

Antagonistic interactions between an invasive alien and a native coccinellid species may promote coexistence

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Summary

1. Despite the capacity of invasive alien species to alter ecosystems, the mechanisms underlying their impact remain only partly understood. Invasive alien predators, for example, can significantly disrupt recipient communities by consuming prey species or acting as an intra-guild predator (IGP).

2. Behavioural interactions are key components of interspecific competition between predators, yet these are often overlooked invasion processes. Here, we show how behavioural, non-lethal IGP interactions might facilitate the establishment success of an invading alien species.

3. We experimentally assessed changes in feeding behaviour (prey preference and consumption rate) of native UK coccinellid species (*Adalia bipunctata* and *Coccinella septempunctata*), whose populations are, respectively, declining and stable, when exposed to the invasive intra-guild predator, *Harmonia axyridis*. Using a population dynamics model parameterized with these experimental data, we predicted how intraguild predation, accommodating interspecific behavioural interactions, might impact the abundance of the native and invasive alien species over time.

4. When competing for the same aphid resource, the feeding rate of *A. bipunctata* significantly increased compared to the feeding in isolation, while the feeding rate of *H. axyridis* significantly decreased. This suggests that despite significant declines in the UK, *A. bipunctata* is a superior competitor to the intraguild predator *H. axyridis*. In contrast, the behaviour of non-declining *C. septempunctata* was unaltered by the presence of *H. axyridis*.

5. Our experimental data show the differential behavioural plasticity of competing native and invasive alien predators, but do not explain *A. bipunctata* declines observed in the UK. Using behavioural plasticity as a parameter in a population dynamic model for *A. bipunctata* and *H. axyridis*, coexistence is predicted between the native and invasive alien following an initial period of decline in the native species. We demonstrate how empirical and theoretical techniques can be combined to understand better the processes and consequences of alien species invasions for native biodiversity.

Key-words: aphid, behaviour, biocontrol, intraguild predation, ladybird, ladybug, natural enemies, non-consumptive interactions

Introduction

Invasive alien species are a significant global driver of biodiversity change and decline (Vitousek *et al.* 1997; Gure-

vitch & Padilla 2004; Hooper *et al.* 2005). Globalization of trade and commerce has led to world-wide, human-mediated dispersal of animals into novel environments (Mack *et al.* 2000). Invading alien species can occupy all trophic levels (*e.g.* herbivore, omnivore and predator) within a community (Kenis *et al.* 2009) and can affect

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native species through resource competition, predation or introduction of novel pathogens (Mack *et al.* 2000; Snyder & Evans 2006; Kenis *et al.* 2009; Vilcinskas *et al.* 2013). Correlations between invasive alien dominance and native decline have been reported (Roy *et al.* 2012); yet, data which confirm a causal link are, in many cases, anecdotal, speculative and based on limited observation (Gurevitch & Padilla 2004). A better understanding of the nature and dynamics of species' invasions is much needed; for example, the mechanistic basis of invasive alien establishment and spread (Mack *et al.* 2000; Traveset & Richardson 2006; Vilà *et al.* 2009; Galiana *et al.* 2014). In particular, the behavioural effects of non-lethal competition between native and invasive animal species may offer an insight on the mechanisms underpinning species invasions (Chapple, Simmonds & Wong 2012; Peck *et al.* 2014).

The occurrence of invasive alien predators often correlates with declines in the abundance of native predators and shared prey, with cascading effects potentially disrupting community function (Moran, Rooney & Hurd 1996; Snyder & Ives 2001; Pratt, Coombs & Croft 2003). For example, invasive alien predators often indirectly compete with native predators via consumption of shared prey (Fig. 1, arrow 1) (Parker *et al.* 1999). Furthermore, they may infiltrate or generate networks of intraguild predation (IGP) whereby the dominant predatory species can directly consume competitors (intraguild prey), thereby reducing the abundance of the weaker competitor (Fig. 1, arrow 3) as well as the shared prey (Polis, Myers & Holt 1989).

As with predator–prey interactions generally, intraguild predators also have the potential to alter prey (Fig. 1, arrow 2) and intraguild prey (Fig. 1, arrow 4) behaviour. This can ultimately alter population dynamics. Such changes in prey behavioural traits could be considered as non-consumptive (or non-lethal) effects. While affecting population dynamics, they are not based directly on changes in density (Preisser, Bolnick & Benard 2005) and include altered prey-foraging, habitat use, life-history shifts and induced changes in morphology (Tollrian & Harvell 1998; Relyea 2001). Competitive interactions between predatory species frequently operate primarily via such behavioural mechanisms (Steffan & Snyder 2010). It is well documented, for example, that intraguild prey can detect and actively avoid encounters with intraguild predators (Choh *et al.* 2010; Steffan & Snyder 2010; Meisner *et al.* 2011). The resulting changes in behaviour can drive alterations in ecosystem function to the same extent as consumptive interactions (Ives, Cardinale & Snyder 2005; Preisser, Bolnick & Benard 2005; Bruno & Cardinale 2008; Steffan & Snyder 2010).

