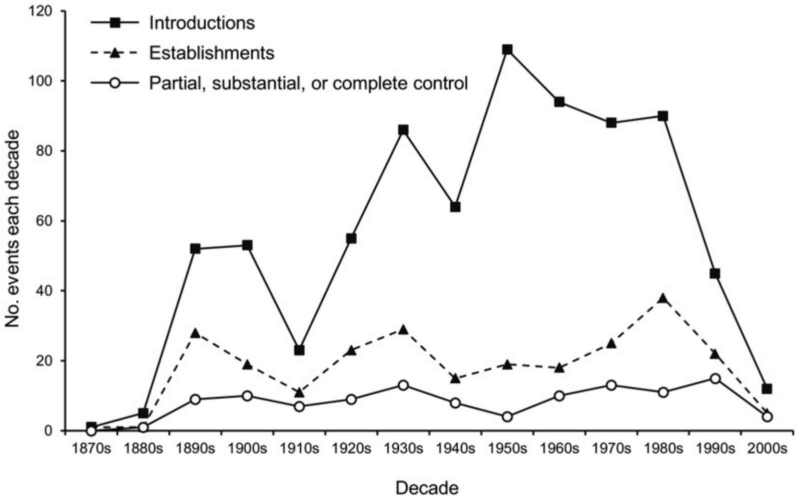

Figure 2 Number of introductions, establishments, and successes (i.e., partial, substantial, or complete control) of ladybirds released under classical biocontrol programs over time. Data from the 2000s are incomplete (see Cock et al., 2016). One introduction event is considered when a biocontrol agent was released in one country/area to control a target pest during a decade.

genera) contributed to at least partial control of the target pest. These have almost entirely been pests of agriculture and horticulture, but a few releases have been made against pests in natural habitats, e.g., *Insignorthezia insignis* (Browne) (Hemiptera: Ortheziidae) on St. Helena (Fowler, 2004), or pests of ornamental plants, e.g., *Maconellicoccus hirsutus* (Green) (Hemiptera: Pseudococcidae) in the Caribbean (Kairo et al., 2000). Ladybird introductions reached the highest peak during the 1950s and remained high until the 1990s, when they steeply decreased (Figure 2). Establishments were higher during the 1980s-2000s than during the 1950s–1970s (Fisher's Exact test: $P<0.001$; $n = 438$). Similarly, there was an increase of successful control reported (Fisher's Exact test: $P = 0.001$; $n = 438$), possibly as a consequence of the rise in the research related to the biology and ecology of BC agents (Sloggett, 2005; Cock et al., 2010). About 30% of the introductions were directed to the USA, 10% to the UK and dependent territories, followed by <2.3% for each of the other 106 countries (Table S2). About 23% of the introductions were carried out in the Pacific region, 22% in the Neartic, 12% in the Afrotropical, 12% in the West

Table 1 Ladybird introductions under classical BC programs, based on target family and herbivorous insect groups. An introduction event is considered if a BC agent was released in one country/area to control a target pest during a decade

Family	Group	No. introductions against target	No. introductions that became established (relative %)	No. introductions that contributed to partial, substantial, or complete control (relative %)
Diaspididae	Coccids	268	61 (22.8)	16 (6.0)
Pseudococcidae	Coccids	177	63 (35.6)	24 (13.6)
Aphididae	Aphids	124	30 (24.2)	7 (5.6)
Monophlebidae	Coccids	81	56 (69.1)	45 (55.6)
Aleyrodidae	Whiteflies	41	18 (43.9)	11 (26.8)
Coccidae	Coccids	32	12 (37.5)	7 (21.9)
Adelgidae	Aphids	31	6 (19.4)	1 (3.2)
Psyllidae	Psyllids	26	12 (46.2)	1 (3.8)
Ortheziidae	Coccids	16	5 (31.3)	5 (31.3)
Asterolecaniidae	Coccids	7	3 (42.9)	2 (28.6)
Eriococcidae	Coccids	2	2 (100)	1 (50.0)
Coccoidea unspecified	Coccids	15	1 (6.7)	0 (0)
Other orders		2	1 (50.0)	0 (0)
Total		822	270 (32.8)	120 (14.6)

Table 2 Ladybird species most frequently introduced (≥10×), the target family, and overview of success rates. An introduction event is considered if a BC agent was released in one country/area to control a target pest during a decade

Ladybird species	Target family	No. introductions	No. establishments (relative %)	No. partial, substantial, or complete successes reported (relative %)
Cryptolaemus montrouzieri	Coccidae, Diaspididae, Monophlebidae, Pseudococcidae	73	46 (63.0)	26 (35.6)
Rodolia cardinalis	Monophlebidae, Pseudococcidae	58	43 (74.1)	35 (60.3)
Cryptognatha nodiceps	Diaspididae	23	6 (26.1)	3 (13.0)
Rhyzobius lophanthae	Coccoidea, Diaspididae	20	11 (55.0)	4 (20.0)
Diomus hennesseyi	Pseudococcidae	17	3 (17.6)	0 (0)
Pseudoazya trinitatis	Diaspididae	17	4 (23.5)	1 (5.9)
Hippodamia convergens	Aphididae, Monophlebidae	16	5 (31.3)	4 (25.0)
Chilocorus bipustulatus	Diaspididae	15	6 (40.0)	3 (20.0)
Chilocorus nigritus	Coccoidea, Diaspididae	15	5 (33.3)	1 (6.7)
Chilocorus cacti	Asterolecaniidae, Diaspididae	13	6 (46.2)	2 (15.4)
Coccinella septempunctata	Adelgidae, Aphididae	13	4 (30.8)	0 (0)
Curinus coeruleus	Asterolecaniidae, Diaspididae, Pseudococcidae, Psyllidae	13	9 (69.2)	0 (0)
Clitostethus oculatus	Aleyrodidae	12	5 (41.7)	4 (33.3)
Halmus chalybeus	Coccidae, Coccoidea, Diaspididae, Eriococcidae, Pseudococcidae	12	3 (25)	0 (0)
Hyperaspis notata	Pseudococcidae	12	5 (41.7)	0 (0)
Chilocorus kuwanae	Adelgidae, Coccoidea, Diaspididae	11	2 (18.2)	1 (9.1)
Harmonia axyridis	Aphididae, Monophlebidae, Psyllidae	10	4 (40.0)	0 (0)
Rodolia pumila	Monophlebidae	10	7 (70.0)	5 (50.0)
Other species (8 or less releases)		462	96 (20.8)	31 (6.7)
Total		822	270 (32.8)	120 (14.6)

Paleartic, and 10% or less in each of the other eight regions (Table S3; see Greathead & Greathead, 1992, for details about the zoogeographical regions).

