

Diet of generalist predators reflects effects of cropping period and farming system on extra- and intraguild prey

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Abstract. The suppression of agricultural pests by natural enemies, including generalist arthropod predators, is an economically important regulating ecosystem service. Besides pests, generalist predators may also consume non-pest extraguild and intraguild prey, which can affect their impact on pest populations. This may either reduce the impact of generalist predators on pest populations, because they are diverted from pest predation, or increase it, as it helps them survive periods of low pest availability. However, the availability of pest prey and alternative, non-pest prey can vary over the crop growing season and between farming systems, potentially affecting predator–prey interactions and the levels of biological control. We have limited information about how farming systems and environmental variation over the crop growing season influence predator diets. This limits our ability to predict the importance of generalist predators as natural enemies of agricultural pests. Here we utilize molecular gut content analyses to assess detection frequencies of extra- and intraguild prey DNA in generalist predator communities in replicated organically and conventionally managed cereal fields at two key periods of the cropping season for aphid biological control. This is done in order to understand how farming system, crop season, prey availability and predator community composition determine the composition of predator diets. Aphid pests and decomposers (springtails) were equally important prey for generalist predators early in the growing season. Later in the season, the importance of aphid prey increased with increasing aphid densities while springtail predation rates were positively correlated to abundance of this prey at both early and late crop growth stages. Intraguild predation was unidirectional: carabids fed on spiders, whereas spiders rarely fed on carabids. Carabids had higher detection frequencies for the two most common spider families in organically compared to conventionally managed fields. Our study documents that predation by generalist predator communities on aphid pests increases with pest numbers independently of their generally widespread consumption of alternative, non-pest prey. Therefore, conservation strategies in agricultural fields could promote biological control services by promoting high levels of alternative non-pest prey for generalist predator communities.

Key words: aphids; Araneae; biological control; Carabidae; intraguild predation; molecular gut content analyses; organic farming.

INTRODUCTION

Food webs are formed by trophic interactions that link consumers and resources and this affects the provision of multiple ecosystem services (Hines et al. 2015). Biological control of agricultural pests by natural enemies is one of the economically most important regulating ecosystem services (Costanza et al. 1997). Generalist arthropod predators, such as spiders and carabids, are abundant natural enemies in many agroecosystems (Lövei and Sunderland 1996, Nyffeler and Sunderland 2003) and are

key contributors to the biological control of pest populations (Symondson et al. 2002). The wide diet breadth of generalist predators (Toft and Bilde 2002) can, however, weaken their role as biological control agents. For example, generalist predators feed on prey from both the above- and belowground subsystem of agroecosystems (Scheu 2001), which may have negative consequences for pest suppression due to a switch from consuming herbivore pests to, for example, decomposer prey (Wise et al. 2006). The consumption of such alternative prey may, however, also promote biological control services, as it provides critically important food resources to generalist predators when pest are scarce (Halaj and Wise 2002, von Berg et al. 2010), for example at the beginning of the growing season of annual crops in temperate regions.

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Generalist predators may also feed on each other (“intraguild predation,” IGP, as opposed to “extraguild predation,” EGP; Wise 2006) and such trophic interactions may constrain their contribution to biological control services (Snyder and Wise 1999, Lang 2003). Intraguild predation may be unidirectional for example in spiders and carabids: carabids may face a lower risk of attack by spiders than vice versa due to their tougher chitinous exoskeletons (Davey et al. 2013). The importance of non-pest prey and IGP for generalist predators are two important, but understudied, aspects of the functional role of these predators.

To improve our ability to predict the importance of generalist predators as natural enemies of agricultural pests, we need to understand how diet composition is modified by farming practices and environmental variation (Winqvist et al. 2011, Diehl et al. 2013). The application of synthetic fertilizers under conventional management, for example, often leads to lower abundances of decomposer prey, but higher numbers of herbivores (Birkhofer et al. 2008). Simultaneously, differences in farming practices may alter the composition of generalist predator communities (Birkhofer et al. 2013), which might affect their contribution to biological control services (Östman et al. 2003, Birkhofer et al. 2015b). It remains less well understood, however, if the diet composition of generalist predators reflects the abundance of potential prey in agricultural fields (Diehl et al. 2013). In fact, generalist predators may not consume prey in a density-dependent manner (Agusti et al. 2003, Kuusk and Ekbom 2010, 2012, Schmidt et al. 2012), but diets may instead reflect specific preferences. The abundances of all major prey groups should therefore be considered when studying effects on pest prey by generalist predators (Gavish-Regev et al. 2008, Kuusk and Ekbom 2012). The presence of weeds in arable fields further complicates predictions about trophic interactions between generalist predators and their prey due to the provision of alternative resources (e.g., seeds) and an altered microclimate (Diehl et al. 2011, Tixier et al. 2013). Moreover, more complex-structured vegetation holds the potential to reduce IGP between generalist predators due to the availability of spatial refuges (Finke and Denno 2002, Janssen et al. 2007, but see Roubinet et al. 2015).

