Research Article

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Alternative prey mediate intraguild predation in the open field

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Abstract

BACKGROUND: Generalist predators that kill and eat other natural enemies can weaken biological control. However, pest suppression can be disrupted even if actual intraguild predation is infrequent, if predators reduce their foraging to lower their risk of being killed. In turn, predator–predator interference might be frequent when few other prey are available, but less common when herbivorous and detritus-feeding prey are plentiful. We used molecular gut-content analysis to track consumption of the predatory bug *Geocoris* sp. by the larger intraguild predator *Nabis sp.*, in organic and conventional potato (*Solanum tuberosum*) fields.

RESULTS: We found that higher densities of both aphids and thrips, two common herbivores, correlated with higher probability of detecting intraguild predation. Perhaps, *Nabis* foraging for these herbivores also encountered and ate more *Geocoris*. Surprisingly, likelihood of intraguild predation was not strongly linked to densities of either *Nabis* or *Geocoris*, or farming system, suggesting a greater importance for prey than predator community structure. Intriguingly, we found evidence that *Geocoris* fed more often on the detritus-feeding fly *Scaptomyza pallida* with increasing predator evenness. This would be consistent with *Geocoris* shifting to greater foraging on the ground, where *S. pallida* would be relatively abundant, in the face of greater risk of intraguild predation.

CONCLUSION: Overall, our findings suggest that while herbivorous prey may heighten intraguild predation of *Geocoris* in the foliage, detritivores might support a shift to safer foraging on the ground. This provides further evidence that prey abundance and diversity can act to either heighten or relax predator–predator interference, depending on prey species identity and predator behavior.
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1 INTRODUCTION

Generalist predators play complex roles in biological control.[1] Their polyphagy allows these predators to subsist on other prey before crops emerge and herbivores colonize, forming a first line of defense.[2,3] Likewise, generalists can switch among prey species throughout the growing season as herbivores become more or less common, contributing to control across diverse pest assemblages.[1,4] But broad feeding habits also bring drawbacks. When pests are not the preferred prey, generalists might focus their attacks on more appealing options and abandon any contribution to biological control.[5–8] Most troubling, perhaps, is that generalist predators often feed on other natural enemies.[9–11] In extreme cases, for example when an aggressive intraguild predator feeds heavily on a key specialist natural enemy, generalists can allow herbivores to escape top-down control.[12–14] Disruption can occur even when predators do not actually kill one another, if a risk-averse predator reduces its foraging in the presence of dangerous intraguild predators.[15,16] The balance of these positive and negative effects of generalists will determine their value as biological control agents, and any management practices that can tip the weighting towards benefit over harm have obvious practical value.[17,18]

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Often, prey communities influence whether intraguild predation is common.[19] When arthropod communities are depauperate and few other options are available, predators may have little alternative but to prey upon one another.[20,21] However, when herbivorous or detritus-feeding prey are plentiful, intraguild predation often becomes less common.[21–23] Abundant floral resources can similarly reduce the frequency of intraguild predation.[24] The opposite effect is possible, however, for example when predators searching for herbivorous prey fall victim to sit-and-wait predators they might not otherwise encounter.[25,26] Therefore, growing prey abundance does not inevitably lead to reduced predator–predator interference, and here again predator behavior can determine the outcome. Snyder[18] suggests that prey diversity, and not just prey abundance, might also influence intraguild predation rates. This is because prey communities that include many abundant prey species might allow predators to move into different, complementary feeding niches that make predator–predator encounters less likely. Perhaps the clearest evidence that prey abundance and diversity mediate intraguild predation comes from laboratory- or field-cage experiments where these factors can be tightly controlled.[9,27] Less is known about the open-field situation, where predator and prey diversity can be relatively high.[9,18]

Here, we use molecular gut-content analysis to assess intraguild predation of the smaller predatory bug *Geocoris sp.* by the larger *Nabis sp.* in potato (*Solanum tuberosum* L.) fields [molecular identification failed to find a consistent species assignment for either predator taxon; Krey *et al.*[28]]. *Geocoris* are generally among the most common insects in potato crops of the northwestern USA, but their small size and active foraging behavior likely exposes these predators to a high risk of intraguild predation.[29,30] Our collection sites were managed by cooperating growers using conventional or organic management practices that influence arthropod communities,[31,32] allowing us to search for any interaction(s) between prey and predator abundance and diversity. *Nabis* appears to forage primarily in the foliage whereas *Geocoris* readily moves between the ground and foliage.[30] We then used a second species-specific primer to examine whether *Geocoris* shifted to feed more on the fly *Scaptomyza pallida* (Zetterstedt), a detritus-feeder that is associated with the soil detrital foodweb,[28] with increasing risk of intraguild predation.