The predatory coccinellid beetle *Harmonia axyridis* (Pallas) has recently spread from Asia into continental Europe and North America (Brown *et al.* 2008a). Since 2004, *H. axyridis* has established itself in the UK, either via accidental human transport or natural dispersal,

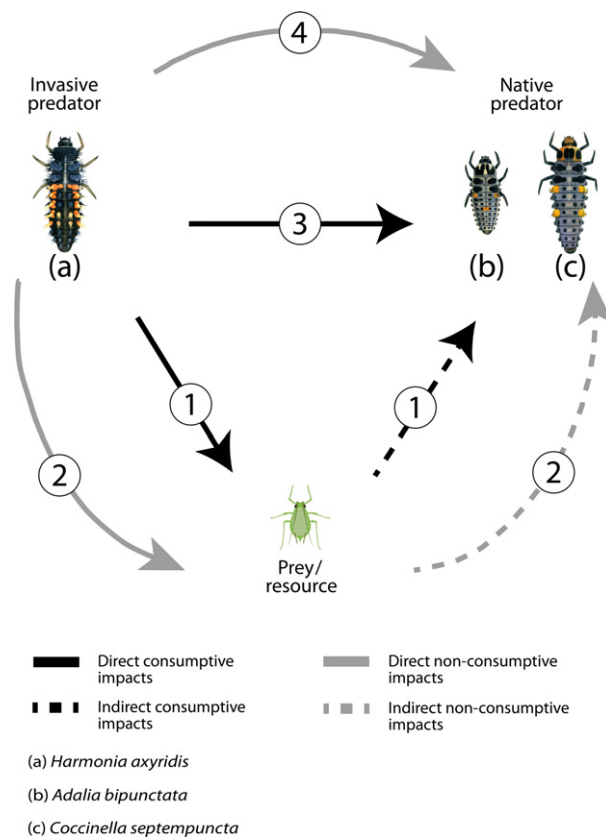


Fig. 1. Major mechanisms by which invasive predators might negatively impact native predators. (1) Predation by invasive species results in resource (prey) depletion; (2) non-consumptive impacts on resource (e.g. modification of prey behaviour such as migration); (3) intraguild predation (IGP) – invasive predator consumes native predator; (4) non-consumptive impacts of invasive predator on native predator (e.g. native alters feeding behaviour). Solid lines represent direct impacts of invasive predator, dashed lines present indirect impacts. Images of fourth larval stage coccinellids show relative sizes differences between species (a) *H. axyridis*, (b) *A. bipunctata* and (c) *C. septempunctata*.

becoming one of the most abundant coccinellid species nationally (Brown *et al.* 2008b). Field observations have revealed that as the abundance of *H. axyridis* has increased, native coccinellid populations, such as *Adalia bipunctata* (L.) and *Propylea quatuordecimpunctata* (L.), have shown a concurrent decline (Brown *et al.* 2011; Roy *et al.* 2012). This, however, is not true for all native coccinellids; *Coccinella septempunctata* (L.) populations, for example, have not declined and have remained stable across Europe despite the arrival of *H. axyridis* (Roy *et al.* 2012).

Intraguild predation occurs between many invasive predatory arthropod species as a result of their generalized feeding habits spanning multiple trophic levels (Snyder & Evans 2006). Laboratory experiments suggest that part of the success of *H. axyridis* may stem from its role as an intraguild predator, readily consuming the eggs and larvae of native coccinellid species (Katsanis *et al.* 2013). Although explicit evidence of egg consumption in the field

is anecdotal (Smith & Gardiner 2013), gut content analysis of *H. axyridis* suggests some consumption of native coccinellids does occur (Thomas *et al.* 2013). Numerous laboratory studies have also documented intraguild predation between *H. axyridis* and other coccinellids across all life stages (Pell *et al.* 2008; Rondoni, Onofri & Ricci 2012; Katsanis *et al.* 2013). In contrast, coccinellids native to the UK such as *A. bipunctata* and *C. septempunctata* have been found to either not attack *H. axyridis* (Rondoni, Onofri & Ricci 2012) or, as intraguild prey, *H. axyridis* represents a very poor diet (Yasuda & Ohnuma 1999). The precise mechanism underpinning the detrimental impact of this invasive alien predator on native predatory coccinellids remains unclear. Non-consumptive trait changes in intraguild predator and prey, for example, as has been observed with a predatory mite (Choh *et al.* 2010) and with a parasitoid (Meisner *et al.* 2011) species does, therefore, have the potential to explain the success of the alien *H. axyridis*.

In this study, the prediction that *H. axyridis* would share a similar preference for aphid prey–nymphal stages as spatially co-occurring native coccinellid species is tested. The occurrence of such sharing would confirm the potential for competitive intraguild interactions. Non-consumptive trait changes in declining and stable native coccinellid species' populations when exposed to *H. axyridis* (Fig. 1, arrow 4) were also investigated. It was predicted that the native *C. septempunctata* (IG prey), which has not declined in the UK since the appearance of *H. axyridis*, would require a higher consumption rate of aphid prey compared to *H. axyridis* to facilitate coexistence, as predicted by IGP theory. In contrast, it was expected that the declining native *A. bipunctata* (IG prey) would not show the compensatory feeding behaviour required for coexistence. Finally, and using the study's data to parameterize, a model of intraguild predation for the two native species and the invasive is constructed. The model captures the impacts of the predicted trait changes on coccinellid abundance over multiple generations and confirms the significance of these behavioural responses on the persistence or extinction of species in IGP systems.

Materials and methods

STUDY SYSTEM

The invasive coccinellid *H. axyridis* (IG predator) and two coccinellid species native to the UK (*C. septempunctata* and *A. bipunctata*, both IG prey) were used in the laboratory experiments. Voltinism in *H. axyridis* and *A. bipunctata* is dependent on temperature and food availability; both are typically reported as bivoltine (Brown *et al.* 2008b). In contrast, *C. septempunctata* is univoltine in the UK, but may be multivoltine in warmer climates (Hodek, Honek & van Emden 2012). Coccinellids were collected from the field in Oxfordshire, UK, during May 2013. Low numbers of *A. bipunctata* from the field required supplementing with individuals obtained from a bio-control supplier (Adavalu S. P. R. L., Burdinne, Belgium). All coccinellid species were reared for

at least one 'laboratory generation' in a controlled environment (20 ± 1 °C, 16-h photoperiod) with a diet of mixed age *Acyrtosiphon pisum* Harris. Field and commercially reared *A. bipunctata* were mixed for the laboratory generation to minimize the impact of the two sources. Coccinellid larvae were starved for 24-h prior to being used in trials.