Previous studies focusing on pest predation by generalist predators have been restricted to predator groups that were suitable for observational studies (Diehl et al. 2013) or relied on manipulative approaches, such as cage experiments (Östman et al. 2001). Recent advances in DNA-based molecular gut content analysis (MGCA) have made it possible to document how communities of generalist predators utilize prey under field conditions. This technique has, so far, mostly been used to identify predators of a given prey (Chen et al. 2000, Lundgren et al. 2009), or target prey groups of individual predator species (Agusti et al. 2003, Kuusk et al. 2008, Davey et al. 2013, Ekbom et al. 2014) or subsets of the predator community (Chapman et al. 2013, Raso et al. 2014, Wirta

et al. 2015). The improvements of molecular approaches to study trophic interactions over recent years (Trautgott et al. 2013, Symondson and Harwood 2014, Furlong 2015) now provide the tools to address the effects of farming practices and environmental variation on trophic interactions within a wider subset of generalist predator and prey communities. Moreover, these techniques allow us to understand if effects are mediated by changes in the composition of predator or prey communities and how they vary over time. The resolution of these techniques is, however, limited by the extent the targeted DNA fragment is shared between predator and prey (e.g., cannibalism cannot be assessed with species-specific primers, and for family primers predation within the same family as the predator cannot be detected).

Here we utilize a series of diagnostic multiplex PCRs to understand which factors determine (1) the composition of extra- and intraguild prey in predator diets and (2) the contribution of predator communities to aphid predation in replicated organic and conventional cereal fields at two different crop growth stages representing key periods for aphid biological control. Assuming that organic farming promotes decomposer populations, we hypothesize that detection frequencies are higher for decomposer prey under organic farming (H1). Assuming that herbivore populations generally increase during the crop growing season, we expect higher detection frequencies for decomposer than for herbivore prey early in the season in both farming systems, but that this pattern is reversed later in the cropping season (H2). We expect that detection frequencies of extraguild prey DNA in predator diets primarily reflect the composition of prey communities in cereal fields (density-dependent detection frequencies). We further hypothesize that detection frequencies for extraguild and intraguild prey reflect the abundance of these prey groups in individual fields (H3) and that higher weed coverage under organic farming reduces detection frequencies for intraguild prey (H4).

MATERIAL AND METHODS

Study sites

We selected 10 spring barley fields surrounding the city of Uppsala, south-central Sweden (59.8° N, 17.6° E). Five of the fields had been managed organically for more than 10 yr and five were under conventional management. Fields were located in pairs with a mean distance between organic and conventional fields of 1.6 km, ranging from 1.1 to 2.2 km. The distance between the furthest pairs was 52.7 km. In this region and in most years, the use of insecticides in cereal systems is low (Statistics Sweden 2011). The differences between organic and conventional fields mainly reside in the use of herbicides and inorganic fertilizers on conventionally managed fields. Weibull et al. (2003) found no significant effect of farming system on carabid diversity and abundance in cereal field margins in our study region.

All field work was carried out from early barley tillering to heading phase (weeks 22–26) in 2011. This includes two periods during the growing season that are critical for biological control of the most abundant aphid in spring barley in this region, *Rhopalosiphum padi* (L.) (Chiverton 1987): when aphids begin colonizing cereal fields (weeks 22 and 23, at barley tillering stage, “early period”) and during a phase of population build-up in aphids (weeks 25 and 26, at barley stem extension/heading stage, “late period”). All sampling was conducted along a 100-m transect approximately 20 m from, and in parallel to, one haphazardly selected field margin, with samples spread evenly across the transect (i.e., wet pitfall traps and weed samples approximately every 17 m, dry pitfall traps at least every 3 m [depending on density], soil samples and clusters of tiller counts every 10 m, and sweeps with sweep nets every 1 m).

Predator and prey composition and weed cover

To study how trophic interactions are altered by predator community composition, we recorded the activity density of generalist ground-dwelling predators each week during the early and late periods. We collected carabids and spiders using six pitfall traps (Sunderland et al. 2005) per field (11.5 cm diameter × 11 cm depth) that were half-filled with water and a small quantity of detergent (traps, Noax Lab, Farsta, Sweden; detergent, Yes, Procter & Gamble, Stockholm, Sweden). Traps were emptied weekly.

