Prey and predator biodiversity mediate aphid consumption by generalists

Karol L. Krey [a], Olivia M. Smith [b], Eric G. Chapman [c], Michael S. Crossley [b], David W. Crowder [a], Zhen Fu [a], James D. Harwood [d], Andrew S. Jensen [e], Christine A. Lynch [a], Gretchen B. Snyder [a], William E. Snyder [b,*]

[a] Department of Entomology, Washington State University, Pullman, WA 99164, USA
[b] Department of Entomology, University of Georgia, Athens, GA 30602, USA
[c] Department of Entomology, University of Kentucky, Lexington, KY 40546, USA
[d] Institute of Plant and Environment Protection, Beijing Academy of Agricultural and Forestry Sciences, Beijing 100097, China
[e] Northwest Potato Research Consortium, 95873 E Goldmohr LN, Lakeview, OR 97630, USA

HIGHLIGHTS

- For two generalist predators, alternative prey generally increased predation of aphids.
- Detection of aphid DNA in *Nabis* and *Geocoris* was more likely with increasing predator richness.
- However, increasing relative abundance of other predators generally reduced aphid predation by *Geocoris*.
- Overall, we found a mix of positive and negative predator and prey diversity effects on aphid consumption.

GRAPHICAL ABSTRACT
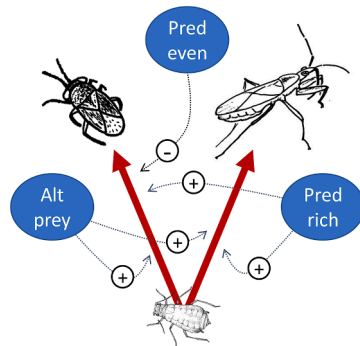
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ABSTRACT

Greater arthropod diversity may promote biological control by bringing together predator species that occupy complementary feeding niches. Diverse prey communities could further accentuate such niche differences and decrease predator-predator antagonism. However, much evidence of these effects comes from simple experiments that do not reflect the ecological complexity of real agricultural fields. Here we used molecular gut-content analysis to examine how predator and prey biodiversity impacted consumption of aphids by two generalists, *Nabis* sp. and *Geocoris* sp., in potato (*Solanum tuberosum*) crops. We show that both predator species were more likely to have fed on aphids when they foraged in fields with greater overall predator richness, an apparent benefit of predator biodiversity for aphid biocontrol consistent with greater complementarity. However, *Geocoris* saw less-frequent aphid predation with increasing predator evenness, perhaps because they foraged less when dangerous intraguild predators were common. For both predator species, higher thrips (*Frankliniella occidentalis*) abundance also correlated with greater aphid predation, as did higher total arthropod richness for *Nabis*. Altogether, beneficial complementarity appeared to be enhanced by greater predator or prey richness, although, for *Geocoris*, this was opposed by a negative effect of predator evenness. Strong prey-species-identity effects

* Corresponding author.
E-mail address: wesnyder@uga.edu (W.E. Snyder).

generally enhanced, rather than disrupted, aphid predation. Overall, the full diversity of biodiversity-biocontrol relationships suggested by smaller-scale experiments also appeared to be impactful in complex, working agricultural fields.

1. Introduction

Greater predator diversity often promotes biological control as species-rich communities can bring together predators that occupy distinct feeding niches, reducing a pest's ability to find refuge from predation (Schmitz, 2009; Dainese et al., 2017; Jonsson et al., 2017; Greenop et al., 2018). For example, suppression of pest Lepidoptera requires different predator species that attack the egg, larva, or adult life stages (Wilby et al., 2005), or both diurnal and nocturnal predator species (Pfannenstiel and Yeargan, 2002). These niche differences also reduce encounters between predator species, making intraguild predation or other types of predator-predator interference less likely (Rosenheim and Corbett, 2003; Rosenheim et al., 2004). Greater natural enemy evenness may provide additional benefits for biological control by ensuring that complementary niches are fully occupied (Crowder et al., 2010; Blubaugh et al., 2021). Unfortunately, as manipulation of natural enemy species richness and/or evenness to isolate their effects is logistically challenging (Loreau, 1998; Gotelli and Colwell, 2001), much evidence for beneficial enemy biodiversity effects comes from laboratory- or field-cage experiments that do not capture the full biodiversity of agricultural fields (Macfadyen et al., 2009a,b). Caging also likely inflates encounter rates among the narrower subset of species that are included. This leaves uncertainty about whether the biodiversity-biocontrol relationships seen in experiments have real-world importance (Straub et al., 2008; Snyder, 2019).

