A window of opportunity: Subdominant predators can use suboptimal prey

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Abstract
Introduced species have been linked to declines of native species through mechanisms including intraguild predation and exploitative competition. However, coexistence among species may be promoted by niche partitioning if native species can use resources that the invasive species cannot. Previous research has shown that some strains of the aphid *Aphis craccivora* are toxic to a competitively dominant invasive lady beetle, *Harmonia axyridis*. Our objective was to investigate whether these aphids might be an exploitable resource for other, subdominant, lady beetle species. We compared larval development rate, survival, and adult weight of five lady beetle species in no-choice experiments with two different strains of *A. craccivora*, one of which is toxic to *H. axyridis* and one that is nontoxic. Two lady beetle species, *Cycloneda munda* and *Coleomegilla maculata*, were able to complete larval development when feeding on the aphid strain that is toxic to *H. axyridis*, experiencing only slight developmental delays relative to beetles feeding on the other aphid strain. One species, *Coccinella septempunctata*, also was able to complete larval development, but experienced a slight reduction in adult weight. The other two lady beetle species, *Hippodamia convergens* and *Anatis labiculata*, demonstrated generally low survivorship when consuming *A. craccivora*, regardless of aphid strain. All five species showed increased survival and/or development relative to *H. axyridis* on the “toxic” aphid strain. Our results suggest that this toxic trait may act as a narrow-spectrum defense for the aphids, providing protection against only some lady beetle enemies. For other less-susceptible lady beetles, these aphids have the potential to provide competitive release from the otherwise dominant *H. axyridis*.

KEYWORDS
Coccinellidae, cowpea aphid, exploitative competition, generalist predators, invasive species, niche partitioning

INTRODUCTION

Competition often plays a large role in shaping community structure (Menge, 1976; Price & Kirkpatrick, 2009). Species that are the most successful in securing food and habitat resources can establish themselves as dominant species, potentially excluding other species that are less adept (Fretwell, 1969; Goldberg, 1987). For these subdominant species, survival in a community then becomes contingent on exploiting alternative resources that cannot or will not be utilized by the dominant species (Hill & Lodge, 1994; Messing & Wang, 2014).
2009). When a competitively dominant invasive species enters a novel ecosystem, it is able to disrupt established community interactions (Blossey & Notzold, 1995) and shift community composition (reviewed in Mooney & Cleland, 2001).

The multicolored Asian lady beetle, Harmonia axyridis, is a notably dominant invasive predator species (Roy et al., 2016). This beetle originated in Asia and has spread to at least 38 new countries since 1988 (Brown, Thomas et al., 2011). The ability of H. axyridis to rapidly expand its range and establish itself in novel communities is largely attributed to its success as a superior competitor and intraguild predator (Lucas, Gagne, & Coderre, 2002; Ware & Majerus, 2008). Additionally, high dispersal capability, multivoltinism, and the capability to survive in a wide variety of habitats have been hypothesized to contribute to the dominance of H. axyridis in novel ecosystems (Roy & Brown, 2015). Overall, native lady beetle populations and species diversity have been in decline (Harmon, Stephens, & Losey, 2007), and it is thought that H. axyridis has played a role in the decreasing biodiversity in some coccinellid communities (Bahlai, Colunga-Garcia, Gage, & Landis, 2015; Brown, Frost et al., 2011).

Harmonia axyridis is an aphidophagous generalist, yet not all aphids are equivalently suitable food sources. For example, some aphids, such as Megoura viciea and Aulacorthum magnolia, cause delayed growth and mortality when consumed by the beetles (Fukunaga & Akimoto, 2007; Tsaganou, Hodgson, Athanassiou, Kavallieratos, & Tomanovic, 2004). Other aphids, such as the cowpea aphid, Aphis craccivora, vary in suitability as food for H. axyridis (Hukusima & Kamei, 1970; Kamo, Tokuoka, & Miyazaki, 2010). Strains of A. craccivora originating from black locust, Robinia pseudoacacia, have been documented as toxic, inducing 100% mortality in H. axyridis larvae (Hukusima & Kamei, 1970; White, McCord, Jackson, Dehnel, & Lenhart, 2017). In contrast, A. craccivora strains that originated from alfalfa, Medicago sativa, are not toxic to H. axyridis larvae (White et al., 2017). This difference between strains is intrinsic to the aphids and is not a function of host plant chemistry. The mechanism of toxicity remains unknown, but aphid strains that originated from locust are consistently and heritably toxic to H. axyridis, even after many generations of rearing on alternate host plant species (White et al., 2017).

