ORIGINAL PAPER

When the adaptive value of intraguild predation between an indigenous and an invasive ladybeetle is altered by an insecticide

Paula Cabrera[1] · Daniel Cormier[2] · Marianne Bessette[1] · Vanessa Cruz[1] · Eric Lucas[1]

Abstract

The multicolored Asian ladybeetle, *Harmonia axyridis* Pallas (Col, Coccinellidae), is recognized as one of the most invasive insects in the world. It has reduced the native coccinellids populations in several areas, and it is considered a threat for biodiversity at large. A significant trait, favoring its invasiveness and its dominance over indigenous ladybeetles, is intraguild predation (IGP). IGP has advantageous adaptive value for individuals: removing competitors and potential predators, and providing an alternative nutritive resource when main resources are scarce. IGP can be affected by several factors, but little is known about the effect of pesticides on this behavior. Previous research demonstrated that the invasive Asian ladybeetle is highly susceptible to the reduced-risk insecticide novaluron, a chitin synthesis inhibitor, whereas the North American indigenous competitor, *Coleomegilla maculata* DeGeer (Col, Coccinellidae), is not. Our study explores the adaptive value of IGP for each of the two coccinellids after preying on each other's larvae, which were previously treated with insecticide. Our first hypothesis is that the invasive ladybeetle, susceptible to the insecticide, should lose the adaptive value of IGP. Our second hypothesis is that the adaptive value of IGP for the invasive predator will recover over time, because of neutralization of the insecticide by the intraguild prey. The results confirm both hypotheses and show that an insecticide can completely remove the adaptive value of IGP for the invader, while the adaptive value of IGP does not change for the indigenous ladybeetle. Moreover, the study demonstrates that if the intraguild prey (non-susceptible to the insecticide) undergoes molt after being exposed to the insecticide, the adaptive value for the intraguild predator is restored.

Keywords Intraguild predation · Biological invasions · *Harmonia axyridis* · *Coleomegilla maculata* · Novaluron · Reduced-risk insecticide

Key message

- In preceding research, we demonstrated that the invasive *Harmonia axyridis* is more susceptible to the reduced-risk insecticide novaluron, than its indigenous competitor, *Coleomegilla maculata*.
- The present study examines the effect of the insecticide on the adaptive value of intraguild predation for both ladybeetle species after preying on each other's larvae.
- The insecticide removes the adaptive value of intraguild predation only for the invasive ladybeetle.
- We illustrate potential impacts of insecticides on intraguild predation and consequences for biocontrol and biological invasions.

✉ Paula Cabrera
cabrera.paula@uqam.ca

1. Laboratoire de Lutte Biologique, Département de Sciences Biologiques, Université du Québec à Montréal, 141 Avenue du Président-Kennedy, Montréal, Québec, Canada

2. Institut de Recherche et de Développement en Agroenvironnement, 335 rang des Vingt-Cinq Est, Saint-Bruno-de-Montarville, Québec, Canada

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Introduction

Biological invasions can interfere with several ecological and evolutionary processes such as species diversity and structure of communities (Mooney and Cleland 2001; Strayer et al. 2006), consequently affecting ecosystem services and causing significant economic losses (Asplen et al. 2015; Pejchar and Mooney 2009; Vilà et al. 2010; Walsh et al. 2016). Some of the traits characterizing invasive species are: high adaptability to the environment, high fecundity and dispersion (Kolar and Lodge 2001; Sakai et al. 2001), and broad diet range (Crowder and Snyder 2010; Evans et al. 2011). Another factor contributing to the success of invaders is their highly competitive ability, and more specifically—intraguild predation (IGP) (Eubanks et al. 2002; Snyder et al. 2004; Pell et al. 2007; Michaud 2012). IGP, defined as the predation on a competitor (Polis and Holt 1992), has a high adaptive value for the intraguild predator: by removing competitors, removing potential predators, and providing an alternative nutritional resource when main extraguild resources are scarce. Therefore, IGP can have important consequences for the distribution, abundance, and evolution of the species involved (intraguild predator, intraguild prey, and shared resource) (Polis et al. 1989), as well as major impacts on conservation management and biological control (Rosenheim et al. 1995; Müller and Brodeur 2002). For example, during the buildup of cereal aphid population, molecular diagnosis used to track trophic interactions showed that generalist predators (carabid and staphylinid beetles, and linyphiid spiders) consumed aphid parasitoids causing the disruption of aphid control. (Traugott et al. 2012).

Intraguild predation interactions may be defined by different proxies such as intensity (frequency, magnitude), direction (mutual or unidirectional), and symmetry (dominance or not) (Lucas 2005). The intensity of the interaction is affected by an array of factors, such as extraguild prey/resource distribution and density, intraguild prey density, or habitat complexity (including potential refuges). The direction and symmetry (in mutual IGP) of the interaction may be also influenced by: the relative size of Intraguild prey and predator, relative thermal tolerance, and by historical factors such as priority of colonization, life cycle duration, growth stages, overwintering stage, and photoperiod (Lucas and Maisonhaute 2019).

A poorly studied factor that may modulate IGP intensity, direction, and symmetry is the exposure of the different organisms involved, to phytosanitary practices, particularly to chemical control. Pesticides have important deleterious effects on ecosystems, such as direct and indirect effects on non-target organisms (Rundlöf et al. 2015; Newman et al. 2016; Mohanty et al. 2017; Muturi et al.