Using natural enemies to control aphid pests of high value covered crops such as raspberry (Wittwer & Castilla 1995) is becoming increasingly common. This is particularly so with global efforts and legislation to reduce pesticide usage [e.g. European Union Regulation (EC) No. 1107/2009]. Generalist predators, such as the coccinellid species used in this study, can be very effective at reducing pest numbers (Symondson, Sunderland & Greenstone 2002). The European large raspberry aphid, *Amphorophora idaei* (Börner), used as the focal prey species in this study, is a specialist phloem-feeding herbivore and the most significant insect pest of raspberry (*Rubus idaeus* L.) (McMenemy, Mitchell, & Johnson 2009). Despite extensive plant breeding campaigns, resistance to this species has now largely broken down in the UK, so it is germane therefore to examine the sustainability of predator control of this species in a wider biological context (Gordon 2008; McMenemy, Mitchell, & Johnson 2009). Moreover, *A. idaei* may extrapolate well to morphologically similar species such as the pea aphid (*A. pisum*), a global pest of legumes. Indeed, this comparability was the rationale for using *A. pisum* for rearing purposes since predator feeding behaviour on either aphid species was indistinguishable. The aphid culture was initiated from field-collected aphids at the James Hutton Institute, Dundee, UK (JHI), and maintained (20 ± 1 °C, 16-h photoperiod) for multiple generations on raspberry (cv. Malling Landmark). Both experiments 1 and 2 took place in a controlled environment room (20 ± 1 °C, 16-h photoperiod); aphid and coccinellid individuals were used only once per replicate arena.

Experiment 1: Do invasive intraguild predators share prey preferences with native predators?

To identify any preferences for specific nymphal stages of their aphid prey, each larval stage of the three coccinellid species was given a choice of 50 *A. idaei* comprising ten apterous adults and ten of each aphid nymphal stage (I–IV). These were placed into a circular arena (185-mm-diam., 25-mm-high Petri dish) with a pane of glass acting as a lid. Fluon® was applied to the dish sides, preventing the escape of aphids and coccinellids. A first larval stage coccinellid was placed in the centre of the arena and left for 1 h, after which, the larva was removed and the number of aphids of each nymphal stage consumed counted. This bioassay was repeated ten times for each coccinellid larval stage (stages I–IV) and then for each coccinellid species ($\times 3$), giving a total of 120 bioassays. Assays were randomly assigned to 12 temporal blocks, 10 assays per block.

Experiment 2: Does intraspecific competition alter coccinellid feeding behaviour?

To assess the impact of competition on preference and feeding rate on a shared prey, 25 *A. idaei*, comprising five apterous adults and five of each of the four nymphal stages, were chilled at -20 °C for 15 min prior to the start of the experiment. This killed the aphids while ensuring that their tissue remained intact and palatable to coccinellid larvae (Roy *et al.* 2008). This also

allowed rapid and accurate identification of the aphid nymphal stage consumed. The aphid cadavers were randomly assigned to 25 points around the circumference of the circular arena. Two coccinellid larvae (larval stage IV) in pairwise hetero- and conspecific combinations were placed in the centre of the arena. One of the two larvae was chosen randomly and marked with non-toxic paint to aid in species identification during subsequent video analysis. Each bioassay ran for 1 h, and behaviour was recorded using a high-definition webcam (Logitech 920). Video footage was later viewed to determine the number of each aphid nymphal stage consumed by each coccinellid larva. Pairs were reversed so that each acted as a focal species. Bioassays were then repeated for each species combination, including a control with no competing hetero- or conspecific individuals ($n = 10$), giving a total of 90 bioassays.

STATISTICAL ANALYSIS

Statistical analysis was performed with R version 3.0.2 (R Core Team 2014). Experiment 1: We estimated prey preference as a function of aphid nymphal stage and coccinellid larval stage by fitting a flexible generalized additive mixed-effects model (GAMM) using the `gamm4` package (Wood & Scheipl 2014) treating 'preference' as a Poisson, count-based response variable (number eaten). Individual coccinellid identity was fitted as a random term because there were multiple observations (*i.e.* the number eaten of each aphid nymphal stage) per individual predator. Temporal block was also fitted as a random term to account for variation across temporal runs. The use of GAMMs allowed for nonlinearities in the surface representing the aphid prey–nymphal stage and predator larval stage pattern of consumption. The model was specified as a tensor product smooth (Wood, Scheipl & Faraway 2013) constructed from the smooths of individual covariates aphid nymphal stage and coccinellid larval stage. In `gamm4`, this is specified as $number\ eaten \sim s(\text{aphid nymphal stage}, \text{coccinellid larval stage}, by = \text{coccinellid species}), random = \sim(I|id) + (I|block)$.

In this instance, the use of GAMM significantly outperforms the equivalent GLMM ($\chi^2_{(33)} = 416.18$, $P < 0.0001$). The model format allows the creation of a response-surface where the interaction effect of aphid nymphal stage and coccinellid larval stage can be clearly seen (Inouye 2001). This model allows the effects of each variable to be assessed and formally allows visualization of peaks, ridges and valleys in preference for each species. A comparison between predatory species can therefore reveal overlapping or non-overlapping preference for each prey–nymphal stage.

Experiment 2: A similar model structure to that described above (Experiment 1) was fitted to feeding rate as a function of competition. Using a GAMM with a binomial error distribution, the response variable, feeding rate, was generated as a proportion of the number of aphids available – number of aphids eaten. The number of aphids available varied depending on the number consumed by the competing coccinellid. Using either the maximum number of aphids available (five) or the number of aphids not consumed by the competitor had minimal effect on the final outcome of the analysis. The latter was, however, the most conservative result and was chosen for use. Individual arena was used as a random term to account for temporal variation between runs. Each focal species was analysed separately.