Prey and predator diversity may interact to make beneficial natural enemy complementarity more or less likely (Woodcock and Heard, 2011). When few prey species are available, predator species may regularly overlap in space and time as they hunt the same prey (Rosenheim et al., 2004; Schmitz, 2009). This can render predator species functionally redundant, such that there is no improvement in biological control with more enemy species (e.g., Straub and Snyder, 2006). In contrast, species-rich prey communities may allow natural enemy species to partition prey and move into different feeding niches (Cardinale et al., 2006; Woodcock and Heard, 2011; Balzan et al., 2016; Dainese et al., 2017); that is, the realized niche moves closer to the fundamental niche (Snyder, 2019). Predator interference can also be reduced as prey diversity increases if predators feed on unique prey and so encounter one another less often (Hironori and Katsuhiro, 1997; Lucas et al., 1998; Venzon et al., 2001; Langellotto and Denno, 2004; Janssen et al., 2007). Of course, greater prey diversity might not inevitably improve biological control. Generalist predators may switch to attacking abundant non-pest prey, freeing key herbivores from predation (Eubanks and Denno, 2000a; Harmon and Andow, 2004; Symondson et al., 2006). Likewise, predators that forage for actively moving prey may be particularly likely to encounter sit-and-wait intraguild predators they might not otherwise meet (Rosenheim and Corbett, 2003). The diversity of possible prey species in an open field situation often is far beyond the small handful of species that logistical concerns allow to be included in cage experiments, so any prey biodiversity effects, positive or negative, that are important in working farm fields might be difficult to capture when arthropod communities are experimentally manipulated (Woodcock and Heard, 2011; Snyder, 2019). This in turn may complicate a grower's ability to correctly identify and conserve the functionally distinct natural enemy species that provide the greatest benefits to biological control.

Here, we used molecular gut-content analysis to track predation of aphid pests of potato (*Solanum tuberosum*) by the predators *Geocoris* sp. (Hemiptera: Geocoridae) and *Nabis* sp. (Hemiptera: Nabidae). Our work was conducted in fields managed by growers using organic or conventional practices, which helped enhance natural site-to-site differences in

predator and prey diversity (Koss et al., 2005; Crowder et al., 2010). Both predator species are generalists, and manipulative experiments suggest they complement one another to enhance aphid predation (e.g., Snyder et al., 2006). Both predator species commonly engage in intraguild predation (Rosenheim, 2005), including of one another (Snyder et al., 2006), that might be reduced in the presence of bio-diverse prey communities (Snyder, 2019). Our central hypothesis was that per-capita aphid predation might be enhanced in fields with greater arthropod biodiversity that could heighten predator complementarity and weaken interference.

2. Materials and methods

Our project had two complementary components. First, we surveyed densities of *Nabis* and *Geocoris* predators, and of other arthropods that might serve as prey, in organic and conventional potato fields managed by cooperating growers (Krey et al., 2017). Second, during these surveys we collected a subsample of *Nabis* and *Geocoris* adults to test for the presence of aphid DNA, taking advantage of a previously developed primer to detect their consumption (Chapman et al., 2010). Aphids are key damaging pests of potato in the region, primarily as vectors of viral pathogens, and thus are the frequent targets of chemical and other control efforts (Murray et al., 2020). The primer that we used generally detects aphids of most species, although in our potato fields *Myzus persicae* Sulzer was the only aphid detected (see below). In total, over 3 years, predators were collected from 41 different potato fields across eastern Washington state (USA) that were managed using either organic or conventional practices.

2.1. Natural history

Consistently, in potato fields in our study region *Geocoris* is the most common predator, sometimes representing 50% or more of all predator individuals found during surveys (Koss et al., 2005; Crowder et al., 2010). These small predators appear to be common victims of intraguild predation by the larger *Nabis* (Straub and Snyder, 2006). Other common predators in these fields include anthocorid bugs, carabid and coccinellid beetles, a diverse community of spiders, and lacewings (Koss et al., 2005). Both predators find green peach aphids (*Myzus persicae*) to be attractive prey (e.g., Koss and Snyder, 2005), such that aphids are commonly eaten even when rare (Krey et al., 2017). The Colorado potato beetle (*Leptinotarsa decemlineata* (Say)), another common pest, appears to be less preferred as prey when other options are available (Koss et al., 2004; Koss and Snyder, 2005). Western flower thrips (*Frankliniella occidentalis*) was the other common herbivore we found in our surveys. A small detritus-feeding fly, *Scaptomyza pallida*, is often the most common insect in both organic and conventionally managed fields (Krey et al., 2017), and may be an important, non-herbivorous prey species for *Nabis* and *Geocoris* (e.g., Settle et al., 1996; Halaj and Wise, 2002; Juen and Traugott, 2005). Manipulative experiments suggest that natural enemies common in annual crops in our study regions are most efficient at controlling aphids when more natural enemy species are present (Snyder et al., 2006; Straub and Snyder, 2008) and those natural enemies are similar in abundance (Crowder et al., 2010). So, both greater natural enemy species richness and evenness may benefit biocontrol. Impacts of prey diversity in this system have not been extensively studied, but generalists like *Nabis* and *Geocoris* might more easily exhibit natural feeding-niche differences as prey biodiversity increases (Snyder, 2019).