2017), leading to a major biodiversity reduction in agricultural ecosystems (Benton et al. 2003; Cattaneo et al. 2006). While most studies focused on lethal effects of pesticides on pests and their natural enemies (Guedes et al. 2017), an increasing attention is being given to sublethal effects (Desneux et al. 2007; Guedes et al. 2016). However, regarding the effect of pesticides on IGP only one study, (Provost et al. 2003) provided evidence that the insecticide lambda-cyhalothrin, a sodium channel modulator, does not modify intraguild predation directly but affects the intraguild predator mobility. IGP can be a key component of biological control programs (Rosenheim et al. 1995), and since pesticides can have lethal and sublethal effects on intraguild preys/predators (Baudrot et al. 2020), they may affect the population dynamics of biocontrol agents and consequently compromise the success of biocontrol.

While pesticides affect behavioral interactions among community members with potential consequences for biological invasions (Guedes et al. 2016), it remains difficult to establish how pesticide may affect the success of an invasive species involved in IGP with indigenous organisms. Therefore, so far this is the first study on this topic.

In southeastern Canada, two ubiquitous ladybeetle competitors occur sympatrically in natural and agricultural landscapes. First, the multicolored Asian ladybeetle, *Harmonia axyridis* Pallas (Col., Coccinellidae), a successful biocontrol agent in a variety of crops (Brown et al. 2011; Riddick 2017), is widely recognized as one of the most invasive insects in the world (Snyder and Evans 2006; Brown et al. 2011; Vandereycken et al. 2012). This species intentionally or accidentally introduced in numerous ecosystems worldwide is involved in competitive interactions through exploitative competition and intraguild predation with native species and has a higher fertility and fecundity than indigenous ladybeetle species (Michaud 2012; Soares et al. 2008; Santos et al. 2013). Furthermore, when engaging in intraguild predation interactions, the invader has a dominant role as intraguild predator (Lucas 2005, 2012; Ware et al. 2009; Hautier et al. 2011; Brown et al. 2015; Mirande et al. 2015).

Second, the indigenous Twelve spotted ladybeetle, *Coleomegilla maculata* (DeGeer) (Col., Coccinellidae), a sympatric native competitor of *H. axyridis*, in numerous agricultural and natural ecosystems (Kabaluk et al. 2006; Lucas et al. 2007; Bélanger and Lucas 2011) is a eurytopic generalist predator (Cottrell and Yeargan 1998; Lucas et al. 2004a, b; Lundgren et al. 2004; Fréchette et al. 2008). It frequently engages in mutual IGP with other coccinellid species and more specifically with the invasive *H. axyridis* (Gagnon et al. 2011).

Both ladybeetle species are exposed to an array of pesticides in different crops (Dai et al. 2020; Lucas et al. 2004a, b). One of them, Novaluron (Rimon® EC 10), considered as a reduced-risk insecticide (RRI), is a chitin synthesis

inhibitor (Cutler and Scott-Dupree 2007), used to control the codling moth, *Cydia pomonella* (L.) (Lep., Tortricidae), in apple orchards (Cormier et al. 2016). The invasive Asian ladybeetle is considerably more susceptible to the insecticide than its indigenous intraguild competitor (Cabrera et al. 2017, 2018).

The aims of this study are (1) to compare the adaptive value of mutual IGP, for the two coccinellids, the invasive and the indigenous species, when the intraguild prey is subject to exposure to an insecticide used in the invaded area and (2) to investigate whether the effect of this exposure on the adaptive value of IGP disappears over time through neutralization of the insecticide by the intraguild prey. We hypothesize that the adaptive value of IGP for the indigenous tolerant twelve spotted ladybeetle will be maintained in the presence of the insecticide, whereas it will be greatly reduced for the susceptible invasive ladybeetle. We also hypothesize that the adaptive value of IGP for the susceptible invasive species will be recovered over time once the indigenous IG prey has neutralized the insecticide.

Materials and methods

Insects

Laboratory rearing of *C. maculata* and *H. axyridis*, morph *Succinea* (Honek et al. 2020), originated from ladybeetle adults collected in the field in Quebec in 2016 at Sainte-Agathe (46°23′0.3″N and 71°24′33.5″W). New individuals coming from the field were added every year to the rearing to improve genetic diversity. These rearings were in a growth chamber at 24 °C, 16L: 8D, and 70% RH at Laboratoire de Lutte Biologique from the Université du Québec à Montréal. Insects were provided with pollen, sweetened water solution (10% sugar), and green peach aphids, *Myzus persicae* (Sulz.) (Hem., Aphididae), reared on potato plants, *Solanum tuberosum* L. Pollen and sweetened water were provided to coccinellids to simulate diet in natural conditions (Berkvens et al. 2007; Michaud and Grant 2005; Lucas et al. 2004a, b; Wolf et al. 2018). Potato plants were grown in a greenhouse and were inoculated with *M. persicae* after two weeks. Plants containing aphids were placed in a rearing chamber at 24 °C, 16L: 8D, and 70% RH and served to maintain a constant source of prey for both ladybeetle species. Coccinellid eggs were removed daily from rearings and were placed in a fridge at 4 °C for no more than 4 days before placing them at the same time in a rearing chamber at 24 °C, 16L: 8D, and 70% RH. Eggs hatched after 3 days and coetaneous larvae were used in bioassays.