Despite the strong negative effects that locust-origin A. craccivora have on H. axyridis, the toxicity might not be ubiquitous across coccinellid predator species. Previous studies on the suitability of A. craccivora as a food source have been conducted with other coccinellid species, often with results suggesting that they are acceptable prey that supports coccinellid development to adulthood (Ferrer, Dixon, & Hemptinne, 2008; Omkar & Mishra, 2005; Omkar & Srivastava, 2003). However, it is not clear which strains of the aphid were evaluated in these trials. These previous studies may have assayed A. craccivora strains on which H. axyridis would have performed well, or they may have assayed strains that would have been toxic to H. axyridis, which would indicate that these other lady beetles are less susceptible to toxic A. craccivora. In other words, the toxic trait may be broad spectrum against a wide range of coccinellid predator species, or narrow spectrum against only a subset of the predators.

Here, we examined whether locust-origin A. craccivora is suitable food for several other coccinellid species. Understanding the specificity of toxicity in these aphids has important ramifications, both for predicting the defensive virtue of the trait for the aphid and community outcomes among coccinellids. If other coccinellid species can use these aphids as a food source, the presence of selectively toxic aphids in an environment could mitigate competitive differentials between H. axyridis and subdominant lady beetle species, facilitating niche partitioning, predator coexistence, and diversity.

2 | MATERIALS AND METHODS

We evaluated the development and survival of five lady beetle species: Anatis lacticula, Coccinella septempunctata, Coleomegilla maculata, Cycloneda munda, and Hippodamia convergens. All species are native to N. America except C. septempunctata, which is native to the Palearctic. All species are also multivoltine habitat generalists commonly found in field crops, except An. lacticula, which is a univoltine arboreal species. Each species co-occurs with both A. craccivora and H. axyridis in the field. Wild caught beetles were collected from Lexington, KY, USA in 2014 and 2015. The beetles were grouped by species and life stage in Petri dishes (100 × 25 mm) and maintained in an incubator at 25°C, 16-hr:8-hr light:dark, 65% humidity. Both juvenile and adult beetles were fed pea aphids (Acrthosiphum pisum). When mating occurred, the paired male and female were removed from the colony and placed in their own Petri dish with folded paper for egg deposition. Egg papers were regularly removed from the parents’ Petri dish to prevent cannibalism.

All aphids (A. craccivora and Ac. pisum) originated from clones originally collected in Lexington, Kentucky, USA and were maintained in colonies on fava bean (Vicia faba) in the laboratory at ambient room temperature. Acrthosiphum pisum clones were initially collected from either black locust or alfalfa as described in Wagner et al. (2015). To date, all clones collected from black locust are intrinsically toxic to H. axyridis, and all clones collected from alfalfa are nontoxic to H. axyridis (White et al., 2017). The toxicity status of the two aphid strains is unknown for non-Harmonia coccinellid species; as such, hereafter locust-origin A. craccivora will be referred to as L-strain and alfalfa-origin A. craccivora will be referred to as A-strain.

For each lady beetle species, we compared beetle development time and survival on the two strains of A. craccivora in no-choice experiments. Neonate larvae were removed from their egg mass before sibling cannibalism could occur and were placed individually in Petri dishes (35 × 10 mm) that had an excised circle of fava bean leaf embedded in 1% agar. We randomly assigned each larva to an aphid treatment. Three lady beetle species (C. septempunctata, Co. maculata, and Cy. munda) had one of two treatments: either L-strain or A-strain A. craccivora. Because the remaining two beetle species, H. convergens and An. lacticula, showed poor survival overall on A. craccivora, we included a third treatment of Ac. pisum aphids as a control. We fed the larvae their assigned aphid diets (mixed instars) ad libitum for the duration of development and monitored daily for mortality and
developmental stage. Once the beetles reached the third instar, we moved them to larger Petri dishes (60 × 15 mm) and provided them with a cotton ball soaked in DI water along with their aphid treatment. For the beetles that survived to adulthood, teneral adults were allowed to sclerotize for 1 day before weighing to the nearest milligram. Sex of each adult beetle was determined through mating observations of the adults. Sex did not statistically affect the differences between treatments and was removed from subsequent analysis. Sample size varied among species based on availability of neonates for each species.