2.2. Identification of predators & prey

Identification of species in the genera *Nabis* and *Geocoris* is currently quite challenging. For both genera, the most recent taxonomic treatments are over 85 years old (*Nabis*: Harris, 1928; *Geocoris*: McAtee, 1914; Barber, 1935), and numerous species have been described since their publications. To attempt to circumvent this morphological difficulty, we generated COI barcode sequences for about 15 representative specimens of each genus following the protocols outlined in Chapman et al. (2010). For *Nabis*, this resulted in 10 COI haplotypes with a maximum sequence divergence of 1.52% (uncorrected p-distances of non-identical sequences ranged from $0.00152 - 0.0152$, mean = 0.0078), and for *Geocoris*, nine COI haplotypes with a maximum sequence divergence of 0.456% (uncorrected p-distances of non-identical sequences ranged from $0.00152 - 0.00456$, mean = 0.00228). We submitted these sequences to the identification engine on the Barcode of Life database on March 13, 2021 (BOLD; Ratnasingham and Hebert, 2007). *Geocoris* barcodes matched three species with >99% similarity (*Geocoris sp.*, *G. pallens* and *G. discopterus*), whereas *Nabis* barcodes matched four species with >99% similarity (*Nabis sp.*, *N. alternatus*, *N. inscriptus*, *N. americoferus*); we know of no examination of ecological differences among these putative possible species within either genus. For search queries of both *Nabis* and *Geocoris* sequences, the identification engine failed to make a confident species identification, therefore, until a modern taxonomic treatment of these genera becomes available, it is prudent to use a genus level identification for both.

Scaptomyza pallida, a common detritovore in WA potato fields, was unambiguously identified usong BOLD (22 COI haplotypes, all unambiguously identified as *S. pallida*). All other potential prey species were identified using conventional taxonomy.

2.3. Arthropod survey and predator collections in commercial potato fields

We sampled from 6 organic and 6 conventional fields in the first year (2009), 9 organic and 8 conventional fields in the second year (2010), and 6 organic and 6 conventional fields in the third year (2011), with all fields managed by growers and located throughout the Columbia Basin of central Washington in Adams, Benton and Grant counties (Krey et al., 2017). Predators were collected in July or early August of each year, which is the approximate midpoint of the growing season (Krey et al., 2017). All predators were collected using a D-vac suction-sampling device using previously described methods (e.g., Koss et al., 2005). Briefly, we haphazardly identified 5 groups of 10 potato plants per field, walking in a zigzag pattern from the field edge towards the center of the field, for sampling. We held the collecting cone over each plant, gently shaking the foliage for 20 s and changed collecting bags between each group of 10 plants (Koss et al., 2005).

Arthropods in D-vac bags were immediately placed on dry ice until up to 80 individuals of *Geocoris* and *Nabis* were removed using forceps, placed individually in 95% ethanol in 1.5-mL microcentrifuge tubes on ice for transport, and then transferred to a $-80\,°C$ freezer to await DNA extraction; Chapman et al. (2010) found that this methodology avoids contamination of predators with prey DNA. Following the removal of predators for gut-content analysis, all other remaining arthropods from each D-vac bag were retained and stored in a $-20\,°C$ freezer before being sorted to allow us to describe overall prey community structure (predators removed from samples for gut-content analysis were included in predator-density estimates for each field). Arthropods were generally identified to family, except for the species included separately in our models because of their expected importance in potato food webs, as described below. D-vac bags were washed with a 10% bleach solution and air-dried before being re-used, to further minimize the risk of cross-contamination of DNA from one sampling period to another.

2.4. Molecular gut-content analysis

Total DNA was extracted from crushed field-collected predators using the QIAGEN DNeasy Kit following the manufacturer's protocol for animal tissue (QIAGEN Inc., Chatsworth, CA, USA). PCRs (25uL) consisted of 1X Takara buffer (Takara Bio Inc., Shiga, Japan), 0.2 mM of each dNTP, 0.25 mM of each primer, 0.625 U Takara Ex Taq TM (Takara Bio Inc.), and template DNA (1uL of total DNA). PCRs were carried out in PTC-200 and C1000 thermal cyclers (Bio-Rad Laboratories, Hercules, CA, USA) following the cycling protocols in Chapman et al. (2010). Electrophoresis was used to confirm amplification using 10 uL of PCR product in 1.5% SeaKem agarose (Lonza, Rockland, ME, USA) stained with GelRed (0.1 mg/uL; Phenix Research, Chandler, NC, USA). Development of the aphid primer is described in Chapman et al. (2010) and was deployed by Krey et al. (2017).