Insecticide

The insecticide Rimon® 10 EC (Makhteshim Agan of North America, Raleigh, NC) was used in all bioassays at a field rate recommended for apple orchards in Quebec (100 g a.i. ha^{-1}). The spray volume most used by apple growers (1000 L ha^1) was considered to calculate concentrations for bioassays: 100 mg a.i. L^{-1} novaluron.

Bioassays

A first bioassay was intended to assess the effect of novaluron on intraguild predation by both coccinellid species on one another. A second bioassay was performed to explore neutralization of the insecticide by the indigenous *C. maculata* as an intraguild prey, and its effect on the invasive *H. axyridis* as the intraguild predator.

Effect of the insecticide on intraguild predation

Experimental units consisted in a newly molted second instar *C. maculata* or *H. axyridis* larvae (intraguild predator), individually weighted with a Metler Toledo AE163 balance, and placed in 5 cm Petri dishes with 5 first instar larvae from the opposite ladybeetle species (intraguild prey), previously treated with novaluron or water with a Potter Tower Burkard Manufacturing (1 mL solution and 2 mg cm^{-2} aqueous insecticide deposit) and killed by freezing to avoid cannibalism (and thawed for 3 min at 20 °C before the bioassay) (Fig. 1). Each experimental unit was replicated 17 times. Intraguild predators and prey were left together during 24 h. Leftovers of intraguild prey were noted and removed afterward. After that, intraguild predators were fed with *M. persicae* aphids daily until the adult stage. Mortality and stage of development were noted every day. Once the individuals became adults, they were weighted again.

Recovery of adaptive value of intraguild predation over time.

Three time points of neutralization of the insecticide by the intraguild prey were considered in this bioassay:

(a) *T0*: first instar larvae of the indigenous ladybeetle or aphids were treated with insecticide or water and immediately killed. Thus, the intraguild prey does not have time to neutralize the insecticide.

(b) *T-24 h*: first instar larvae of the indigenous ladybeetle or aphids were treated with insecticide or water and killed 24 h after. Thus, the intraguild prey has 24 h to neutralize the insecticide.

(c) *T-Molt*: first instar larvae of the indigenous ladybeetle or aphids were treated with insecticide or water and killed after molting to 2nd instar, which occurred between 4 and 5 days after treatment. Thus, the intragu-

Intraguild predator	*H. axyridis*	*C. maculata*
Intraguild prey	*C. maculata*	*H. axyridis*
Intraguild prey treated with water		
Intraguild prey treated with insecticide (novaluron)		

: First instar *C. maculata* larvae

: First instar *H. axyridis* larvae

: Second instar *C. maculata* larvae

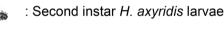: Second instar *H. axyridis* larvae

Fig. 1 Experimental design used to assess the effect of novaluron on IGP. Each experimental unit consisted of a second instar larva (intraguild predator) placed with five first instar newly hatched larvae from the opposite coccinellid species. Each experimental unit was replicated 17 times

ild prey has more than 24 h to neutralize the insecticide and undergoes molt.

In order to compare the effect of insecticide neutralization by the intraguild prey on the intraguild predator, three treatments were included in each time point of neutralization (Fig. 2):

1. *XG-Water*: Aphids treated with water, representing optimal extraguild prey, and offered ad libitum to intraguild predators,
2. *IG-Water*: 1st instar larvae of the indigenous lady beetle, treated with water, and
3. *IG-Insecticide*: 1st instar larvae of the indigenous lady beetle, treated with the insecticide (novaluron).

A Potter tower was used to treat larvae (1 mL solution and 2 mg/cm^2 aqueous insecticide deposit). All preys were weighted prior to freezing. There were twelve replicates of experimental units consisting of five *C. maculata* larvae, thawed during 3 min at 20 °C, and placed in a 5-cm Petri dish with a newly molted 3rd instar *H. axyridis* larva, previously starved during 24 h. Third instar larvae were used as

intraguild predators in this bioassay, in order to encourage IGP by reducing the prey/predator body mass ratio. Intraguild predators were in contact with extraguild and intraguild prey for 24 h. Intraguild and extraguild prey leftovers were noted and removed afterward, and intraguild predators were fed with fresh green peach aphids daily until the adult stage. Mortality was assessed daily, and *H. axyridis* individuals were weighed after reaching adult stage.

Statistical analyses

Differences in frequencies of mortality in both bioassays were evaluated with a χ^2 test ($\alpha = 0.05$) (Sokal and Rohlf 1995). Bonferroni corrections of the *p* value were performed to detect differences among treatments (McDonald 2009). Survival was analyzed by means of Kaplan–Meier survival analysis and a proportional hazard model to detect differences among groups (SAS Institute 2016).