We compared survival to adulthood among treatments using Kaplan–Meier survival analysis followed by the Mantel-Cox test. For species in which all individuals survived to adulthood in one or more treatments, Kaplan–Meier statistics could not be calculated and we instead used Fisher’s exact test to compare survival between treatments. We similarly used Kaplan–Meier analysis to compare development time (time to pupation) among treatments, coding individuals that died as censored values. For An. labiculata, all individuals died in the L-strain treatment, so we were only able to compare development time between the A-strain treatment and the Ac. pisum control treatment. Finally, we compared adult weight between treatments using two-sample t-tests for each species. All weight data conformed to homoscedasticity and normality assumptions. For Hi. convergens, only three adults were produced across the L- and A-strain A. craccivora treatments, so we combined these two diet treatments for comparison with the Ac. pisum control treatment. For An. labiculata, we again only compared the A-strain treatment to the Ac. pisum control treatment, as there were no adults produced in the L-strain treatment. We conducted all statistical analyses in IBM SPSS v.24.

3 | RESULTS

In contrast to H. axyridis, which experiences 100% mortality when exposed to L-strain A. craccivora, the tested lady beetle species showed a wide range of tolerance. Two species, Cy. munda and Co. maculata, were only slightly affected by the L-strain of A. craccivora. For Cy. munda, all of the beetle larvae survived to adulthood when reared on either L-strain (n = 13/13) or A-strain (n = 14/14) aphids (Figure 1a; Fisher’s exact test p = 1.0). Cycloneda munda larvae exhibited a slight delay in development when reared on L-strain aphids, taking approximately 10% longer to pupate than those on A-strain aphids (L-strain mean ± SE = 11.7 ± 0.3 days, A-strain = 10.7 ± 0.2 days; Mantel-Cox χ² = 8.4, df = 1, p = .008). However, there was no significant

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**FIGURE 1** Survivorship of larvae of (a) Cycloneda munda, (b) Coleomegilla maculata, (c) Coccinella septempunctata, (d) Hippodamia convergens, and (e) Anatis labiculata lady beetles when fed on different aphids. All five beetle species included L-strain and A-strain A. craccivora treatments; L-strain aphids cause rapid mortality of Harmonia axyridis larvae, A-strain aphids do not. Hippodamia convergens (d) and An. labiculata (e) additionally included a control treatment of Acrithosiphum pisum aphids. Trials were concluded when all beetles had reached adulthood or died.
difference between the adult weights of Cy. munda reared on the two treatments (Figure 2a; $t = .60$, $df = 25$, $p = .55$). Similarly, Co. maculata experienced high survival on both L-strain ($n = 26/28$ survived) and A-strain ($n = 23/24$ survived) A. craccivora (Figure 1b; Mantel-Cox $\chi^2 = 0.04$, $df = 1$, $p = .84$) and had 12% slower development on L-strain than A-strain A. craccivora (L-strain = 18.5 ± 0.4 days, A-strain = 16.8 ± 0.5 days; Mantel-Cox $\chi^2 = 4.24$, $df = 1$, $p = .049$). There was no difference in adult weight of Co. maculata between treatments (Figure 2b; $t = .84$, $df = 47$, $p = .40$).

Coccinella septempunctata showed a moderately negative response to L-strain A. craccivora. There was a trend toward reduced survival on L-strain aphids, with 76.9% ($n = 10/13$) surviving, relative to 100% ($n = 14/14$) survival on A-strain aphids (Figure 1c; Fisher’s exact test $p = .098$). The beetles feeding on L-strain aphids took approximately 2 days longer (15.6%) to pupate than beetles feeding on A-strain aphids (L-strain = 17.0 ± 0.8 days, A-strain = 14.7 ± 0.2 days; Mantel-Cox $\chi^2 = 10.9$, $df = 1$, $p = .001$) and showed a 24% reduction in adult weight (Figure 2c; $t = 4.0$, $df = 22$, $p < .001$).

