Oecologia Australis
21(3): 268-279, 2017
10.4257/oeco.2017.2103.04

ENVIRONMENTAL IMPACTS OF ARTHROPODS AS BIOLOGICAL CONTROL AGENTS

Camila Fediuk de Castro-Guedes[1] & Lúcia Massutti de Almeida[1]*

[1]*Universidade Federal do Paraná (UFPR), Departamento de Zoologia, Laboratório de Sistemática e Bioecologia de Coleoptera (Insecta). Caixa Postal 19030, Curitiba, Brasil. CEP: 81531-980*
E-mails: camifc@yahoo.com, lalmeida51@gmail.com

ABSTRACT
Biological control is an important component in the integrated management of pests. It is used to reduce or mitigate pests and it has been the focus of discussions for a long time. Hundreds of species of natural enemies were introduced, resulting in the successful control of various pests. However, the ecological processes involved for its success are generally very complex. In this way, this review focused on all the process of introducing species of arthropods as biological control agents and how they can affect the environment. The evaluation of environmental risk is the most critical and difficult part of the procedures and should contain some elements such as the identification of potential risks to which the environment will be exposed. The problems caused by the invasion of exotic species have increased and the high frequency of invasion is associated in large part with human activities, such as accidental transport and introduction. All these questions should be analysed based on rigorous studies and risk analysis, in which ecological interactions, competition, intraguild predation, and the effects of introduction on non-target organisms as well are considered.

Keywords: *Harmonia axyridis*; intraguild predation; invasive species; non-target organisms; pests' control.

INTRODUCTION

Biological control, which is the use of live organisms as control agents against pests, has been the focus of discussions for a long time, but currently, this has been established as an important component in the integrated management of pests (Waage 1997, Van Lenteren *et al.* 2003, Hoelmer & Kirk 2005, Bebber *et al.* 2014, Cock *et al.* 2016). In more than a hundred years of biological control, several natural enemy species were imported, bred and released in nature, resulting in the successful control of various pest species (Van Lenteren *et al.* 2003). However, the ecological processes involved for successful biological control are generally very complex (Rosenheim *et al.* 1995, Cock *et al.* 2016).

Up to the mid-1980s, it was widely accepted that the practice of biological control was much more efficient in relation to chemical control in terms of environmental safety (DeBach & Rosen 1991, Messing *et al.* 2006). However, since then, evidence has indicated that the introduction of predators and parasitoids has the potential to impact non-target species (Messing *et al.* 2006, Frehse *et al.* 2016). An important difference between biological control and the utilization of chemical pesticides is that natural enemies are generally self-perpetuating and self-dispersing, and as a result, biological control is often irreversible (Messing *et al.* 2006).

The most important decision in a biological control program is making sure that the utilization of the agent is appropriate for the target pest in question. This decision should be based on a critical scientific evaluation, which will give a reasonable guarantee that the efforts will not be wasted with ineffective agents (Hoelmer & Kirk 2005). Thus, when choosing biological agents for pest control, we need to know its effectiveness. There are various reasons for not using ineffective natural enemies, including the possibility of undesirable impacts on non-target organisms and on the ecosystem in which these organisms occur (Van Lenteren *et al.* 2003, Özsisli & Prischmann-Voldseth 2016).

Investigators have discussed the viability of predicting the efficacy of arthropod biological control agents before releasing them in the field. However, no planning or preliminary studies can replace the empirical testing of natural enemies in the field, and there are no reliable criteria for determining *a priori* which attribute is the best for choosing a biological control agent (DeBach & Huffaker 1971, Cock *et al.* 2016).

The procedures of evaluation of environmental risk related to the release of natural enemies is the most critical and difficult part concerning biological control. This evaluation involves the identification of potential risks to which the species will be exposed in the environment, based on experimental and observational information (Van Lenteren *et al*. 2003, 2006, Prakash *et al.* 2011, Fujitani *et al.* 2017). There should also be a summary of the risks and benefits of the release of an exotic natural enemy in comparison with alternative control methods. Finally, a post-release report is necessary, describing any adverse effect that could be minimized and adjusted in possible future releases ("Guidelines for Registration Requirements for Invertebrate Biological Control Agents" - OECD working group) (Van Driesche & Bellows Jr. 1996, Van Lenteren *et al.* 2003).

The voluntary introduction of species should be regulated in a very restrictive manner, with a very good justification for the need of utilizing an exotic species. Besides, there should be an economic evaluation for the benefit of such an introduction, and studies need to be conducted on the impact of the exotic species in the natural environment. The potential risks of the release of exotic natural enemies have only recently received attention in biological control (Van Lenteren *et al.* 2003, Özsisli & Prischmann-Voldseth 2016).

In the last 100 years, many exotic natural enemies (*e.g.*, *Rodolia cardinalis* (Mulsant), *Adalia bipunctata* (L.), *Harmonia axyridis* (Pallas), *Rhizobius lophanthae* (Blaisdell), and *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) were released as biological control agents (Greathead 1995, Gurr & Wratten 2000, Van Lenteren *et al.* 2003). However, there have been few reports about the negative environmental effects caused by the introduction of these species (Lynch & Thomas 2000, Howarth 2001, Lynch *et al.* 2001).

An important difference between biological control and the use of chemical insecticides is that natural enemies are often definitive and self-dispersing. These irreversible characteristics are appreciated in classic biological control programs, because when correctly executed, they are sustainable and quite economical in comparison with any other control method (Bellows & Fisher 1999, Van Lenteren 2001).

Until recently, tests with native non-target species had rarely been done as part of evaluation programs of natural enemies of arthropods (Van Lenteren & Woets 1988, Waage 1997, Barratt *et al.* 1999, Wolfenbarger *et al.* 2008, Romeis *et al.* 2011, Biondi *et al.* 2012, Özsisli & Prischmann-Voldseth 2016, Riedel *et al.* 2016). However, the number of tests has been increasing, as researches are paying attention to its importance. In the case of arthropods, there are proposals for the methodology of risk evaluation of biological control agents as a basis for the regulation of the introduction and inundative releases of exotic natural enemies. This evaluation integrates information on the diverse potential and characteristics of the species, for example, ability to disperse, range of possible hosts, and possible direct and indirect effects on non-target species (Van Lenteren *et al.* 2003, Özsisli & Prischmann-Voldseth 2016). These studies of risk evaluation can indicate whether the species has high or low risk indices for its introduction.

Therefore, this review approaches the risks involved in the process of introducing species of arthropods as biological control agents and in what ways these introductions can affect the environment and the intra and interspecific relationships.

MATERIAL AND METHODS

This review was based on books, scientific papers, theses and dissertations present in the library of the Universidade Federal do Paraná (UFPR), as well as scientific articles available on specialized search databases. We searched for information about species introductions acting as biological control agents and about successful cases of introductions. In addition, information about the benefits and harms of these introductions has been raised and organized into topics discussed throughout the text.