Relative to the most frequently released species (with 10 or more introduction events), the establishment rate was 30.8–40.0% for the aphidophagous species and 17.6–74.1% for the coccidophagous species (Tables 1 and 2). The overall rate of introductions that led to at least partial control (i.e., reduced pest status but other control means, including other BC agents, were needed; Cock et al., 2010) or better (e.g., substantial or complete control; Cock et al., 2010) was 14.6%. Nevertheless, this may be an underestimation because the control impact has not always been assessed, with 27% of the cases reported as 'result unknown' (Table S1). Compared to outcomes for the two most widely used species, *C. montrouzieri* and *R. cardinalis*, the overall rates of establishment (26.2%) and BC success (8.5%) of other ladybirds were lower (for both comparisons; Fisher's Exact test: $P<0.001$; $n = 822$). Overall, there was no correlation between the number of introduction cases of a given species and its rate of establishment (Spearman rank test: $r = 0.05$, $P = 0.84$). Conversely, the number of introductions that led to at least partial control (proportion of successful control) was positively correlated with the proportion of establishments (Spearman rank test: $r = 0.54$, $P = 0.021$; Figure 3). Successful establishments, however, varied across geographic regions. *Harmonia axyridis* established more successfully in central and northern Europe than in southern Europe. Some oceanic islands, e.g., Azores, seem to be unsuitable for *H. axyridis* (Soares et al., 2008, 2017; Ameixa et al., 2019). *Harmonia axyridis* thrives better when food resources are abundant to sustain large populations of this large species, which occurs less frequently on typical vegetation of southern Europe and small oceanic islands (Honěk et al., 2017; Soares et al., 2017).

Considering the most represented target groups (820 introductions; Table 1), establishment success was 33.9% against coccids, 43.9% against whiteflies, and 46.2% against psyllids (Fisher's Exact test: $P = 0.19$; $n = 665$).

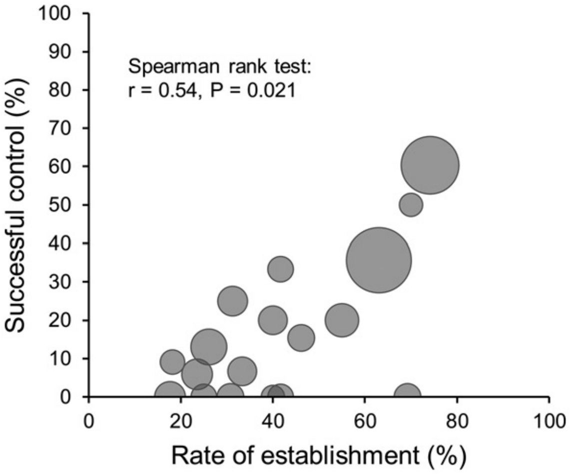

Figure 3 Correlation between establishment of the most frequently introduced (≥10×) ladybirds in classical biocontrol programs and success of control (partial, substantial, or complete). The size of the symbols is proportional to the number of introduction cases. Each case represents an introduction of a biocontrol ladybird that was released in one country/area to control a target pest within a decade period [see Table 2 for details of data used in the figure and Cock et al. (2010, 2016) for the BIOCAT database].

Establishment success against aphids (23.2%) was lower than for the other target groups (Fisher's Exact test: P = 0.004; n = 820). The rate of introductions that led to at least partial success was 16.7% against coccids and 26.8% against whiteflies, altogether higher compared to 5.2% against aphids and 3.8% against psyllids (Fisher's Exact test: P<0.001; n = 820). In particular, success in BC was higher against coccids compared to aphids (Fisher's Exact test: P<0.001; n = 753). Kindlmann & Dixon (1999) proposed the 'generation time ratio' hypothesis to explain the difference in the efficacy of aphidophagous and coccidophagous ladybirds as BC agents. Because the generation time of the aphid-eating predators is greater than that of aphids, the predator is limited in the level of control of the prey population. On the other hand, the generation times of coccidophagous ladybirds and coccids are similar, so the predator can easily follow the prey population oscillations. A comparison between phylogenetically close aphidophagous and coccidophagous ladybird species showed that the predator lifestyle mirrors that of their prey (Borges et al., 2006, 2011), as suggested by Dixon (2000).

Rodolia cardinalis is considered the most effective among the ladybirds released (Table 2) as it completely controlled *I. purchasi* in several countries and *Icerya aegyptiaca* (Douglas) (Hemiptera: Monophlebidae) in parts of Africa (Ragab, 1995; reviewed by Cock et al., 2010). The Australian *C. montrouzieri* was used for the first time in 1908 to control *Planococcus citri* (Risso) (Hemiptera: Pseudococcidae) mealybug in Italy and is considered established in almost all the countries where it was intentionally introduced against mealybugs (Roy & Migeon, 2010; Kairo et al., 2013). *Clitostethus oculatus* (Blatchley) specifically preys upon aleyrodids (Hodek & Evans, 2012) and significantly contributed to the suppression of *Aleurodicus dispersus* Russell (Hemiptera: Aleyrodidae) in American Samoa, Hawaii (USA), Guam, and Fiji (Table S1), although it is reported that substantial control was enhanced in combination with *Encarsia* spp. parasitoids (Tables 2 and 3; Michaud, 2012). *Rhyzobius lophanthae* (Blaisdell) originated from Australia as did most of its target prey species (reviewed by Roy & Migeon, 2010). After introduction into a new area, *R. lophanthae* established well to become present now in several countries around the world (Roy & Migeon, 2010; Pellizzari & Porcelli, 2014; Table S1). Although initial releases were not or only partially successful, the ladybird significantly contributed to the suppression of *Diaspidiotus perniciosus* (Comstock) and *Pseudaulacaspis pentagona* (Targioni Tozzetti) in Europe (Gerber & Schaffner, 2016), and provided complete control of *Aulacaspis tegalensis* (Zehntner) on sugarcane in Tanzania and substantial control of *Aonidiella aurantii* (Maskell) (all Hemiptera: Diaspididae) on citrus orchards in South Africa (Table S1). The introduction of *Rodolia pumila* Weise in the Pacific Islands adequately contributed to control of *I. aegyptiaca* on fruit trees (reviewed by Clausen, 1978).

None of the classical BC involving other ladybird species – i.e., *H. axyridis*, *Coccinella septempunctata* L., *Curinus coeruleus* Mulsant, and *Hyperaspis notata* Mulsant – were reported as successful, albeit these species exhibited good establishment rates. *Curinus coeruleus* originated from South America and was released during the 1980s-1990s in several countries against *Heteropsylla cubana* Crawford (Hemiptera: Psyllidae). In spite of its high establishment rate, the ladybird failed to control the psyllid (Table S1). *Curinus coeruleus* was also introduced in Florida (USA) to control *Toxoptera citricida* (Kirkaldy) (Hemiptera: Aphididae) but without remarkable control; some populations of the ladybird, however, successfully contributed to suppression of this aphid in Hawaii (Michaud, 2012). The low dispersal capability of this ladybird may explain its failure in citrus groves in Florida (Michaud, 2002).

