Wetlands Provide a Source of Arthropods Beneficial to Agriculture: A Case Study from Central Georgia, USA[1]

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Abstract We described the overlap of arthropod communities between agricultural lands and adjacent wetlands using transect sampling, to determine if these juxtapositions might be influencing abundances of beneficial arthropods in agricultural lands. We further assessed experimentally whether these beneficial arthropods migrating from wetlands may potentially enhance crop productivity. Large numbers of predaceous carabid beetles and spiders moved from the wetlands into the agricultural lands; both of these groups can be important to biological control of crop pests. However, our exclusion experiments did not detect significant impacts of these predators on herbivorous insects or on crop productivity. Numerous studies have established that natural habitats adjacent to crop lands serve as refuge to beneficial arthropod communities and enhance overall biodiversity. Wetlands adjacent to agricultural lands appear to serve the same function. Our study suggests that wetlands may provide the ecosystem service of enhancing numbers of arthropods beneficial to agriculture, a service not established previously, and a factor that may motivate farmers to conserve wetlands that they own.

Key Words agroecosystem, biocontrol, ecosystem services, habitat heterogeneity, landscape

Wetlands often occur in juxtaposition with agricultural lands, and their proximities suggest wetlands and agricultural lands likely interact in many ways. Ecologically, wetlands are key habitats for sediment retention, nutrient cycling, and high biodiversity (Brinson and Malvárez 2002, Heimlich et al. 1998, Matteson et al. 2020). Wetland bacteria can metabolize components of fertilizers, especially nitrate, improving soil and water quality (Heimlich et al. 1998). By retaining water and sediment, wetlands prevent crop runoff from reaching downstream habitats (Brinson and Malvárez 2002, Matteson et al. 2020, Steinman et al. 2003). Wetlands abate floods and maintain soil moisture by retaining water in dense plant stands and clay soils. Besides plants, wetlands provide habitat for a range of animal species (e.g., arthropods, amphibians, birds).

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Historically, vast amounts of wetland in the United States have been drained for agriculture (Brinson and Malvárez 2002, Steven and Lowrance 2011), and farmers often consider wetlands as wastelands (Rijsberman and de Silva 2006). Yet, many of the remaining wetlands still occur on farms and ranches, which makes their conservation and preservation a challenge (Brinson and Malvárez 2002, Heimlich et al. 1998). Although draining a wetland to convert it to agricultural land may seem more profitable to a farmer than keeping it in its natural state, once drained, wetlands lose their ability to provide various ecosystem services to agriculture (Brinson and Malvárez 2002, Lemly 1994). These "free" services from wetlands would otherwise be very costly to obtain (Denny 1994, Heimlich et al. 1998). If the negative perception of wetlands to farmers can be changed and the benefits of wetlands to agriculture made better known, perhaps farmers would be induced to voluntarily preserve wetlands on their lands.

Natural habitats adjacent to crop lands allow the preservation of arthropod biodiversity and, consequently, improve ecosystem resilience in an otherwise homogeneous environment (Duelli et al. 1999, Duelli and Obrist 2003, Wood and van Halsema 2008). Wetlands adjacent to agricultural lands likely serve as refuge for arthropod communities beneficial to crops (Brinson and Malvárez 2002, Denny 1994). We hypothesize that significant overlap exists in the invertebrate communities between agricultural lands and adjacent wetlands and that beneficial arthropods (i.e., predators, parasitoids, pollinators) and possibly pests (herbivores) will move from the wetlands into the agricultural lands. We further suspect that natural enemies from the wetlands will enhance productivity of crops by controlling pests.

Materials and Methods

We tested our hypotheses by monitoring distributions of invertebrates (predators, parasitoids, pollinators, herbivores) in adjacent wetland-cropland systems and by experimentally excluding large natural enemies of pests from crops adjacent to wetlands to assess if the natural enemies are affecting crop yields.