Voracity of the intraguild predator was calculated by assessing 1st instar larvae (intraguild prey) leftovers after 24 h of IGP. Mass of consumed prey (mg) was estimated from percentages of leftover prey and weight of prey before freezing (See section of insecticide neutralization by the

Neutralisation time points	Intraguild prey		Extraguild prey
T0: Indigenous ladybeetle L1 and aphids treated and immediately consumed.	**IG-water**	**IG-insecticide**	**XG-water**
T-24 h: Indigenous ladybeetle L1 and aphids treated and consumed 24 h after	**IG-water**	**IG-insecticide**	**XG-water**
T-Molt: Indigenous ladybeetle L1 treated and consumed after molt. Treated aphids consumed.	**IG-water**	**IG-insecticide**	**XG-water**

: First instar *C. maculata* larvae

: Third instar *H. axyridis* larvae
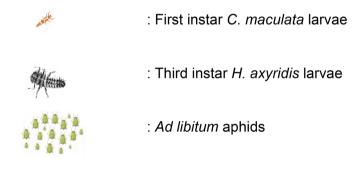
: *Ad libitum* aphids

Fig. 2 Experimental design used to assess recovery of the adaptive value of IGP over time. Experimental units consisted of a third instar *H. axyridis* larva (intraguild predator) placed with five first instar *C. maculata* larvae or a third instar *H. axyridis* larva with ad libitum aphids. Each experimental unit was replicated 17 times

intraguild prey). Weight gained by the intraguild predators at adult stage was calculated subtracting initial third instar larval weight from final adult weight (g). Weight gained as well as voracity was analyzed with independent samples Student's t test ($\alpha = 0.05$) in order to investigate the effect of novaluron on both ladybeetle species. Analysis of variance and the Tukey test or the nonparametric Wilcoxon test and the Steel–Dwass All Pairs test ($\alpha = 0.05$) (SAS Institute 2016) were used to detect differences among treatments in

the case of neutralization by intraguild prey on *H. axyridis,* since data did not always meet the normality assumption. Developmental time of *C. maculata* as the intraguild predator was examined with independent samples Student's t test ($\alpha = 0.05$) in the first bioassay (Sokal and Rohlf 1995), and developmental time of *H. axyridis* in the second bioassay was investigated with the Wilcoxon test ($\alpha = 0.05$) (SAS Institute 2016). JMP software v.12.1 (SAS Institute, Cary, NC) was used to perform all statistical analyses.

Table 1 Voracity of intraguild predators after 24 h feeding on intraguild prey treated with water or insecticide

	Intraguild prey consumed (% ± SE)	
	Control	Insecticide
Indigenous ladybeetle	42.81 ± 7.27 **A**	58.06 ± 7.41 **A**
Invasive ladybeetle	61.56 ± 7.33 **a**	40.00 ± 5.96 **b**

Comparisons are done across rows. Lowercase and uppercase letters indicate statistical comparisons between treatments. Means denoted by a different letter indicate significant differences within treatments. Student's t test ($p < 0.05$)

Results

Effect of the insecticide on intraguild predation

Voracity of intraguild predators

There were no differences in voracity between the insecticide treatment and the control, $t_{(30.99)} = 1.469$, $p = 0.152$ for the indigenous ladybeetle. A different trend was found for the invasive ladybeetle. Less prey were ingested in the insecticide treatment than in the control $t_{(29.37)} = -2.283$, $p = 0.0299$ (Table 1).

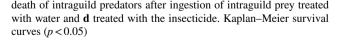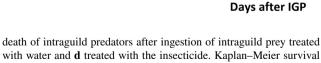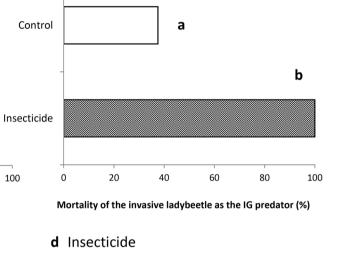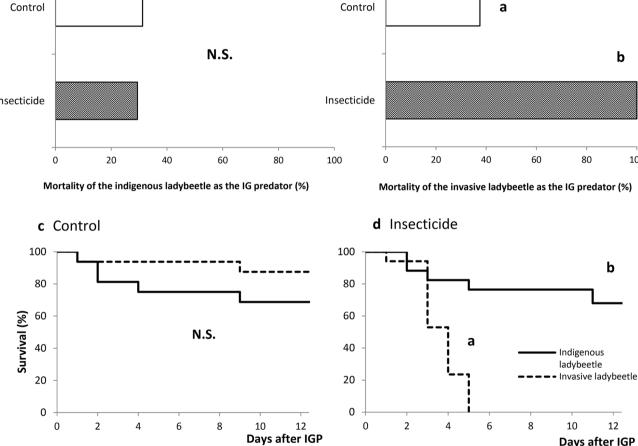**Fig. 3** **a** Mortality of the indigenous ladybeetle as the intraguild predator, **b** mortality of the invasive ladybeetle as the intraguild predator, after 24 h exposure of second instar larvae (intraguild preys) to water or insecticide-treated preys. χ^2 ($p < 0.05$), **c** Survival and time of death of intraguild predators after ingestion of intraguild prey treated with water and **d** treated with the insecticide. Kaplan–Meier survival curves ($p < 0.05$)

Mortality–survival of intraguild predators

After feeding on intraguild prey (first instar invasive ladybeetle) treated with novaluron, the mortality of second instar indigenous ladybeetle larvae was not different from the control, $X^2_{(1)} = 0.01$, $p = 0.908$ (Fig. 3a). Surviving individuals molted normally and completed development until the adult stage. In the case of the invasive ladybeetle, all larvae died after IGP in the insecticide treatment, in which mortality was significantly higher than the control, $X^2_{(1)} = 15.24$, $p < 0.0001$ (Fig. 3b). Survival analysis for intraguild predators, preying on intraguild prey treated with the insecticide, reveals a significant difference between survival of both species over time, $X^2_{(1)} = 12.73$, $p = 0.0004$. All invasive ladybeetle larvae died between the first and fifth day following IGP, and none of the predators were able to molt before death, whereas 70% of indigenous individuals reached the adult stage (Fig. 3d). No significant differences were detected for survival between both ladybeetle species in the control (Fig. 3c).