Minimum adequate models for experiments 1 and 2 were determined from the stepwise exclusion of parameters from a full model using log-likelihood tests (Lewis, Butler & Gilbert 2011).

Model fit was assessed using the diagnostics specified within the `gamm4` package.

POPULATION DYNAMIC MODEL

To predict the impact altered feeding behaviour might have on the population dynamics of competing coccinellid species, a modified version of the classic intraguild predation dynamic model based on the Lotka–Volterra framework (Holt & Polis 1997) was developed. The expected outcomes of three potential intraguild interactions were given by:

$$\text{Shared resource } (H) \quad \frac{dH}{dt} = bH \left(1 - \left(\frac{H}{K} \right) \right) - NaH - Pa'H$$

$$\text{Intraguild Prey } (N) \quad \frac{dN}{dt} = e(NaH) - sN - P\alpha N$$

$$\text{Intraguild Predator } (P) \quad \frac{dP}{dt} = e'(Pa'H) + \beta(P\alpha N) - s'P$$

where b is the per capita birth rate and k is the carrying capacity of H ; treated as constants for the purpose of this study, parameters were based on Holt & Polis (1997). Parameters a and a' are the attack rates of N and P on shared resource H , respectively. Feeding rate recorded in Experiment 2 was used as a proxy for attack rate and was used to parameterize a and a' . The attack rate of the intraguild predator on the intraguild prey is denoted by α ; the conversion efficiency of prey into predators is represented by e , e' and β , which is relative to body size in coccinellids (Mishra, Omkar Kumar & Pandey 2012). Using mass as a proxy for size, the fourth instar *A. bipunctata* larvae used in Experiment 2 were found to be approximately 50% smaller than *C. septempunctata* and *H. axyridis* which were a similar size. The parameter used for the conversion efficiency of *A. bipunctata* was therefore half that of the other coccinellid species. The conversion efficiency of intraguild prey into intraguild predator β was treated as a constant based on Holt & Polis (1997). Finally, s and s' are the death rates of N and P , respectively, independent of predator or prey densities. The invasive-native parameters for s and s' were estimated from *a priori* knowledge of factors affecting coccinellid death rate (*e.g.* relative immunity of *H. axyridis* from shared natural enemies and interspecific differences in body size, a proxy for resilience to environmental stochasticity) (Hodek, Honek & van Emden 2012). The population dynamic model was simulated using R using the package 'deSolve' (Soetaert, Petzoldt & Setzer 2010).

Results

EXPERIMENT 1: INDIVIDUAL FEEDING PREFERENCES

All three coccinellid species consumed larger (*i.e.* older) aphid prey as they developed (Fig. 2 – areas in red indicate higher levels of consumption compared to yellow). Both coccinellid larval stage and aphid nymphal stage were significant predictors of the number of aphids consumed by each coccinellid species (Table 1). Furthermore, the effect of coccinellid larval stage and aphid nymphal stage differed between coccinellid species (Table 1). The

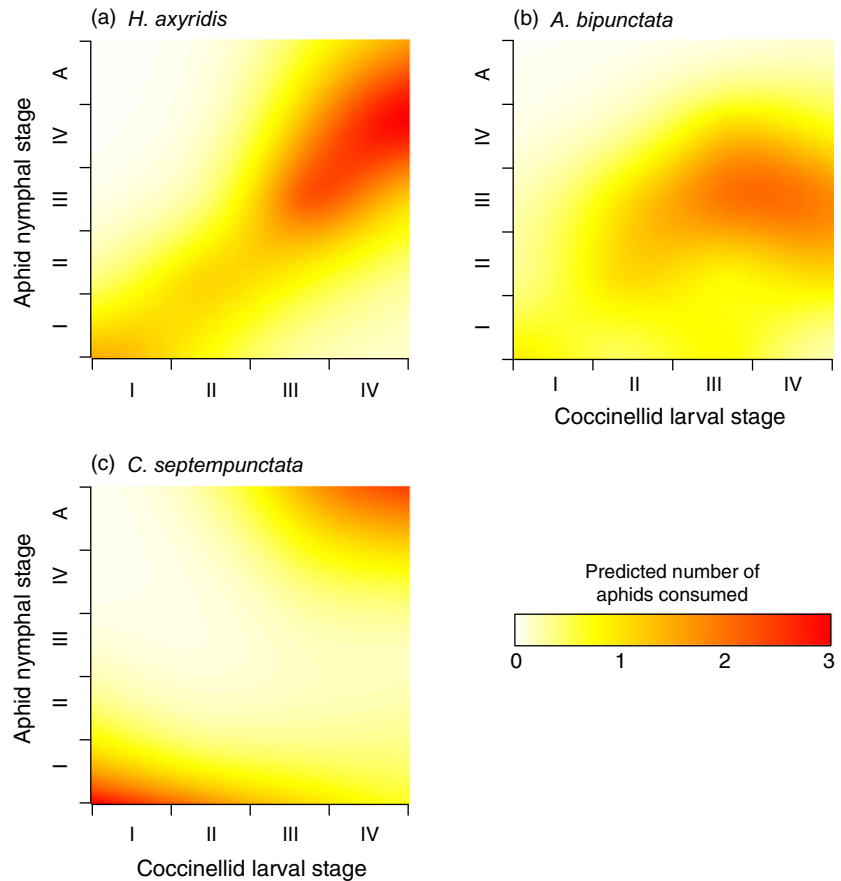


Fig. 2. Predicted output from generalized additive mixed-effect model (GAMM) with mean number of aphids consumed in response to coccinellid larval stage and aphid nymphal stage for the coccinellid species (a) *Harmonia axyridis*, (b) *Adalia bipunctata* and (c) *Coccinella septempunctata*. The heat map gives a qualitative indication of the number of aphids consumed and is derived from GAMM output. For quantitative analysis, see Table 1. Coccinellid larval stage \times aphid nymphal stage = 10 replicates of each.