Study sites. All studies were conducted at the Iron Horse Farm (33°43′37.1″N 83°18′03.3″W); an agricultural research facility of the University of Georgia located in Greene Co., GA. Associated with the farm are extensive wetlands, including wet meadows, alluvial swamps, and floodplains (see Matteson et al. 2020 for maps and a geological description of the farm). We worked with a wet meadow site (0.2 ha) that was bordered by row crop agriculture and an alluvial swamp (10 ha) that was bordered by managed grasslands initially (2016, 2017) and then subsequently by soybean, *Glycine max* (L.) Merrill, row crop (2018). The alluvial swamp was a bottomland hardwood forest with an embedded beaver wetland, and the wet meadow comprised assorted emergent moist-soil herbaceous and grassy vegetation.

Distributional sampling. At both the wet-meadow/row-crop setting and the alluvial-swamp/grassland setting, we selected 4 parallel 50-m transects as our treatment units: (1) in the wetland interior (~20 m from the agricultural lands); (2) along the wetland edge (~2 m from the agricultural lands); (3) along the agricultural land edge (~5 m from the wetlands); and (4) in the interior of the agricultural lands (~20 m from the wetlands). To monitor a range of invertebrate types, we employed 3 sampling approaches: (1) pitfall traps sampled ground-dwelling invertebrates; (2) sweep netting sampled plant-dwelling invertebrates; and (3) "bee bowls" sampled pollinators and parasitoids.

Pitfall traps consisted of open wide-mouth glass jars (volume 237 ml, diameter 100 mm) sunk to their rims into the soil at random locations (6–8) along each transect. We filled them approximately half-way with 95% ethanol as a preservative. We used ethanol to ensure the croplands would not become contaminated by spilled preservative for possible future research efforts at the farm. We acknowledge that some aerially colonizing insects (e.g., vinegar and fruit flies, bark beetles) might be attracted to the ethanol, so we only quantified ground-dwelling organisms. Further attractivity of traps would then be similar in all transects. Pitfall traps were left in place for 24 h. If needed, additional ethanol was added to jars to preserve captured invertebrates, the samples were returned to the laboratory, and invertebrates were removed via hand-sorting, identified, and quantified.

Sampling was initiated ~2 wk after the crop plants had sprouted and then every 6 wk thereafter, until crops had matured (in late summer). Sampling was conducted in both agriculture-wetland settings over the 2016 and 2017 seasons.

In conjunction with pitfall sampling, we used sweep netting (40 cm diameter) of vegetation to collect invertebrates living on plants (crops, grasses, wetland plants), at randomly selected locations (6–10) along each transect (described above). Each 1-m long sweep was transferred to a labeled plastic bag, samples were transported to the lab and frozen to kill invertebrates, and specimens were hand-picked under a dissecting scope, identified, and quantified.

In 2017, we additionally sampled pollinators and parasitoids using yellow, white, and blue colored "bee bowls." The small plastic bowls were placed at random locations (8) along the same transects used for pitfall and sweep net sampling, partially filled with soapy water, and left in place for 24 h. Upon retrieval, specimens captured were preserved in ethanol and transported to the lab for identification and quantification.

Exclusion experiments. Distributional sampling suggested that ground beetles (Carabidae) and ground-dwelling spiders (Araneae) were readily moving from the wetlands into the croplands. Moreover, it is known that these beneficial organisms can be efficiently sampled with pitfall traps (Duelli et al. 1999), as verified by our distributional sampling. Thus, we targeted those organisms to examine if the wetland fauna was enhancing productivity of adjacent crops. In a transect inside the croplands, and ~10 m from the wetland edges, we erected circular cages (60 cm diameter) of 3 designs as our treatment units: (1) exclusion cages had walls of 12-mm wire mesh, from the soil surface to a height of 40 cm to limit entry of large, ground-dwelling carabid beetles and spiders; (2) "faux" exclusion cages were of the same design but with a 5-cm gap along the bottom edge to permit entry of large ground-dwelling beetles and spiders, and (3) open habit with no cage (6 replicates of each cage design/experiment). Studies were initiated ~2 wk after the crop plants had sprouted and continued for the subsequent 4 wk in summer 2018. We conducted studies in 1 corn, *Zea mays* L., field, adjacent to the wet meadow, and 1 soybean field, adjacent to the alluvial swamp.