To study how densities of herbivore and decomposer prey are related to trophic interactions, prey density was assessed in each field during the growing season using tiller counts (aphids on 100 tillers/week during each period, from 10 spatially clustered batches of 10 tillers), soil samples (springtails, thrips, and earthworms in 10 soil samples of 5 cm diameter × 10 cm depth once at each period, extracted into ethanol via a Tullgren funnel over 48 hours), and sweep-netting (dipterans in 100 sweeps with sweep nets of 35 cm diameter × 80 cm shaft length [Ento Sphinx, Pardubice, Czech Republic] weekly during each period). Prey densities per sampling unit were averaged per week in the early and late periods for each field, and they were estimated on the same day within field pairs and within a maximum of four days among field pairs. To study whether trophic interactions were altered by weed cover, we estimated weed coverage in

each field in six quadrats (1 m²), divided in four sub-quadrats (0.25 m²), i.e., 24 measures were taken in each field weekly during each period. In each sub-quadrat, ground cover by arable weeds was estimated based on six categories: <1%, 1–4.9%, 5–12.4%, 12.5–24.9%, 25–49.9% and ≥50%. We then transformed the categorical data into a continuous variable, using the median coverage in each category (i.e., 0.5, 2.5, 8.75, 18.75, 37.5, and 75) and averaged weed cover at each period for each field.

Molecular gut content analysis

We collected live arthropods for MGCA weekly following practices recommended by King et al. (2008). We used dry pitfall traps (11.5 cm diameter × 11 cm depth) containing clay balls (Weibulls, Åby, Sweden) to decrease the likelihood of predation in the traps (Sunderland et al. 2005), a method that is recommended as a best practice for MGCA (King et al. 2008). To assess trap predation occurring despite the clay balls, we carefully searched about one-half of the traps for prey remains when they were emptied. Within each period during the growing season, 12–35 traps (number depending on predator abundances) were open for 24 h each week (weeks 22–23 and 25–26), in each field. All predators were individually collected in 1.5-mL microtubes (Saarstedt, Nümbrecht, Germany) and immediately frozen on dry ice, then stored at –80°C until subsequent identification and DNA extraction. A total of 3680 individuals, belonging to the eight most common generalist predator species (Table 1), were processed. We pooled data from the two weeks within each period (the sample size from each individual week was considered too small to allow analysis at that temporal resolution).

After morphological species identification each sample was subjected to whole-body DNA extraction and screened with diagnostic multiplex PCR assays as described in Staudacher et al. (2016). These assays were designed for assessing arthropod predator–prey interactions in cereal systems. A first group-specific multiplex PCR assay (MPI) allowed the examination of a predator’s prey choice on a more general level (targeting extraguild [aphids, dipterans, springtails, and earthworms] and intraguild [lacewings, spiders, beetles/thrips] prey groups) followed by two additional assays enabling the assessment of IGP at a higher taxonomic resolution (MPII spiders [Lycosidae, Linyphiidae, *Pachygnatha*]

TABLE 1. Number of individual generalist predators processed for molecular gut content analysis.

Class	Order	Family	Scientific name	Sample size
Insecta	Coleoptera	Carabidae	<i>Pterostichus melanarius</i> (Illiger)	629
Insecta	Coleoptera	Carabidae	<i>Poecilus cupreus</i> (L.)	494
Insecta	Coleoptera	Carabidae	<i>Harpalus rufipes</i> (Degeer)	788
Insecta	Coleoptera	Carabidae	<i>Bembidion lampros</i> (Herbst)	547
Insecta	Coleoptera	Carabidae	<i>Trechus secalis</i> (Paykull)	164
Arachnida	Aranea	Lycosidae	<i>Pardosa agrestis</i> (Westring)	485
Arachnida	Aranea	Linyphiidae	<i>Oedothorax apicatus</i> (Blackwall)	348
Arachnida	Aranea	Linyphiidae	<i>Agynera rurestris</i> (Koch)	175

and MPII beetles/thrips [thrips, *Pterostichus*, *Poecilus*, *Harpalus*, *Bembidion*, *Coccinella septempunctata*]). The screening was conducted as per the recommendations for molecular diagnostic work; DNA extraction process and assay sensitivity were highly standardized, and PCRs largely followed the protocols presented in Staudacher et al. (2016) with some modifications (for details, see Appendix S1). The standardization of the assay sensitivity (i.e., the number of copies of DNA fragments amplifiable by each of the primer pairs employed in the assays) improves the comparability of the detectability of all prey in all predators (Sint et al. 2012). Although recommended by some researchers (e.g., Greenstone et al. 2014), we did not determine post-feeding prey DNA detection probabilities for the various predator and prey interactions discovered in this study. First, due to the large number of predator–prey interactions, it would have been practically impossible to run all these experiments and, second, as in addition to predator identity, factors such as frequency of prey consumption, meal size, and meal composition, as well as the level of hunger could also impact DNA degradation rates; such adjustments would be questionable (Traugott et al. 2013). Furthermore, because the analysis of prey DNA detection was always carried out for the same predator community (for all extraguild prey in analysis a, and all intraguild prey in analysis b and c), all prey DNA-specific post-feeding detection probabilities were affected by the same factors for all prey types, and the effect of varying detection probabilities on our results should therefore be minor. Note that predation within family (for spiders) and genus (for carabids), including cannibalism, cannot be measured with our assays. We performed separate analyses of IGP for (a) carabids feeding on spiders and (b) spiders feeding on carabids. With this approach, it was possible to utilize information on all spider prey eaten by carabids (in analysis a) and on all carabid prey eaten by spiders (in analysis b), so that detection frequencies within carabids or spiders covered an identical range of taxa. All prey detected at less than 1% in a predator species over the cropping season were removed from the analysis, as the contribution of these prey to the predator's diet was assumed to be marginal, and to avoid false predation events that could be misleading in the analyses.