Table 1. GAMM results summary for the numbers of aphids consumed in relation to coccinellid species (CS), coccinellid larval stage (CL) and aphid prey–nymphal stage (AN). Main effects were evaluated using log-likelihood ratio tests. Graphical output from GAMM presented in Fig. 2

Test	Likelihood ratio test (full vs. reduced)	χ^2	d.f.	<i>P</i>
Coccinellid species (CS)	AN + CL + CS vs. AN + CL	125.19	2	Alk0.0001
Coccinellid larval stage (CL)	AN + CL + CS vs. AN + CS	223.67	3	
Aphid nymphal stage (AN)	AN + CL + CS vs. CL + CS	308.12	4	

number of aphids consumed of each aphid nymphal stage by the larval stages of *H. axyridis* (IG predator) was linear (Fig. 2a), indicating that older *H. axyridis* larvae selected progressively larger aphid prey items. *Harmonia axyridis* (IG predator) and *A. bipunctata* (IG prey) selected similar aphid nymphal stages during their development (Fig. 2a,b, respectively). The *A. bipunctata* prey–nymphal stage relationship was, however, nonlinear, with later coccinellid larval stages (stages III and IV) preferring third nymphal stage aphids (Fig. 2b), compared to *H. axyridis*'s preference for fourth nymphal stage aphids (Fig. 2a). In contrast, prey preference of the stable native coccinellid, *C. septempunctata* (IG prey), differed to the other coccinellids (Fig. 2c). The prey selection of *C. septempunctata* was more complex over its larval development (Fig. 2c). Early larval stages (stages I and II) preferred early aphid nymphal stages, after which prey selection became bimodal with consumption of both early and late

aphid nymphal stages, and finally a strong preference for adult aphids by the fourth larval stage (Fig. 2c).

EXPERIMENT 2: INTERSPECIFIC COCCINELLID COMPETITION

In the absence of interspecific competition (experimental control), the fourth larval stage of all three coccinellid species had a preference for later aphid nymphal stages (Fig. 3a–c with no competitor), mirroring the results from *Experiment 1*. There was no significant interaction between the presence of a competing coccinellid species and aphid nymphal stage consumed (Table 2). Additionally, no intraguild aggression or predation was observed during any of the experiments.

Feeding rate (number of aphids consumed within an hour) of coccinellid larvae in the presence of a competitor differed between focal species (Table 2). The presence of a

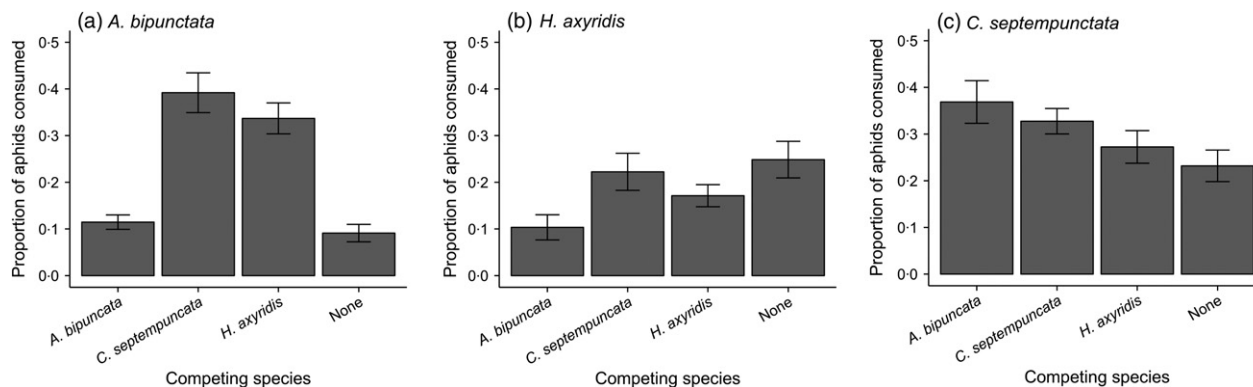


Fig. 3. Proportion (\pm SE) of aphids predicted by generalized additive mixed-effect model (GAMM) to be consumed by (a) *Adalia bipunctata*, (b) *Harmonia axyridis* and (c) *Coccinella septempunctata* in response to the presence of other coccinellids: *A. bipunctata*, *C. septempunctata*, *H. axyridis* or none/control.

Table 2. Generalized additive mixed-effect model (GAMM) results' summary for number of aphids consumed per focal coccinellid species in relation to competing coccinellid species and aphid prey–nymphal stage. Interaction and main effects were evaluated using log-likelihood ratio tests. Entries in bold are statistically significant effects. AN, aphid nymphal stage; CC, competing coccinellid

Focal species	Test	Likelihood ratio test (full vs. reduced)	χ^2	d.f.	<i>P</i>
(a) <i>H. axyridis</i>	Interaction	AN * CC vs. AN + CC	0.63	12	0.996
	Aphid nymphal stage (AN)	AN + CC vs. CC	6.67	2	0.0355
	Competing coccinellid (CC)	AN + CC vs. AN	9.561	3	0.0226
(b) <i>C. septempunctata</i>	Interaction	AN * CC vs. AN + CC	2.402	12	0.879
	Aphid nymphal stage (AN)	AN + CC vs. CC	22.616	2	< 0.0001
	Competing coccinellid (CC)	AN + CC vs. AN	7.797	3	0.05
(c) <i>A. bipunctata</i>	Interaction	AN * CC vs. AN + CC	1.004	12	0.985
	Aphid nymphal stage (AN)	AN + CC vs. CC	10.64	2	0.005
	Competing coccinellid (CC)	AN + CC vs. AN	50.42	3	< 0.0001