After exclusion cages were erected, 2 pitfall traps were set in each cage for 24 h to assess population levels of ground-dwelling arthropods and to facilitate removal of residual beetles and spiders from full exclusion cages. After 4 wk, pitfall traps were re-set and retrieved after 24 h. Then, plants inside the cages were swept with a sweep net to collect plant-dwelling arthropods. Finally, the central plant in each cage was harvested, including the roots, to obtain above-ground and below-ground material. In the lab, invertebrates collected in pitfalls and sweeps were sorted, identified, and quantified. Plant material both above ground (leaves, stems, and fruits) and below it (roots) was oven dried (105°C) for 48 h and weighed to assess dry mass. Roots were gently rinsed to remove soil prior to drying.

Analyses. For distributional sampling, organisms in pitfall, sweep net, and bee bowl samples were identified to family (or order; depending on their life stage or if they were not insects) using standard keys (Triplehorn and Johnson 2005). We relied on the family level as a finer level taxonomic determination was not practical for many groups and specimens (immatures); Mueller et al. (2013) report that for community analyses, results at the family-level are typically congruent with analyses at the genus level, but we interpret analyses with caution. We then determined which groups were likely to be ecologically influential by identifying those taxa that occurred in at least 25% of the samples and restricted our analyses to them. We assessed samples in the wet-meadow/row-crop and alluvial-swamp/grassland systems, and samples from the 2016 and 2017 study years, independently. We assessed spatial and temporal distributions of ecologically important invertebrates using 2-way ANOVA in R (version 3.4.0) that accounted for transects (wetland interior, wetland edge, agricultural edge, and agricultural interior) as treatments and the sample date, and their interaction; with individual samples (pitfalls, sweeps, bee bowls) as statistical replicates. If the edge and interior transects within a habitat (wetland, agricultural land) displayed similar levels for a metric, displayed by similar behaviors in their graphed statistical interactions, they were pooled and evaluated simply as either wetland or agricultural land. Data were log $(x+1)$ transformed prior to analyses to meet assumptions of normality and equal variance. Because a case study approach was used (2 wetland-agricultural associations), we cannot infer broader application of specific results, but simply use the analyses to demonstrate potential links between wetlands and croplands.

Based on these analyses, we divided the taxa into 3 categories. (1) Generalist taxa occurred in similar abundances in both habitat types. For these taxa, the existence of a juxtaposition of wetlands and agricultural lands was of minimal consequence. (2) Specialist taxa were significantly more abundant in a single habitat type (wetland or agricultural land), and they exhibited minimal movements between the habitats. For these taxa, as for generalists, the existence of a juxtaposition of wetlands and agricultural lands was of minimal consequence. (3) Transient taxa had population levels that changed over the season between habitats; they were initially more abundant in 1 habitat type but then migrated to the other. For these taxa, the existence of a juxtaposition of wetlands and agricultural lands was consequential.

To identify transient taxa, we used the following winnowing process, based on our ANOVA results: (1) when habitat type (i.e., transect type) was not significant in the ANOVA and no significant interaction existed between habitat and sample date, taxa were considered generalists; (2) when habitat type was significant but no significant interaction existed between habitat and sample date, taxa were considered specialists; (3) when a significant interaction existed between habitat and sample date, taxa were considered potential transients; and (4) if the statistical interaction between habitat and sample date developed because the organism was largely absent from 1 habitat and only abundant in the other habitat on certain dates, the taxon was reassigned as a specialist.

In summary, transient taxa were at least occasionally abundant in both wetland and agricultural habitats, but at different times. We then assessed whether transient taxa potentially were beneficial (predators, parasitoids, pollinators), pestiferous (herbivorous), or agriculturally neutral (detritivorous). For taxonomic groups that include taxa falling in more than 1 classification, we assigned them based on their most common designation (Triplehorn and Johnson 2005). Further, it is likely that some predators and parasitoids preyed on other beneficials. Thus, our broad classification should be viewed with caution.