DISCUSSION

Biological invasions

With the destruction of biogeographic barriers because of anthropic action, there has been a strong acceleration of biological invasions. As humans colonize new environments, they take domesticated plants and animals for food, pets and ornaments, providing conditions for their dispersion. The rapid and uncontrolled implementation of transport on a global scale over the last four centuries allowed previously isolated species to overcome geographic barriers and to become established in new regions (Ricciardi & MacIssac 2000, Roderick & Najavas 2015, Peterson *et al.* 2016).

This species displacement is called bioinvasion or bioglobalization of pests, that is, the displacement of organisms by another in a region, inadvertently or intentionally, which can result in incalculable harm on an environmental, economic, social and cultural scope. The term bioinvasion is also used to explain the introduction and/or dispersion of pests around the world (MMA 2014).

The definition of exotic invasive species is any organism which is found outside its natural distribution area and threatens ecosystems, habitats or species, and through its competitive advantages, favoured by the absence of predators and by the degradation of natural environments, it dominates the niches occupied by native species, principally in fragile and degraded environments (MMA 2014). Invasive exotic species are recognized as one of the greatest biological threats to the environment, with enormous harm to the natural ecosystems, where they are considered the second major cause of loss of biodiversity. Problems caused by these species in agricultural systems are well known, but the extent of the damage to natural ecosystems has been recently recognized (Sala *et al.* 2000).

Once introduced, the species can establish itself successfully in the new environment and eventually become an invasive species, disrupting the composition of the local community. When an invasion occurs, it is necessary to consider factors such as adaptation to the environment, the biodiversity of the ecosystem where the species are introduced, the existence of natural enemies, its rate of growth, etc (Williamson 1996).

The invasion of communities by exotic species is not only a concern for the academic and scientific community, but also for different segments of the society, since this phenomenon has increased dramatically in the whole world (Mooney & Hobbs 2000, Roderick & Navajas 2015). To tackle the problems brought about by the invasions of species, it is necessary to determine clearly the modalities of decontamination or of quarantine and these guidelines need to be based on rigorous scientific studies.

A classic example of biological invasion was the case of the harlequin ladybird *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae), a native species from Northeast Asia (Hukusima & Kamei 1970) and used in biological control of aphids considered as pests worldwide (Koch 2003).

Harmonia axyridis was introduced as a biological control agent in different periods in the United States of America, however, its establishment occurred only in 1988 (Chapin & Brou 1991). It was also introduced in some localities of Mexico (Koch *et al.* 2004), Canada (Koch 2003) and in several European countries, such as Grece (Katsoyannos *et al*. 1997), Southeast France (Iperti & Bèrtand 2001), Germany (Klausnitzer 2002), Belgium (Adriaens *et al.* 2003) and England (Majerus *et al.* 2006). In South America, *H. axyridis* was intentionally introduced in Mendoza, Argentina, in the late 1990s for biological control, and in 2001, it was detected in Buenos Aires (Saini 2004).

In Brazil, this species was observed for the first time in 2002, in Curitiba (PR), probably introduced accidentally, feeding on *Tinocallis kahawaluokalani* (Kirkaldy, 1907) (Hemiptera, Aphididae) in *Lagerstroemia indica* Linnaeus (Lythraceae), an ornamental species utilized in urban landscaping in the southern region, and on the aphid *Cinara atlantica* (Wilson, 1919) (Hemiptera: Aphihidae) in *Pinnus* sp. (Pinaceae) (Almeida & Silva 2002). After the introduction of this Coccinellidae species, studies were carried out in order to determine its impact on the native species. Martins *et al.* (2009) studied the impact of *H. axyridis* on native species and found that there was a reduction and variation in the diversity of the Coccinellidae collected, with a predominance of *H. axyridis*, indicating the displacement of native species.

Harmonia axyridis behaviour has been studied in the laboratory at different temperatures for the evaluation of its performance as a predator, showing that there can be competition with the native species (Castro *et al.* 2011, Castro-Guedes & Almeida 2016). It shows a high rate of consumption (Santos *et al.*

2014), even being able to utilize alternative food resources, such as cultivated fruits in the absence of a preferred food, representing a risk to fruit crops in the country (Guedes & Almeida 2013). According to the literature, little is known about the potential impacts of the natural enemies of *H. axyridis on its populations*. Some authors include the pathogenic fungus *Metarhizium anisopliae* (Metchnikoff) Sorokin (Deuteromycotina: Hyphomycetes), *Beauveria bassiana* (Balsamo) Vuillemin (Deuteromycotina: Hyphomycetes), and *Hesperomyces virescens* Thaxter (Laboulbeniales: Ascomycetes) as its most important natural enemies (Kenis *et al.* 2008). In addition, some birds species are also considered as natural enemies of *H. axyridis*, such as *Picus canus* (Gmelin, 1788) (Piciformes: Picidae) and *Sitta europaea* (L. 1758) (Passeriformes: Sittidae). The parasitoid *Dinocampus coccinellae* (Schrank, 1802) (Hymenoptera: Braconidae), which occurs in sympatry with *H. axyridis*, seems to be a main natural enemy of this species and has been reported as larvae, pupae and adult parasitoid, with a low rate of parasitism (Hoogendoorn & Heimpel 2002, Koyama & Majerus 2008, Berkvens *et al.* 2010, Castro-Guedes & Almeida 2016). *Strongygaster triangulifera* (Loew, 1863) (Diptera: Tachinidae), *Medina luctuosa* (Meigen, 1824) (Diptera: Tachinidae), *Medina separata* (Meigen, 1824) (Diptera: Tachinidae) (Kenis *et al.* 2008), *Oomyzus scaposus* (Thomson, 1878) (Hymenoptera: Eulophidae) (Riddick *et al.* 2009) and *Phalacrotophora philaxyridis* (Disney, 1997) (Diptera: Phoridae) (Comont *et al.* 2014) are also used as biological controls for *H. axyridis*. Other predators of *H. axyridis* are the nematodes *Heterorhabditis bacteriophora* Poinar (Rhabditida: Heterorhabditidae) and *Steinernema carpocapsae* (Weiser) (Rhabditida: Steinernematidae) which occur in laboratory (Kenis *et al.* 2008) and the parasitic mite *Coccipolipus hippodamiae* (McDaniel & Moril, 1969) (Actinedida: Podapolipidae) (Riddick *et al.* 2009).