competing coccinellid significantly affected the rate of aphid consumption in both the native *A. bipunctata* (IG prey) (Fig. 3a) and the invasive *H. axyridis* (IG predator) (Fig. 3b; Table 2). In the absence of competition (*i.e.* feeding in isolation), the feeding rate of *A. bipunctata* on aphid prey (Fig. 3a) was 63% lower than that of *H. axyridis* (Fig. 3b). When these two species were competing, the feeding rate of *A. bipunctata* (Fig. 3a) was 68% higher (Fig. 3b). When compared to other treatments (no competition, conspecific and *C. septempunctata* competitor), aphid consumption by *H. axyridis* was reduced in the presence of *A. bipunctata* (Fig. 3b). The aphid consumption rate of *A. bipunctata* doubled in the presence of interspecific competition from either *C. septempunctata* or *H. axyridis* (Fig. 3a). In contrast, the feeding rate of *C. septempunctata* did not significantly change in the presence of competitors (Table 2, Fig. 3c). In the presence of *H. axyridis* (IG predator), the feeding rate of *C. septempunctata* (IG prey) was 10% lower than when feeding alone; this reduction was not statistically significant (Fig. 3c).

POPULATION DYNAMIC MODEL

Parameter values used for *H. axyridis* (IG predator) and *A. bipunctata* (IG prey) when feeding in isolation ($b = 1$,

$k = 1$, $a = 0.33$, $d' = 1$, $e = 1$, $e' = 0.5$, $\alpha = 0.5$, $s = 0.5$, $s' = 0.2$, $\beta = 1$) and when competing are same except for $a = 1$ and $a' = 0.32$. Parameter values used for *H. axyridis* (IG predator) and *C. septempunctata* (IG prey) when feeding independently are the same as above, except $a = 0.88$ and $a' = 1$. Again, when *H. axyridis* (IG predator) and *C. septempunctata* (IG prey) are competing, the values are the same, except $a = 1$, $d' = 0.77$, $e = 1$ and $e' = 1$. Contrary to our original predictions, only the declining *A. bipunctata* (IG prey) showed the feeding characteristics of the intraguild prey (*e.g.* greater prey consumption rate than the intraguild predator on the shared resource), whereas the stable *C. septempunctata* (IG prey) did not. In addition, this feeding behaviour was plastic, only changing when the intraguild predator and prey occupied the same physical space. The population dynamic model predicted that coexistence with *H. axyridis* (IG predator) is possible for one (*A. bipunctata*) of the two native intraguild prey species. The model indicates that after an initial period of decline, the observed plasticity in the *A. bipunctata* (IG prey) feeding rate in the presence of *H. axyridis* (IG predator) (Fig. 3a) can allow coexistence between this intraguild prey and predator (Fig. 4b) after approximately 50 generations. The equilibrium between *A. bipunctata* and *H. axyridis* was robust to variation in parameters such as

attack rate of IG predator on IG prey (Fig. S1c) and conversion efficiency of IG prey into IG predators (Fig. S1d). A decrease in the feeding rate of *A. bipunctata* (Fig. S1e) or an increase in the feeding rate of *H. axyridis* (Fig. S1f) increased time to equilibrium to the same degree as reducing the carrying capacity (Fig. S1b).

In contrast, if the feeding rate of these two species, when competing for a shared resource, remained unchanged from their feeding rate in the absence of a competitor, then coexistence would be impossible and the intraguild prey would become extinct (Fig. 4a). For example, the alternative intraguild prey *C. septempunctata* (IG prey) did not significantly alter its feeding rate in the presence of the intraguild predator *H. axyridis* (IG predator) (Fig. 3c) and, consequently, the population dynamic

model predicted rapid decline and extinction of this intraguild prey (Fig. 4c,d).

Discussion

This is one of the few studies to demonstrate the importance of combining empirical and theoretical approaches to understanding the dynamics of invasive alien and native coccinellid species. Empirical evidence shows that when the native *A. bipunctata* (IG prey) and the invasive alien *H. axyridis* (IG predator) are competing for a shared resource, both species alter their feeding rate, but not their preference (*i.e.* prey–nymphal stage/size), for a shared prey resource. On its own, while this novel finding is an interesting example of the