Developmental time and weight gain (indigenous ladybeetle)

Since all invasive ladybeetle individuals in the insecticide treatment died during the second larval instar, results of developmental time and weight gain were obtained only for the indigenous ladybeetle in this treatment. Developmental time until the adult stage after IGP (for the indigenous ladybeetle in the insecticide treatment) was not different from the control $t_{(21)} = 0.622$, $p = 0.541$ (Fig. 4a).

Weight gain was not statistically different between the control and insecticide treatments, $t_{(17.97)} = 2.08$, $p = 0.052$ (Fig. 4b).

Recovery of adaptive value of intraguild predation over time.

Voracity of the invasive ladybeetle

The invasive ladybeetle consumed similar mass of intraguild prey in all three neutralization time points treated with water: $X^2_{(1)} = 5.0$, $p = 0.082$. When comparing the voracity of the invasive ladybeetle preying upon the indigenous ladybeetle treated with insecticide, there were slightly more intraguild preys consumed in T0 compared to T-24h or T-Molt. However, the insecticide-treated intraguild preys consumed at T-24h were not different from T-Molt: $F_{(2)} = 11.12$, $p = 0.0002$ (Table 2).

Mortality–survival of the invasive ladybeetle as the intraguild predator

Mortality of the invasive *H. axyridis* was not different among the three time points of prey neutralization (T0, T-24h and
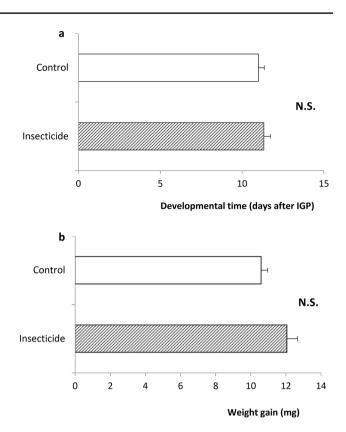

Fig. 4 a Developmental time (days + SE) and **b** weight gain (mg ± SE) of the indigenous ladybeetle, from second instar larvae until adult stage, after 24 h feeding on intraguild prey treated with water or insecticide. Student's *t* test ($p < 0.05$)

Table 2 Voracity of the invasive *H. axyridis* after 24 h preying upon extraguild (XG) and intraguild (IG) prey treated with insecticide or water. Comparisons are done across rows

Treatment	Consumed prey (mg ± SE)		
	T0	T-24 h	T-Molt
XG-Water	7.37 ± 1.95 **a**	9.76 ± 1.20 **a**	7.79 ± 0.93 **a**
IG-Water	0.77 ± 0.10 **A**	0.92 ± 0.17 **A**	1.16 ± 0.18 **A**
IG-Insecticide	1.07 ± 0.05 **A′**	0.40 ± 0.04 **B′**	0.69 ± 0.16 **B′**

Lowercase and uppercase letters indicate statistical comparisons between treatments. Means denoted by a different letter indicate significant differences within treatments. ANOVA or Wilcoxon test ($p < 0.05$)

T-Molt), when consuming water-treated extraguild prey (green peach aphids): $X^2_{(2)} = 0.31$, $p = 0.851$. Similarly, no differences were found among time points when intraguild predators consumed the indigenous *C. maculata* first instar larvae treated with water, $X^2_{(2)} = 0.85$, $p = 0.652$. However, when comparing mortality frequencies of the invasive ladybeetle after feeding on the indigenous ladybeetle treated with novaluron, T-Molt showed significantly less mortality $X^2_{(1)} = 23.22$, $p < 0.0001$; T-24h versus T-Molt: $X^2_{(1)} = 13.55$,

$p = 0.0002$; T0 versus T-Molt: $X^2_{(1)} = 13.38$, $p = 0.0003$ (Bonferroni $\alpha = 0.025$). Moreover, it was found that intraguild predators feeding on prey treated with novaluron in T0 and T-24h had a higher mortality than their controls of extraguild prey and intraguild prey treated with water ($X^2_{(1)} = 20.28$, $p < 0.0001$; T0-IG-Insecticide vs T0-XG-Water: $X^2_{(1)} = 14.4$, $p < 0.0001$; T0-IG-Insecticide vs T0-IG-Water: $X^2_{(1)} = 17.14$, $p < 0.0001$ and $X^2_{(1)} = 19.21$, $p < 0.0001$; T-24 h-IG-Insecticide vs T-24 h-XG-Water: $X^2_{(1)} = 16.22$, $p < 0.0001$; T-24 h-IG-Insecticide vs T-24 h-IG-Water: $X^2_{(1)} = 13.55$, $p = 0.0002$, Bonferroni $\alpha = 0.017$, respectively) (Fig. 5a).

When comparing the survival of the invasive ladybeetle over time among neutralization time points after IGP on prey treated with the insecticide, it was found that 70% of individuals consuming T-Molt prey became adults, whereas all individuals died before nine days after consumption of T0 and T-24h prey (Fig. 5b). The proportional hazard model indicated that this difference was significant: $X^2_{(2)} = 19.91$, $p < 0.0001$. Moreover, individuals in T0/IG-Insecticide were ± 15 times more prone to die than T-Molt/IG-Insecticide individuals ($p < 0.0001$). Similarly, T-24h/IG-Insecticide predator larvae had ± 11 times probabilities of dying than T-Molt-IG-Insecticide larvae ($p = 0.0002$).

