

Ecological effects of invasive alien species on native communities, with particular emphasis on the interactions between aphids and ladybirds

Pavel Kindlmann · Olga M. C. C. Ameixa ·
Antony F. G. Dixon

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Abstract The ecological effects of introduced species on native organisms can sometimes, but not always be significant. The risks associated with invasive alien pests are difficult to quantify. This paper concentrates on the ecological effects of invasive insect predators that feed on pest insects, because the former may potentially affect the biological control of the latter. The literature indicates that invasive predatory insects generally are resistant to changes in environmental conditions, long-lived and voracious with a high reproductive rate, high dispersal ability, able to spread very rapidly across landscapes and exhibit phenotypic plasticity.

Their colonization of patches of prey may induce native predators to leave, but the evidence that invaders negatively affect the abundance of the native species is scarce and not persuasive. Insect predators do not substantially affect the abundance of their prey, if the ratio of generation time of the predator to that of the prey is large (the generation time ratio hypothesis), therefore the effect of an invasion by long-lived alien predators on systems consisting of long-lived native predators and short-lived prey on the abundance of the prey is hard to detect.

Keywords Invasive alien species · Predators · Insect pests · Ecological effects · Intraguild predation

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P. Kindlmann · O. M. C. C. Ameixa (✉) ·
A. F. G. Dixon
Department of Biodiversity Research, Global Change
Research Centre AS CR, Na sádkách 7,
České Budějovice, Czech Republic
e-mail: olgameixa@portugalmail.pt

P. Kindlmann
Institute for Environmental Studies, Charles University,
Benatska 2, Prague, Czech Republic

O. M. C. C. Ameixa
Faculty of Sciences, University of South Bohemia,
Branišovská 31, České Budějovice, Czech Republic

A. F. G. Dixon
School of Biological Sciences, University of East Anglia,
Norwich NR4 7TJ, UK

Introduction

The ecological effects of introduced species on native organisms can sometimes but not always be significant (Vitousek et al. 1996). For example, Nedvěd et al. (2011) report that invasive spiders pose little threat to biodiversity. The risks associated with invasive alien pests (e.g., of widespread establishment or ecological effect) are difficult to quantify, as they involve interactions between factors operating across a range of spatial and temporal scales, such as the population dynamics of an invader, environmental conditions in the invaded region and the status of potential dispersal pathways (Barney and Whitlow 2008).

Import and establishment of exotic natural enemies with the purpose of reducing pest populations below levels at which they cause economic injury to crops, has gained a special place in crop management. Among these, insect predators (the group that is focused on in this paper) used to control insect pests are important. However, the introduction of a new organism into a new environment is in itself a form of contamination and can have a significant effect on species conservation (De Clercq et al. 2011; Elliott et al. 1996). For example, recently the ladybird *Harmonia axyridis* (Pallas) made the headlines in some countries. It is native to Asia, introduced several times into USA and more recently also European countries, mainly for the biological control of aphids (Koch 2003; Roy and Wajnberg 2008). It is currently the commonest invasive coccinellid in the US and Canada (Harmon et al. 2007). The possible adverse effect of this coccinellid on native species is a matter of considerable concern not only in the USA where it is said to be responsible for the decline of native ladybirds, but also in Europe. This paper will concentrate on the ecological effects of invasive insect predators (mainly ladybirds) that feed on pest insects (usually aphids), because the former may potentially affect the biological control of the latter and have economic consequences.

What characterizes a successful invader?

An invasive species can share traits and compete with resident native species or have different traits and occupy “empty niches” (Levine and D’Antonio 1999; Mack 1996). Invasive species are generally resistant to changes in environmental conditions, long-lived (Hemptinne et al., personal communication), chemically well defended (Sloggett et al. 2011), sometimes even synanthropic (Nedvĕd et al. 2011), voracious, highly fecund, exhibit phenotypic plasticity and spread actively and rapidly (Hemptinne et al., personal communication). In the absence of natural enemies, they can dominate an ecosystem and compete with native species.