Certainly, there are successful cases of biological control. Some examples are *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) to control *Diatraea saccharalis* (Fabricius) (Lepidoptera: Crambidae); *Ageniaspis citricola* Logvinovskaya (Hymenoptera: Encyrtidae) to control the citrus leaf miner, *Phyllocnistis citrella* Stainton (Lepidoptera: Gracillariidae), and parasitoids of the genera *Praon*, *Ephedrus* and *Aphidius* (Hymenoptera: Braconidae) to control the wheat aphids (Hemiptera: Aphididae) (Parra *et al.* 2004, Parra 2014).

Risk analysis

The biological control of invasive species utilizing natural enemies has been considered safe, effective and a good tool for the management of pests, but recent studies have questioned the negative impacts of imported natural enemies on the populations of non-target species (Messing & Wright 2006, Obrycki *et al.* 2009, Almeida & Ribeiro-Costa 2012, Van Lenteren 2012, Parra 2014, Cock *et al.* 2015). The disruption of ecological processes by invasive species is a serious threat and has been well documented (Mooney & Hobbs 2000). The threat of invasive species can be faced by quantitative procedures that impede its entrance, and one of the most important procedure is the adoption of risk analysis before importing any species (Lodge *et al.* 2006). This procedure has also been suggested for the introduction of biological control agents, because it can represent a threat to non-target species (Louda *et al.* 2003, Van Lenteren *et al.* 2003, Messing *et al.* 2006).

Such procedures have been implemented in a safe manner and there is important progress for the application of quantitative procedures of risk analysis for each proposed introduction of biological control agents (Messing *et al.* 2006). Meanwhile, any type of risk assessment is complex because of the large number of factors documented, scarcity of data on these risk factors, nature of the analyses (Simberloff 2003, Messing & Wright 2006) and determination of how much risk is acceptable.

The analysis and evaluation of the risks for the introduction of control agents should consist in the correct identification and studies of potential risks (Wapshere 1989, Greathead 1995, Messing 2000). Laboratory tests for specificity and adequate knowledge of basic ecological relations are also needed (McCoy & Frank 2010). Risk analyses of non-target organisms were carried out systematically in the introduction of control agents in Florida (USA), for example, clearly illustrating the complexity and urgency of this establishment. Such results showed that 42% of the agents established had native species in their range of potential hosts and that the release of widely generalist agents occurred. However, the risk was restricted to a small number of species belonging to ten families, and the documented cases of the effects on non-target organisms were rare (McCoy & Frank 2010). This example demonstrates that the risk factors should always be analysed to provide a balance between risks and their associated costs (Shrader-Frechette & McCoy 1992, Frehse *et al.* 2016).

Ecological interactions

To understand and predict the dynamics of a pest and its control agent, efforts are generally focused on the direct interactions between them, but the host-parasitoid or predator-prey interactions are not independent of the rest of the community they belong. The direct and indirect effects of the community on this type of interactions can significantly influence the pests' species and their control agents (Brodeur & Boivin 2006).

Knowledge about the life history of native species is essential for the understanding of their relationships with the environment. The dynamics in plant-pest-predator/parasitoid interactions is essential for the use of species in biological control.

Interferences of predators and parasitoids

Several characteristics of a natural enemy are likely to make it an effective control agent, including a high degree of prey specificity, short development time relative to prey, and high reproductive potential (Debach & Rosen 1991, Snyder & Ives 2003). Among entomophagous arthropods, predators and parasitoids are the most commonly used species. Hymenoptera and Diptera parasitoids exemplify better these characteristics, since parasitoids generally attack only a few prey species and develop within their prey. Thus, parasitoids and host must have similar generation time and, generally, parasitoids have highly fertile adult females that can attack many hosts during their lifetime (Parra 2014, Castro-Guedes & Almeida 2016, Peterson *et al*. 2016). Therefore, it is very important to know the population dynamics of these agents and their hosts and prey.

When the biological control agent and another natural enemy exploit the same resource, both can survive most of the time or maybe one succeeds and the other fails (competitive exclusion) (Tilman 1982, González-Changa *et al.* 2016, Hajek *et al.* 2016). In some cases, the release of polyphagous predators has not only led to a decimation of pests but has also affected non-target organisms, resulting in declines in populations of native predators and even other populations (Simberloff 1992, Hajek *et al.* 2016, Riedel *et al.* 2016).

Interspecific competition is difficult to be detected in nature. Therefore, even though introduced control agents quite often compete with native species, it is not surprising that their effects on natural communities are not documented (Simberloff & Stiling 1996). However, a few studies assessed this issue. One of the cases that called substantial attention was the introduction of the European species *Coccinella septempunctata* (Linnaeus, 1758) (Coleoptera: Coccinellidae), the seven-spot ladybird, in North America to control the Russian wheat aphid (Gordon & Vandenberg 1991, Elliott *et al.* 1996), displacing various native species of Coccinlellidae. Also, in Brazil, like in other countries, *H. axyridis* displaces native species (Martins *et al.* 2009), and is a more effective predator in a guild of aphidophagous insects, because besides utilizing available food resources more efficiently and competing for food with other species of aphidophagous coccinelids, it can also prey on other predators (Hodek *et al.* 2012). However, in both cases, all effects of such dramatic change in numerous taxa in diverse communities and ecosystems are unknown and greater impacts probably occurred.

Intraguild predation (IGP), which is defined as "an association of competitive species that kill and prey for feeding, utilizing the same resources", can reduce the efficacy of biological control (Dixon 2000). IGP was initially seen as a rare interaction and with few effects on food web dynamics (Janssen *et al.* 2006). This view was partially due to the theoretical prediction that omnivory and IGP destabilize food web dynamics and could thereby be unimportant, which led to a scarcity of studies on this interaction (Janssen *et al.* 2006, Mirande *et al.* 2015). Studies of IGP generally model populations of three species: an intraguild predator, an intraguild prey and a shared source or a prey that is attacked by the predator and by the intraguild prey (Janssen *et al.* 2006, Mueller *et al.* 2016). Consequently, IGP can produce diverse indirect effects between the co-existing species (Müller & Brodeur 2002). Their consequences on the dynamics of the prey population and community structure have become one of principal topics concerning biological control (Müller & Brodeur 2002, Mueller *et al.* 2016), because it represents a possible threat to the control success (Rosenheim *et al.* 1995).

Intraguild predation may influence the suppression of pest species because it occurs in various communities. When the target pest species is a plant, for example, IGP appears to be less common. On the contrary, communities of biological control agents associated with arthropods appear to be replete with IGP (Rosenheim *et al.* 1995, Peterson *et al.* 2016).

When the biological control agent is an intraguild predator of another natural enemy, its suppression can indirectly reduce predation in its prey population, generally herbivores (Rosenheim *et al.* 1995). This can lead to temporal outbreaks or to an increase in predators that are freed from their competitors (Van Lenteren *et al.* 2003).