It is also important to note that there were no significant differences of survival between the XG treatments and the water IG treatments within the T0 ($X^2_{(1)} = 0.2807$, $p = 0.5962$) and T-24 h ($X^2_{(1)} = 0.0099$, $p = 0.9206$) neutralization time points.

Developmental time and weight gain of the invasive ladybeetle

Data from T0 and T-24 h related to insecticide-treated intraguild preys are absent, since no individual reached the adult stage.

When comparing treatments among all time points, no significant differences were found in the developmental time after IGP, from third instar to adult stage: $X^2_{(6)} = 1.16$, $p = 0.98$ (Fig. 6a).

Similarly, to developmental time, no significant differences were detected in weight gain among treatments: $X^2_{(6)} = 11.93$, $p = 0.064$ (Fig. 6b).

Discussion

The present study demonstrates a drastic differential effect of a reduced-risk pesticide treatment on the adaptive value of intraguild predation for two intraguild predator species. Furthermore, the results demonstrate that these negative effects on the adaptive value of intraguild predation for the invasive participant are annulated over time.

Effect of the insecticide on the adaptive value of IGP for the invasive and the indigenous predators

Our results support our first hypothesis that the adaptive value of IGP, for the invasive *H. axyridis*, is completely lost when preying on intraguild prey treated with the insecticide. Unlike its competitor, the adaptive value of IGP was maintained for the tolerant indigenous *C. maculata* after preying on intraguild insecticide-treated prey for 24 h. Survival success was not different than survival in the absence of the insecticide, and neither voracity weight gain nor the developmental time was altered. Furthermore, this is in accordance with previous research, confirming a different susceptibility of both predator species to the reduced-risk insecticide novaluron (Cabrera et al. 2017, 2018).

IGP is particularly advantageous for the adaptive value of intraguild predators, by removing competitors and potential predators, gaining energy and nutrition, and consequently surviving, developing, and reproducing when extraguild prey densities are low (Polis et al. 1989). For instance, pollen is consumed by coccinellids at the beginning of the growing season in temperate regions, when prey densities are low. But it does not allow maturation of the ovaries, and therefore, IGP is beneficial at that period (Lucas 2012). Additionally, by the end of the season, IGP, for several species including *H. axyridis*, can help immature stages to reach the overwintering stage (adult stage for ladybeetles) (Labrie et al. 2008; Hodek 2012). However, our results show that an insecticide can drastically alter the outcome of IGP and even completely cancel out its adaptive value for the intraguild predator.

Intraguild prey containing novaluron do not deter the invasive ladybeetle from consuming it, and therefore, mortality is devastating for this insect after being exposed to contaminated prey for only 24 h. This means that in the presence of novaluron, IGP is no longer an advantage for this predator. The adaptive value is completely lost, and IGP becomes a highly risky behavior, which it is not the case for the indigenous *C. maculata*. Thus, consequences of IGP for both the indigenous and the invasive ladybeetles are reversed by the insecticide.

At a population level, a shift in the dominance of species on the coccinellid assemblage might be expected, particularly under conditions favoring IGP, such as scarcity of extraguild prey (Lucas et al. 1998) or habitats with little structure (Janssen et al. 2007; Gagnon and Brodeur 2014). In this context, an insecticide might reduce populations of an invasive species, releasing populations of indigenous coccinellids as well as other natural enemies. Declines of natural enemies of Hemipterans, especially indigenous lady beetles in several regions where *H. axyridis* has established, have been attributed to interspecific competition for resources and the strong intraguild predation abilities of this
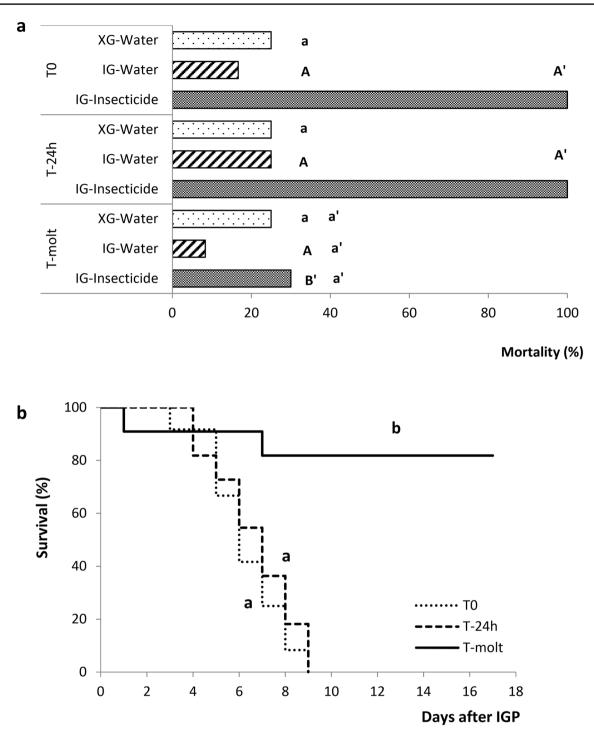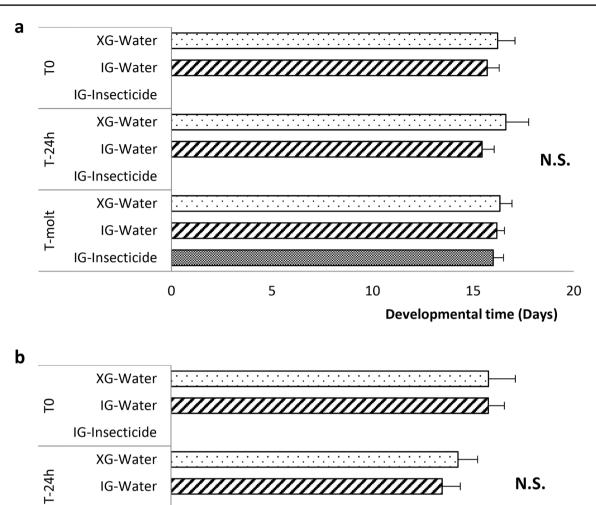
Fig. 5 a Mortality of the invasive ladybeetle (intraguild predator), after 24 h exposure of third instar larvae to water or insecticide-treated intraguild preys (IG-Water and IG-Insecticide, respectively), and for extraguild prey treated with water (XG-Water) at three time points of neutralization of the insecticide by the intraguild prey (χ^2 ($\alpha = 0.05$)) and **b** survival of intraguild predators after ingestion of intraguild prey treated with insecticide at three time points of neutralization. Kaplan–Meier survival curves ($p < 0.05$). *T0*: first instar larvae of the indigenous ladybeetle or aphids, insecticide or water treated, and immediately killed; *T-24 h*: first instar larvae of the indigenous ladybeetle or aphids, insecticide or water treated and killed 24 h after; *T-Molt*: first instar larvae of the indigenous ladybeetle or aphids, insecticide or water treated and killed after molting to second instar; *XG-Water*: Aphids treated with water; *IG-Water*: first instar larvae of the indigenous ladybeetle, treated with water; and *IG-Insecticide*: first instar larvae of the indigenous ladybeetle, treated with insecticide (novaluron). Lowercase and uppercase letters indicate statistical comparisons between treatments