Invasive success is closely associated with the invaders being large (Hemptinne et al., personal communication). However, it is not their size *per se*, but more likely their potential reproductive rate and dispersal ability, which are both positively associated

with size, which apparently determines their invasive success (Hemptinne et al., personal communication).

Not all introduced species become invasive as many are unable to establish for some reason. For example, of the 179 coccinellid species introduced into North America only 27 became established in the US and Canada (Gordon 1985; Gordon and Vandenberg 1991).

Ecological effects of invasive insect predators

Invasive predators can have a direct effect on the abundance of native herbivores (Sakai et al. 2001). Alternatively, invasive predators may have an indirect effect on the abundance of native herbivores by lowering the abundance of local predators (Sakai et al. 2001). The mechanism causing the latter may be quite complicated: (i) competition between native and invasive predators for food and/or intraguild predation (Pell et al. 2008), or (ii) emigration of native predators from patches colonized by the invasive predatory species (Evans 2004). Whatever the reason, lowering the abundance of native predators reduces their predatory pressure on herbivores at the same time as the predator pressure of the invasive species increases. This can result in either a decline or increase in the abundance of herbivores. To make things even more complicated, the negative effects of introduced exotics can also include suppression or extinction of non-target species of prey (herbivore), some of which may be beneficial (Elliott et al. 1996).

The main interest is usually in the effect of invasive species on the abundance of both herbivore pests and non-target species. For this it is necessary to explore each of the possibilities listed above and determine which have significant effects. This is the task of the subsequent sections.

Intraguild predation and competition between native and invasive predators

Intraguild predation (IGP), defined as feeding on species that use the same resources in a similar way (guild—Polis et al. 1989), has become a major research topic in biological control and conservation ecology. It is assumed to occur widely in many, but not all, communities of biological-control agents (Holt and Polis 1997; Rosenheim et al. 1995). As a

consequence, IGP combines two important ecological forces: competition and predation (Polis and Holt 1992; Polis and Winemiller 1996) and may generate a diversity of indirect effects among co-occurring species (Miller and Brodeur 2002).

Some studies have revealed that predator diversity often favours biological control (Cardinale et al. 2003; Losey and Denno 1998; Snyder 2009), but other studies suggest the opposite (Finke and Denno 2003, 2004; Rosenheim et al. 1993; Snyder and Ives 2001). The latter argue that because of intraguild interactions, increasing predator diversity may disrupt the suppression of a pest species, thus leading to higher pest densities. The implications for biological control of the introductions of strong IGP competitors that reduce or eliminate other intraguild members should therefore be considered.

Good examples of a system in which IGP may potentially affect the structure of the community are ladybird guilds invaded by exotic species. For example, the exotic *H. axyridis* is often supposed to negatively affect native coccinellids and in some aphidophagous guilds is considered to be a top predator. Since 1916, *H. axyridis* has been repeatedly released as a classical biological control agent in the USA (Gordon 1985). It did not establish until the 1980s, but then spread and increased in abundance, so that it is now the most numerous of all ladybirds throughout North America (Hesler et al. 2001). In Europe it has been commercially available for both classical and inundative biological control since 1982 (Ipert and Bertand 2001) and is still widely used (Brown et al. 2008). The rapid expansion of the range of *H. axyridis* in Europe has caused considerable concern both from ecological and anthropogenic perspectives (Roy and Wajnberg 2008). The role of *H. axyridis* as an intraguild predator is the focus of many studies (Pell et al. 2008). At many locations, *H. axyridis* is the dominant predator in arboreal habitats (Brown and Miller 1998; LaMana and Miller 1996) and many agronomic crops (Colunga-Garcia and Gage 1998).

Weber and Lundgren (2009) state: “In recent years, populations of several coccinellid species endemic to North America and Europe have experienced steep declines, and exotic coccinellids released as biological control agents are implicated as causal agents (Alyokhin and Sewell 2004; Brown 2003; Elliott et al. 1996; Evans 2004; Hesler et al. 2004;

Losey et al. 2007; Michaud 2002; Mizell 2007; Snyder and Evans 2006; Ware et al. 2009)”. However, whether or not the exotic coccinellids are really responsible for the observed declines is unclear for several reasons.