The remaining two species, Hi. convergens and An. labiculata, had generally poor survival, and additionally included an Ac. pisum control treatment. Hippodamia convergens performed poorly in all treatments. On L-strain aphids, only 6.7% ($n = 2/30$) survived, on A-strain aphids only 3.8% ($n = 1/26$) survived, and on the control Ac. pisum aphids, 34.6% ($n = 9/26$) survived. Survival time was significantly longer on control aphids than either A. craccivora strain (Figure 1d; Mantel-Cox $\chi^2 = 15.6$, $df = 2$, $p < .001$). Time to pupation also tended to be slower on either A. craccivora strain than the Ac. pisum control (L-strain = 19 ± 1 days, A-strain = 20.5 ± 0.4 days, control = 17.3 ± 0.9 days), but low survival numbers precluded statistical significance (Mantel-Cox $\chi^2 = 5.26$, $df = 2$, $p = .07$). For these few survivors on A. craccivora, adult weight was 40% lower than on the Ac. pisum control (Figure 2d; $t = 3.92$, $df = 9$, $p = .003$), but could not be compared statistically between L-strain and A-strain aphid diets.

For An. labiculata, 0% ($n = 0/13$) of larvae survived to adulthood on L-strain aphids, but only 15% ($n = 2/13$) survived on A-strain aphids, and 50% ($n = 6/12$) survived on the Ac. pisum control. There was no difference in survival between beetles fed L-strain versus A-strain A. craccivora (Fisher’s exact test $p = .48$), but the survival on any A. craccivora diet was significantly lower than the Ac. pisum control (Fisher’s exact test $p = .007$). Time to death did not differ significantly among any of the treatments, due to some early mortality of beetles on control aphids, and relatively long larval survival on both A. craccivora strains before dying (Figure 1e; Mantel-Cox $\chi^2 = 3.75$, $df = 2$, $p = .05$).

**FIGURE 2** Mean ± 1 SE adult weight of (a) Cycloneda munda, (b) Coleomegilla maculata, (c) Coccinella septempunctata, (d) Hippodamia convergens, and (e) Anatis labiculata lady beetles when fed on different aphids. All five beetle species included L-strain and A-strain A. craccivora treatments; Hi. convergens (d), and An. labiculata (e) additionally included a control treatment of Acrithosiphum pisum aphids. Sample sizes of beetles surviving to adulthood per treatment are inset within each column. Brackets indicate statistical contrasts: An asterisk indicates a contrast that was significant at $p < .05$, n.s. indicates a contrast that was not significantly different.
p = .15). On L-strain aphids, An. lobiclata larvae exhibited some development before dying; 54% of beetles survived into the second instar and 23% survived to the third. For the two beetles that survived to adulthood on A-strain A. craccivora, time to pupation was 15% longer than the survivors on Ac. pismum (A-strain = 17.4 ± 0.3 days, control = 15.1 ± 0.5 days; Mantel-Cox $\chi^2 = 8.10$, df = 1, $p = .004$), and adult weight was nearly 50% lower (Figure 2e; $t = 5.43$, df = 6, $p = .002$).

4 | DISCUSSION

Coccinellid species varied in their ability to use L-strain A. craccivora. Three species, Cy. munda, Co. maculata, and C. septempunctata, showed only slight negative effects of consuming L-strain versus A-strain A. craccivora: All or most beetles survived to adulthood feeding on L-strain aphids and exhibited only modest delays in development. Of these three species, only C. septempunctata demonstrated a lower adult weight when feeding on L-strain aphids, which may be indicative of lower adult fitness (Honěk, 1993). The remaining two beetle species, Hi. convergens and An. lobiclata, performed poorly on L-strain A. craccivora, but also performed poorly on A-strain A. craccivora. For these two beetle species, few larvae reached adulthood on either A. craccivora strain, and the survivors exhibited substantially reduced adult size when compared to beetles reared on Ac. pismum control aphids. Thus, A. craccivora in general appears to be an alternate rather than essential food source for these two beetle species (Hodek & Evans, 2012). It should be noted, however, that even on Ac. pismum, survival to adulthood was low for both beetle species (35-50%). It is not unusual for Hi. convergens to exhibit relatively low survival on pea aphids in the laboratory (e.g., Costopoulos, Kovacs, Kamins, & Gerardo, 2014), suggesting that beetle sensitivity to laboratory-rearing conditions may have contributed to poor survival in general and exacerbated the negative effects of A. craccivora.