The utilization of complexes of natural enemies or a single natural enemy in biological control programs has been discussed for a long time (Dixon 2000). There are cases in which it is assumed that complexes of enemies provide an increase in the suppression of the pest, but there are cases in which the complexes of predators appear to be less effective than a single natural enemy in the reduction of pest populations (Rosenheim *et al.* 1995, Dixon 2000, Mirande *et al*. 2015).

IGP is generally recognized as influencing the interactions between multiple predators and their control effects on the prey (Snyder 2009). IGP between predators can be intense, resulting in high mortality of intraguild prey, while additional mortality imposed on the shared prey population can be minimal (Katsanis *et al.* 2013).

Investigators interested in the use of arthropod predators as biological control agents have conducted studies to determine if they act in a simple additive manner or if the addition of another predator species improves or reduces the ability of native predators in reducing the number of pests (Dixon 2000). Therefore, it is very important, from a theoretical-practical point of view, to know if the mortality caused by all species in a guild of natural enemies on a prey population is greater than the sum of mortalities caused by each species.

Harmonia axyridis is a predator that is often involved in IGP, in most of cases with predators of aphids (Pell *et al.* 2008, Hodek *et al.* 2012, Katsanis *et al.* 2013) but also with parasitoids and entomopathogens (Roy *et al.* 2008, Meisner *et al.* 2011). It has some characteristics that can explain the success of its establishment as an invasive species and intraguild predator, as well as an optimal biological control agent. One of its characteristics is the chemical protection against predation from aphidophagous species (Sato & Dixon 2004). It has a high rate of fecundity (Iablokoff-Khnzorian 1982, Castro *et al.* 2011) and rapid development of immatures in relation to native species (Lanzoni *et al.* 2004). In addition, it shows an aggressive behaviour (Yasuda & Ohnuma 1999), which gives it advantages over its competitors, high mobility (Osawa 2000), allowing it to take refuge in unfavourable situations, to procure food and to have low susceptibility to pathogens (Hoogendoorn & Heimpel 2002).

IGP is a very important interaction in biological control systems (Hodek *et al.* 2012), where it can often lead to their collapse (Katsanis *et al.* 2013). Still, there is limited evidence for the positive effect of IGP on the densities of pest species. Thus, IGP does not appear to have negative effects on biological control (Janssen *et al.* 2006). The use of generalist natural enemies (generally intraguild predators) does not appear to be as risky for biological control as predicted up to now (Van Lenteren *et al.* 2003).

What still needs to be explained is if IGP really has no negative effects on biological control and why. The theory predicts that intraguild predators would always have positive effects on shared pest species, as long as they are inferior competitors. However, the effects of IGP on the population dynamics of intraguild prey and shared prey can be unpredictable due to the complexity of the food web and to anti-predator behaviour (Janssen *et al.* 2006). Although there is a consensus about the effects of IGP regarding the use of arthropods as control of pests, empirical studies are needed to test the possible damage caused by multiple predators and to determine whether only one or various enemies should be released to achieve the maximum control of the pest.

Effects on non-target organisms

Many exotic species have caused various impacts on the communities where they were introduced or invaded. These impacts may be amplified if the species is an invasive generalist insect predator (IGIP), which generally reaches much greater densities than similar native species (Snyder & Evans 2006, Frehse *et al.* 2016). The commercial trade and the introduction of generalist predators for use as biological control agents have increased the frequency of invasions by IGIP (Mack *et al.* 2000, Parry 2009, Mirande *et al.* 2015).

The frequency with which IGIP ecologically displace similar native species during their course of invasion is impressive (Snyder & Evans 2006), because they compete with native predators for shared sources and use mechanisms of interference, such as IGP (Polis *et al.* 1989, Rosenheim *et al.* 1995). However, those mechanisms are still poorly understood (Crowder & Snyder 2010).

Some studies showed the connection between the exploitation of resources and the displacement of native predator species (Crowder & Snyder 2010). Evans (2004) sampled alfafa fields in Utah before and after the invasion of the coccinelid *Coccinella septempunctata* Linnaeus, 1758 (Coleoptera: Coccinellidae). Before the invasion, various native species of Coccinellidae were abundant in the fields, and afterwards, those species were widely displaced. However, when the density of aphids was experimentally restored, the native coccinelids returned to the fields, suggesting that competition for resources drove the native species out of the habitats and that the alternative food source maintained the populations of ladybugs. In this case, the biological control of aphids was improved by the invasion of ladybugs to the detriment of the biodiversity of native coccinelids (Crowder & Snyder 2010).

In Brazil, tritrophic relationships of aphids-plants-coccinelids and the occurrence, abundance and population dynamics of *H. axyridis* were studied in comparison with native species, and the authors observed that this species competes mainly with *Cycloneda sanguinea* (Linnaeus, 1763), the most common species recorded. A large reduction in coccinellid abundance and diversity occurred after the introduction of *H. axyridis* in 2002, suggesting a possible displacement of native or established coccinellid species (Martins *et al.* 2009).

One way of reducing the risks of the release of natural enemies to non-target species would be to conduct prior tests as part of a pre-release evaluation for arthropod control agents (Barratt *et al.* 1999, Van Lenteren *et al.* 2003, Frehse *et al.* 2016). Another way of reducing these risks would be to limit the number of releases, increasing the utilization of native natural enemies. However, many exotic biological control agents have been imported and released without a complete evaluation of their characteristics (Van Lenteren *et al.* 2003).

For an analysis of environmental risk, any known or potential direct effects should be reported, especially in relation to species introduced as control agents. Based on the ability of intraguild species to establish themselves, their rate of attack on non-target species and the regulatory mechanisms present in the non-target population, potential effects of the biological control agent and the occurrence of IGP should be investigated. When considering the possibility of large impacts on the natural communities, additional tests are required (Van Lenteren *et al.* 2003, Frehse *et al.* 2016).

Secondary effects

Several indirect effects in the ecosystems can be expected when using biological agents for pest control due to the complexity of the trophic interactions, such as protection, pollination and dispersion impairment (Van Lenteren *et al.* 2003, Lourenço *et al.* 2014, Frost *et al*. 2016).

Apparent competition is a type of indirect interaction between two species that is mediated by a third species. In the last decades, there was an increase in interest in indirect interactions among ecologists (Schmitt 1987, Wootton 1994, Müller & Godfray 1999, Werner & Peacor 2003, Van Veen *et al.* 2006), and they are usually classified as density (or trophically) mediated or trait (or behaviorally) mediated (Werner & Peacor 2003, Van Veen *et al.* 2006, Frost *et al.* 2016). The simplest model of apparent competition suggests that predators and hosts cannot coexist in the same environment if they share a natural enemy, which is equivalent to the principle of competitive exclusion. The species that survives is the one that, in equilibrium, withstands the greater density of natural enemies (Van Veen *et al.* 2006, Frost *et al.* 2016).