First, some of the time series used are very short and therefore, even if they might indicate that the cause of the decline of the native coccinellids might be the alien ladybirds, the results are not significant and longer time series should therefore be collected, as stated by Hesler and Kieckhefer (2008) and Mizell (2007). There are, to our knowledge, only two analyses of data sets spanning at least three or more years before and three or more years after the invasion of the alien ladybirds (Colunga-Garcia and Gage 1998; Elliott et al. 1996). Neither of these two indicates a uniform decline in the abundance of the whole guild of native coccinellids. This means that in these studies some species (e.g., *A. bipunctata*) decline, some species do not, and some species even increase in abundance—e.g., *H. glacialis* in Colunga-Garcia and Gage’s (1998) study and *H. parenthesis* in Elliott et al.’s (1996) study. Also Brown (2003), using data sets of one year before and four years after the invasion of *H. axyridis* concludes: “Principal component analysis indicated that although individual species were affected, the overall effect of *H. axyridis* invasion on the predator guild as a whole was negligible”. To summarize: Statistically significant differences between ladybird abundances one or two years before and one or two years after the invasion cannot be used as a proof of a long-term decline in the abundance of native ladybirds after the invasion of alien species, bearing in mind the variability in ladybird numbers between years. None of the existing longer data series (spanning three years or more) indicates a uniform decline of all native species: after the establishment of the alien species, some native species declined, some increased and the abundance of some was unchanged.

Second, a negative relationship between the abundances of the native species and those of the invaders (decline in time of the former accompanied by increase in time of the latter) may not necessarily mean a cause-and-effect relationship (Losey et al. 2007; Wheeler and Hoebeke 1995). The true reasons for the decline of the natives may be different. For example, in the Czech Republic, Honek et al. (personal communication) show, using 30-years of data,

that the decline in the abundance of certain native species started before the introduction of *H. axyridis*, and relate this to changes in agricultural practices and landscape. Honek et al. (personal communication) show that, although *H. axyridis* is now very common in the Czech Republic, there were no evident changes in the abundances of the native species after 2006, when *H. axyridis* was first recorded. No other species invaded the Czech Republic during the period studied by Honek et al. (personal communication). However, there were substantial changes in agriculture management and landscape composition after political changes in 1989. Some other studies indicate a negative relationship between the abundance of *A. bipunctata* and *H. axyridis*, but they also suggest that *A. bipunctata* may have declined in abundance even prior to the arrival of *H. axyridis* (Boiteau et al. 1999; Brown and Miller 1998; Colunga-Garcia and Gage 1998). In North America, *Adalia bipunctata* (L.), *Coccinella novemnotata* Herbst and *Coccinella transversoguttata* Faldermann were once the most abundant coccinellids in many habitats. These species are now rarely recorded in certain habitats (Losey et al. 2007) and populations of the exotic coccinellids *Coccinella septempunctata* and *Harmonia axyridis* Pallas now abound in habitats formerly dominated by the above species. Again, whether or not this is a causal relationship or mere coincidence is unknown (Losey et al. 2007).

Third, some of these analyses, even those using long-term data sets, use proportions of individual species in total catches for comparison (e.g., Alyokhin and Sewell 2004). However, a decline in the proportion of natives can result either from a decrease in the absolute abundance of native species or from a simple increase in the total coccinellid abundance (natives + exotic) due to the invasion of exotic species, without any absolute decrease in the abundance of the native species. Thus Harmon et al. (2007) report reductions in the proportion of native species in coccinellid assemblages, after the mid 1980s, and even though they attribute this to the introduction of *C. septempunctata* and *H. axyridis*, they stress that care must be taken to not over-interpret these results.