Processing of gut content data

We calculated the DNA detection frequencies (i.e., the proportion of positively tested predators for a given prey) at early and late season of (1) extraguild prey taxa (herbivores and decomposers: aphids, thrips, dipterans, earthworms, springtails) for all predator species pooled; (2) carabid intraguild prey (from the genera *Harpalus*, *Pterostichus*, *Poecilus*, and *Bembidion*) for all three spider species pooled (for analysis a of IGP); and (3) spider intraguild prey (from the families Lycosidae and Linyphiidae, the genus *Pachygnatha*, and from other

spiders) for all five carabid species pooled (for analysis b of IGP).

For each analysis (EGP, IGP a and b), we combined the pooled detection frequencies for each prey at each site and season into one data frame (with 20 rows and 5, 4, or 3 columns, respectively). We then constructed resemblance matrices between sites based on Euclidean distances.

Statistical analyses

We first tested if differences between farming systems and sampling periods affected the multivariate composition of detected herbivore and decomposer prey in the predator community, to test hypotheses H1 & H2. For this multivariate assessment of prey detection, we used permutational analyses of variance models (PERMANOVA; Anderson 2001) with farming system (two levels: organic or conventional) and sampling period (two levels: early or late) as fixed factors and location (five levels: pairs of a single organic and conventional field) as a random factor to reflect the paired design in our study. In the first PERMANOVA model, we tested if farming system or sampling period significantly altered DNA detection frequencies across the community of five potential extraguild prey groups (dependent variables: DNA detection frequencies of aphids, thrips, dipterans, earthworms, and springtails DNA in all predators). In the second PERMANOVA model, we tested if the farming system or sampling period significantly altered DNA detection frequencies across the community of four spider intraguild prey groups in carabids (dependent variables: detection frequencies of linyphiid, lycosid, *Pachygnatha*, or other spider DNA, analysis a). These permutational analyses of variance models were based on 9999 permutations of residuals under a reduced model. Detection frequencies for intraguild prey DNA of carabids in spiders (analysis b) were not analyzed statistically due to very low detection frequencies.

We then tested if detection frequencies for multivariate intraguild and extraguild prey merely reflect the availability of prey in each field and if DNA detection frequencies are affected by weed cover in line with hypotheses H3 and H4. We used distance-based linear models with the predictors (1) prey and (2) predator composition (wet pitfall trap data) and (3) weed cover in individual fields. The choice of this model was motivated by the fact that predictors and dependent data were multivariate compositional data and that this technique has explicitly been developed for this purpose (Legendre and Anderson 1999, McArdle and Anderson 2001). The models are similar to multivariate multiple regression analyses, but use distance matrices instead of raw data, which is a more appropriate approach for community-type data (McArdle and Anderson 2001). Model 1 used the abundances of extraguild prey, activity densities of predators and weed cover in each field at each sampling date as predictors to explain variation in the detection frequency

TABLE 2. Permutational analyses of variance for a mixed-effects model with fixed factors farming system and sampling period and random factor location for DNA detection frequencies of (a) five individual extraguild prey groups in generalist predators (spiders and carabids) and (b) three individual intraguild (spider) prey groups in carabids.

Source	df	(a) Extraguild prey			(b) Intraguild prey Carabidae		
		SS	F	P	SS	F	P
Location	4	0.41	4.38	0.013	0.04	3.15	0.107
Farming system	1	0.05	2.37	0.142	0.04	10.60	0.021
Period	1	1.30	14.84	0.012	0.00	0.43	0.643
Location × Farming system	4	0.08	0.82	0.623	0.01	1.10	0.454
Location × Period	4	0.35	3.73	0.026	0.04	2.74	0.117
Farming system × Period	1	0.00	0.12	0.944	0.00	3.06	0.129
Residuals	4	0.09			0.01		
Total	19	2.28			0.15		

Note: Fixed factors or interactions that are significant at $\alpha = 0.05$ level are shown in boldface type.

of the five extraguild prey groups. Model 2 used the activity densities of spider intraguild prey and of carabid predators, and the weed cover in each field at each sampling date as predictors to explain variation in the detection frequency of the three intraguild prey groups. Intraguild carabid prey composition in spiders was not tested due to the very low detection.