Although classical BC towards coccids was overall quite successful, the results were highly variable depending on the target pest species (Table 3). *Aspidiotus destructor* (Signoret) (Hemiptera: Diaspididae) was the target of the largest proportion of classical BC programs (Table 3). The

Table 3 Number of introductions of ladybirds under classical BC programs by insect pests targeted (≥10×). An introduction event is considered if a BC agent was released in one country/area to control a target pest during a decade

Target species	No. introductions against target	No. introductions that became established (relative %)	No. introductions that contributed to partial, substantial, or complete control (relative %)
Aspidiotus destructor	80	21 (26.3)	6 (7.5)
Icerya purchasi	53	37 (69.8)	33 (62.3)
Carulaspis carueli	35	3 (8.6)	0 (0)
Aonidiella aurantii	34	7 (20.6)	2 (5.9)
Phenacoccus manihoti	30	9 (30.0)	0 (0)
Planococcus citri	28	18 (64.3)	12 (42.9)
Adelges piceae	24	4 (16.7)	1 (4.2)
Maconellicoccus hirsutus	23	11 (47.8)	9 (39.1)
Aleurodicus dispersus	17	10 (58.8)	8 (47.1)
Icerya aegyptiaca	17	10 (58.8)	7 (41.2)
Diaspidiotus perniciosus	14	3 (21.4)	0 (0)
Saissetia oleae	14	5 (35.7)	2 (14.3)
Heteropsylla cubana	13	9 (69.2)	0 (0)
Aulacaspis tegalensis	11	2 (18.2)	1 (9.1)
Pseudaulacaspis pentagona	11	2 (18.2)	1 (9.1)
Diuraphis noxia	10	4 (40.0)	0 (0)
Dysmicoccus brevipes	10	2 (20.0)	0 (0)
Parlatoria blanchardii	10	3 (30.0)	3 (30.0)
Other target species	219	72 (32.9)	28 (12.8)
Target not specified to species level	169	38 (22.5)	7 (4.1)
Total	822	270 (32.8)	120 (14.6)

species originated in the Pacific islands and is currently distributed worldwide (Burger & Ulenberg, 1990). The ladybird *Cryptognatha nodiceps* Marshall completely controlled this pest in Fiji and São Tomé and Príncipe and was more successful than parasitoids (Spennemann, 2020; Table S1). Several ladybirds were introduced in Africa to control the cassava mealybug, *Phenococcus manihoti* Matile-Ferrero (Hemiptera: Pseudococcidae). In spite of the reasonable establishment rate, none of the species used were effective, e.g., *Diomus hennesseyi* Fürsch and *H. notata* (Table 3).

Use of ladybirds in augmentative biological control

Augmentative release of ladybirds can provide a within-season reduction of pest density. To date, at least 35 species (reviewed by Cock et al., 2010; van Lenteren, 2012; van Lenteren et al., 2018) of exotic or native species have been reared by suppliers for seasonal field releases. Intriguingly, only two of them, *H. axyridis* and *C. montrouzieri*, were sold in large numbers globally. Concerning the European releases, nine out of 23 species were of exotic origin; most important among them were *H. axyridis* and *Delphastus pusillus* Leconte (thousands to millions of individuals sold per week). Most of the exotic species provided a substantial level of seasonal control; exceptionally, *H. axyridis* was recorded to provide complete control of some aphid species (Cock et al., 2010). In spite of the positive impact of *H. axyridis* on aphid control (Koch & Costamagna, 2017), the commercialization of the ladybird by biocontrol suppliers has been interrupted due to the awareness of potential non-target effects on native predators (reviewed by Roy et al., 2016). *Hippodamia convergens* Guerin-Meneville was released multiple times in France and Italy (Gerber & Schaffner, 2016; Soares et al., 2018). However, this species did not permanently establish, as confirmed by its absence in the European checklist (de Jong et al., 2014) and by the fact that it has not been detected in recent ladybird survey monitoring programs (Honěk et al., 2016; Viglášová et al., 2017).

A limitation of using adult ladybirds for augmentative BC is that they tend to disperse once released in high number. For example, overwintering individuals of *H. convergens* were commercially available in the USA for farmers, but once released in the field they suddenly disappeared to the surrounding habitats (reviewed by Obrycki et al., 2009). Research studies have been conducted to improve the residence period of ladybird adults in the crop, thereby increasing their efficacy. For instance, naturally obtained flightless strains of *H. axyridis* performed better in suppressing *Aphis gossypii* Glover, *Myzus persicae* Sulzer, and *Aulacorthum solani* (Kaltenbach) (all Hemiptera: Aphididae) compared to winged strains (Lommen et al., 2008; Seko et al., 2008). Other novel approaches may include, for instance, the use of semiochemical lures for attracting and maintaining the ladybirds in crop (reviewed by Kaplan, 2012) and selective breeding of flightless strains (Lommen et al., 2017, 2019).

Case study 1: Introductions of *Coccinella septempunctata* and *Harmonia axyridis* in the USA

Introduction, establishment, efficacy

Coccinella septempunctata and *H. axyridis* are very abundant, widespread species that attack multiple species of pest aphids in diverse field and orchard crops, often occurring as the dominant ladybirds in these crops in their native range (Hodek et al., 2012). Consequently, these species were intentionally released on numerous occasions across the USA during the 20th century (Gordon, 1985; Schaefer et al., 1987; Koch, 2003; Table S1), with multiple species of aphids considered as potential pests for which these predators might contribute to BC. Repeatedly, initial introductions of individuals of these two species imported from the Old World seemingly failed to result in establishment (see above 'Use of ladybirds in classical biological control'; Table S1). In the case of *C. septempunctata*, these first attempts were followed during the 1970s with vigorous redistribution across the USA of more than half a million adults, as collected from naturally occurring populations found in 1973 in the northeastern USA (Angalet et al., 1979). Similar naturally occurring source populations were discovered for *H. axyridis* in the southeastern USA in 1988 (Tedders & Schaefer, 1994) and in the northwestern USA in 1994 (LaMana & Miller, 1996). These populations, along with an additional population of *C. septempunctata* in Quebec, Canada, first detected in 1973 (Larochelle & Larivière, 1979), may well have resulted unintentionally from transoceanic shipping (Day et al., 1994). With the arrival of the Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), in the western USA in the 1980s, *C. septempunctata* was reared in the laboratory by the USDA and shipped in large numbers to western states to combat the newly establishing pest (Gordon & Vandenberg, 1991; Prokrym et al., 1998). Both *C. septempunctata* and *H. axyridis* also proved capable of strong, rapid dispersal over large distances on their own (Turnock et al., 2003; Hemptinne et al., 2012). The net result is that by the early 21st century, *C. septempunctata* and *H. axyridis* had become two of the most common and most widely distributed species of Coccinellidae throughout the USA.