2.5. Data analyses

We used the extensive literature on ecological interactions among arthropods in potato fields in our study region, described above, to construct a set of putative models (Tables 1, S1). The factors we considered in our modeling effort were abundances of the key herbivore species *M. persicae*, *L. decemlineata*, *F. occidentalis*, *S. pallida*; abundances of the focal predators *Nabis* and *Geocoris*; total abundance, richness, and evenness of predators; and total abundance, richness, and evenness of all arthropods (Table S1). The biodiversity metrics were calculated without rarefaction as described in Crowder et al. (2012). First, we modeled arthropod community metrics (response variables) as a function of farming system alone (fixed effect; predictor variables) using generalized linear mixed-effects models (GLMMs) (glmmTMB package in R) (Magnusson et al., 2016). Models of abundance used a negative binomial distribution to account for overdispersion in count data, models of richness used a gaussian distribution, and models of evenness used a beta distribution. Model assumptions were examined using the DHARMa package in R (Hartig, 2020). Models included random effects of field and year. We then constructed 35 candidate models (including a random effects-only null model) that tested the relative importance of each of the arthropod community metrics and their potential additive and interactive effects with farming system (predictor variables) on the probability that aphids would be detected in both *Geocoris* and *Nabis* guts (response variables; Table S1). While we considered all combinations of arthropod community metrics and farming system, we did not consider all possible combinations of arthropod community metrics because (1) they are often highly correlated, which would cause multicollinearity issues (Fig. S3), and (2) the possible candidate model set considering all possible combinations is quite large. We then ranked models based on Akaike Information Criterion corrected for small sample sizes (AICc) and identified those that were most supported (ΔAICc < 2.0) (Burnham and Anderson, 2002) using the bbmle package in R (Bolker and R Development Core Team, 2020). Briefly, AICc is a statistical technique intended to select a "best" model among a series of candidate models. AICc has a second order bias correction for AIC (AICc = AIC + (2 K (K + 1))/(n-K-1)) for when sample sizes are small but converges to AIC as sample sizes increase. Change (Δ) in AICc values are on a continuous scale of information relative to other models in the set, where low Δ values have higher relative support (Burnham & Anderson, 2002; Burnham et al., 2011). We assessed multicollinearity for candidate models using the performance package in R (Ludecke et al., 2020). Because models were fully nested, if we found multicollinearity to be an issue (VIF < 5), models were removed from further consideration.

3. Results

3.1. Predator and prey communities in potato fields

The dominant predatory insects in these fields were the predatory

bugs *Geocoris* sp., *Nabis* sp., and *Orius* spp., representing, respectively, ca. 24.6%, 7.8%, and 14.5% of all predators collected; carabid and coccinellid beetles (together ca. 6.9% of all predators); lacewings in the families Chrysopidae and Hemerobiidae (together ca. 3.2% of all predators); and a diverse community of spiders primarily in the families Araneidae, Thomisidae, and Linyphiidae (together representing ca. 42.8% of the total). Among all arthropods, the detritus-feeding fly *S. pallida* sp. is overwhelmingly most abundant, representing ca. 57.2% of all arthropod individuals collected, with the most abundant herbivores being leafhoppers (Cicadellidae: Sternorrhyncha; ca. 4.6% of all arthropods) and the thrips *F. occidentalis* (ca. 2.0% of all arthropods). Among adult aphids that we collected, all were *M. persicae*, which generally is the numerically dominant potato aphid in this region (Koss et al., 2005). However, juvenile aphids could not be reliably identified, so other species may have been present as well.

Both *Nabis* (β = 1.23 ± 0.39 (SE), P = 0.002) and *Geocoris* (β = 0.93 ± 0.27 (SE), P = 0.005) were more abundant on organic compared to conventional farms (Table 1; Fig. 1). Aphids were similarly abundant on organic and conventional farms (β = 0.98 ± 0.63 (SE), P = 0.12; Table 1; Fig. 1). Predator abundance (β = 0.75 ± 0.26 (SE), P = 0.004) and richness (β = 1.53 ± 0.62 (SE), P = 0.013) were both higher on organic versus conventional farms (Table 1; Fig. 1). Total arthropod richness was also higher on organic farms (β = 7.34 ± 2.11 (SE), P = 0.0005). However, we did not detect differences in other species or groups between the two farming systems (Table 1; Fig. S1).

3.2. Impacts of arthropod communities and farm management on aphid predation

Aphid predation by both *Nabis* and *Geocoris* increased as predator richness increased (Table 2, 3; Fig. 2; Tables S2–S3). However, aphid predation by *Geocoris* decreased when predator evenness was higher; predator evenness did not affect aphid predation by *Nabis* (Table 2; Table S3). For both focal predators, higher thrips abundance correlated with more-frequent aphid predation (Table 2, 3; Fig. 4; Tables S2–S3). For *Nabis*, greater total arthropod richness also was correlated with aphid predation (Table 2; Fig. S2; Table S2); predator richness and total arthropod richness were themselves correlated, making it difficult to statistically isolate the effect of one from the other (Fig. S3). Overall, aphid predation by both predators did not differ between the two

Table 1

Impact of organic (1) vs. conventional (0) management on arthropod community metrics from generalized linear mixed effects models (GLMMs) with a random effect of field and year. Mean (standard error) for organic and conventional treatments show. Estimate (SE) is from GLMMs. Models of abundance used a negative binomial distribution, models of richness used a gaussian distribution, and models of evenness used a beta distribution. * P < 0.05, ** P < 0.01, *** P < 0.001.