Thus neither empirical observations, nor their analysis indisputably support the claims that there have been regional reductions in native coccinellid diversity coupled with the range expansion of

invasive species. Targeted long-term studies should therefore be performed in countries, which recently suffered invasion by alien species and for which data exist on the past abundances of native species. Only such studies would clearly show which factors really caused the recent declines in the abundances of the native species. European countries, where *H. axyridis* is now spreading, are good candidates. In some of these countries (at least in the Czech Republic), appropriate long-term data on ladybird numbers before invasion by *H. axyridis* exist, so that only a few more years of data after the invasion are needed for performing very reliable tests of the effect of the invader on native communities. Direct observation of the numbers of individuals should be accompanied by gut analyses or similar techniques, in order to determine whether or not intraguild predation on native ladybirds by *H. axyridis* is common enough to cause the suppression of the former.

Emigration of native predators from patches colonized by invasive predatory species

Evans (2000, 2004) records in the USA that although native ladybirds declined dramatically in Utah alfalfa fields after the establishment of the exotic ladybird, *Coccinella septempunctata*, they were still dominant in native habitats. He suggests that native ladybirds may have abandoned alfalfa fields to forage and reproduce elsewhere because of the reduction in prey density caused by the arrival of invasive alien ladybirds. The support for this hypothesis comes from field experiments, in which native ladybirds “reappeared” in alfalfa fields in response to artificially created, local aphid outbreaks (Evans 2004). Therefore, in some cases, native species may still dominate in non-agricultural habitats, but are replaced by invasive alien ladybird species in agricultural ecosystems. This conclusion was inferred by the authors, since non-agricultural habitats were not monitored. This form of resource partitioning and optimal feeding is referred to as the “compression hypothesis” (MacArthur and Pianka 1966; MacArthur and Wilson 1967).

On the other hand, Finlayson et al. (2008) did not find any evidence that native ladybirds retreat to and remain dominant in non-agricultural habitats after the arrival of invasive alien ladybirds in agricultural habitats in Maine, USA. They report that captures of

native ladybirds were never greater than those of invasive alien ladybirds in any habitat, regardless of their location or proximity to agriculture. Finlayson et al. (2008) attribute this discrepancy: (i) to the possibility that invasive alien lady beetles in Utah (Evans 2000, 2004) might not have spread into more natural habitats at the time of the surveys; (ii) to differences in landscape and habitat structure, which might have made non-agricultural habitats in Maine more prone to invasion than the non-agricultural habitats in Utah; and (iii) to the fact that “the invasive *P. quatuordecimpunctata* and *H. axyridis*, which were the dominant species in their survey, but absent in Utah (Evans 2000, 2004), are more invasive than *C. septempunctata*, which was the invasive species in Utah (Evans 2000, 2004)” (Finlayson et al. 2008). To conclude: there is some evidence that native species may not colonize agricultural habitats if they are invaded by another species (Evans 2004) and there is no evidence that refutes this. Thus it may be true that spatio-temporal differences in habitat-use lead to complementary effects on prey by encouraging different predator species to attack different subsets of the prey population (Snyder 2009).

Effect of invasive predators on the abundance of herbivorous pests

From an evolutionary perspective, both predator and prey species strive to maximize their own reproductive potentials or, more strictly, their genetic fitness. However, whilst prey can exist perfectly well in the absence of predators, predators require prey. Therefore, it is in the predator’s interest to practice conservation. The optimal strategy of the predator then involves the counteracting pressures to maximize its own reproduction and survival, usually through the use of efficient hunting tactics, and yet conserve enough prey for its offspring (Berryman and Kindlmann 2008).

This is nicely exemplified by the case of long-lived insect predators feeding on short-lived prey (the “Generation time ratio (GTR) hypothesis”). As most of these predators suffer high egg and larval mortality due to cannibalism and intraguild predation, selection acts mainly by optimizing their oviposition strategies in terms of maximizing the likelihood that their offspring will survive until reproductive age. The oviposition strategy of a predator with a long larval

developmental time relative to that of its prey depends on a longer projection of the future prey abundance in the patch, and therefore the possibility of experiencing more bottlenecks or a higher probability of a bottleneck in prey abundance than a predator with a short developmental time, and consequently must be more conservative in terms of preserving their prey (Kindlmann and Dixon 1999, 2001 and references therein). The GTR hypothesis is strongly supported by recent empirical results: Mills (2006) and Mills and Latham (2009) show that generation time ratio is an important life history trait that determines the effect of natural enemies in biological control. They conclude that a small generation time ratio (coupled with a broad window of host attack) can facilitate the suppression of pest abundance by parasitoids and is positively associated with success in biological control.