As in Europe, *C. septempunctata* is especially abundant in the USA in agricultural habitats (e.g., Evans, 2000, 2017; Finlayson et al., 2008; Hesler & Kieckhefer, 2008). So too is *H. axyridis*, which in addition occurs in the Nearctic as well as the Palearctic in large numbers on trees, including in urban settings (LaMana & Miller, 1996; Honěk et al., 2016). The potential impact of these two introduced predators in reducing numbers of pest aphids has received considerable attention (Lucas et al., 2007; Kindlmann et al., 2015; Koch & Costamagna, 2017). The two species, *C. septempunctata* and *H. axyridis*, often occur together in the USA alongside at least several native species of ladybirds attacking an aphid population, such that it can be challenging to tease out the contributions of individual predator species to observed reductions in prey numbers. Although *C. septempunctata* often occurs as the most abundant species in these ladybird assemblages, the question remains as to whether its impact simply replaces rather than adds to the impact of other species that it may have displaced (Elliott et al., 1996). The establishment of *C. septempunctata* in large numbers in the spring in alfalfa fields of northern Utah in the 1990s was associated with a decline in numbers of pea aphid, *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae) (Evans, 2004). In contrast, however, similar establishment of *C. septempunctata* in potato fields of northern Maine in the 1980s was not associated with subsequent decline in aphid numbers. Interestingly, a clear decline in aphid numbers was detected subsequently with the displacement of *C. septempunctata* by *H. axyridis* in the 1990s as the dominant ladybird species in these potato fields (Alyokhin & Sewell, 2004). Similarly, displacement of *C. septempunctata* by *H. axyridis* in apple orchards of eastern West Virginia around the same time was associated with decline in numbers of the pest, *Aphis spiraecola* Patch (Hemiptera: Aphididae) (Brown & Miller, 1998). Most recently, field caging experiments and season-long sampling to address the spatial scale of entire fields have implicated *H. axyridis*, but not *C. septempunctata*, as contributing significantly to prevention and suppression of outbreaks of the soybean aphid, *Aphis glycines* Matsumura, following the appearance of this exotic pest in Minnesota and neighbouring states (Bannerman et al., 2018).

Ecological impact on native insect communities

As *C. septempunctata* rapidly became well-established throughout the USA, concern was expressed widely that its abundance could result in substantial reductions of native ladybirds (Schaefer et al., 1987; Ehler, 1990; Ruesink et al., 1995; Obrycki et al., 2000). Similar concerns were raised with the subsequent establishment of *H. axyridis*, both in the USA and across the globe (Koch & Galvan, 2008; Roy et al., 2016). Indeed, substantial declines in numbers of native North American ladybirds have been recorded in diverse habitats, albeit mainly agricultural and urban, following the establishment of *C. septempunctata* and *H. axyridis* (e.g., Elliott et al., 1996; Ellis et al., 1999; Turnock et al., 2003; Alyokhin & Sewell, 2004; Harmon et al., 2007). Although there is little consensus yet concerning the relative importance of multiple causes (Evans et al., 2011; Bahlai et al., 2015), one prominent mechanism proposed for such adverse effect is intraguild predation (IGP), especially as involving *H. axyridis* (Cottrell & Yeargan, 1998; Snyder et al., 2004; Yasuda et al., 2004). Alternatively, or in addition, it has been proposed especially for *C. septempunctata* that indirect (scramble or exploitative) competition for shared prey (aphids) might favour the introduced species over native species. In northern Utah, for example, numbers of adults of native ladybirds have declined with numbers of pea aphids in spring alfalfa fields following the arrival of *C. septempunctata*, which colonizes these fields early in the growing season when aphid numbers are still low. Numbers of native ladybirds can be restored in these fields, however, by experimentally creating local outbreaks of aphids (Evans, 2004). This suggests that these native species may persist regionally but no longer colonize spring alfalfa fields in large numbers as aphid densities are kept in check in these fields by *C. septempunctata*. Mobile native ladybirds, which disperse as adults frequently and widely across landscapes in tracking ephemeral populations of their prey, instead may persist by colonizing and occupying other habitats (Evans, 2017). During the summer, when *C. septempunctata* numbers often are low and aphid populations may reach high densities in alfalfa fields of northern Utah, native ladybirds at times outnumber the introduced species.

The impact of *C. septempunctata* and *H. axyridis* on local communities of insects in alfalfa fields in the USA likely extends well beyond intraguild interactions among species of ladybirds. Aphid consumption by *C. septempunctata*, for example, may undercut BC of diverse insect pests other than aphids, by reducing the availability of a key food, aphid honeydew, for foraging parasitoid adults (e.g., Evans & England, 1996; Rand & Lundgren, 2018). The ability of *C. septempunctata* and *H. axyridis* to reach high populations in consuming aphids within agricultural habitats may also have implications for insect populations and communities beyond these habitats. Spillover of *C. septempunctata*, *H. axyridis*, and other ladybird species maturing within agricultural fields and dispersing thereafter as adults into adjacent, non-agricultural habitats, reduced aphid numbers on an indigenous thistle in native grassland (Rand & Louda, 2006). Similarly, field observations and modelling suggest high numbers of *C. septempunctata* and *H. axyridis*, which feed readily on many insect prey in addition to aphids (Koch, 2003; Evans, 2009), could further threaten small populations of endangered lycaenid and monarch butterflies in non-agricultural habitats (Horn, 1991; Koch, 2003; Schellhorn et al., 2005). Although each of these possible impacts of *C. septempunctata* and *H. axyridis* on local insect communities remains to be evaluated more fully, they illustrate the range of ecological implications likely associated with the introduction of these generalist predators for BC of aphids.

Case study 2: Biological control of aphids by exotic ladybirds in Canada

Introduction, establishment, efficacy

In eastern Canada, the ladybird assemblage has been greatly modified by the arrival of four exotic species. First, the 14-spotted ladybird, *Propylea quatuordecimpunctata* (L.), arrived probably in 1968 (Day et al., 1994), the 7-spotted ladybird, *C. septempunctata*, in 1973 (Larochelle & Larivière, 1979), *Hippodamia variegata* (Goeze) in 1984 (Gordon, 1985), and finally *H. axyridis* in 1994 (Coderre et al., 1995). In western Canada, *C. septempunctata* was found in Manitoba in 1988, in Saskatchewan in 1989, and in British Columbia and Alberta in 1990 (Turnock et al., 2003; Acorn, 2007; Marriott et al., 2009). *Coccinella septempunctata* became the dominant species in the initial years after its arrival in crops and natural areas, but later became second in abundance to the native *Hippodamia tredecimpunctata* (L.) (Turnock et al., 2003). *Harmonia axyridis* was found in British Columbia in 1995, in Manitoba in 2000, and is currently present in Alberta (Turnock et al., 2003; Acorn, 2007; Marriott et al., 2009). In Manitoba, a 2-year survey using bidirectional Malaise traps located in the borders of soybean fields, found that currently *C. septempunctata* is the dominant species (59.8%), followed by *H. tredecimpunctata* (23.6%), *H. axyridis* (13.8%), and *H. variegata* (1.2%), suggesting the dominance of exotic species in agricultural landscapes (Samaranayake & Costamagna, 2019).

In soybean fields, for instance, *H. axyridis* and *C. septempunctata* represented 58.3–61.5% and 5.0–16.9%, respectively, of the total ladybirds observed between 2010 and 2012 (Lucas et al., 2007; J-E Maisonhaute, G Labrie & E Lucas, unpubl.). Over the 3 years of the study, exotic species (including *H. axyridis*, *C. septempunctata*, and *P. quatuordecimpunctata*) accounted for 86.0–92.6% of the total ladybird abundance. The increase in areas dedicated to soybean cultivation may have favoured the expansion of the distribution of *H. axyridis*. Oscillations of the populations of the soybean aphid in Eastern Canada have decreased gradually since 2005, and a common hypothesis is that the changes in the ladybird assemblage, more specifically the arrival of *H. axyridis*, may have improved the level of control of the aphid (Maisonhaute et al., 2017). In Manitoba, suppression of soybean aphid was related to the movement of aphidophagous predators from field borders, including ladybird assemblages dominated by *C. septempuncata* (38.8%), *H. axyridis* (35.8%), and *H. tredecimpunctata* (22.4%) (Samaranayake & Costamagna, 2018).