Response	Organic (SE)	Conventional (SE)	Estimate (SE)	*P*-value
Aphids	400.0 (353.9)	45.8 (26.1)	0.86 (0.65)	0.14
Colorado potato beetle	1.67 (1.06)	0 (0)	21.7 (18,818)	0.99
Geocoris	35.8 (5.93)	14.1 (2.84)	0.93 (0.27)	0.0005 ***
Nabis	28.8 (11.1)	7.80 (3.01)	1.23 (0.39)	0.002 **
Scaptomyza pallida	905.7 (217.1)	1650 (411)	−0.45 (0.32)	0.16
Thrips	50.4 (12.4)	56.4 (18.7)	0.39 (0.32)	0.22
Total abundance	2774 (534)	2447 (443)	0.088 (0.24)	0.72
Total richness	37.6 (1.37)	30.1 (1.87)	7.34 (2.11)	0.0005 ***
Predator abundance	428.5 (107.2)	182.6 (37.9)	0.75 (0.26)	0.004 **
Predator richness	9.38 (0.43)	7.85 (0.47)	1.53 (0.62)	0.013 *
Predator evenness	0.68 (0.021)	0.66 (0.031)	0.031 (0.15)	0.84

farming systems (Tables 2, 3; Tables S2–S3; Fig. S4). Interestingly, aphid abundance was not a competitive predictor of aphid predation by either predator species (Tables 2, 3).

4. Discussion

When searching for effects of predator diversity on biological control, the standard practice is to manipulate the number of species while keeping total predator abundance constant (Snyder et al., 2006). Carefully deployed, such manipulations are a powerful technique for separating the effects of species number from confounding effects of predator abundance or species identity (Letourneau et al., 2009; Jonsson et al., 2017; Greenop et al., 2018). Of course, in the open field we might expect different facets of predator community structure to co-vary with one another, or with prey abundance and biodiversity, making the ultimate driver(s) difficult to untangle (Macfadyen et al., 2009a,b). So, it is intriguing that, for both predator species we considered, we found correlations between predator richness and aphid predation (Fig. 2). These patterns are consistent with the view that species-rich predator communities bring together species with different feeding habits, exposing a greater fraction of the prey population to attack in space and time (e.g., Schmitz, 2009; Greenop et al., 2018). That is, predators occupy complementary niches that allow greater total exploitation of the prey resource, consistent with early ideas about such niche differences fostering consumer coexistence (Finke and Snyder, 2008). This suggests that the type of beneficial predator-predator complementarity seen in cage experiments might also be impactful in the open field. However, we note that predator richness was positively correlated with total arthropod richness (Fig. S3), so that it was not possible to entirely isolate correlations with predator richness from overall arthropod richness at the community level.

Alternative prey can indirectly impact predation on a pest through several different channels, some helpful and some not (Harmon and Andow, 2004; Symondson et al., 2002, 2006). At small spatiotemporal scales, alternative prey can draw generalists' attacks away from a target pest and thus disrupt biological control (e.g., Eubanks and Denno, 2000a). However, over longer periods, a rich prey community can support more predator individuals and species and promote biological control (e.g., Evans et al., 1999; Eubanks and Denno, 2000b; Agustí et al., 2003; Szendrei et al., 2010; Blaauw and Isaacs, 2012; Gurr et al., 2017). We showed greater aphid predation in fields with higher abundance of the thrips *F. occidentalis* (Fig. 4), suggesting an indirect enhancement of aphid suppression by these common herbivores. This does not appear to operate by altering abundance of *Nabis* or *Geocoris*, as densities of these two predators were not retained in models (Table 2, 3). Thrips abundance also did not clearly correlate with predator richness (Fig. S3), suggesting that thrips were not simply supporting species-rich predator communities that correlated with greater per capita aphid predation by both generalists. One possibility is that predators foraged more often, or more extensively, when thrips were abundant as prey (e. g., Xu et al., 2006; Rim et al., 2015), leading to incidental predation of aphids as the predators encounter them. Of course, it is also possible that thrips abundance correlates with some other factor that we did not consider in our models, leading to a spurious correlation. Further experimental work will be needed to differentiate among these mechanisms. Regardless, the correlations between thrips abundance and aphid predation suggested an important effect of this particular prey species on aphid biological control.