2 MATERIALS AND METHODS

Our project had three complementary components. First, we developed and verified taxon-specific polymerase chain reaction (PCR) primer pairs that allowed us to infer consumption of *Geocoris* by *Nabis*, or of the detritus-feeding fly *S. pallida* by either predator. Second, we surveyed densities of *Nabis* and *Geocoris* predators, and of other arthropods that might serve as prey, in organic and conventional potato fields that were managed by cooperating commercial growers. Third, we used the primers to test for the presence of *Geocoris* and/or *Scaptomyza* DNA in a subset of the predators that we had collected.

2.1 Natural history

Consistently, *Geocoris* is among the most common generalist predators in potato fields in our study region in central Washington state, USA, sometimes representing 50% or more of all predator individuals found during intensive surveys.[28,31,32] These relatively small predators appear to be common victims of intraguild predation by the larger predatory bug *Nabis*.[29,33] However,

predator–predator interference appears to be relaxed with increasing predator richness or evenness, perhaps because predators that forage in different niches have relatively little opportunity to encounter and eat one another.[34,35] Both predators seem to find green peach aphids [*Myzus persicae* (Sulzer)] to be relatively attractive prey (*e.g.*,[36]) that are commonly eaten even when rare in the field.[37] The Colorado potato beetle (*Leptinotarsa decemlineata* Say), another common herbivore, appears to be less preferred.[36] Western flower thrips (*Frankliniella occidentalis* Pergande) is among the most abundant herbivores,[28] and the detritus-feeding fly, *S. pallida*, is the most common insect overall often making up >50% of the community.[28] It has been hypothesized the greater prey biodiversity might allow predatory arthropods to move into distinct feeding niches that relax intraguild predation,[18] although this has not been tested in this system.

Earlier, we described arthropod communities in the same fields considered here, while examining predation of aphids by these same predator individuals.[28,38] When comparing arthropods in organic *versus* conventional fields, we found that both *Nabis* and *Geocoris* were significantly more abundant under organic management, and total predator abundance, predator richness, and total arthropod richness were also higher.[28] All other arthropod community attributes that we considered (*i.e.*, abundances of aphids, thrips and *S. pallida* flies; and total arthropod abundance and predator evenness) did not significantly differ between the two farming systems.[28]

2.2 Primer design

To design primers to test for *Geocoris* or *S. pallida* consumption, all of the Lygaeoidea and Drosophilinae COI sequences available on GenBank were downloaded with the search criterion 'Lygaeoidea and (coi or co1 or cox1)' or "Drosophilinae and (coi or co1 or cox1) (GenBank searches conducted in June and April, 2010, respectively). An additional 15 COI *Geocoris* sp. and 18 *S pallida* COI barcodes were obtained from specimens collected in WA potato fields using the primers LCO1490[39] and HCO-700ME[40] and using the PCR reagents and following the thermal cycling protocols in Chapman *et al.*[41] We found nine *Geocoris* and 18 *S. pallida* COI haplotypes among them (GenBank accession numbers: *Geocoris*: MZ677017- MZ677025; *S. pallida*: OK429345-OK429362). To obtain COI data sets for primer design, we added these additional sequences to the GenBank data sets, removed sequences that would not align (using MUSCLE[42]); with the COI barcode region,[43] and removed duplicate sequences using MacClade.[44] After using maximum likelihood (Garli 0.95, default settings[45]) to build a tree from these terminals, taxa were arranged in the data sets in similar fashions to the relationships shown in the maximum likelihood trees. This facilitated easy searches for DNA sites that were different from the other species (the most similar sequences were in close proximity to our targets), and therefore potentially taxon-specific.