Different numbers of individuals were screened per predator species at each site and this difference in composition of screened predator individuals per species may introduce a bias for the analysis of detection frequencies. We accounted for this potential bias by first partialing out the variation in detection frequencies that was explained by the composition of screened predators. To build models 1 and 2, we further grouped individual predictor variables into indicator groups: prey composition (five variables of extraguild prey abundances for model 1 or three variables of intraguild prey abundances for model 2), predator composition (eight variables for predator abundances for model 1 or five variables of carabid abundances for model 2), the composition of screened predators (number of screened individuals per predator species in each model) and weed cover at each site. All predictors were $\log(x + 1)$ transformed after examination to improve the distribution and reduce the impact of outlier values in the subsequent analyses (as recommended in Anderson et al. 2008). The five best models among all models based on the AIC are shown, alternative models are considered if they were within 2 Δ AIC units of the best model. To visualize relationships between individual predictor variables in the selected indicator groups we use scatterplots between these variables and the dependent variables.

RESULTS

Extraguild predation

Considering the whole predator community, there was no difference in detection frequencies of extraguild prey between farming systems (Table 2a, $P = 0.142$). The detection frequencies of extraguild prey generally

increased from the early to the late period (Fig. 1, Table 2a, $P = 0.012$): they increased by a factor of 4.4 for aphids (Fig. 1a), but only slightly for the other extraguild prey groups (Fig. 1b–e). The composition of extraguild prey explained 26% of the variation in detection frequencies (Table 3b, $P = 0.017$) while predator composition and weed cover were not selected in the final model. More specifically, DNA detection frequencies of the two most common extraguild prey groups (aphids and springtails) were positively related to their abundances (Fig. 2a, b). For aphid prey, density and detection frequencies were only positively related in the late period (Fig. 2a), but springtail abundances and DNA detection frequencies were positively related in both sampling periods (Fig. 2b). The detection frequencies of dipterans, thrips, and earthworms showed no density dependence (Appendix S1: Fig. S1). In the only alternative model within 2 Δ AIC units, weed cover was selected as an additional predictor with a generally positive relationship to extraguild prey detection frequencies. Aphid (Pearson $R = 0.57$), thrips ($R = 0.50$), and earthworm ($R = 0.43$) detection frequencies were most strongly related to weed cover.

Intraguild predation

The frequency of IGP detected could be increased by predation occurring within dry pit fall traps. However, we used clay balls in the traps to minimize this and found visible prey remains in only 4% of the traps emptied, suggesting that within trap predation was limited. Intraguild predation was less common than EGP (Figs. 1f–i and 3d–f). On average, less than 1% of the spiders tested positive for carabid intraguild prey across study sites (range 0–5%). No spider tested positive for prey from the carabid genus *Harpalus*, even though this potential prey group was present at all sites. In contrast, on average more than 16% of the carabids tested positive for spider intraguild prey across study sites (range 0–55%, distributed to 0–16% for Linyphiidae, 0–31% for Lycosidae, and 0–9% for other spider prey). Carabids did not feed on spiders from the genus *Pachygnatha*, even though this group was present at 8 out of the 10 sites.

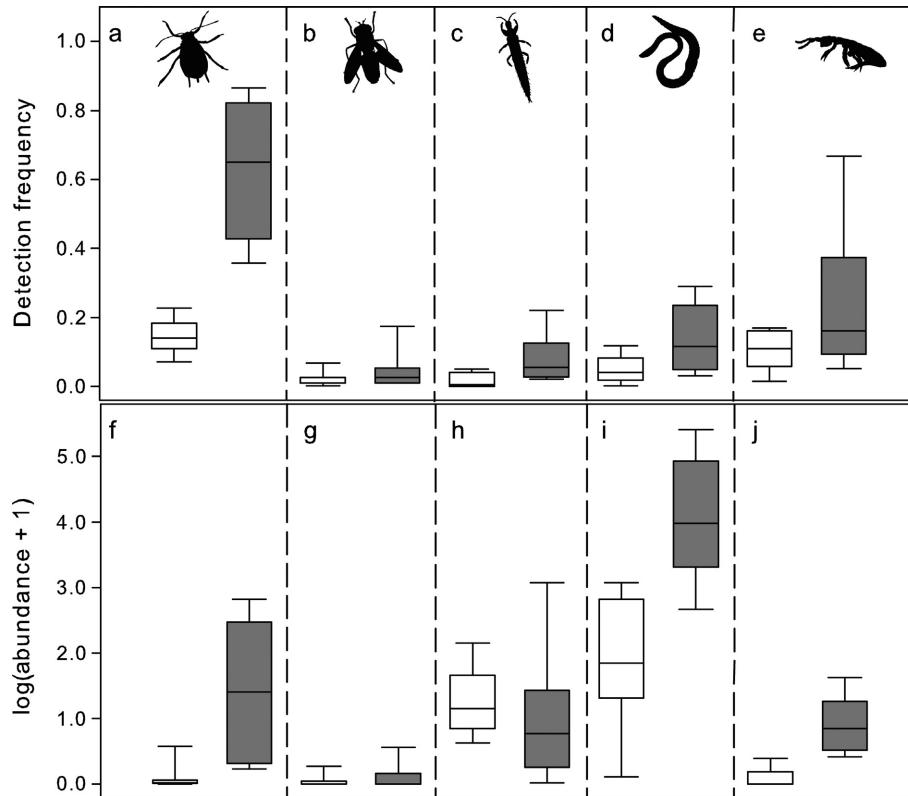


FIG. 1. Within-season effects of (a–e) detection frequencies in predator communities and (f–j) abundances of extraguild prey per field for (a, f) aphids, (b, g) dipterans, (c, h) thrips, (d, i) earthworms, and (e, j) springtails in the early (white) and late (gray) sampling periods. Box plots show medians (horizontal line), 25th and 75th percentiles (upper and lower box limits), and extreme observations (bars).