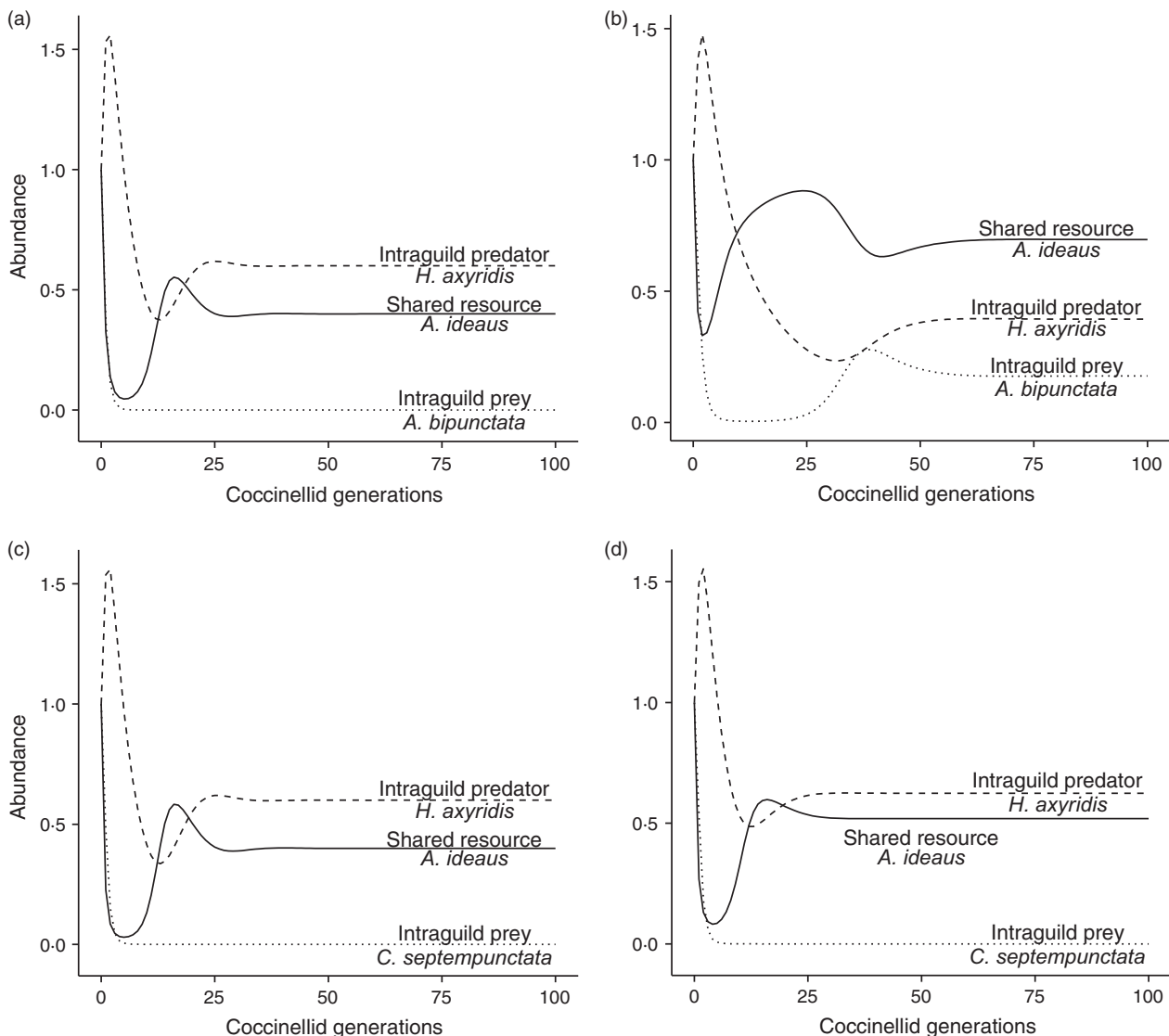


Fig. 4. Dynamics of intraguild predation model adapted from Morin (2011) using feeding rate values derived from Experiment 2 of the current study where intraguild predator *H. axyridis* and intraguild prey (a) *A. bipunctata* and (c) *C. septempunctata* are feeding in isolation (Experiment 1). Intraguild predator and prey (b) *A. bipunctata*, (d) *C. septempunctata* are competing (Experiment 2). Parameter values for (a): $b = 1$, $k = 1$, $a = 0.33$, $d' = 1$, $e = 1$, $e' = 0.5$, $\alpha = 0.5$, $s = 0.5$, $s' = 0.2$, $\beta = 1$. Parameter values for b–d are same as (a), except for a and d' which are as follows: (b) $a = 1$, $d' = 0.32$; (c) $a = 0.88$, $d' = 1$; (d) $a = 1$, $d' = 0.77$.

behavioural plasticity of competing predators, it does not offer an explanation for the significant declines observed in this native coccinellid species. By incorporating the empirical data into a well-established model, it was possible to make predictions of how the observed non-consumptive trait changes might impact the invasion process. After an initial period of significant decline in the native coccinellid species, the model predicts coexistence can only occur between native and invasive alien when both species modify their behaviour (*i.e.* feeding rate). Specifically, the feeding rate of the native predator on the shared prey must be significantly higher than that of the invasive alien. Without this behavioural modification, extinction of the native species is predicted to follow.

Using the data derived from the experiments, the population-level consequences of the observed behavioural trait changes were predicted. Intraguild predation between competing predators has the potential to stabilize food web structure (Polis, Myers & Holt 1989) when the intraguild prey is a better competitor on the shared resource (Morin 2011). The precise outcome is dependent on the interplay between various traits, which include the attack rates on shared prey and on intraguild prey, conversion efficiency of prey and the mortality rate from sources other than intraguild predation or resource abundance (*e.g.* environmental stochasticity, Holt & Polis 1997). The population dynamic model presented in this study does not take into account many of the complexities of predation and competition [such as size and life stage structured dynamics (de Roos *et al.* 2008)] nor the limitations of small-scale and short-term experiments (*e.g.* the long-term impacts of altered feeding rate by IG predators and prey) (Briggs & Borer 2005). Instead, the model provides a demonstration of how one trait change can significantly alter population dynamics between competing predatory species (Holt & Huxel 1997).

Extinction of the intraguild predator would require density-independent mortality of the intraguild predator to be higher than that of the intraguild prey. This is unlikely as an invasive species, *H. axyridis* is currently less susceptible to many forms of predation (Soares *et al.* 2008; Sloggett *et al.* 2011), parasitism (Pell *et al.* 2008) and disease (*e.g.* from fungal pathogens – see Roy *et al.* 2008) that afflict native species such as *A. bipunctata* and *C. septempunctata*. Additionally, greater body size (*H. axyridis* is the largest of these species) has been shown to reduce density-independent mortality, increasing resilience to abiotic variability such as extreme climatic events (Parmesan, Root & Willig 2000). Plasticity in body size, as seen in *H. axyridis* and *C. septempunctata*, can also confer an advantage, such as optimizing predation for different size prey (Sloggett 2008) and creating 'ecological flexibility' when expanding to new ranges (Evans 2000).

For extinction to occur, the feeding rate of the intraguild predator on the shared resource must only be slightly lower (<10%) than that of the intraguild prey.