Using *Primer3*,[46] we designed three forward and three reverse primers for *Geocoris* and four each for *Scaptomyza pallida*. Our goal was to design primers such that the 3′ base in at least one of the primers was unique to the focal taxon using *Primer3*.[46] Initial testing allowed us to identify one primer pair for each focal taxon that worked better than the others, so we optimized them for amplification of *Geocoris* or *S. pallida* from gut contents (see protocols below). For *Geocoris*, our final primers were Geo-294-F (5′- TAT CAA GAA GTA TAG TAG AAA TAG GAG CT −3′) and Geo-449-R (5′- AAA TAA AAT TAA TAG CTC CAA GAA TAG AAC -3′). For *S. pallida*, our primers were Scap-93-F (5′- TAA TTG GAG ATG

ACC AAA TTT ACA −3′) and Scap-234-R (5′- AAA GCT ATA TCA GGA GCT CCT AAC A – 3′). The numbers in the primer names reflect the position of the 5′ base relative to an alignment of the barcode region of COI[43] that is amplified by the Folmer *et al.*[39] COI primers. The *Geocoris* primers amplify a 156 bp amplicon whereas the *S. pallida* primers amplify a 142 bp amplicon. Primers were tested for specificity by attempting PCR amplifications with around 90 non-target taxa, 71 of which were from WA potato fields (Appendix S1).

Identification of species in the genera *Nabis* and *Geocoris* is currently quite challenging, as discussed in Krey *et al.*[28] In summary, sequencing approximately 15 individuals of each genus from WA potato fields resulted in multiple COI haplotypes for each, with intraspecific uncorrected p-distances of 1.52% for *Nabis* and 0.456% for *Geocoris*. Even with over 99.5% similarity among them, our *Geocoris* COI sequences had best matches to three different species on the Barcode of Life Database (BOLD[47]), whereas the approximately 98.5% sequence similarity among our *Nabis* sequences led to four best matches. Taxonomically, multiple species have been described in each genus since their most recent revisions, which are both over 85 years old. Therefore, it is prudent to leave predator identification at the genus level, as these genera are in serious need of modern taxonomic treatments. Identification of *Scaptomyza* was more clear-cut. All 18 COI haplotypes created unambiguous matches on BOLD to *S. pallida* at either 100% or 99.85% sequence similarity.

2.3 Arthropod survey and collections in commercial potato fields

We sampled from six organic and six conventional fields in the first year (2009), nine organic and eight conventional fields in the second year (2010), and six organic and six conventional fields in the third year (2011), with all fields managed by cooperating growers and located in Adams, Benton and Grant counties in central Washington state (see[28,37,38]). Different fields were sampled each year; organic fields met US Department of Agriculture criteria for certification; and all fields of both farming system were approximately 50 ha circles under center pivot irrigation. Predators were collected in July–early August of each year, from 50 plants in each field using a D-vac suction-sampling device as described previously.[28,32,37] Briefly, we haphazardly identified five 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.[32] D-vac bags containing arthropods were immediately placed on dry ice, and *Geocoris* and *Nabis* were removed using forceps, placed individually in 95% EtOH 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.*[41] found that this methodology avoids contamination of predators with prey DNA. We tested between five and 71 *Geocoris* per field (mean = 48.7 ± 2.32 SE) and between one and 82 *Nabis* per field (mean = 30.5 ± 2.73 SE).

Following the removal of predators for gut-content analysis, all other remaining arthropods from each D-vac bag were retained from vacuum samples 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 specific species included in our models 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 Blood and Tissue Kit following the manufacturer's animal tissue protocol (QIAGEN Inc., Chatsworth, CA, USA). PCRs (12.5 μL) consisted of 1× 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 (1 μL of total DNA). PCRs were carried out in Bio-Rad PTC-200 and C1000 thermal cyclers (Bio-Rad Laboratories, Hercules, CA, USA). The PCR cycling protocols for the *Geocoris* primers were 94 °C for 1 min followed by 45 cycles of 94 °C for 45 s, 61 °C for 45 s, 72 °C for 30 s and a final extension of 72 °C for 5 min. The *S. pallida* primers had an identical protocol except that the annealing temperature was 63 °C. Electrophoresis was used to confirm amplification using 10 μL of PCR product in 3% SeaKem agarose (Lonza, Rockland, ME, USA) stained with GelRed (0.1 mg uL^{-1}; Phenix Research, Chandler, NC, USA).

2.5 Data analyses

Based on the known natural history described above, the factors we considered in our modeling efforts were individual abundances of the key herbivore species *M. persicae*, *L. decemlineata*, and *F. occidentalis*; the detritus-feeding fly *S. pallida*; the focal predators *Nabis* and *Geocoris*; total abundance, richness, and evenness of predators; and total abundance, richness, and evenness of all arthropods (Table S1). Richness was calculated as the sum of species and evenness using the metric E_{var} (*e.g.*,[48]). We examined the impact of arthropod community metrics and farming system on the probability of detecting *S. pallida* DNA in *Geocoris* and *Nabis*, and of detecting *Geocoris* DNA in *Nabis*, using GLMMs with a binomial distribution and logit link function in the glmmTMB package in R.[49] Models included random effects of field and year.