In urban areas, the dominance of exotic ladybirds is even more obvious. In the urban ecosystem of Montreal island, ladybird communities observed on wild plants were composed with exotic ladybirds accounting for 91% (2012) and 94% (2013) of individuals (F Dumont, L Fraser & E Lucas, unpubl.). *Harmonia axyridis* (36%), *H. variegata* (30%), *C. septempunctata* (17%), and *P. quatuordecimpunctata* (8%) were among the most abundant ladybird species, whereas native ladybirds were overall negligible (F Dumont, L Fraser & E Lucas, unpubl.).

Exotic ladybirds seem to dominate also undisturbed areas (Bélanger & Lucas, 2011). For instance, in a wild meadow ecosystem, *H. axyridis* alone accounted for 69% of the ladybird community, with 84% of the community that was formed by exotic ladybirds (Bélanger & Lucas, 2011).

The population dynamics of the various ladybird species are relatively similar, except for *H. axyridis*. This ladybird species does not survive outside in Canada during the winter; its behaviour to enter in human houses at the end of the fall allows a proportion of the population to reach the next spring (Labrie et al., 2008). Thus, the northern distribution of the ladybird is dependent on the presence and proximity of human houses, whereas winter survival and population dynamics of the other species usually are more influenced by melting-freezing events at the end of the winter.

Ecological impact on native communities of aphid predators

The dominance of exotic over native ladybirds in agricultural, natural, and urban environments suggests that native ladybirds are exploiting similar ecological niches. Whereas some species, such as *H. tredecimpunctata*, seem to be drastically affected by the establishment of the exotic species, others, such as *Coleomegilla maculata lengi* Timberlake and *H. convergens*, maintain their relative abundance in the ladybird assemblages (Lucas et al., 2007; Bélanger & Lucas, 2011). The adaptability of these native ladybirds may be based on a significant change in their diet and/or on some level of habitat preference. For example, *C. maculata* can complete its entire life cycle and reproduction on a plant diet only (including pollen) (Michaud & Jyoti, 2008). Physiological (e.g., body size reduction) and genetic (underlying food preference) changes may have occurred since the invasions of exotic ladybirds. Thus, the role of these indigenous ladybirds in biological control may have changed. Increased pollen exploitation may favour encounters between *C. maculata* ladybirds and prey that also use floral resources (Aubry et al., 2017). Finally, *C. maculata* was highly influenced by the abundance of uncultivated areas (e.g., woods, field margins, uncultivated fields), compared to *H. axyridis* (Maisonhaute & Lucas, 2011).

The replacement of indigenous ladybirds with exotic species may have implications for the role of other aphidophagous predators, like predatory bugs, in BC. Takizawa & Snyder (2012) reported asymmetric IGP favouring *H. axyridis* in its interaction with *Nabis* spp. and *Geocoris* spp. bugs. In contrast, IGP between the bugs and the exotic ladybird *C. septumpunctata* was more symmetric. Aquilino et al. (2005) observed an increase in aphid predation in a system including both the native *C. maculata* ladybird and *Nabis* spp. compared to a single predator system. Cardinale et al. (2003) reported that this synergistic effect between ladybirds and predatory bugs is observable also in a system that includes the exotic *H. axyridis*. As Nabidae also play a role in regulating tarnished plant bugs and leafhoppers – prey rarely exploited by ladybirds (Lattin, 1989) – we can speculate that a reduction of Nabidae populations, due to *H. axyridis* invasion, may favour outbreaks of these pests.

Globally, the successive invasion waves in Canada have greatly modified the assemblage of predators. However, no drastic change has been observed concerning pest natural control in agricultural, natural, or urban areas. One study in Quebec demonstrated that the functional diversity of natural enemies (based on seven specific groups) was the only natural enemy variable positively associated with an increased control (negative effect on the cumulative number of aphids per day) (Maisonhaute et al., 2017). Our hypothesis is that some ecological redundancy within guilds of natural enemies may prevent drastic changes. And finally, we desperately need long-term field surveys of pest abundance and ladybird assemblages for many agricultural or natural ecosystems.

Case study 3: Biological control by exotic ladybirds in Chile

Introduction, establishment, efficacy

Chile has 119 ladybird species, of which approx. 13% are exotic (González, 2006). Most species are concentrated in the central part of the country, where most agriculture is developed, and therefore their role in pest control may be crucial (Alaniz et al., 2018). For example, in alfalfa fields in this area ladybirds account for approximately 50% of aphid predation (Ximenez-Embun et al., 2014).

Fifteen species have been introduced to the country as part of classical BC projects, as early as 1902; only seven of them established successfully (Table S1). None of these introductions, with the exception of *H. convergens*, came directly from their native geographic range, and most of them came from the USA and South Africa, regions with similar crops to central Chile and with a Mediterranean climate (Table S1). This means that, in general, Chile relies on previously successful BC programs in other regions of the world, possibly explaining the overall good establishment rate and BC success in this country. Of those introduced, *C. montrouzieri* and *R. lophanthae* are now commercialized by BC companies.

Presently, *H. variegata* is among the most common species in Chile, reaching very high abundances in crops like alfalfa, cereals, and fruit crops (Grez et al., 2013). This is surprising because in other countries where it has been introduced, such as in the USA, it has only attained very low numbers (Gardiner et al., 2009). In contrast, *C. septempunctata*, which has been very successful and even invasive in North America, did not establish in Chile (Rojas, 2005; Gardiner et al., 2009; Table S1). The other exotic species of ladybirds present in Chile, some of them with very abundant populations, arrived accidentally, e.g., *H. axyridis*, *Harmonia quadripunctata* (Pontoppidan), *Olla v-nigrum* (Mulsant), *Parastethorus histrio* Chauzeau, and *Scymnus loewii* Mulsant. A special case is *H. axyridis*, which was first unsuccessfully introduced from France in 1998 for the BC of pest insects in greenhouses. Later, feral populations were recorded, and genetic analyses demonstrated that they originated in eastern North America (Grez et al., 2010; Lombaert et al., 2014). Notably, these introduced populations independently originated from those populations that established in Argentina or Brazil (Lombaert et al., 2014). Over the years, *H. axyridis* spread widely and became dominant in Chile, as well as in other locations in South America (Mirande et al., 2015; Hiller & Haelewaters, 2019). The ladybird is especially abundant in alfalfa fields and urban settings, with negative effects on the diversity and abundance of resident ladybirds, particularly natives (Mirande et al., 2015; Grez et al., 2016).