The observed feeding rate on the shared prey by *H. axyridis* was approximately 50% lower than that of *A. bipunctata*, whereas the *H. axyridis* and *C. septempunctata* feeding rates on the shared prey were almost identical. These results imply a low and high extinction risk for the intraguild prey, *A. bipunctata* and *C. septempunctata*, respectively. Out of the eight species tested by Roy *et al.* (2012), only *C. septempunctata* populations have not experienced significant declines since the appearance of *H. axyridis* in the UK. The intraguild predation model presented here predicts that *C. septempunctata* (IG prey) would become extinct when competing with *H. axyridis* (IG predator), but field evidence suggests the contrary (Roy *et al.* 2012). Despite all three species co-occupying a broad range of habitats throughout the year (Honěk 2012), habitat partitioning among the three coccinellid species may offer some explanation as to why *C. septempunctata* does not fit within the conceptual framework presented by the intraguild predation models. Both *A. bipunctata* (IG prey) and *H. axyridis* (IG predator) often occupy the same arboreal habitat for most of the growing season; *C. septempunctata* (IG prey) occupies herbaceous vegetation (Roy *et al.* 2012) and niche overlap with *H. axyridis* (IG predator) will be markedly less than that experienced by *A. bipunctata* (IG prey).

Additionally, other behavioural traits specific to *C. septempunctata* (IG prey) may be allowing this species to escape intraguild predation by *H. axyridis* in the field. For example, in the presence of *H. axyridis*, nearly 50% of *C. septempunctata* larvae have been observed to drop from the feeding site to avoid the intraguild predator, whereas *A. bipunctata* does not demonstrate this behaviour (Sato, Yasuda & Evans 2005).

The interaction between *A. bipunctata* (IG prey) and *H. axyridis* (IG predator), but not *C. septempunctata* (IG prey) and *H. axyridis* (IG predator), mapped onto the classic assumptions and predictions of IGP theory (Polis, Myers & Holt 1989). The theory predicts that *H. axyridis* (IG predator) and *A. bipunctata* (IG prey) can coexist as a result of the trait differences between both species in response to competition. Attack rate on the shared resource by the intraguild predator should be approximately 50% lower compared to the intraguild prey, which this study supports. Current field evidence, however, suggests the opposite, with significant declines in *A. bipunctata* abundance (Brown *et al.* 2008b). One possible explanation revealed by our population models is that the observed decline in abundance of *A. bipunctata* in the field may correspond to an initial period of significant decline in this intraguild prey species, prior to a new equilibrium being reached (Fig. 4b). To test this hypothesis requires accurate census data of *H. axyridis* and *A. bipunctata* populations since the introduction of *H. axyridis* in 2004.

The feeding rate of *H. axyridis* (IG predator) and *A. bipunctata* (IG prey) on a shared prey resource varied depending on the presence and identity of the interspecific

competitor. This, in itself, indicates a degree of plasticity in this trait. The cue used by coccinellids for this trait change remains unknown, and therefore, its specificity is also unknown. The feeding rate of *A. bipunctata* was not affected by the presence of a conspecific suggesting the cue may be species specific. This type of plastic behavioural response is commonly seen in many organisms when threatened by different predators (Relyea 2001) and demonstrates the significant cost incurred by its occurrence. Heterospecific cues such as faeces and trails have been shown to alter feeding and oviposition, suggesting olfactory identification of predator species occurs (Agarwala, Yasuda & Kajita 2003). This may ultimately weaken the strength of IGP allowing for intraguild predator–prey coexistence (Choh *et al.* 2010). Future work with different larval stages (and therefore sizes) of coccinellids would be required to determine the cue that elicits the observed change in feeding behaviour in these predators. These empirical data can then be used to inform a more complex population dynamic model which incorporates life stage structured predation within IG predators and their prey (Faria, Costa & Conde Godoy 2011; Zhou, Fujiwara & Grant 2013). Despite evidence of *H. axyridis* consuming *A. bipunctata* (Thomas *et al.* 2013), at no point prior to the experiment did any coccinellid species come in contact with each other; therefore, the change in feeding rate observed in *H. axyridis* and *A. bipunctata* to other coccinellid species is evidence of behavioural plasticity.

CONCLUSIONS

Animal behaviour is considered an essential component of invasion biology (Holway & Suarez 1999). This study provides mechanistic insights from controlled laboratory-based experiments, which, when coupled with theoretical modelling, has contributed to a greater understanding of native and invasive predator population dynamics. Investigating the behavioural interspecific interactions between native and invasive alien species revealed that the correlation between invasive success and native decline is not necessarily linear, resulting in the extinction of the native, but can over time result in an alternative, potentially stable, coexistence. This study suggests that coexistence is possible and that an increase in the abundance of *A. bipunctata* may occur 25 years after the introduction of *H. axyridis* (assuming that food availability and temperature will allow for two generations of each species per year, Hodek, Honek & van Emden 2012). To test this prediction will require field census data in space for time substitution models at large spatial scales. This would create a valuable link between small-scale laboratory experiments, theoretical models and population dynamics at species distribution scales. Integrating non-consumptive effects into the intraguild predation framework adds a substantial amount of trophic complexity to attempts at understanding the invasion process. Additional details that may be worthwhile considering in the future would be the subsequent impact of polyphagy and

prey switching of more palatable aphid prey at driving the invasion process.

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Data accessibility

Data are available at the NERC Environment Information Data Centre: <http://doi.org/10.5285/c8c3f4ef-889b-457a-a05b-1b2214d5802c> (Hentley & Brien 2016).

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Supporting Information

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

Figure S1. Qualitative sensitivity analysis for the number of generations until the start of equilibrium predicted by a population

dynamic model between *A. bipunctata* and *H. axyridis*, presented in Figure 4b.