We constructed 35 candidate models that tested the relative importance of each of the arthropod community metrics and their potential additive and interactive effects with farming system (Table S1). We generated our candidate model set based on
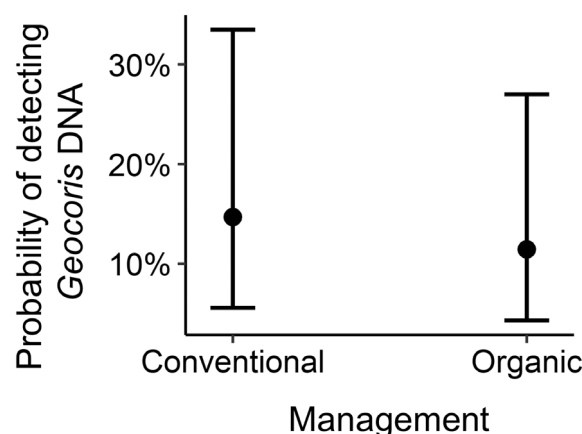

Figure 1. Probability of detection of *Geocoris* DNA in *Nabis* in organic *versus* conventional potato fields. Figure shows the predicted values from the models including farming system alone using the 'plot_model' function in the sjPlot package in R. Bars show 95% confidence interval.

Table 1. Model selection results for arthropod community and farm management (conventional = 0, organic = 1) variables that influence the probability of detecting *Geocoris* DNA in *Nabis* guts. Only models having >5% of model weights are shown. Numbers in columns Aphid abundance through Management indicate model estimate ± SE. Bolded values indicate $P < 0.05$. Year and field were included as random effects. The next-best model not shown had $\Delta AIC_c = 3.6$ and weight = 0.036. ** $P < 0.01$, * $P < 0.05$, · $P < 0.10$ but >0.05

Model	Aphid abundance	Colorado potato beetle abundance	Thrip abundance	Management	ΔAIC_c*	df	Weight
Aphid abundance	**0.36 (0.15)** *				0	4	0.22
Colorado potato beetle abundance		**−0.67 (0.33)** *			0.3	4	0.19
Thrips abundance			**0.27 (0.11)** *		0.6	4	0.16
Management + aphid abundance	**0.38 (0.15)** *			−0.39 (0.43)	1.8	5	0.090
Management + thrips abundance			**0.27 (0.11)** *	−0.30 (0.40)	2.7	5	0.056
Management + Colorado potato beetle abundance		−0.67 (0.34) ·		−0.013 (0.41)	2.9	5	0.051

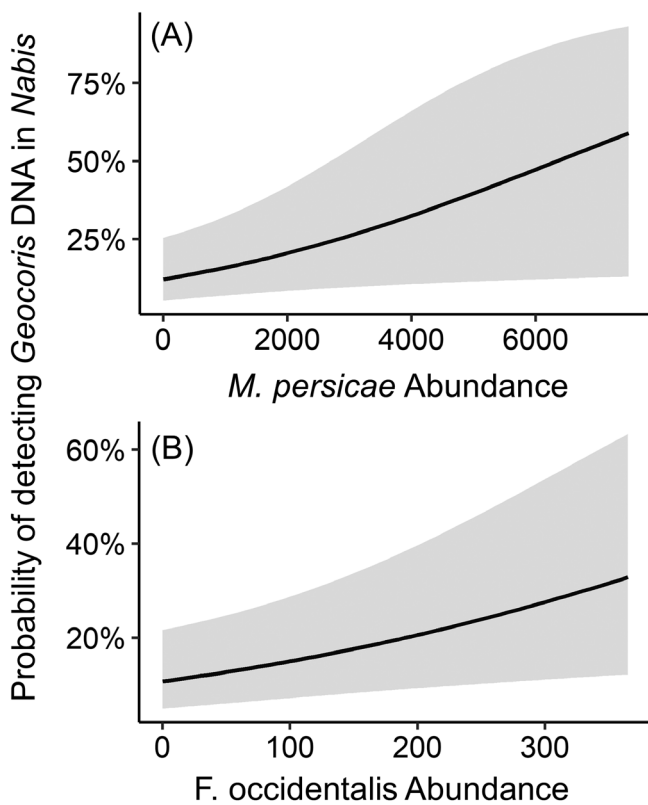*Akaike Information Criterion with a correction for small sample sizes.