TABLE 3. Distance-based linear model for extraguild predation (EGP) with results for the final model resulting from selection of predictors according to the Akaike information criterion (AIC) selection criterion and the five best alternative models.

Model	AIC	R^2	Predictors
1	-66.51	0.92	1, 2
2	-65.07	0.92	1, 2, 4
3	-49.26	0.88	1, 2, 3
4	-48.94	0.86	1, 3
5	-47.79	0.7	1, 4

Note: Predictors are (1) the composition of screened predators, (2) the composition of available prey, (3) the composition of active predators, and (4) the weed cover in each field.

The composition of spider intraguild prey in carabid diets was significantly affected by farming system (Table 2b, $P = 0.021$), but not by periods (Table 2b, $P = 0.643$). DNA detection frequencies for Linyphiidae and Lycosidae prey in carabids were higher in fields under organic farming management while no differences were observed for other spiders (Fig. 3a–c). Neither spider prey composition ($P = 0.117$), nor carabid predator composition ($P = 0.285$), nor weed cover ($P = 0.225$) significantly explained the variation in the intraguild spider prey detection frequencies in carabids, but were selected in the best model (Table 4b).

DISCUSSION

We examined the effects of farming system, period within the growing season, predator and prey composition, and weed abundance on the diet of generalist predator communities and their contribution to cereal aphid biological control under field conditions during two key periods for aphid biological control.

We found that detection frequencies for decomposer (springtails) prey in generalist predators did not differ between the two farming systems (refuting H1). Detection frequencies for aphid prey only increased with aphid densities late in the cropping season, resulting in a higher detection frequency for herbivores compared to decomposer prey at this growth stage (partly supporting H2). For springtails, in contrast, detection frequencies were positively related to prey abundance in both periods. Intraguild predation was unidirectional, with carabids feeding on spiders, and less common than EGP (supporting H3). The composition of spider intraguild prey for carabids was affected by farming system. Carabid predators in organically managed fields had higher detection frequencies for the two most common spider groups, partly reflecting spider prey abundances in different farming systems, but not weed coverage (refuting

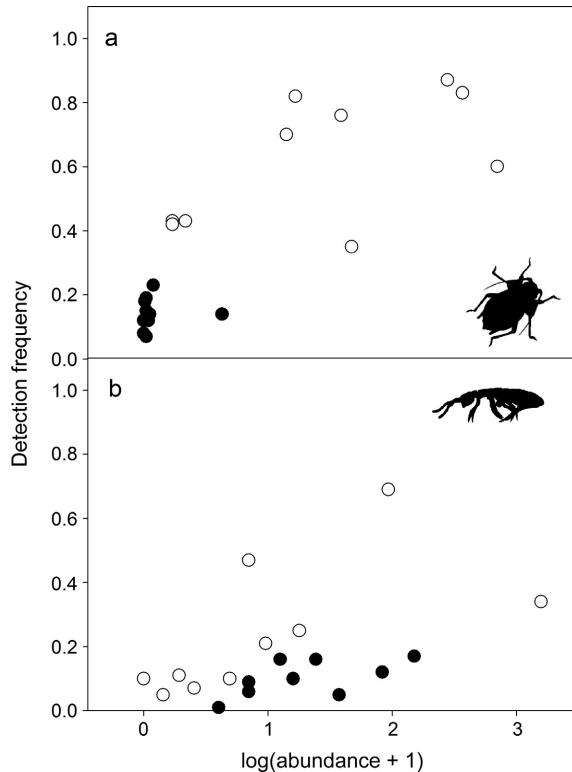


FIG. 2. Abundance and detection frequencies for (a) aphid and (b) springtail extraguild prey early (solid symbols) and late (open symbols) in the growing season.

H4). In the following sections, we discuss the implications of these results concerning EGP and IGP for the functional role of generalist predators and biological control.

Extraguild predation

All five extraguild prey taxa targeted by MGCA were detected in the gut of generalist predators. Detection frequencies were generally higher for aphid and springtails than for dipterans, thrips, and earthworm prey. The use of this wide range of prey taxa confirms, under field conditions, the previously suggested broad diet of ground-dwelling arthropod generalist predators in agroecosystems (Nyffeler et al. 1994, Toft and Bilde 2002, Birkhofer et al. 2013).