All the beetle species in the present study were more capable of using L-strain A. craccivora than the multicolored Asian ladybeetle, H. axyridis. In a previous study, we found that H. axyridis invariably failed to complete larval development on L-strain A. craccivora, typically dying within a few days and without ever molting (White et al., 2017). In contrast, H. axyridis completed larval development and reproduced normally when fed A-strain A. craccivora (White et al., 2017). The present study shows that this dramatic variation in ability to consume the aphid strains is not a widespread phenomenon among lady beetles. While L-strain A. craccivora seemed to be a poorer food source than A-strain A. craccivora for all tested beetle species, the fitness differential between beetles fed on L-strain and A-strain aphids was generally quite subtle. These results deepen the mystery regarding the mechanism of L-strain aphid toxicity for H. axyridis. Previous work has eliminated aphid host plant and facultative bacterial symbionts as explanatory factors (White et al., 2017). The present study indicates that the toxic effect is particular to certain predator species and that comparative mechanistic investigations between susceptible and non-susceptible predator species may be informative.

Regardless of mechanism, the consequence for L-strain A. craccivora is that its “toxic” trait may act as a narrow-spectrum defense, negatively affecting some but not all enemy species. How common and effective such partial defenses might be for herbivores remains to be seen. There are certainly other aphid examples in which individuals are protected from some enemies but vulnerable to others (e.g., Asplen et al., 2014; Cayetano & Vorburger, 2015; Michaud, 2000; Müller, Adriaanse, Belshaw, & Godfray, 1999). Whether an herbivore population will benefit from such narrow-spectrum defenses ultimately depends on the composition of susceptible versus less susceptible enemies in the local community (Lenhart & White, 2017), and the degree to which compensatory attack by less susceptible enemies undercuts the defensive virtue of the selectively toxic trait for the herbivore (Letourneau, Jedlicka, Bothwell, & Moreno, 2009).

In turn, narrow-spectrum herbivore defenses have the potential to structure the predator community. Consumers that are able to exploit such resources have access to a niche that susceptible consumers do not, and may benefit from reduced interspecific competition and reduced intraguild predation (Jeffries and Lawton 1984, Snyder, 2009). Such benefits would be particularly likely in systems where the susceptible enemy is otherwise dominant, as is the case H. axyridis (Hesler, Kieckhefer, & Catangui, 2004). Prey such as L-strain A. craccivora represent a niche that cannot be substantially exploited by H. axyridis, an aggressive invasive species that typically outcompetes and consumes many other species of coccinellids (Koch, 2003; Lucas et al., 2002; Snyder, Clevenger, & Eigenbrode, 2004; Ware & Majerus, 2008). In theory, it is possible that selectively toxic prey allow for resource partitioning (Chesson, 2000) and represent a window of opportunity for subdominant predators to persist in communities where H. axyridis has invaded. Future empirical efforts should test how differential prey toxicity affects predator community assembly in the field and investigate whether this process may predict lady beetle community resilience to H. axyridis invasion.

In conclusion, our research highlights that prey can exhibit in-specific heterogeneity in toxicity (White et al., 2017) and that generalist predator species can be heterogeneous in their sensitivity to such prey. Together, these findings suggest that niche partitioning among generalist predators may be more nuanced than previously appreciated and that dynamic ecological and evolutionary interactions between generalist predators and their prey may be ongoing.

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CONFLICT OF INTEREST

None declared.

AUTHOR CONTRIBUTIONS

KJ and JSM collected the data, KJ and JAW analyzed the data and wrote the initial draft of the article, and all authors revised and approved of the final version.