Figure 2. Probability of detection of *Geocoris* DNA in *Nabis*, against abundance of (A) aphids (*M. persicae*) and (B) Western flower thrips (*F. occidentalis*). Figure shows the predicted values from the best-supported models using the 'plot_model' function in the sjPlot package in R.[53] X-variables were standardized in the candidate model set but are plotted on the original scale for visualization. Gray bands are 95% confidence intervals.
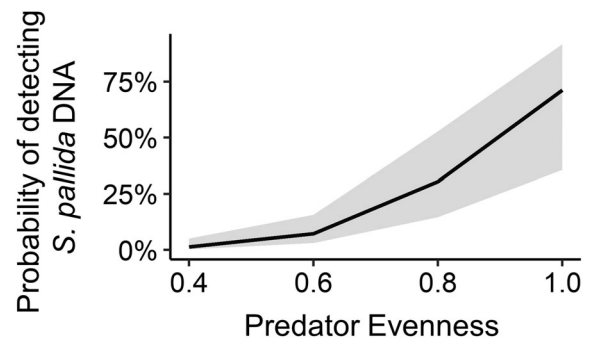

FIGURE 3. Probability of detecting *S. pallida* DNA in *Geocoris*, *versus* predator evenness. Figure shows the predicted values from the model using the 'plot_model' function in the sjPlot package in R.[53] X-variables were standardized in the candidate model set but are plotted on the original scale for visualization. Gray bands are 95% confidence interval.

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.[50,51] We assessed multicollinearity for candidate models using the performance package in R.[52] Multicollinearity was not an issue (VIF < 5).

3 RESULTS

3.1 *Geocoris* and *S. pallida* primers

Geocoris and *S. pallida* primers were tested for cross-reactivity against a variety of non-target arthropod species including three phyla, 10 orders, and at least 50 families (Appendix S1). Given the mismatches in both primer pairs to non-targets in our data sets and the completely negative non-target test results (Appendix S1), we can be reasonably assured that our primers are specific to the strains of *Geocoris* and *S. pallida* that occur in Washington potato fields.

3.2 Factors impacting predation

When ignoring arthropod community attributes or abundance of particular species, and making a simple comparison between organic and conventional potato fields, we found no difference

arthropod community metrics that have previously been important in predator–prey dynamics in our system and similar systems (*e.g.*,[31]). We z-score transformed arthropod community metrics prior to running our models. We then ranked models based on Akaike Information Criterion (AICc) and identified those that were most supported (ΔAICc <2.0).[50] Briefly, AICc is a statistical technique intended to select a 'best' model among a series of

Table 2. Model selection results for arthropod community and farm management (conventional = 0, organic = 1) variables that influence the probability of detecting *S. pallida* DNA in *Geocoris* guts. Only models having >5% of model weights are shown. Numbers in columns Predator Evenness through *S. pallida* Abundance * Management indicate model estimate ± SE. Bolded values indicate $P < 0.05$. Year and field were included as random effects. The next-best model not shown had $\Delta AIC_c = 4.2$ and weight = 0.048. ** $P < 0.01$, * $P < 0.05$, · $P < 0.10$ but >0.05

Model	Predator Evenness	Management	Predator evenness * Management	*S. pallida* Abundance	*S. pallida* Abundance * Management	ΔAIC_c*	df	Weight
Predator evenness	**1.02 (0.24)** ***					0	4	0.38
Predator evenness + Management	**1.00 (0.23)** ***	−0.80 (0.51)				0.2	5	0.35
Predator evenness * Management	**1.12 (0.28)** ***	−0.75 (0.51)	−0.34 (0.36)			2.1	6	0.14
S. pallida Abundance * Management		−0.17 (0.57)		**0.64 (0.33)** *	**1.24 (0.55)** *	3.9	6	0.055

*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) variables that influence the probability of detecting *S. pallida* DNA in *Nabis* guts. Only models having >5% of model weights are shown. Numbers in columns Management through Management * *S. pallida* Abundance indicate model estimate ± SE. Bolded values indicate $P < 0.05$. Year and field were included as random effects. The next-best model not shown had $\Delta AIC_c = 4.9$ and weight = 0.029. ** $P < 0.01$, * $P < 0.05$, · $P < 0.10$ but >0.05