The most frequently used means of evaluating the efficiency of natural enemies to suppress the abundance of their prey in the field are exclusion techniques, such as cages (Luck et al. 1988). The growth rates and peak densities of aphid populations within cages that exclude natural enemies are usually larger than those in un-caged populations (e.g., Basky 2003; Cardinale et al. 2003; Chambers et al. 1983; Elliott and Kieckhefer 2000; Michels et al. 2001; Schmidt et al. 2003). However, the use of exclusion techniques was criticized, because they change the microenvironment (Hand and Keaster 1967) and prevent aphids from emigrating (Kindlmann and Dixon 2010). Some cages used in these “exclusion” experiments (Schmidt et al. 2003) even do not reduce predator densities within cages (Kindlmann and Dixon 2010). Therefore, it is surprising that cage exclusion experiments are still used to assess the effectiveness of predators in reducing aphid population growth and such flawed results are presented as proof of their effectiveness. Cages can provide us with a very good insight into the mechanisms governing inter-specific interactions, including intra-guild predation (Rosenheim et al. 1993; Snyder and Ives 2001 etc.), so long as like-with-like is compared. They should not be used, however, to determine the effectiveness of predators in reducing the numbers of their prey.

In summary: if insect predators are unlikely to affect population densities of their prey too much, is there any point in discussing, whether or not invasive

species can affect biological control of native pests? There is a common tendency to believe that invasive species reduce the abundance of their aphid prey substantially, as exemplified by, e.g., Alyokhin and Sewell (2004). They claim that “the abundance of aphid prey was substantially reduced after the establishment of *H. axyridis*”, but their own multiple regression analysis reveals that the abundances of only two out of all ladybird species they studied were significantly correlated with aphid densities in the same year—and one of them (*H. tredecimpunctata*) even positively (more ladybirds—more aphids). In this context it should be noted that a positive correlation in this case means that ladybirds concentrate in places, where there are many aphids. A good test of ladybird efficiency in suppressing aphids would be to correlate ladybird densities during the season with aphid densities at its end, while considering other effects (including aphid see-saw effect) as correlates, which was not done by Alyokhin and Sewell (2004). In view of this, the significant negative correlation between the numbers of *H. axyridis* and the abundances of aphids (their Table 3) is much less persuasive, but for a rigorous conclusion of what it really means the original raw data are needed.

Conclusions

Invasive predatory insects are generally resistant to changes in environmental conditions, long-lived, voracious, highly fecund, actively disperse, rapidly spread across landscapes and exhibit phenotypic plasticity. Native predators may leave or avoid patches colonized by invasive species, but the evidence that the latter negatively affect the abundance of native species is scarce and not persuasive. Insect predators do not substantially affect the abundance of their prey, if the ratio of generation time of the predator to that of the prey is large (the generation time ratio hypothesis, Kindlmann and Dixon 1999, 2001, 2010), therefore the effect of an invasion by long-lived alien predators on systems consisting of long-lived native predators and short-lived prey on the abundance of the prey is hard to detect. A careful design of the experiments dealing with ecological effects of invasive insects is a good starting point to address this problem. Such designs should include a long (at least three years) period

before and a period after the invasion. Proportions of individual species in total catches should not be used for comparison. This is because the decline in the proportion of natives can result either from a decrease in the absolute abundance of native species or from an increase in the total coccinellid abundance due to the invasion of exotic species, without any absolute decrease in the abundance of the native species.

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Author Biographies

Pavel Kindlmann is studying life history strategies of aphids and their predators, with particular attention to their implications in population dynamics.

Olga M. C. C. Ameixa This research is part of a PhD project of Olga Ameixa devoted to the interactions among aphid predators.

Anthony F. G. Dixon is studying life history strategies of aphids and their predators, with particular attention to their implications in population dynamics.