This interaction may occur when the control agent affects non-target organisms by sharing natural enemies (Van Veen *et al.* 2006). For example, an herbivorous insect introduced to control a weed could be attacked by generalist native parasitoids, which also have native hosts (Hawkins & Marino 1997). When the biological agent and the weed share the same parasitoids, competition may occur between them (Van Veen *et al.* 2006).

CONCLUSIONS

The indirect harmful effects caused by the introductions of biological controls cannot be ignored and should always be assessed. Many exotic natural enemies were released in nature as biological control agents without information about their negative effects on the environment, as the case of *H. axyridis*. Most studies involving the risks and impacts caused by biological control only report successful cases and, for many regions, there are no reports of introductions that were previously tested. Moreover, the lack of evidence of negative environmental impacts does not mean they do not occur.

The arrival of individuals in a new habitat does not necessarily imply in its establishment. The colonization success of a species depends on its adaptation to the environment, biodiversity of the ecosystem, existence of predators and its population growth rate. Regarding ecological impacts, competition with autochthonous species can lead to the disappearance of natural species, including their extinction. These changes can cause multiple variations in the ecosystem functioning and, consequently, lead to a decline in biodiversity. Such problems are increasing with worldwide consequences, and several invasions of exotic species are associated with human activities, such as accidental transport and purposeful introduction.

In the last years, the scientific community has considered the question of the introduction of exotic species, based on the ecological and economic impacts resulting from the invasion of various ecosystems by those species. However, the question of biological invasions overcomes the academic interests. The consequences of biological introductions need to be addressed based on rigorous scientific studies and not only on bureaucratic requirements. All these questions should be analysed based on rigorous studies and risk analysis, in which ecological interactions, such as competition and intraguild predation, and the effects of introduction on non-target organisms are taken into account.

ACKNOWLEDGMENTS

We thank Dr. Al Leyva who helped with the English translation of the manuscript. To Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (CFCG, 401366/2014-6), and (LMA, 309764/2013-0).

REFERENCES

Adriaens, T., Branquart, E., & Maes, D. 2003. The multicoloured Asian ladybird *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae), a threat for native aphid predators in Belgium? Belgium Journal of Zoology, 133(2), 195-196.

Almeida, L. M., & Silva, V. B. 2002. Primeiro registro de *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae): um coccinelídeo originário da região Paleártica. Revista Brasileira de Zoologia, 19(3), 941-944.

Almeida, L. M., & Ribeiro-Costa, C. S. 2012. Predatory beetles (Coccinellidae). In: A. R. Panizzi & J. R. P. Parra (Eds.), Insect bioecology and nutrition for integrated pest management. pp. 571-591. Boca Raton: CRC Press.

Barratt, B. I. P., Ferguson, C. M., McNeil, M. R., Goldson, S. L. 1999. Parasitoid host specificity testing to predict field host range. In: T. M. Whithers, L. B. Browne & J. N. Stanley (Eds.), Host specificity testing in Australia: towards improved assays for biological control. pp. 70-83. Brisbane: CRC for Tropical Pest Management.

Bebber, D. P., Holmes, T., & Gurr, S. J. 2014. The global spread of crop pests and pathogens. Global Ecology and Biogeography, 23(12), 1398-1407.

Bellows, T. S., & Fisher, T. W. (Eds.). 1999. Handbook of biological control. Principles and applications of biological control. San Diego: Academic Press: p. 1046.

Berkvens, N., Moens, J., Berkvens, D., Samih, M. A., Tirry, L., De Clercq, P. 2010. *Dinocampus coccinellae* as a parasitoid of the invasive ladybird *Harmonia axyridis* in Europe. BioControl, 53(1), 92-99.

Biondi, A., Mommaerts, V., Smagghe, G., Viñuela, E., Zappalà, L., Desneux, N. 2012. The non-target impact of spinosyns on beneficial arthropods. Pest Management Science, 68(12), 1523-1536.

Brodeur, J., & Boivin, G. (Eds.). 2006. Trophic and guild interactions in biological control. Dordrecht: Springer Netherlands: p. 249.

Castro, C. F., Almeida, L. M., & Penteado, S. R. C. 2011. The impact of temperature on biological aspects and life table of *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). Florida Entomologist, 94(4), 923--932.

Castro-Guedes, C. F., & Almeida, L. M. 2016. Laboratory investigations reveal that *Harmonia axyridis* (Coleoptera: Coccinellidae) is a poor host for *Dinocampus coccinellae* (Hymenoptera: Braconidae) in Brazil. Journal of Insect Science, 16(1), 1-9.

Chapin, J. B., & Brou, V. A. 1991. *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera, Coccinellidae). Proceedings of the Entomological Society of Washington, 93(3), 630-635.

Cock, M. J. W., Day, R. K., Hinz, H. L., Pollard, K. M., Thomas, S. E., Williams, F. E., Witt, A. B. R., Shaw, R. H. 2015. The impacts of some classical biological control successes. CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources, 10(42), 1-58.

Cock, M. J. W., Murphy, S. T., Kairo, M. T. K., Thompson, E., Murphy, R. J., Francis, A. W. 2016. Trends in the classical biological control of insect pests by insects: an update of the BIOCAT database. BioControl, 61(4), 349-363.

Comont, R. F., Purse, B. V., Phillips, W., Kunin, W. E., Hanson, M., Lewis, O. T., Harrington, R., Shortall, C. R., Rondoni, G., Roy, H. E. 2014. Escape from parasitism by the invasive alien ladybird, *Harmonia axyridis*. Insect Conservation and Diversity, 7(4), 334-342.

Crowder, D. W., & Snyder, W. E. 2010. Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. Biological Invasions, 12(9), 2857-2876.

DeBach, P., & Huffaker, C. B. 1971. Experimental techniques for evaluation of the effectiveness of natural enemies. In: C. B. Huffaker (Ed.), Biological control. pp. 113-140. Boston: Springer.

DeBach, P., & Rosen, D. 1991. Biological control by natural enemies. 2nd ed. Cambridge, UK: Cambridge University Press: p. 456.

Dixon, A. F. G. 2000. Insect predator-prey dynamics: ladybird beetles and biological control. Cambridge, UK: Cambridge University Press: p. 268.

Elliott, N., Kieckhefer, R., & Kauffman, W. 1996. Effects of an invading coccinellid on native coccinellids in an agricultural landscape. Oecologia, 105(4), 537-544.

Evans, E. W. 2004. Habitat displacement of North American ladybirds by an introduced species. Ecology, 85(3), 637-647.