In the exclusion studies, we assessed the experiments in corn and soybean independently. Using 1-way ANOVA, we first assessed possible cage artifacts by contrasting faux cages (with open gaps at their bases) with completely open habitats, for invertebrate abundances and crop plant biomass. If there were no differences between faux-cage and open habitats, these treatments were pooled as "open" habitat. Invertebrate abundances and crop plant biomass between open and exclusion habitats were then contrasted using 1-way ANOVA (with cages as replicates). Data were log $(x+1)$ transformed prior to analyses to meet assumptions of normality and equal variance.

Results

We collected a range of invertebrate taxa (Table 1) across the wetland-agricultural land complexes. However, $<$20% of them were common (occurred in at least 25% of samples). The most abundant taxa collected were Cicadellidae, Araneae, Formicidae, Gryllidae, and Carabidae.

Distributional studies. Most invertebrate taxa that were common across the wetland-agricultural land complex were either generalists or specialists (Table 2), and their distributions did not appear to be affected by the juxtaposition of habitats. However, distributions of several taxa were affected by the juxtaposition, where populations in 1 habitat appeared to affect populations in the other (i.e., transients). The most responsive transient taxa were 2 large, mobile predatory groups, carabid ground beetles and ground-dwelling spiders. In the 2016 sampling effort, pitfall sampling indicated that large numbers of ground beetles initially occurred in the wetlands, both the alluvial swamp and the wet meadow, whereas few occurred in the agricultural lands, either the soybean field or the pasture grassland (Fig. 1A, B). However, as the season progressed, numbers declined in the wetlands while they simultaneously increased in the agricultural habitats (i.e., highly significant habitat by date interaction terms existed, both $P < 0.001$). In the 2017 season, the same pattern developed in the wet-meadow/row crop complex, albeit somewhat weaker (interaction $P = 0.007$; Fig. 1C). That year in the alluvial-swamp/pasture system, the opposite pattern developed where the ground beetles appeared to migrate from the grassland to the swamp as the season progressed (interaction $P = 0.0002$; Fig. 1D).

Table 1. Invertebrate taxa collected in wetland and agricultural land ecosystems in 2016–2017 according to sampling method. Taxa highlighted in bold were present in at least 25% of the samples in the respective sampling method and year.

2016		2017		
Pitfalls	**Sweeps**	**Pitfalls**	**Sweeps**	**Bee Bowls**
ARACHNIDA	ARACHNIDA	MOLLUSCA	MOLLUSCA	ARACHNIDA
Acari	**Araneae**	Gastropoda	Gastropoda	Araneae
Araneae	Opiliones	MYRIAPODA	ARACHNIDA	COLLEMBOLA
DIPLURA	ORTHOPTERA	Diplopoda	Araneae	Entomobryidae
COLLEMBOLA	**Acrididae**	Chilopoda	ODONATA	Hypogastruridae
Entomobryidae	**Gryllidae**	ARACHNIDA	Coenagrionidae	Sminthuridae
Hypogastruridae	Tetrigidae	**Araneae**	Lestidae	ODONATA
Isotomidae	Tettigoniidae	COLLEMBOLA	ORTHOPTERA	Lestidae
Sminthuridae	HEMIPTERA	**Entomobryidae**	Acrididae	ORTHOPTERA
MICROCORYPHIA	Anthocoridae	**Isotomidae**	Gryllidae	Acrididae
Machilidae	Aphididae	Hypogastruridae	Tetrigidae	Gryllidae
ORTHOPTERA	Berytidae	Poduridae	Tettigoniidae	Tetrigidae
Acrididae	Blissidae	Sminthuridae	HEMIPTERA	Tettigoniidae
Gryllidae	Cercopidae	ORTHOPTERA	Alydidae	HEMIPTERA
Tetrigidae	**Cicadellidae**	**Acrididae**	Anthocoridae	Aleyrodidae
Tettigoniidae	Cixiidae	**Gryllidae**	Aphididae	Aphididae

Table 1. Continued.