REFERENCES

Asplén, M. K., Bano, N., Brady, C. M., Desneux, N., Hopper, K. R., Malouines, C., ... Heimpel, G. E. (2014). Specialization of bacterial endosymbionts that protect aphids from parasitoids. *Ecological Entomology, 39*, 736–739.

Bahle, C. A., Colunga-Garcia, M., Gage, S. H., & Landis, D. A. (2015). The role of exotic ladybeetles in the decline of native ladybeetle populations: Evidence from long-term monitoring. *Biological Invasions, 17*, 1005–1024.

Blossey, B., & Notzold, R. (1995). Evolution of increased competitive ability in invasive nonindigenous plants: A hypothesis. *Journal of Ecology, 83*, 887–889.

Brown, P. M. J., Frost, R., Doberski, J., Sparks, T., Harrington, R., & Roy, H. E. (2011). Decline in native ladybird species in the arrival of *Harmonia axyridis*: early evidence from England. *Ecological Entomology, 36*, 231–240.

Brown, P. M. J., Thomas, C. E., Lombaert, E., Jeffries, D. L., Estoup, A., & Handley, L. J. L. (2011). The global spread of *Harmonia axyridis* (Coleoptera: Coccinellidae): distribution, dispersal and routes of invasion. *BioControl, 56*, 623–641.

Cayetano, L., & Vorburger, C. (2015). Symbiont-conferred protection against Hymenopteran parasitoids in aphids: How general is it? *Ecological Entomology, 40*, 85–93.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics, 31*, 343–366.

Costopoulos, K., Kovacs, J. L., Kamins, A., & Gerardo, N. M. (2014). Aphid facultative symbionts reduce survival of the predatory lady beetle *Hippodamia convergens*. *BMC Ecology, 14*, 5.

Ferrer, A., Dixon, A. F. G., & Hemptinne, J. (2008). Prey preference of ladybird larvae and its impact on larval mortality, some life-history traits of adults and female fitness. *Bulletin of Insectology, 61*, 5–10.

Fretwell, S. (1969). Dominance behavior and winter habitat distribution in juncos (Junco hyemalis). *Bird-Banding, 40*, 1–25.

Fukunaga, Y., & Akimoto, S. I. (2007). Toxicity of the aphid *Aulacorthum magnoliae* to the predator *Harmonia axyridis* (Coleoptera: Coccinellidae) and genetic variance in the assimilation of the toxic aphids in *H. axyridis* larvae. *Entomological Science, 10*, 45–53.

Goldberg, D. E. (1987). Neighborhood competition in an old-field plant community. *Ecology, 68*, 1211–1223.

Harmon, J., Stephens, E., & Losey, J. (2007). The decline of native coccinellids (Coleoptera: Coccinellidae) in the United States and Canada. In T. R. New (Ed.), *Beetle conservation* (pp. 85–94). Netherland: Springer.

Hesler, L. S., Kieckhefer, R. W., & Catangui, M. A. (2004). Surveys and field observations of *Harmonia axyridis* and other Coccinellidae (Coleoptera) in eastern and central South Dakota. *Transactions of the American Entomological Society, 130*, 113–113.

Hill, A. M., & Lodge, D. M. (1994). Diet changes in resource demand - competition and predation in species replacement among crayfishes. *Ecology, 75*, 2118–2126.

Hodek, L., & Evans, E. W. (2012). Food relationships. In I. Hodek, H. F. Van Emden, & A. Honek (Eds.), *Ecology and behaviour of the ladybird beetles (Coccinellidae)* (pp. 141–274). Chichester, West Sussex, UK: John Wiley and Sons.

Honěk, A. (1993). Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos, 66*, 483–492.

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

Jeffries, M. J., & Lawton, J. H. (1984). Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society, 23*, 269–286.

Kamo, T., Tokuoka, Y., & Miyazaki, M. (2010). Influence of aphid-host plant pairs on the survivorship and development of the multicolored Asian ladybird beetle: implications for the management of vegetation in rural landscapes. *Ecological Research, 25*, 1141–1149.

Koch, R. L. (2003). The multicolored Asian lady beetle, *Harmonia axyridis*: A review of its biology, uses in biological control, and non-target impacts. *Journal of Insect Science, 3*, 1–16.