Fig. 6 **a** Developmental time (days) of the invasive *H. axyridis*, from third instar larvae until adult stage, after 24 h feeding on intraguild prey treated with water or insecticide and extraguild prey; **b** Weight gain (mg) of *H. axyridis* from third instar larvae until adult stage, after 24 h feeding on intraguild prey treated with insecticide or water and extraguild prey. Wilcoxon test ($\alpha = 0.05$). *T0*: first instar larvae of the indigenous ladybeetle or aphids, insecticide or water treated, and immediately killed; *T-24 h*: first instar larvae of the indigenous ladybeetle or aphids, insecticide or water treated and killed 24 h after; *T-Molt*: first instar larvae of the indigenous ladybeetle or aphids, insecticide or water treated and killed after molting to second instar; *XG-Water*: aphids treated with water; *IG-Water*: first instar larvae of the indigenous ladybeetle, treated with water; and *IG-Insecticide*: first instar larvae of the indigenous ladybeetle, treated with insecticide (novaluron)

invasive species (Pell et al. 2007). Yet, the outcome of these repercussions in communities will depend on susceptibilities of intraguild members to the toxic compound. Responses to insecticides are a consequence of stress related to dose/ concentrations of insecticides, as well as the result of differences in tolerance and resistance between species and populations. As insecticides affect individuals in several ways, they also affect subsequent interrelated components, such

as heterospecific interactions among co-occurring species. Thus, shifts in species dominance can be the result of insecticide-induced responses (Guedes et al. 2017). For example, a confrontation experiment showed that individuals of the native Southern ant *Monomorium antarcticum* exposed to the neonicotinoid insecticide imidacloprid had decreased aggression toward the invasive Argentine ants *Linepithema humile*. When exposed individuals of this invasive species confronted non-exposed native ants, they were significantly more aggressive, although their survival decreased. Non-exposed individuals of the invasive species were less aggressive but more likely to survive when interacting with exposed native ants (Barbieri et al. 2013).

Recovery of adaptive value of intraguild predation over time.

Our second hypothesis stating that the adaptive value of IGP, lost due to intraguild prey contamination by an insecticide, is recovered over time is also supported by the results. This might be linked to neutralization of the compound by the intraguild prey. Survival of the intraguild predator is significantly higher after feeding on contaminated intraguild prey having molted to the next stage compared to intraguild prey more recently treated. Results of voracity show that this finding is not due to a lower consumption of treated intraguild prey compared to the T-24h treatment. Weight gained by the intraguild predator after predation on treated intraguild prey does not differ from weight gained after consumption of extraguild prey or intraguild prey treated with water at the longest time of insecticide neutralization by the prey, when this has undergone molt. The same trend is observed for the developmental time of the intraguild predator. Therefore, benefits of intraguild predation are recovered over time. In this context, IGP is advantageous for the intraguild predator, when the period between the exposure of the prey to the insecticide and the intraguild predation event is long enough for the prey to neutralize the compound to a non-toxic level for the intraguild predator.