Sometimes, intraguild predation or other forms of predator-predator interference can disrupt biological control as arthropod diversity increases (Jonsson et al., 2017). Most often this happens when a particularly effective (often large) intraguild predator species is added (Finke and Denno, 2004). We observed a negative correlation between overall predator evenness and apparent aphid predation by *Geocoris* (Fig. 3). This potential harmful evenness effect is surprising, because the few other published examples report positive relationships between
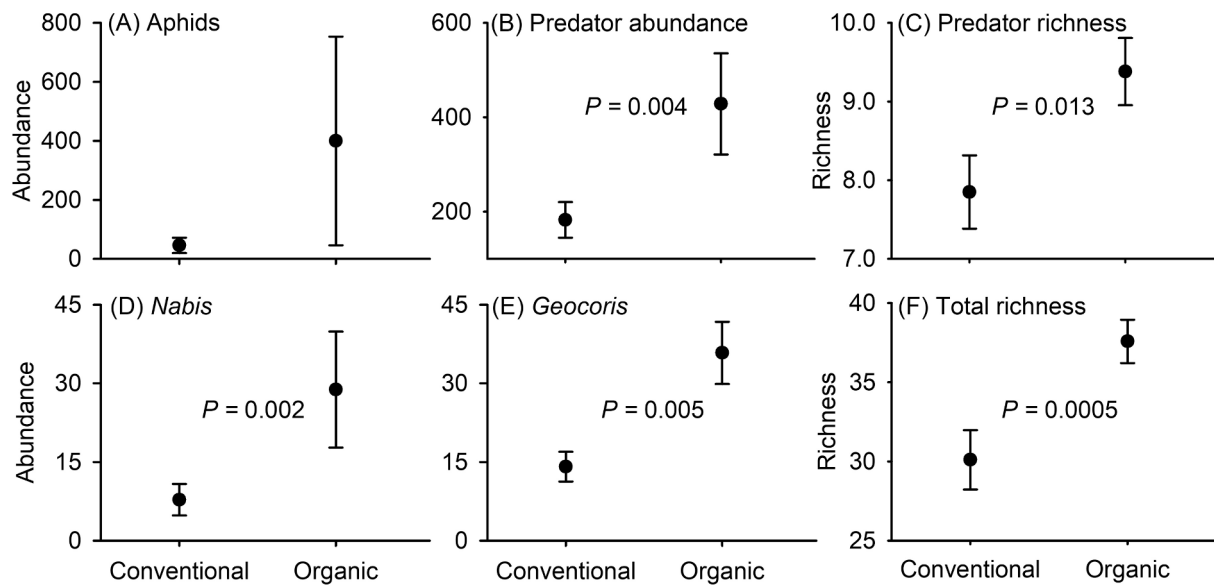
Fig. 1. In potato fields managed using conventional or organic practices, mean abundance ± SE of (A) aphids (all adults keyed as *M. persicae*), (B) predator abundance, (C) predator species richness, (D) *Nabis*, (E) *Geocoris*, and (F) total arthropod species richness.

Table 2
Model selection results for arthropod community and farm management (conventional = 0, organic = 1) that influence the probability of detecting aphids in *Nabis* guts. Only models having > 5% of model weights (95% confidence set of models) are shown. Numbers in columns thrips abundance through total arthropod richness indicate model estimate ± SE on that individual model. Bolded values indicate 95% confidence intervals do not overlap zero. Year and field were included as random effects. The next-best model not shown had ΔAIC_c = 3.5 and weight = 0.038. ** 99% confidence interval does not overlap zero, * 95% confidence interval does not overlap zero, · 90% confidence interval does not overlap zero. The marginal R^2 on the best-supported model was 0.013.

Model	Thrips abundance	Management	Predator richness	Total arthropod richness	ΔAIC_c*	df	Weight
Thrips abundance	0.21 (0.087) *				0	4	0.22
Thrips abundance + Management	0.21 (0.087) *	0.46 (0.38)			1.2	5	0.12
Predator richness			0.35 (0.17) *		1.6	4	0.098
Total arthropod richness				0.37 (0.19) *	1.8	4	0.089

* Akaike Information Criterion with a correction for small sample sizes

Table 3
Model selection results for arthropod community and farm management (conventional = 0, organic = 1) that influence the probability of detecting aphids in *Geocoris* guts. Only models having > 5% of model weights (95% confidence set of models) are shown. Numbers in columns thrips abundance through predator richness indicate model estimate ± SE. Bolded values indicate 95% confidence intervals do not overlap zero. Year and field were included as random effects. The next-best model not shown had ΔAIC_c = 3.3 and weight = 0.030. ** 99% confidence interval does not overlap zero, * 95% confidence interval does not overlap zero, · 90% confidence interval does not overlap zero. The marginal R^2 on the best-supported model was 0.037.