Model	Management	*S. pallida* Abundance	Management * *S. pallida* Abundance	ΔAIC_c*	df	Weight
Management + *S. pallida* Abundance	**−0.70 (0.35)** *	**0.55 (0.17)** **		0	5	0.33
Management * *S. pallida* Abundance	−0.69 (0.36) ·	0.37 (0.20) ·	0.54 (0.34)	0.1	6	0.31
S. pallida Abundance		**0.66 (0.17)** ***		1.1	4	0.19

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

in the probability of detection of possible intraguild predation ($\beta = -0.29 \pm 0.43$ (SE), $P = 0.50$; Fig. 1). However, we did find important predictors of probability of detecting intraguild predation within our full model set. For the probability of detection of *Geocoris* DNA in *Nabis*, four models had high support (*i.e.*, ΔAIC_c <2.0; Table 1). Two models included a positive correlation increased probability of detecting intraguild predation and aphid density (among adult aphids, only *M. persicae* was found in these fields[28] (Table 1, Fig. 2(A)). Similarly, one model included a positive relationship between probability of detecting intraguild predation and increasing abundance of *F. occidentalis* (Table 1, Fig. 2 (B)). A fourth competitive model included *L. decemlineata* abundance, although we only collected *L. decemlineata* on five organic farms, and never on conventional farms, across our arthropod community sampling. No other arthropod community attribute was included in competitive models (Table 1).

For the probability of detecting *S. pallida* DNA in *Geocoris*, all three models with high support included a positive relationship with predator evenness (Table 2, Fig. 3). No other arthropod or system effects were included in best-supported models (Table 2). For the probability of detecting *S. pallida* DNA in *Nabis*, two of three competitive models included, perhaps not surprisingly, increasing probability of detection with increasing *Scaptomyza* abundance (Table 3, Fig. S1). Farming system also appeared in the best-supported model, with *Scaptomyza* detection in *Nabis* more likely in conventional than organic potato fields (Table 3, Fig. S2).

4   DISCUSSION

We found positive correlations between aphid and thrips abundance, and the probability of detecting intraguild predation of *Geocoris* by the larger predator *Nabis*. Aphids appear to be relatively appealing prey for *Nabis*, attacked in preference to other prey like *L. decemlineata* that have stronger chemical and/or behavioral defenses.[32,54] Indeed, *Nabis* tested positive for aphid DNA even in fields where aphids were too rare to be detected during intensive field sampling.[37] Aphids are relatively stationary feeders, and so, to efficiently hunt them *Nabis* would have to actively forage.[33] This increased foraging, in turn, could lead to more chance encounters with *Geocoris* that lead to intraguild predation.[25,55] Something similar could be at play with thrips, if they too are perceived as relatively desirable prey. This is in line with the common observation that any ecological factor that enhances predator–predator encounters might lead to enhanced intraguild predation.[22,56] For example, removing straw thatch often leads to predators bumping into and eating one another more often,[23,57,58] and spatiotemporal niche overlap strongly predicts predator–predator interference across systems.[18,55]

Often, when prey detect predators, they alter their foraging behavior to reduce their risk of being eaten.[59–61] Within predator communities, this can lead to a disruption of natural pest control that is similar to the effects of actual intraguild predation.[18] For example, Prasad and Snyder[62] found that a relatively large ground beetle species that was a dangerous intraguild predator disrupted biological control of pest-fly eggs, because the smaller ground

beetles that ate the most fly eggs stopped foraging when the larger beetle was active. Similarly, Hosseini *et al.*[63] found that predatory gall midge fly larvae leave patches of aphid prey when they detected the alarm pheromones the aphids release when being attacked by other predator species. *Geocoris* appears to readily move between foraging on the ground and in potato foliage.[35] In contrast, *Nabis*, along with other likely intraguild predators of *Geocoris* such as thomisid spiders and reduviid bugs, spend much of their time in plant foliage.[30,32,35,64] This means that *Geocoris* might find a refuge from intraguild predation by foraging on the ground rather than in the foliage. Consistent with this, detection of *Scaptomyza* DNA in *Geocoris* increased with increasing predator evenness; because *Geocoris* is often the most abundant predator in these fields, growing evenness would typically reflect higher relative abundance of other predator species (*e. g.*,[31]). *Scaptomyza* flies are detritus feeders, and so likely are most-often encountered when a predator forages on the soil surface. Of course, future direct observations of *Geocoris* foraging behavior will be needed to confirm that these predators do indeed shift to greater ground-surface foraging as the abundance of other predators increases.