Contrary to our initial hypothesis (H1), we found no support for a higher detection frequency of decomposer prey in organic farming systems. Organic farming practices are known to increase the organic matter content of agricultural soils and thereby often support higher abundances of decomposers (Birkhofer et al. 2008). Decomposers are a potentially valuable resource for ground-dwelling predators and may increase their contribution to biological control by sustaining their populations during periods when pest are scarce (Scheu 2001). However, we found no difference in detritivorous prey abundances between organic and conventional fields

(Appendix S1: Table S2) in south-central Sweden. In this region, the differences between the two farming systems are not as pronounced as in other areas in Europe, as conventional field management is generally of low intensity (Statistics Sweden 2011). It has also been suggested that biological control of pests is higher under organic farming due to higher predator abundances (e.g., Östman et al. 2001, Birkhofer et al. 2015a), but not always (Winqvist et al. 2011). This assumption is also not supported in our study as the densities of aphids (Appendix S1: Table S2a) and activity density of predators (Appendix S1: Table S3) did not differ significantly between farming systems, although a trend toward higher densities of aphids (Fig. 1f), earthworms (Fig. 1i), and Lycosidae in organic fields was observed (Fig. 3e). We, however, acknowledge that our results are based on detection frequencies of prey DNA and not on actual per capita predation rates.

In addition to the numerical effects of organic farming on predator and prey populations, other properties of organically managed fields may cause predators to prefer herbivores over decomposer prey. It has, for example, previously been documented that structural properties of cereal fields (crop physiognomy; Birkhofer et al. [2011],

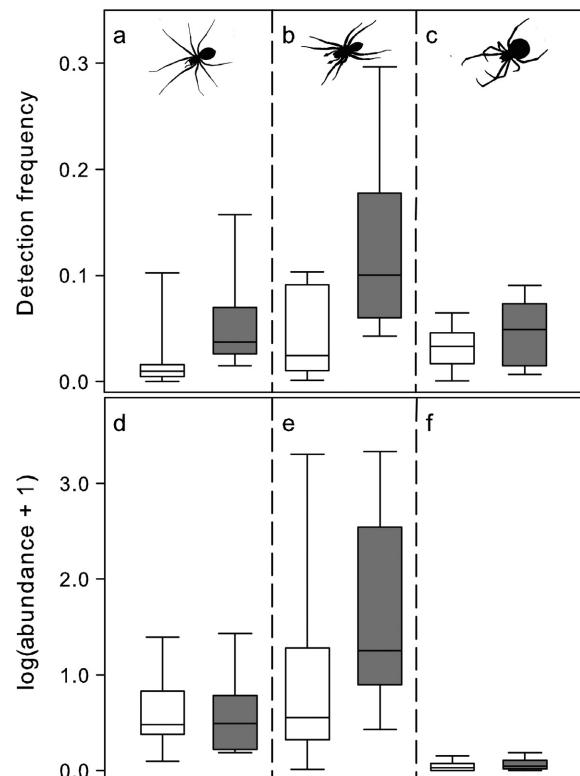


FIG. 3. Farming system effect on (a–c) detection frequencies and (d–f) abundances of intraguild prey in carabid communities in each field for (a, d) Linyphiidae, (b, e) Lycosidae, and (c, f) other spider prey in conventionally (white) and organically (gray) managed fields. Box plots show medians (horizontal line), 25th and 75th percentiles (upper and lower box limits), and extreme observations (bars).

TABLE 4. Distance-based linear model for intraguild prey in Carabidae with results for the final model resulting from selection of predictors according to the AIC selection criterion and the five best alternative models.

Model #	AIC	R ²	Predictors
1	-111.52	0.90	1, 2, 3, 4
2	-106.50	0.86	1, 2, 3
3	-97.47	0.64	1, 2
4	-97.04	0.70	1, 3, 4
5	-96.29	0.65	1, 2, 4

Note: Predictors are (1) the composition of screened predators, (2) the composition of available prey, (3) the composition of active predators, and (4) the weed cover in each field.

mulching; Sereda et al. [2015]) affect generalist predator–prey interactions. Our results do not support such a direct effect of organic farming on prey selection in ground-dwelling predators potentially due to less pronounced differences between the farming systems in our study area (see *Materials and Methods: Study sites*).

Aphids and springtails were the most frequently detected prey in generalist predators and aphids became much more important prey during the population build-up phase later in the growing season. These high detection frequencies for aphid prey emphasize the potential of generalist predators as antagonists of aphids in cereal fields. This beneficial role is further supported by the fact that aphid prey was detected in predators also at very low aphid abundances early in the growing season (detection frequencies ranging from 0.23 to 0.66 for aphid densities ranging from 0.00 to 0.88 aphids/tiller), when aphids start to colonize fields. During this colonization phase, cereal aphids occur in distinct patches at the base of the tillers (Östman 2002) and generalist predators, already present in the field, may be most efficient in finding and suppressing aphids (Edwards et al. 1979, Chiverton 1988, Birkhofer et al. 2008). The positive relationship between detection frequencies and aphid or springtails abundances in the late growing season indicates that predators at least partially consume prey in a density-dependent manner (see also Birkhofer et al. 2013). Carabids are indeed able to adapt their prey search behavior in relation to prey density (Firle et al. 1998) and prey distribution in the field (Griffiths et al. 2008). However, to fully support the argument of density-dependent predation, additional information on per capita consumption of prey at different prey densities would be needed.