Harmonia axyridis could be regarded as a good BC agent because it has much higher voracity than other ladybird species common in alfalfa fields in Central Chile, consuming twice as many aphids as *H. variegata* and the native *Eriopis chilensis* Hofmann (Zaviezo et al., 2019). Nevertheless, *H. axyridis* is only present in this crop during a short period of time at the beginning of spring, whereas the other two remain for a longer period, suggesting that maintaining a higher diversity of ladybirds, including native species, would result in enhanced BC. In fact, in alfalfa fields, better BC of aphids is associated with higher abundance of native ladybirds, but not with exotics (Grez et al., 2014).

Effect of landscape on ladybird abundance and biological control

Like other natural enemies, during the growing season ladybirds forage within several habitats (Evans, 2003). Therefore their establishment and BC success in a given crop may depend on local habitat and landscape characteristics at different spatial scales, and this may vary between exotic and native species (Gardiner et al., 2009; Werling et al., 2011; Grez et al., 2013; Raymond et al., 2015). Regarding local habitat characteristics, in Central Chile exotic species are more abundant and specialized in human-disturbed habitats, especially in intensively managed crops, compared with native species. One exception is the exotic *Clitostethus arcuatus* (Rossi), which is more abundant in the native sclerophyllous Matorral, although it is also abundant in urban greenspaces where whiteflies, their prey, are abundant (Grez et al., 2013, 2019). Because of this differential habitat use, the abundance of exotic and native ladybirds and their efficacy as BC agents in a given crop may be modulated by the composition and configuration of the landscape surrounding a given crop (Gardiner et al., 2009; Werling et al., 2011; Woltz et al., 2012; Zhao et al., 2013). In alfalfa fields in Chile, the diversity and abundance of ladybirds increase with the compositional and configurational heterogeneity of landscapes. Additionally, the abundance of both native and exotic ladybirds decrease as the area covered by cultivated lands, such as annual crops and orchards, increases (Grez et al., 2014).

Ladybirds are not only important BC agents of pests in crops but also in other anthropogenic habitats, including parks and gardens. Rich communities of native and exotic species have been found in these green spaces. Nevertheless, these communities vary depending on the urbanization of the surrounding landscapes (Gardiner et al., 2014; Egerer et al., 2017, 2018). For instance, in green spaces within a rural-to-urban gradient in Santiago Metropolitan Region, total richness and abundance of ladybirds are negatively affected by urbanization, but lesser so for exotics than for natives. Even when total exotic species abundance does not respond to landscape urbanization, *C. arcuatus* is more abundant in green spaces within more urbanized landscapes, presumably because its prey is very abundant in ornamental trees in cities. Contrary to *C. arcuatus*, fungivorous and aphidophagous ladybirds are negatively affected by urbanization (Grez et al., 2019). Therefore, in these anthropogenic landscapes, urbanization filters ladybird composition and functional groups, and possibly the BC service they provide in urban and rural environments.

Case study 4: Introduction of exotic species in Europe and the case of *Harmonia axyridis*

Introduction, establishment, dispersal

The use of exotic ladybirds for classical and augmentative BC in Europe has resulted in several examples of safe, sustainable, and successful pest control. Five exotic species are listed by EPPO as successful classical biolcontrol agents. Concerning augmentative BC, EPPO lists eight exotic ladybird species to Europe. These species have been used for at least 5 years in five EPPO countries and have shown no negative environmental effects (EPPO, 2019). However, the use of generalist predators, as many ladybird species are, has slowed down markedly within the last 2 decades (van Lenteren, 2012; Hajek et al., 2016). This is largely due to the national regulations that require risk assessments for agents to be introduced (Hajek et al., 2016; Mason et al., 2017). Risk assessments consider whether the agent is able to establish (i.e., the temporal scale of potential effects) and its dispersal capacity (i.e., the spatial scale of effects), as well as direct and indirect effects that might result from the release, in particular the extent to which non-target organisms might be affected (Bigler et al., 2006; EPPO, 2018; Collatz et al., 2021).

Harmonia axyridis was first experimentally released in the 1990s in central and southern Europe to control aphids, e.g., *Macrosiphon rosae* L. and *Phorodon humuli* (Schrank) (Hemiptera: Aphididae) in France (Ferran et al., 1996; Trouve et al., 1997), *A. gossypii* in Italy (Bazzocchi et al., 2004), and various species in citrus orchards and maize fields in Portugal (Algarve and Azores) (Soares et al., 2018). From 1994 it was commercially available in several countries including France, The Netherlands, and Belgium, against a variety of aphids and scales (van Lenteren et al., 2008; Poutsma et al., 2008). In contrast to Switzerland, most of these countries at that time did not have a regulation requiring risk assessment. Although in Switzerland a license for the release of *H. axyridis* was refused, the species was commercially sold for more than a year (van Lenteren et al., 2008; Franz Bigler, pers. comm.). During the first years of release no persistent populations were observed, but within a few years *H. axyridis* had established in most European countries, including countries where it was not released such as the UK in 2003 and Norway in 2006 (Roy et al., 2016). Microsatellite analyses have revealed that the invasive *H. axyridis* in Europe today stems from a North American population, accidentally introduced into Belgium, that cross-bred with individuals present locally and in other locations in Europe (Lombaert et al., 2010; Turgeon et al., 2011; Brown et al., 2011b). It is clear that humans mediated this long-range dispersal. Additionally, *H. axyridis* is a strong flyer. Using a citizen science approach, Brown et al. (2008) tracked the rate of dispersal at 58 km per year north and 144.5 km per year westwards. In aphidophagous ladybirds, body size, as tied to both reproductive potential and speed of movement, is a good predictor of potential dispersal ability (Hemptinne et al., 2012). In Europe, potential dispersal ability of *H. axyridis* is significantly higher than that of native species or the closely related exotic *Harmonia conformis* (Boisduval) and *H. convergens* (Soares et al., 2018).

Environmental risks of *Harmonia axyridis* establishment

Besides feeding on non-target organisms, *H. axyridis* competes with native aphidophagous ladybird species by exploiting their food resources, for instance through interference competition (Soares & Serpa, 2007). In absence of aphids, *H. axyridis* is able to sustain itself on prey- and plant-derived alternative food sources, which might give it a competitive advantage over those species that largely rely on aphids for survival and reproduction (Berkvens et al., 2010; Wolf et al., 2018). Furthermore, it has been hypothesized that IGP by *H. axyridis* is one of the current causes of the decline of native ladybirds in Central Europe (Pell et al., 2008). In contest with European native species, *H. axyridis* is often superior leading to an asymmetric effect, for example on *Aphidecta obliterata* (L.) and *Adalia bipunctata* (L.), as well as many other native species (reviewed by Roy et al., 2016). Also, in the introduced areas, *H. axyridis* might benefit from escaping attacks of natural enemies, such as predators and parasites (Comont et al., 2014; Ceryngier et al., 2018).