Intraguild predation rates are generally thought to reflect, at least in part, the abundance of other prey and the abundance of intraguild predators. This is because a low abundance of other prey paired with high predator densities might lead to hungry predators regularly encountering one another.[19,20] In contrast, rare predators foraging among bountiful prey might find little need or opportunity to prey on one another.[22] Extrapolating, we might then expect intraguild predation to be relatively rare in organic fields where arthropod diversity is generally higher.[48,65] Our results failed to follow these expectations. Overall, per-capita intraguild predation of *Geocoris* by *Nabis* did not significantly differ between organic and conventional potato fields, and farming system was not retained in 3 of 4 well-supported models even though organic fields generally had higher total prey abundance. Organic fields did have consistently higher abundances of both *Nabis* and *Geocoris*, seemingly heightening the opportunity for predator–predator encounters. For example, Roubinet *et al.*[66] found that intraguild predation of spiders by carabids was more frequently detected in organic than conventional cereal fields. Yet, for our work in potato fields, abundances of *Geocoris* and *Nabis* predators were not retained in the best-supported models. Additional work may be needed, ideally in the open-field conditions explored here, to see whether it is common for abundance of appealing prey to heighten, rather than reduce, intraguild predation rates independent of predator abundances.

It is important to point out several caveats of this study, shared with many other gut-content studies and observational work more generally. First, DNA detection reveals relatively little about how many prey of what stage were eaten.[67–69] Of course, it is also possible that the predator has eaten another predator that ate that prey, or scavenged the insect, reflecting harm or no contribution to biological control.[70,71] Our models suggest correlations where we might not be truly getting at causation, if some other factor not included co-varies with two or more factors that we did consider. Similarly, while we chose our model set based on earlier experimental findings, we do not know the full range of prey the predators have eaten and so cannot rigorously define prey that would or would not be common diet items. So, it is important to reinforce that direct observations of predator behavior are needed to gain greater confidence that the correlations we report are revealing interactions that are truly important in the field.

Using these same predator individuals, we have looked at evidence of predation of two herbivorous prey, aphids and the Colorado potato beetle, with the same statistical model set. This allows us to look at evidence for predator–predator interference as a factor mediating consumption of these two prey items.[28,38] As we saw here for *Scaptomyza* as prey, our probability of detecting *Geocoris* consumption of aphids decreased with increasing predator evenness.[28] This provides further support for a niche shift to more ground-foraging as relative abundance of intraguild predators increases. Likewise, our probability of detecting *Nabis* predation of Colorado potato beetles generally decreased with increasing overall predator abundance, consistent with increasingly-disruptive predator–predator interference or a switch to acting as an intraguild predator.[38] All else being equal, we would expect increasing predator richness to foster greater foraging niche complementarity, and thus fewer predator–predator encounters[72–75]; this did correlate with greater detection of aphid DNA in both *Nabis* and *Geocoris*.[28] So, molecular gut-content work to-date generally supports the view that these generalist predators have great potential to interfere with one another and other predators in the community, but that the frequency of these interactions can be relaxed or heightened based on predator and prey abundance and biodiversity.[28,38]

5 CONCLUSION

In general, intraguild predation rates are thought to decrease with increasing abundance of alternative prey, especially of relatively attractive prey such as aphids.[19] Here, we found just the opposite, that intraguild predation was more often detected when aphids or thrips were more abundant. This result is roughly analogous to the scenario reported by Rosenheim *et al.*,[26] who found that lady beetle predators actively hunting for spider mite prey heightened their risk of encountering and falling victim to sit and wait spiders. The difference of course is that mobile *Nabis* in our potato fields were the perpetrator, rather than victim, of intraguild predation. Our findings did closely align with the observation that predators might react to heightened intraguild predation risk by reducing their foraging,[61] as suggested by greater *Geocoris* feeding in the detrital foodweb (Fig. 2) and reduced feeding on herbivores[28] when other predators were relatively more abundant. The common thread is that the specifics of behavior by each predator species, and how they react both to prey and predator communities, determines the extent of intraguild predation and its implications for consumption of any particular prey species.[25]

AUTHOR CONTRIBUTIONS

DATA AVAILABILITY STATEMENT

SUPPORTING INFORMATION

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

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