Model	Thrips abundance	Management	Colorado potato beetle abundance	Predator evenness	Predator richness	ΔAIC_c*	df	Weight
Thrips abundance	0.40 (0.15) **					0	4	0.16
Management + Colorado potato beetle abundance		0.56 (0.34) ·	−1.03 (0.54) ·			0.4	5	0.13
Colorado potato beetle abundance			−0.79 (0.45) ·			0.5	4	0.13
Predator evenness				−0.35 (0.12) **		0.7	4	0.11
Predator richness					0.41 (0.16) **	0.8	4	0.11
Management + thrip abundance	0.40 (0.15) **	0.31 (0.36)				1.9	5	0.063
Management + predator evenness		0.34 (0.32)		−0.37 (0.12) **		2.1	5	0.055

* Akaike Information Criterion with a correction for small sample sizes.

predator evenness and pest suppression (Crowder et al., 2010, Blubaugh et al., 2021). In potato fields in our region, *Geocoris* is smaller than other common generalists like *Nabis*, and so may be more likely to be the victim of intraguild predation (Koss and Snyder, 2005, Straub and Snyder, 2006). *Geocoris* also is the most abundant predator (Koss et al., 2005), such that increasing evenness usually arises from the other, often large predator species becoming more common. So, it may be that *Geocoris* is reducing its foraging activity in more even predator communities in response to growing threat of intraguild predation (Langellotto and Denno, 2004). Or, these predators may be foraging more on

the surface of the ground, rather than in the foliage, and so are less likely to encounter aphids (e.g., Schmitz, 2009). Of course, the correlation might arise from some indirect channel that was not considered in our models, and so be a statistical artifact rather than reflecting any real causal relationship.

There are several caveats to our study that must be noted, that are typical of molecular gut content studies and correlational field work more generally. First, as just noted, correlation does not equal causation, and the feeding links proposed here must be interpreted with caution. Of course, carefully controlled manipulative experiments in laboratory or
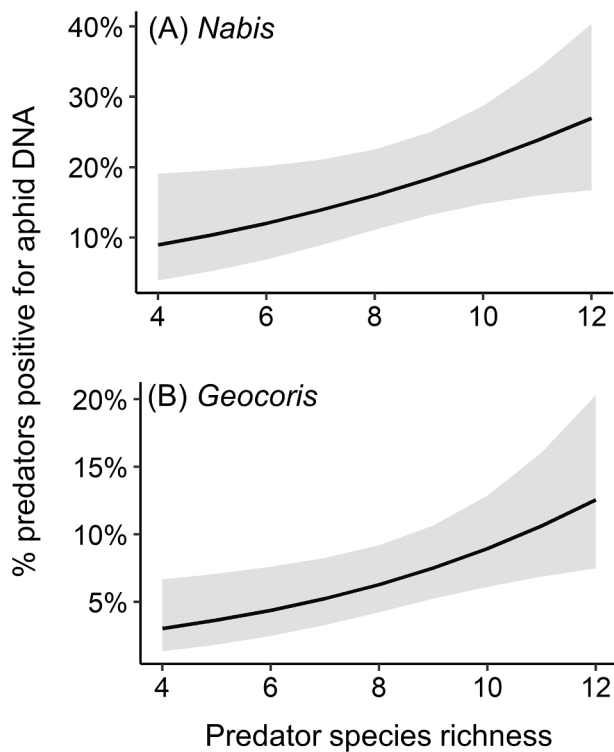
Fig. 2. Probability of detecting aphid DNA (solid line) in (A) *Nabis* and (B) *Geocoris*, by predator species richness. Gray bands indicate 95% confidence intervals.
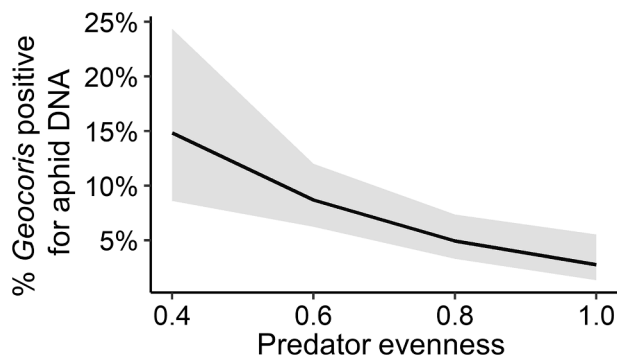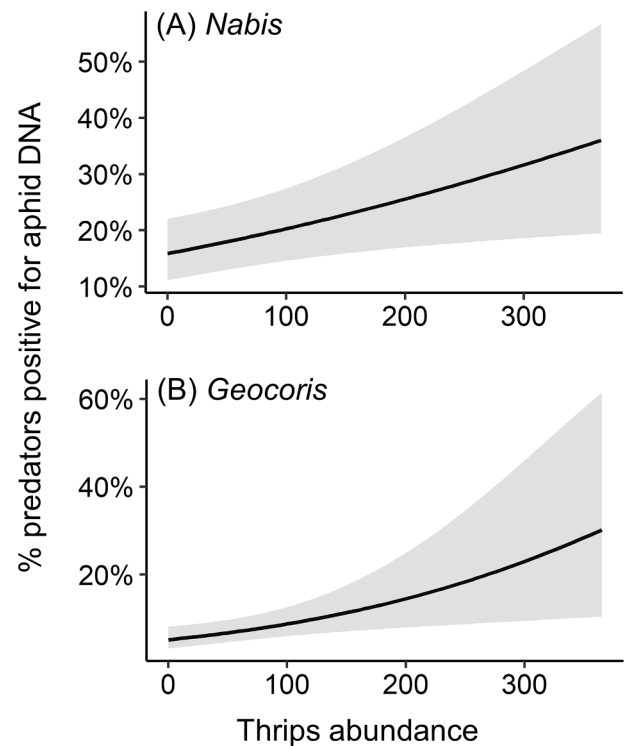