Feeding or competing with non-target organisms does not necessarily mean that long-lasting, measurable population-scale effects are observable in non-targets (Collatz et al., 2021). Although it is often difficult to determine the strength of the relationship that would lead to considerable effects, less than 10% short-term population suppression is considered to be of minor concern, whereas more than 40% short-term population suppression or more than 10% permanent suppression of the population is deemed critical (van Lenteren et al., 2003). Although some studies have reported the decline of local populations with the arrival of *H. axyridis* (see case study 5 below), establishing a causal link to the interaction with *H. axyridis* in the field remains difficult. A recent study by Kenis et al. (2017a) took a different approach and estimated the risk of *H. axyridis* for 30 native European ladybird species. Based on the data on the likelihood of encounters in the field, competition for food, and IGP, the study concluded that *A.*

bipunctata, *Adalia decempunctata* (L.), *Calvia decemguttata* (L.), and *Oenopia conglobata* (L.) are at greatest risk by *H. axyridis* in Europe.

Case study 5: Field evaluation of non-target effects of *Harmonia axyridis* in Europe

Field evaluation of non-target effects

In Europe, the ecological impact of *H. axyridis* in open field settings has received much more attention than pest suppression efficacy (Roy et al., 2016; but see Viglášová et al., 2017). Several field studies in Europe, briefly reviewed below, demonstrate that IGP and exploitative competition may occur in aphidophagous communities. Those studies sampled *H. axyridis* co-occurring with other aphidophagous species over 1- to 6-month periods between 2008 and 2011 and were delimited by well-defined habitat patches of *Tilia* spp., largely in urban areas. Hautier et al. (2011) used gas chromatography-mass spectrometry to screen *H. axyridis* third and fourth instars collected from *Tilia* spp. in 20 parks in Brussels for native ladybird alkaloids. Intraguild predation was detected in 20.5% of *H. axyridis* larvae, with the largest proportion (17.6%) screening positive for adaline, signalling predation of *Adalia* spp. Thomas et al. (2013) employed DNA gut-content analysis to determine rates of IGP in local ladybird populations at four sites dominated by *Tilia* × *europaea* L. (Tiliaceae) in East Anglia, UK, sampling between late-June and early-July over 3 years. Overall, 7.7% of *H. axyridis* larvae tested positive for *A. bipunctata* DNA and 4.5% for *A. decempunctata*. Specifically, the rate of IGP by *H. axyridis* against *A. bipunctata* increased from 3.7% in 2008 to 11.4% in 2010. In northern Italy, Rondoni et al. (2015) found a lower frequency of IGP on *A. bipunctata*, whereby DNA was detected in 1.5% of fourth-instar *H. axyridis*. In comparison, a higher frequency (5%) of *H. axyridis* larvae tested positive for *O. conglobata*. Although the lower IGP level on *A. bipunctata* compared to previous studies may in part be due to the target DNA amplicon sizes (Rondoni et al., 2015), it also suggests that in some local populations direct impacts on non-targets through IGP may be negligible. Interestingly, the presence of *Eucallipterus tiliae* L. (Hemiptera: Aphididae) DNA was detected in 73% of the collected larvae.

Attempting to unveil the extent of resource sharing between *H. axyridis* and *Anthocoris nemoralis* Fabricius (Heteroptera: Anthocoridae), Howe et al. (2016) determined *E. tiliae* predation in five urban parks in Copenhagen, Denmark, from May to October. Overall, aphid DNA was detected in 54.8% of *H. axyridis* larvae and 45.9% of adults, whereas 63.8% of adult *A. nemoralis* screened positive for aphid DNA. In stark contrast, the frequency of IGP on *A. nemoralis* was 2.7% for larvae and 3.4% for adults. Here, it was hypothesized that the high density of *H. axyridis* larvae negatively interfered with aphid predation by *A. nemoralis*, suggesting the possibility of indirect competition by *H. axyridis*. Finally, covering the largest geographic scale, Brown et al. (2015) collected *H. axyridis* larvae from 10 sites in five countries (UK, France, Germany, Slovakia, and Czech Republic), largely from *T.* × *europaea* (eight sites). Using DNA gut-content analysis, this study revealed a low IGP rate on *A. bipunctata* (2.8% of sampled *H. axyridis*) across countries, 9.6% tested positive for *A. decempunctata*, whereas 2.8% of larvae screened positive for *Episyrphus balteatus* (De Geer) (Diptera: Syrphidae) DNA; no *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) DNA was detected. Albeit, secondary predation or scavenging events cannot be distinguished from IGP and could contribute to false positives (e.g., Aebi et al., 2011). Even so, these studies clearly demonstrate the potential for direct deleterious effects (e.g., IGP) and indirect effects (e.g., exploitative competition) by *H. axyridis* on non-target natural enemies co-occurring under field conditions. However, studies have focussed on preferred habitats of *H. axyridis*, namely arboreal settings, which in its invasive European range are often in urban areas (Adriaens et al., 2008; Purse et al., 2015). Trophic studies conducted in other habitat types exploited by *H. axyridis* and/or across multiple years would be valuable in order to validate the extent of non-target impacts beyond studied systems (van Lenteren et al., 2006). Thus, determining the potential direct and indirect non-target effects of *H. axyridis* on native insect populations over larger spatial and temporal scales, and the magnitude of potential impacts, is somewhat more difficult.

Trends of ladybird populations before and after the arrival of *Harmonia axyridis*

Honěk et al. (2016, 2019) followed ladybird populations over large spatial scales of 50-77 km^2 in the Czech Republic. Sampling in arboreal habitats in May and June during three distinct intervals between 1976 and 2014, Honěk et al. (2016) traced populations of 21 native species. Declines of *A. bipunctata*, *Coccinella quinquepunctata* L., and *P. quatuordecimpunctata* were revealed, but populations of these species were already in decline prior to the invasion by *H. axyridis* in 2006/2007. Declines of *A. decempunctata* and *Calvia quatuordecimguttata* (L.) occurred after the arrival of *H. axyridis* in the Czech Republic, yet over the entire period their populations remained stable. Honěk et al. (2019) compared ladybird densities in trees, herbaceous plants and cereal habitats between 2010 and 2016. *Harmonia axyridis* dominated tree habitats where adult abundances were 7.5 × higher than on herbaceous plants and 89 × higher than on cereals; conversely, native ladybirds were dominant in herbaceous and cereal habitats. Comparison with data of native species sampled in similar habitats from 1976 to 1986 uncovered overall declines, with an average abundance 3.1 × greater than in 2010-2016. Declines among native populations were most pronounced in tree habitats, highlighting the overall negative effect of *H. axyridis* on ladybird species. The encouraging mention of the persistence of *A. decempunctata* in tree habitats shared with *H. axyridis* could be due to its alternating temporal presence during a season (Honěk et al., 2015). However, the authors highlight that long-term declines of ladybird abundance are not solely due to *H. axyridis*, with habitat and climate change playing critical roles (Honěk et al., 2017). At smaller spatial scales, Masetti et al. (2018) compared ladybird communities in farmland hedgerow and herbaceous field margin habitats in two periods spanning 20 years at six sites in Bologna, Italy. Although community diversity indices in the hedgerow arboreal habitats did not differ significantly between sampling periods, in 2015-2016 *H. axyridis* dominated hedgerows, accounting for 66.5% of total sampled adults. The authors suggest that significant decline of *A. bipunctata* is most likely driven by *H. axyridis*.