Frehse, F. A., Braga, R. R., Nocera, G. A., Vitule, J. R. S. 2016. Non-native species and invasion biology in a megadiverse country: scientometric analysis and ecological interactions in Brazil. Biological Invasions, 18(12), 3713-3725.

Frost, C. M., Peralta, G., Rand, T. A., Didham, R. K., Versani, A., Tylianakis, J. M. 2016. Apparent competition drives community-wide parasitism rates and changes in host abundance across ecosystem boundaries. Nature Communications, 7, 12644.

Fujitani, M., McFall, A., Randler, C., Arlinghaus, R. 2017. Participatory adaptive management leads to environmental learning outcomes extending beyond the sphere of science. Science Advances, 3(6), e1602516.

González-Changa, M., Wratten, S. D., Lefort, M-C., Boyer, S. 2016. Food webs and biological control: A review of molecular tools used to reveal trophic interactions in agricultural systems. Food Webs, 9, 4-11.

Gordon, R. D., & Vandenberg, N. 1991. Field guide to recently introduced species of Coccinellidae (Coleoptera) in North America, with a revised key to North American genera of Coccinellini. Proceedings of the Entomological Society of Washington, 93, 845-867.

Greathead, D. J. 1995. Benefits and risks of classical biological control. In: H. M. T. Hokkanen & J. M. Lynch (Eds.), Biological control: benefits and risks. pp. 53-63. Cambridge: Cambridge University Press.

Guedes, C. F. C., & Almeida, L. M. 2013. The potential os different fruit species as food for *Harmonia axyridis* (Pallas, 1773) (Coleoptera: Coccinellidae). Revista Brasileira de Fruticultura, 35(4), 1025-1031.

Gurr, G., & Wratten, S. (Eds.). 2000. Biological control: measures of success. Dordrecht: Springer Netherlands: p. 429.

Hajek, A. E., Hurley, B. P., Kenis, M., Garnas, J. R., Bush, S. J., Wingfield, M. J., Van Lenteren, J. C., Cock, M. J. W. 2016. Exotic biological control agents: a solution or contribution to arthropod invasions? Biological invasions, 18(4), 953-969.

Hawkins, B. A., & Marino, P. C. 1997. The colonization of native phytophagous insects in North America by exotic parasitoids. Oecologia, 112(4), 566-571.

Hodek, I., Emden, V. H. F., & Honek, A. (Eds.). 2012. Ecology and Behaviour of the Ladybird Beetles (Coccinellidae). New Jersey: Wiley-Blackwell Publishing: p. 561.

Hoelmer, K. A., & Kirk, A. A. 2005. Selecting arthropod biological control agents against arthropod pests: can the science be improved to decrease the risk of releasing ineffective agents? Biological Control, 34(3), 255-264.

Hoogendoorn, M., & Heimpel, G. E. 2002. Indirect interactions between an introduced and a native ladybird beetle species mediated by a shared parasitoid. Biological Control, 25(3), 224-230.

Howarth, F. G. 2001. Environmental issues concerning the importation of non-indigenous biological control agents. In: J.

A. Lockwood, F. G. Howarth & M. F. Purcell (Eds.), Balancing nature: assessing the impact of importing non-native biological control agents, an international perspective. pp.70-99. Maryland: Entomological Society of America.

Hukusima, S., & Kamei, M. 1970. Effects of various species of aphids as food on development, fecundity and longevity of *Harmonia axyridis* Pallas (Coleoptera, Coccinellidae). Research Bulletin of the Faculty of Agriculture, Gifu University, 29, 53-66.

Iablokoff-Khnzorian, S. M. 1982. Les coccinelles, coléoptères-Coccinellidae. Paris: Société Nouvelle des Éditions Boubée: p. 568.

Iperti, G., & Bèrtand, E. 2001. Hibernation of *Harmonia axyridis* (Coleoptera, Coccinellidae) in South-Eastern France. Acta Societatis Zoologicae Bohemicae, 65(3), 207-210.

Janssen, A., Montserrat, M., HilleRisLambers, R., Roos, A. M., Pallini, A., Sabelis, M. W. 2006. Intraguild predation usually does not disrupt biological control. In: J. Brodeur & G. Boivin (Eds.), Trophic and guild in biological interactionscontrol. pp. 21-44. Dordrecht: Springer.

Katsanis, A., Babendreier, D., Nentwig, W., Kenis, M. 2013. Intraguild predation between the invasive ladybird *Harmonia axyridis* and non-target European coccinellid species. BioControl, 58(1), 73-83.

Katsoyannos, P., Kontodimas, D. C., Stathas, G. J., Tsartsalis, C. T. 1997. Establishment of *Harmonia axyridis* on *Citrus* and some data on its phenology in Greece. Phytoparasitica, 25(3), 183-191.

Klausnitzer, B. 2002. *Harmonia axyridis* (Pallas, 1773) in Deutschland (Coleoptera, Coccinellidae). Entomologische Nachrichten Berichte, 46, 177-183.

Kenis, M., Roy, H. E., Zindel, R., Majerus, M. E. N. 2008. Current and potential management strategies against *Harmonia axyridis*. In H. E. Roy & E. Wajnberg (Eds.), From biological control to invasion: the Ladybird *Harmonia axyridis* as a model species. pp. 235-252. Dordrecht: Springer.

Koch, R. L. 2003. The Multicolored Asian Lady beetle, *Harmonia axyridis*: a review of its biology, uses in biological control and non-target impacts. Journal of Insect Science, 3, 1-16.

Koch, R. L., Burkness, E. C., Burkness, S. J. W., Hutchison, W. D. 2004. Phytophagous preferences of the multicolores Asian Lady Beetle (Coleoptera: Coccinellidae) for autumn-ripering fruit. Journal of Economic Entomology, 97(2), 539-543.

Koyama, K., & Majerus, M. E. N. 2008. Interactions between the parasitoid wasp *Dinocampus coccinellae* and two species of coccinellid from Japan and Britain. BioControl, 53(1), 253-264.

Lanzoni, A., Accinelli, G., Bazzocchi, G. G., Burgio, G. 2004. Biological traits and life table of the exotic *Harmonia axyridis* compared with *Hippodamia variegata,* and *Adalia bipunctata* (Col., Coccinellidae). Journal of Applied Entomology, 128(4), 298-306.

Lodge., D. M., Williams, S., MacIsaac, H. J., Hayes, K. R., Leung, B., Reichard, S., Mack, R. N., Moyle, P. B., Smith, M., Andow, D. A., Carlton, J. T., McMichael, A. 2006. Biological invasions: recommendations for U.S. policy and management. Ecological Applications, 16(6), 2035-2054.

Louda, S. M., Pemberton, R. W., Johnson, M. T., Follett, P. A. 2003. Nontarget effects: the Achilles's heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annual Review of Entomology, 48(1), 365-396.