Fig. 4. Probability of detecting aphid DNA (solid line) in (A) *Nabis* and (B) *Geocoris*, by thrips (*F. occidentalis*) abundance. Gray bands indicate 95% confidence intervals.

Fig. 3. Probability of detecting aphid DNA (solid line) in *Geocoris*, by predator species evenness. Gray bands indicate 95% confidence intervals.

field cages also have their weaknesses, and it is reassuring how often the correlations we report here align with results from earlier experiments (e.g., Koss and Snyder, 2005; Straub and Snyder, 2008). Second, molecular gut content analysis cannot distinguish between true predation and scavenging of dead prey, or consumption of other natural enemies that had eaten the prey detected (e.g., Juen and Traugott, 2005; King et al., 2008). Likewise, we cannot determine how many prey of what stage were consumed. All of these limitations make it difficult to directly relate the percentage of predators positive for aphids to resulting aphid suppression. Finally, while it appears that both *Geocoris* and *Nabis* are broad generalists, we do not know the full range of arthropod species they attack or how often. In turn, this means that crude metrics of arthropod diversity like total richness or evenness of all arthropods will only be a rough measure of prey biodiversity from the perspective of the predators.

Several data syntheses have shown higher richness and evenness of natural enemies and other taxa in fields under organic compared to

conventional management (Bengtsson et al., 2005; Hole et al., 2005; Crowder et al., 2012). However, so many farming and thus ecological factors differ between the two systems that the specific underlying cause of these differences can be difficult to unravel (Birkhofer et al., 2011; Schmidt et al., 2014). Greater biodiversity in organic fields is generally attributed to some combination of a greater abundance and/or biodiversity of resources alongside fewer disruptive pesticide applications (e. g., Crowder et al., 2010, 2012). We found higher total arthropod richness in organic fields, and also higher abundance of both of the focal predator species and greater predator richness (Table 1). It was notable that farming system itself, and diversity and abundance characteristics that significantly differed between the two, generally were not retained in models (Tables 2-3). Indeed, for both predators, aphid predation rates did not statistically differ between farming types in simple pairwise comparisons (Fig. S4). So, differences in aphid predation appeared to reflect ecological conditions that varied broadly among fields, independent of farming system, which aligns with a common inability to find clear predator feeding differences when comparing predation in organic versus conventional fields (e.g., Macfadyen et al., 2009ab; Schmidt et al., 2014).

Biodiversity-biocontrol relationships are generally thought to reflect some combination of complementarity, interference, and species identity effects (Snyder, 2019). However, much evidence for the importance of each comes from relatively tightly controlled manipulations in experimental laboratory or field arenas. Thus, it was reassuring that each appeared influential, in one response variable or another, within our open-field study. Complementarity was suggested by positive correlations between predator richness and aphid predation by both *Geocoris* and *Nabis*, while interference was suggested by the negative correlation between predator evenness and *Geocoris* feeding on aphids. Correlations with thrips abundance suggested identity effects for this key herbivorous prey. An obvious weakness of the results presented here is that we can only infer causal relationships, rather than directly demonstrate them. Nonetheless, our findings suggest reason for

optimism that the type of biodiversity effects suggested by experimental manipulations in simpler arenas, might yield some insight into mechanisms operating in real world production fields. Although no simple undertaking, this in turn suggests it may be possible to develop conservation biological control plans that allow growers to heighten predator-predator complementarity and reduce interference.

CRediT authorship contribution statement

Karol L. Krey: Conceptualization, Investigation, Methodology, Writing - original draft. **Olivia M. Smith:** Formal analysis, Writing - original draft. **Eric G. Chapman:** Formal analysis, Investigation, Methodology, Writing - original draft. **Michael S. Crossley:** Formal analysis, Writing - original draft. **David W. Crowder:** Conceptualization, Formal analysis, Funding acquisition. **Zhen Fu:** Investigation, Methodology. **James D. Harwood:** Conceptualization, Funding acquisition, Methodology. **Andrew S. Jensen:** Conceptualization, Funding acquisition. **Christine A. Lynch:** Investigation, Methodology. **Gretchen B. Snyder:** Conceptualization, Funding acquisition, Supervision. **William E. Snyder:** Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocontrol.2021.104650.

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