Several phenomena may explain predator susceptibility to insecticides, among these, penetration, absorption, and neutralization may be significant. Penetration through the cuticle and rate of absorption of the compound in the arthropod body following topical contact or gut wall after ingestion may differ among species (Croft 1990; Cutler and Scott-Dupree 2007). Neutralization can also be different among species. Toxic compounds can be neutralized by insects through sequestration (storage of compounds in an unaltered form), increased rates of excretion (removal of the toxic substance without altering its integrity), and detoxification (biochemical transformation of the compound in a way that it won't harm the insect) (Cabrera et al. 2018). Although we do not know how these mechanisms are involved, we

formulate two hypotheses that might explain the recovery of the adaptive value of IGP by the intraguild predator over time: (a) The Molt–Neutralization hypothesis: low penetration of the insecticide through the cuticle/gut wall of the intraguild prey, which is shed during the next molt. Low penetration through the cuticle of other benzoylureas, such as diflubenzuron, has been shown in the literature (Medina et al. 2002). Then, molt can be an opportunity for the insect to eliminate toxic compounds from their bodies, or/and (b) The Excretion–Detoxification–Neutralization hypothesis of the insecticide by the intraguild prey, occurring over time. Detoxification and excretion affect susceptibility of natural enemies to pesticides (Oppenoorth and Welling 1976; Croft 1990), and increased capacity to metabolize and eliminate the toxic compound has been associated with the development of resistance to benzoylureas (Kostyukovsky and Trostanetsky 2006). Thus, the outcome of IGP for the intraguild predator depends on the time that has passed, after exposure of the intraguild prey to the insecticide, specifically the time that is required for the intraguild prey to shed the contaminated cuticle or/and excrete or detoxify the insecticide to levels that will not harm the predator. The ability of the indigenous *C. maculata* to neutralize the insecticide could be explained by a preadaptation to deal with toxic secondary plant compounds, since this species seems to be more phytophagous than the invasive *H. axyridis* (Cottrell and Yeargan 1998; Moser et al. 2008). This hypothesis has already been mentioned in previous articles (Cabrera et al. 2017, 2018), but it must be tested in future research.

The present investigation demonstrates the drastic effects of chemical exposure to beneficial insects and suggests that pesticide regime should be taken in consideration when assessing the ecological and economical impacts of invasive species in a new environment, including potential shifts of species dominance. Studies of lethal and sublethal effects of compounds used in the environment involved (Cabrera et al. 2017, 2018; Desneux et al. 2007; Guedes et al. 2016), including effects on behavior of invaders, and intraguild interactions at a population level, in field and semifield conditions, should be envisaged. Moreover, we are currently conducting research in field conditions, over an entire season.

Novaluron is a larvicide with a broad spectrum of activity on several insects (Mills et al. 2015) and is highly toxic for the invasive *H. axyridis* (Cabrera et al. 2017, 2018), as well as for other natural enemies found in orchards, such as the lacewing *Chrysoperla carnea* (Stephens) (Neur., Chrysopidae), the predatory plant bug *Deraeocoris brevis* (Uhler) (Hem., Miridae), the ladybeetle *Hippodamia convergens* Guérin-Méneville (Col., Coccinellidae), and the mite predators *Galendromus occidentalis* (Nesbitt) (Mills et al. 2015) and *Neoseiulus fallacis* (Garman) (Aca., Phytoseiidae) (Lefebvre et al. 2012). Yet, certain natural

enemies are less susceptible to it, as it is the case of *C. maculata* (Cabrera et al. 2017, 2018) and the parasitoid *Aphelinus mali* (Hald.) (Hym., Aphelinidae) (Mills et al. 2015). Because pesticides affect the organisms involved in IGP differentially, impacts of this interaction depend on two main factors: (1) susceptibility of each species to the toxic compound, which can offer refuges for the intraguild prey, and (2) the period between exposure of the prey to the pesticide and the ecological interaction. Accordingly, as mentioned in the previous section, the impact of IGP on coccinellid assemblages as well as on aphidophagous guilds facing pesticides will be determined by the variability of susceptibilities among guild members as well as the timing of the treatment and of the interaction (neutralization of toxic compounds by intraguild preys). Moreover, insecticides can modify the composition of guilds, altering occurrences of competitors (Lucas et al. 1998), which changes the dynamics of the guild and the frequency of encounters for IGP. Consequently, and considering other effects of pesticides on natural enemies (Guedes et al. 2016), we infer that the composition of guilds as well as the subsequent interactions within the entomophagous guilds is greatly modified by pesticide treatments, which means that functional diversity is also altered and therefore the efficacy of the guild as the main tool for natural control of insect pests.

Global pesticide use in 2014 was estimated at 2.7 kg ha^{-1} (Zhang 2018). Novaluron, a "reduced-risk insecticide", is only one of the pesticides used worldwide. Our research highlights its side effects on the guild of beneficial organisms and their ecological consequences. Yet, we do not know the direct and indirect effects of other compounds in agroecosystems, nor the consequences on the ecosystem services of guilds, particularly on biocontrol by interfering with IGP.

The present study reports the impact of an insecticide on an adaptive behavior for a top predator, which is one of the key factors associated with the invasive status of the multicolored Asian ladybeetle worldwide (Castro-Guedes et al. 2020). At an ecological level, our findings show that an insecticide might alter not only guild composition but also disturb intraguild interactions and consequently alter cascade effects in trophic systems.

Author Contribution

PC and EL conceived and designed the study. MB and VC conducted the bioassays, and PC analyzed data and mainly wrote the manuscript. DC and EL revised the manuscript. All authors contributed to and approved the manuscript.

Declaration

Conflict of interest The authors declare that they have no conflict of interest.

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