Lourenço, R., Penteriani, V., Rabaça, J. E., Korpimäki, E. 2014. Lethal interactions among vertebrate top predators: a review of concepts, assumptions and terminology. Biological Review, 89(2), 270-283.

Lynch, L. D., & Thomas, M. B. 2000. Nontarget effects in the biocontrol of insects with insects, nematodes and microbial agents: the evidence. Biocontrol News and Information, 21(4), 117N-130N.

Lynch, L. D., Hokkanen, H. M. T., Babendreier, D., Bigler, F., Burgio, G., Gao, Z. H., Kuske, S., Loomans, A., Menzler-Hokkanen, I., Thomas, M. B., Tommasini, G., Waage, G. J., Van Lenteren, J. C., Zeng, Q. Q. 2001. Indirect effects in the biological control of arthropods with arthropods. In: E. Wajnberg, J. K. Scott & P. C. Quimby (Eds.), Evaluating indirect ecological effects of biological control. pp. 99-125. Wallingford: CABI Publishing.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., Bazzaz, F. A. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications, 10(3), 689-710.

McCoy, E. D., & Frank, J. H. 2010. How should the risk associated with the introduction of biological control agents be estimated? Agricultural and Forest Entomology, 12(1), 1-8.

Majerus, M. E. N., Strawson, V., & Roy, H. 2006. The potential impacts of the arrival of the harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae), in Britain. Ecological Entomology, 31(3), 207-215.

Martins, C. B. C., Almeida, L. M., Zonta-de-Carvalho, R. C., Castro, C. F., Pereira, R. A. 2009. *Harmonia axyridis*: a threat to Brazilian Coccinellide? Revista Brasileira de Entomologia, 53(4), 663-671.

Meisner, M., Harmon, J. P., Harvey, C. T., Ives, A. R. 2011. Intraguild predation on the parasitoid *Aphidius ervi* by the generalist predator *Harmonia axyridis*: the threat and its avoidance. Entomologia Experimentalis et Applicata, 138(3), 193-201.

Messing, R. H. 2000. The impact of nontarget concerns on the practice of biological control. In: P. A. Follett & J. J. Duan (Eds.), Nontarget effects of biological control. pp. 45-55. Boston: Springer.

Messing, R. H., & Wright, M. G. 2006. Biological control of invasive species: solution or pollution? Frontiers in Ecology and the Environment, 4(3), 132-140.

Messing, R., Roitberg, B., & Brodeur, J. 2006. Measuring and predicting indirect impacts of biological control: competition, displacement and secondary interactions. In: F. Bigler, D. Babendreier & U. Kuhlmann (Eds.), Environmental impact of invertebrates for biological control of arthropods. Methods and risk assessment.. pp. 64-77. Wallingford: CABI International.

Ministério do Meio Ambiente (MMA). 2014. Espécies exóticas invasoras. Retrivied April 25, 2014, from http://

www.mma.gov.br/biodiversidade/biosseguranca/

Mirande, L., Desneux, N., Haramboure, M., Schneider, M. I. 2015. Intraguild predation between an exotic and a native coccinellid in Argentina: the role of prey density. Journal of Pest Science, 88(1), 162-165.

Mooney, H. A., & Hobbs, R. J. 2000. Global change and invasive species: where do we go from here? In: H. A. Mooney & R. J. Hobbs (Eds.), Invasive species in a changing world. pp. 425-434. Washington: Island Press.

Mueller, A. K., Chakarov, N., Heseker, H., Krüger, O. 2016. Intraguild predation leads to cascading effects on habitat choice, behaviour and reproductive performance. Journal of Animal Ecology, 85(3), 774-784.

Müller, C. B., & Godfray, H. C. J. 1999. Indirect interactions in aphid-parasitoid communities. Researches on Population Ecology, 41(1), 93-106.

Müller, C. B., & Brodeur, J. 2002. Intraguild predation in biological control and conservation biology. Biological Control, 25(3), 216-223.

Obrycki, J. J., Harwood, J. D., Kring, T. J., O'neil, R. J. 2009. Aphidophagy by Coccinellidae: application of biological control in agroecosystems. Biological Control, 51(2), 244-254.

Osawa, N. 2000. Population field studies on the aphidophagous ladybird beetle Harmonia axyridis (Coleoptera: Coccinellidae): resource tracking and population characteristics. Population Ecology, 42(2), 115-127.

Özsisli, T., & Prischmann-Voldseth, D. A. 2016. Beyond focal pests: impact of a neonicotinoid seed treatment and resistant soybean lines on a non-target arthropod. Insects, 7(4), 1-12.

Parra, J. R. P. 2014. Biological Control in Brazil: An overview. Scientia Agricola, 71(5), 345-355.

Parra, J. R. P., Bento, J. M. S., Chagas, M. C. M., Yamamoto, P. T. 2004. O controle biológico da larva-minadora-dos-citros. Visão Agrícola, 2, 64-67.

Parry, D. 2009. Beyond Pandora's box: quantitatively evaluating non-target effects of parasitoids in classical biological control. In: D. W. Langor & J. Sweeney (Eds.), Ecological Impacts of Non-Native Invertebrates and Fungi on Terrestrial Ecosystems. pp. 47-58. Dordrecht: Springer.

Pell, J. K., Baverstock, J., Roy, H. E., Ware, R. L., Majerus, M. E. N. 2008. Intraguild predation involving *Harmonia axyridis*: a review of current knowledge and future perspectives. BioControl, 53(1), 147-168.

Peterson, J. A., Ode, P. J., Oliveira-Hofman, C., Harwood, J. 2016. Integration of plant defense traits with biological control of arthropod pests: challenges and opportunities. Frontiers in Plant Science, 7, 1-23.

Polis, G. A., Myers, C. A., & Holt, R. D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annual Review of Ecology, Evolution, and Systematics, 20(1), 297- 330.

Prakash, D., Verma, S., Bhatia, R,. Tiwary, B. N. 2011. Risks and precautions of genetically modified organisms. International Scholarly Research Network, 2011, 1-13.

Ricciardi, A., & Maclssac, H. J. 2000. Recent mass invasion of the North-American Great Lakes by Ponto-Caspian species. Trends in Ecology & Evolution, 15(2), 62-65.

Riddick, E. W., Cottrell, T. E., & Kidd, K. A. 2009. Natural enemies of the Coccinellidae: parasites, pathogens, and parasitoids. Biological Control, 51(2), 306-312.