Brown & Roy (2018) sampled two *T. europeae* churchyard sites, one herbaceous (*Urtica dioica* L., Urticaceae) and one pine tree (*Pinus sylvestris* L., Pinaceae) site over an 11-year period following invasion by *H. axyridis* in 2006. Comparing native species in early (2006/2008-2011) and late (2012-2016) periods revealed a significant decline of *A. bipunctata* densities at only one churchyard, and significantly reduced Shannon diversity index at the other *T. europeae* site. In addition, a negative correlation was found between densities of *H. axyridis* and *A. bipunctata*, but not of other native species, in both churchyard sites. Based on average proportions and considering 2006 as a baseline year for *H. axyridis* invasion of these communities, *H. axyridis* comprised 50.9 and 57.6% of individuals at churchyard sites, and 5.3 and 11.4% at pine and nettle sites, respectively. Here, the decline of *A. bipunctata* in *T. europeae* habitats echoes this species' widespread decline as *H. axyridis* dispersed across the UK and Belgium (Brown et al., 2011a; Roy et al., 2012).

In summary, the picture in Europe depicts widespread decreases in ladybird population densities in a range of habitats, with numerous studies illustrating greatest population changes where *H. axyridis* occupies arboreal habitats (Roy et al., 2012). However, other factors including agriculture and habitat changes operating at large spatial scales, and desynchronization of the host plants, prey, and ladybird phenologies due to climate change at local scales, are also important drivers (Honěk et al., 2017). Overall, despite reported declining densities, there is no evidence to support local extinctions of native European aphidophagous species due to the spread of *H. axyridis* through Europe, nor any known extinctions from other causes (Honěk et al., 2017). However, it is also worth mentioning that the available, very valuable long-term data obviously cannot capture population fluxes beyond periods sampled by these studies; noteworthy is the posited return of European *A. bipunctata* populations back to pre-industrial levels following invasion by *H. axyridis* (Sloggett, 2017). *Harmonia axyridis* presents an example of how accidental or intentional introductions of a BC agent can lead to negative environmental consequences and a plethora of studies investigating this case have contributed to highlight the importance of assessing the risk of BC agents before their release. Today the characteristics of *H. axyridis* would most likely preclude such a species from being licensed in European countries that possess a regulatory system for the release of BC agents. Finally, it is important to note that the prominent case of *H. axyridis* should not overshadow the many successful examples of agents that allow safe, sustainable and successful BC most often with much less severe environmental effects than their pesticide alternatives (Collatz et al., 2021).

Conclusions

In 130 years of classical BC programs, ladybirds have been extensively released for controlling herbivorous pests. Although the results with ladybirds highlighted in this review were variable, the establishment and BC success rate of ladybird species were similar to those obtained from previous analysis of the 6 158 introductions for all kinds of natural enemies (predators and parasitoids) of herbivorous insects and recorded in the complete BIOCAT database (Cock et al., 2016). The increased establishment and success of ladybirds in the most recent decades may be due to the increased research on their biology and ecology (e.g., Hagen, 1962; Hodek & Honěk, 1996; Dixon, 2000). Nevertheless, there is still important information missing about the pest control success by exotic ladybirds, particularly when they are part of a larger guild attacking a pest. Being generalist in terms of food diet and habitat use is helpful for establishment (Comont et al., 2012) and our analysis confirms that predator-prey life cycle synchronization is favourable for effective control (Dixon, 2000). Concerning the establishment of introduced ladybirds, the case studies for the USA, Canada, and Chile illustrate that initial individuals of *H. axyridis* and *C. septempunctata* failed to establish. Intriguingly, feral populations of these species were later able to colonize agroecosystems, eventually providing effective control. This may be due to various fitness-related traits between BC and natural or invasive strains. Recent investigations on *H. axyridis* populations revealed that selection of BC strains favoured a faster life history, lower cannibalism, higher susceptibility to pathogens, and lower resistance to low temperatures compared to feral invasive strains (Tayeh et al., 2012, 2015). This may suggest that commercial strains reared in biofactories and released for BC purposes show a higher efficacy and lower non-target risks compared to feral, accidentally introduced populations.

Additionally, exotic ladybirds tend to dominate aphidophagous communities in the USA, Canada, Chile, and Europe, but temporal and spatial niche segregation with native species often occur, with no repercussion or even positive effects for BC. Understanding how composition and configuration of the habitat surrounding a given crop can be manipulated to foster coexistence is therefore crucial.

During recent decades, there was reduced use of generalist natural enemies for classical BC (Cock et al., 2016), due to an increased awareness of possible risks of classical BC. Similarly, augmentative BC using exotic generalist species, including aphidophagous ladybirds, should not be recommended in principle (Lucas, 2012). However, some exotic aphidophagous species, i.e., *H. variegata* or *P. quatuordecimpunctata*, became very abundant (e.g., in Chile or part of Canada) and successfully contributed to pest control. Considering their moderate risk to engage in IGP (e.g., Grez et al., 2012; Rondoni et al., 2018), releases of these species might be a safe choice whenever necessary.

To reach the target of sustainable pest control, ladybird efficacy should be sometimes improved. For instance, the use of synthetic semiochemicals, e.g., methyl salicylate-based lures, has been proposed as a way to recruit ladybird adults in the crop, thus improving pest suppression (reviewed by Rodriguez-Saona et al., 2011; Kaplan, 2012). Therefore, research and application on the manipulation of ladybird behaviour using semiochemicals or attractive plants, i.e., 'attract and reward', should be prioritized. Finally, post-release evaluation using molecular-based methods, long-term field surveys, and citizen science programs might help to understand the ecological impact of releases in agricultural, natural, or urban areas.

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Author contributions

All authors contributed to the structure, writing, and review of the paper. GR and EC conceived the idea of the article and designed the layout. GR coordinated the paper, wrote the general parts, and conducted statistical analyses. MJWC provided the information from the BIOCAT database and contributed to the discussion of it. IB and AOS contributed on several aspects of the introduction, discussion of the BIOCAT database, and case studies. EWE wrote the case study for the USA. ACC, FD, EL, and J-EM focused on the case study for Canada. AG and TZ focused on the case study for Chile. JC wrote on the legislation part. JC and AGH wrote on the establishment, risk assessment, and post-release evaluation of *H. axyridis* in Europe.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Extract from the BIOCAT2010.4 database. The list includes all introductions where the biocontrol agent (BCA) ladybird is identified to species level. Note that only published information is included and only literature to the end of 2010 (with a few exceptions). Each case represents an introduction of a BC ladybird that was released in a target country/area within a decade period (for more details of fields and categories, see Cock et al., 2016). Classification of ladybird subfamilies and tribes was updated according to Nedvěd & Kovář (2012).

Table S2. Breakdown of the use of ladybirds as BC agents by countries that have made 10 or more introductions. An introduction event is considered if a BC agent was released in one country/area to control a target pest during a decade.

Table S3. Summary of the use of ladybirds as BC agents by zoogeographical regions. One introduction event is considered when a BC agent was released in one country/area to control a target pest during a decade.