Detection frequencies for dipterans, thrips, and earthworms prey did not reflect the abundances of these prey groups. This might be best explained by the life cycle of these organisms and/or the life stages during which they are most vulnerable to predation by ground-dwelling predators. For instance, larvae of many dipterans are soil-living, and these early life stages are probably more accessible prey than the flying adults. Thrips, on the other hand, are mostly plant-living, although they are more accessible to predators on the ground. In our study, we only analyzed the abundances of dipterans in the

vegetation and of thrips on the ground, a limitation that could explain the weak relationship between abundance and detection frequency for these taxonomic groups.

The only alternative model within 2 Δ AIC units showed a positive relationship between weed cover and detection rates of extraguild prey. Although the mechanisms behind these effects are uncertain, the results are in line with previous findings that showed an increased herbivore predation with increased structural complexity (Finke and Denno 2002, 2006).

Intraguild predation

The detection of IGP in the guts of predators varied according to predator and prey taxa: it was unidirectional as carabids consumed spiders at considerable frequencies, but spiders rarely preyed on carabids (see also Dinter 1998, Davey et al. 2013, Raso et al. 2014). Spiders are known to frequently prey on other spiders (Finke and Denno 2002, Rypstra and Samu 2005, Raso et al. 2014), but to consume carabids, spiders need to penetrate their chitinous exoskeleton. Additionally, most Linyphiidae are of smaller size than most carabids, contributing to their attractiveness as carabid prey (Brose 2010). Given the relatively common IGP by carabids on spider prey in our study, high densities of spiders early in the growing season may contribute to larger carabid populations in cereal fields (Östman 2004). Spiders are early colonizers of arable fields (Bishop and Riechert 1990, Birkhofer et al. 2013) and may attract predator groups that frequently consume spiders. There is, however, no indication from this study that carabids rely more on intraguild spider prey early in the growing season, when herbivore prey are scarce, compared to later in the growing season (Davey et al. 2013). We did not detect any intraguild predation by carabids on *Pachygnatha*, which might result from the spiders' nightly transition to the foliage where they might be protected from carabids (Madsen et al. 2004). Due to the limitations of our molecular assay, intraguild predation might, however, be underestimated as cannibalism and predation within the same genus/family is likely to occur by generalist predators.

Differences between farming systems significantly affected the composition of intraguild spider prey in carabid diets. Both Linyphiidae and Lycosidae were more frequently detected as prey under organic management, a result that could partly be explained by the observed trend of higher activity density of Lycosidae in organically managed fields. Differences in the structural complexity of fields under organic and conventional farming may additionally contribute to this effect. However, the structural property of fields measured in this study (weed cover) did not affect the detection frequencies of intraguild spider prey in carabids. Previous studies, however, showed that IGP between spiders was lower in habitats with more complex vegetation structure (Finke and Denno 2002, Schmidt and Rypstra 2010) and that spatial associations between ground-dwelling spiders

and carabids can be affected by crop physiognomy (Birkhofer et al. 2011).

CONCLUSION

This study shows that the diet composition of extraguild prey among ground-dwelling arthropod predators reflects the composition of the most abundant extraguild prey communities in cereal fields (aphids and springtails) during two key periods for aphid biological control. Our findings suggest that, under field conditions, generalist predators feed in an almost density dependent manner on aphids and springtail prey. However, our results also show that aphids are consumed early in the growing season even under very low local densities and independently of high densities of alternative decomposer prey (springtails). The strong positive relationship between aphid numbers and aphid prey detection frequencies later in the growing season further emphasizes the important functional role of generalist predators as aphid biological control agents. Organic farming practices hold the potential to attract more generalist predators, but IGP by carabids on spider prey also increases with spider numbers. The net effect of these factors on aphid predation requires more attention in future studies. However, our study documents that predation by generalist predator communities on aphid pests increases with pest numbers independently of their generally widespread consumption of alternative, non-pest prey. Therefore, conservation strategies in agricultural fields, e.g., through organic fertilization, could promote high levels of alternative non-pest prey to generalist predator communities, without risking reduced pest predation (Bell et al. 2008). If such strategies are implemented during periods when pest abundances are low they are likely to result in a positive numerical response of predators that should result in improved biological control.

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B. Ekblom, M. Jonsson, and M. Traugott conceived the project; K. Staudacher realized the molecular analysis; E. Roubinet and K. Birkhofer analyzed the data and wrote the first draft of the paper; all authors edited the manuscript.

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DATA AVAILABILITY

Data associated with this paper have been deposited in figshare <https://doi.org/10.6084/m9.figshare.4560409.v1>