Riedel, J., Romeis, J., & Meissle, M. 2016. Update and expansion of the database of bio-ecological information on non-target arthropod species established to support the environmental risk assessment of genetically modified crops in the EU. EFSA-Q-2013-00291; p. 109. Zurich: Agroscope, Institute for Sustainability Sciences ISS – Biodiversity and Environmental Management – Biosafety. Retrieved from http://onlinelibrary.wiley.com/doi/10.2903/sp.efsa.2016.EN-956/epdf

Roderick, G. K., & Navajas, M. 2015. Invasions of terrestrial arthropods: mechanisms, pathways, and dynamics. In: J. Canning-Clode (Ed.), Biological invasions in changing ecosystems: vectors, ecological impacts, management and predictions. pp. 75-87. Berlin: De Gruyter Open.

Romeis, J., Hellmich, R. L., Candolfi, M. P., Carstens, K., Schrijver, A., Gatehouse, A. M. R., Herman, R. A., Huesing, J. E., McLean, M. A., Raybould, A., Shelton, A. M., Waggoner, A. 2011. Recommendations for the design of laboratory studies on non-target arthropods for risk assessment of genetically engineered plants. Transgenic Research, 20(1), 1-22.

Rosenheim, J. A., Kaya, H. K., Ehler, L. E., Marois, J. J., Jaffee, B. A. 1995. Intraguild predation among biological-control agents: theory and evidence. Biological Control, 5(3), 303-335.

Roy, H. E., Baverstock, J., Ware, R. L., Clark, S. J., Majerus, M. E. N., Baverstock, K. E., Pell, J. K. 2008. Intraguild predation of the aphid pathogenic fungus *Pandora neoaphidis* by the invasive coccinellid *Harmonia axyridis*. Ecological Entomology, 33(2), 175-182.

Saini, E. D. 2004. Presencia de *Harmonia axyridis* (Pallas) (Coleoptera, Coccinellidae) en la Provincia de Buenos Aires. Aspectos biológicos y morfológicos. Revista de Investigaciones Agropecuarias, 33(1), 151-160.

Sala, O. E., Chapin III, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., Poff, N. L., Sykes, M. T., Walker, B. H., Walker, M., Wall, D. H. 2000. Global biodiversity scenarios for the year 2100. Science, 287(5459), 1770-1774.

Santos, A. A., Almeida, L. M., Castro-Guedes, C. F., Penteado, S. R. C. 2014. Life table analysis and consumption capacity for *Harmonia axyridis* (Coleoptera: Coccinellidae), feeding on *Cinara atlantica* (Hemiptera: Aphididae). Florida Entomologist, 97(4), 1702-1709.

Sato, S., & Dixon, A. F. G. 2004. Effect of intraguild predation on the survival and development of three species of aphidophagous ladybirds: consequences for invasive species. Agricultural and Forest Entomology, 6(1), 21-24.

Schmitt, R. J. 1987. Indirect interactions between prey: apparent competition, predator aggregation, and habitat segregation. Ecology, 68(6), 1887-1897.

Shrader-Frechette, K., & McCoy, E. D. 1992. Statistics, costs and rationality in ecological inference. Trends in Ecology & Evolution, 7(3), 96-99.

Simberloff, D. 1992. Conservation of pristine habitats and unintended effects of biological control. In: W. C. Kaufmann & R. J. Nichols (Eds.), Selection criteria and ecological consequences of importing natural enemies. pp. 104-117. Maryland: Entomological Society of America.

Simberloff, D., & Stiling, P. 1996. How risky is biological control? Ecology, 77(7), 1965-1974.

Simberloff, D. 2003. How much information on population biology is needed to manage introduced species? Conservation Biology, 17(1), 83-92.

Snyder, W. E. 2009. Coccinellids in diverse communities: which niche fits? Biological Control, 51(2), 323-335.

Snyder, W. E., & Ives, A. R. 2003. Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. Ecology, 84(1), 91-107.

Snyder, W. E., & Evans, E. W. 2006. Ecological effects of invasive arthropod generalist predators. Annual Review of Ecology, Evolution, and Systematics, 37(1), 95-122.

Tilman, D. 1982. Resource competition and community structure. Monographs in Population Biology 17. R. M. May, Ed. Princeton: Princeton University Press: p. 296.

Van Lenteren, J. C., & Woets, J. 1988. Biological and integrated pest control in greenhouses. Annual Review of Entomology, 33(1), 239-269.

Van Driesche, R. G., & Bellows Jr., T. R. 1996. Biological control. 1st ed. Boston, MA: Springer: p. 539.

Van Lenteren, J. C. 2001. Harvesting safely from biodiversity: natural enemies as sustainable and environmentally friendly solutions for pest control. In: J. A. Lockwood, F. G. Howarth & M. F. Purcell (Eds.), Balancing nature: assessing the impact of importing non-native biological control agents, an international perspective. pp. 15-30. Maryland: Entomological Society of America.

Van Lenteren, J. C. 2012. The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. BioControl, 57(1), 1-20.

Van Lenteren, J. C., Babendreier, D., Bigler, F., Burgio, G., Hokkanen, H. M. T., Kuske, S., Loomans, A. J. M., Menzler-Hokkanen, I., Van Rijn, P. C. J., Thomas, M. B., Tommasini, M. G., Zeng, Q-Q. 2003. Environmental risk assessment of exotic natural enemies used in inundative biological control. BioControl, 48(1), 3-38.

Van Veen, F. J. F., Memmott, J. H., & Godfray, C. J. 2006. Indirect effects, apparent competition and biological control. In: J. Brodeur & G. Boivin (Eds.), Trophic and guild interactions in biological control. pp. 145-169. Dordrecht: Springer Netherlands.

Waage, J. K. 1997. Global developments in biological control and the implications for Europe. In: I. M. Smith (Ed.), EPPO/CABI Workshop on Safety and Efficacy of Biological Control in Europe. pp. 5-13. Oxford: Blackwell Science Ltd.

Wapshere, A. J. 1989. A testing sequence for reducing rejection of potential biological control agents for weeds. Annals of Applied Biology, 114(3), 515-526.

Werner, E. E., & Peacor, S. D. 2003. A review of trait-mediated indirect interactions in ecological communities. Ecology, 84(5), 1083-1100.

Williamson, M. 1996. A framework for the study of invasions. In: M. Williamson (Ed.), Biological invasions. pp. 1-27. London: Chapman and Hall.

Wolfenbarger, L. L., Naranjo, S. E., Lundgren, J. G., Bitzer, R. J., Watrud, L. S. 2008. Bt crop effects on functional guilds of non-target arthropods: a meta-analysis. PlosOne, 3(5), 1-11.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology, Evolution, and Systematics, 25, 443-466.

Yasuda, H., & Ohnuma, N. 1999. Effect of cannibalism and predation on the larval performance of two ladybirds beetles. Entomologia Experimentalis et Applicata, 93(1), 63-67.

Submitted: 18 April 2017
Accepted: 06 September 2017