2016		2017		
Pitfalls	**Sweeps**	**Pitfalls**	**Sweeps**	**Bee Bowls**
DERMAPTERA	Coreidae	Tetrigidae	Blissidae	Blissidae
Anisolabididae	Delphacidae	Tettigoniidae	Cercopidae	Cercopidae
HEMIPTERA	Derbidae	DERMAPTERA	**Cicadellidae**	**Cicadellidae**
Alydidae	Geocoridae	Anisolabididae	Coreidae	Delphacidae
Aphididae	Membracidae	HEMIPTERA	Delphacidae	Geocoridae
Blissidae	**Miridae**	Alydidae	Geocoridae	Membracidae
Cicadellidae	Nabidae	Anthocoridae	Membracidae	**Miridae**
Gelastocoridae	Pentatomidae	Aphididae	Miridae	Nabidae
Geocoridae	Plataspidae	Blissidae	Nabidae	Pachygronthidae
Membracidae	Reduviidae	Cercopidae	Pachygronthidae	Pentatomidae
Miridae	Tingidae	**Cicadellidae**	Pentatomidae	Psyllidae
Pachygronthidae	COLEOPTERA	Cydnidae	Reduviidae	Reduviidae
Pentatomidae	Anthicidae	Geocoridae	Tingidae	Tingidae
Psyllidae	**Chrysomelidae**	Membracidae	PSOCOPTERA	**THYSANOPTERA**
Reduviidae	Coccinellidae	Miridae	COLEOPTERA	COLEOPTERA
THYSANOPTERA	Curculionidae	Pachygronthidae	Carabidae	Carabidae
Phlaeothripidae	Mordellidae	Pentatomidae	Chrysomelidae	Chrysomelidae

Table 1. Continued.

2016		2017		
Pitfalls	**Sweeps**	**Pitfalls**	**Sweeps**	**Bee Bowls**
COLEOPTERA	Ptinidae	Psyllidae	Coccinellidae	Coccinellidae
Anthicidae	Scarabaeidae	Reduviidae	Curculionidae	Curculionidae
Carabidae	Staphylinidae	Tingidae	Laemophloeidae	Laemophloeidae
Chrysomelidae	HYMENOPTERA	THYSANOPTERA	Meloidae	Ptiliidae
Coccinellidae	Apidae	Phlaeothripidae	Mordellidae	Staphylinidae
Curculionidae	Braconidae	COLEOPTERA	Nitidulidae	HYMENOPTERA
Elateridae	Eulophidae	Anthicidae	Ptiliidae	Andrenidae
Endomychidae	Formicidae	**Carabidae**	Ptinidae	Apidae
Meloidae	Ichneumonidae	Chrysomelidae	Staphylinidae	Chrysididae
Monotomidae	Vespidae	Coccinellidae	Tenebrionidae	Cynipidae
Nitidulidae	LEPIDOPTERA	Curculionidae	NEUROPTERA	Diapriidae
Ptiliidae	Geometridae	Elateridae	Chrysopidae	Dryinidae
Ptinidae	Noctuidae	Laemophloeidae	HYMENOPTERA	Encyrtidae
Scarabaeidae	Sesiidae	Meloidae	Braconidae	Eulophidae
Staphylinidae	Attevidae	Monotomidae	Cynipidae	**Formicidae**
Tenebrionidae	DIPTERA	**Nitidulidae**	Diapriidae	**Halictidae**
HYMENOPTERA	Calliphoridae	Ptiliidae	Encyrtidae	Ichneumonidae

Table 1. Continued.