Lenhart, P. A., & White, J. A. (2017). A defensive facultative endosymbiont fails to protect aphids against the parasitoid community present in the field. *Ecological Entomology, doi: 10.1111/een.12419.*

LeTourneau, D. K., Jedlicka, J. A., Bothwell, S. G., & Moreno, C. R. (2009). Effects of natural enemy biodiversity on the suppression of arthropod herbivores in terrestrial ecosystems. *Annual Review of Ecology Evolution and Systematics, 40*, 573–592.

Lucas, E., Gagne, I., & Codere, D. (2002). Impact of the arrival of *Harmonia axyridis* on adults of *Coccinella septempunctata* and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *European Journal of Entomology, 99*, 457–463.

Menge, B. A. (1976). Organization of new-england rocky intertidal community: Role of predation, competition, and environmental heterogeneity. *Ecological Monographs, 46*, 355–393.

Messing, R. H., & Wang, X.-G. (2009). Competitor-free space mediates non-target impact of an introduced biological control agent. *Ecological Entomology, 34*, 107–113.

Michaud, J. P. (2000). Development and reproduction of lady beetles (Coleoptera: Coccinellidae) on the citrus aphids *Aphis spiraecola* Patch and *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphiididae). *Biological Control, 18*, 287–297.

Mooney, H. A., & Cleland, E. E. (2001). The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences, 98*, 5446–5451.

Müller, C. B., Adriaanse, I. C. T., Belshaw, R., & Godfray, H. C. J. (1999). The structure of an aphid-parasitoid community. *Journal of Animal Ecology, 68*, 364–370.

Omkar, & Mishra, G. (2005). Preference-performance of a generalist predatory ladybird: A laboratory study. *Biological Control, 34*, 187–195.

Omkar, & Srivastava, S. (2003). Influence of six aphid prey species on developmental impact and reproduction of a ladybird beetle, *Coccinella septempunctata*. *Biocontrol, 48*, 379–393.

Price, T. D., & Kirkpatrick, M. (2009). Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society B: Biological Sciences, 276*, 1429–1434.

Roy, H. E., & Brown, P. M. (2015). Ten years of invasion: *Harmonia axyridis* (Pallas)(Coleoptera: Coccinellidae) in Britain. *Ecological Entomology, 40*, 336–348.

Roy, H. E., Brown, P. M. J., Adriaens, T., Berkvens, N., Borges, I., Ciusella-Trullas, S., ... Zhou, Z. (2016). The harlequin ladybird, *Harmonia axyridis*: global perspectives on invasion history and ecology. *Biological Invasions, 18*, 997–1044.

Snyder, W. E. (2009). Coccinellids in diverse communities: Which niche fits? *Biological Control, 51*, 323–335.

Snyder, W. E., Clevenger, G. M., & Eigenbrode, S. D. (2004). Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia, 140*, 559–565.

Tsganou, F. C., Hodgson, C. J., Athanassiu, C. G., Kavalleratos, N. G., & Tomanovic, A. (2004). Effect of *Aphis gossypii* Glover, *Brevicoryne
brassicae (L.), and Megoura viciae Buckton (Hemiptera: Aphidoidea) on
the development of the predator Harmonia axyridis (Pallas) (Coleoptera: 
Coccinellidae). Biological Control, 31, 138–144.
Wagner, S. M., Martinez, A. J., Ruan, Y. M., Kim, K. L., Lenhart, P. A., Dehnel, 
A. C., … White, J. A. (2015). Facultative endosymbionts mediate dietary 
breadth in a polyphagous herbivore. Functional Ecology, 29, 1402–1410.
Ware, R. L., & Majerus, M. E. N. (2008). Intraguild predation of immature 
stages of British and Japanese coccinellids by the invasive ladybird 
Harmonia axyridis. BioControl, 53, 169–188.
White, J. A., McCord, J. M., Jackson, K. A., Dehnel, A. K., & Lenhart, P. A. 
(2017). Differential aphid toxicity to ladybeetles is not a function of 
host plant or facultative bacterial symbionts. Functional Ecology, 31, 
334–339.

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window of opportunity: Subdominant predators can use 
suboptimal prey. Ecol Evol. 2017;7:5269–5275. 
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