2016		2017		
Pitfalls	**Sweeps**	**Pitfalls**	**Sweeps**	**Bee Bowls**
Cynipidae	Ceratopogonidae	Ptinidae	Eulophidae	Megachilidae
Diapriidae	Chironomidae	Scarabaeidae	Formicidae	Mymaridae
Encyrtidae	Culicidae	Staphylinidae	Halictidae	Platygastridae
Eulophidae	Dolichopodidae	Tenebrionidae	Ichneumonidae	Scelionidae
Formicidae	Drosophilidae	HYMENOPTERA	Mymaridae	Scoliidae
Ichneumonidae	Empididae	Cynipidae	Platygastridae	Sphecidae
Mymaridae	Mycetophilidae	Diapriidae	Torymidae	Torymidae
Platygastridae	Psychodidae	Encyrtidae	Trichogrammatidae	Trichogrammatidae
Pompilidae	Simuliidae	**Formicidae**	Vespidae	Vespidae
Pteromalidae	Syrphidae	Mymaridae	LEPIDOPTERA	LEPIDOPTERA
Scelionidae	Tachinidae	Platygastridae	Erebidae	Geometridae
Scoliidae	Tipulidae	Scelionidae	Geometridae	Hesperiidae
Sphecidae	Ulidiidae	Scoliidae	Noctuidae	Noctuidae
Tenthredinidae		Torymidae	DIPTERA	DIPTERA
Torymidae		Trichogrammatidae	Agromyzidae	Asilidae
Trichogrammatidae		LEPIDOPTERA	Anthomyzidae	Cecidomyiidae
Vespidae		Geometridae	Cecidomyiidae	Chironomidae

Table 1. Continued.

2016		2017		
Pitfalls	Sweeps	Pitfalls	Sweeps	Bee Bowls
LEPIDOPTERA		Noctuidae	Chironomidae	**Dolichopodidae**
Erebidae		DIPTERA	Chloropidae	**Drosophilidae**
Noctuidae		Asilidae	Culicidae	Empididae
Pieridae		Cecidomyiidae	Dolichopodidae	Mycetophilidae
DIPTERA		Chloropidae	**Drosophilidae**	Phoridae
Cecidomyiidae		Dolichopodidae	Empididae	Sciaridae
Chironomidae		Empididae	Mycetophilidae	Syrphidae
Chloropidae		Mycetophilidae	Phoridae	Tabanidae
Dolichopodidae		Phoridae	Sciaridae	Tachinidae
Empididae		Sciaridae	Syrphidae	
Lauxaniidae		Tachinidae	Tachinidae	
Mycetophilidae		Tipulidae	Tephritidae	
Phoridae			Ulidiidae	
Psychodidae				
Sciaridae				
Simuliidae				
Tachinidae				

Table 2. Commonly occurring arthropods (collected in >25% of samples, in at least 1 type of sampler) that did not exhibit obvious movement between wetland and agricultural lands (transient taxa are listed in Fig. 1).*

Specialists		Generalists		
Pitfalls	**Sweeping**	**Pitfalls**	**Sweeping**	**Bee Bowls**
Wetland taxa				
Potential beneficial				
Araneae (RC, 17)	Tachinidae (RC, 17)	Araneae (P, 17)	Araneae (P, 16)	Parasitoids (P/RC, 17)
		Formicidae (P/RC, 17)		Pollinators (P/RC, 17)
		Staphylinidae (P, 16; P/RC, 17)		Halictidae (P/RC, 17)
Potential pest				
Blissidae (RC, 17)	Cicadellidae (RC, 17)	Nitidulidae (RC, 17)		
	Miridae (RC, 16)	Curculionidae (P, 17)		
	Drosophilidae (RC, 17)	Acrididae (RC, 17)		
Potential neutral				
Entomobryidae (P/RC, 16; P, 17)	Gryllidae (RC, 16)	Isotomidae (P, 17)	Gryllidae (P, 16)	
Isotomidae (P/RC, 16; RC, 17)		Gryllidae (P/RC, 16; RC, 17)		
Hypogastruridae (P, 16)				
Sminthuridae (RC, 16)				

Table 2. Continued.

Specialists		Generalists		
Pitfalls	Sweeping	Pitfalls	Sweeping	Bee Bowls
Agricultural land taxa				
Potential beneficial				
Formicidae (P, 16)				
Potential pest				
Cicadellidae (P, 17)				
Acrididae (P, 17)				
Potential neutral				
Entomobryidae (RC, 17)				
Edge taxa				
Potential pest				
Nitidulidae (P, 17)	Cicadellidae (P, 16)			
	Miridae (P, 16)			
Potential neutral				
Hypogastruridae (RC, 16)				

* Classified by: general function (specialists or generalists); collecting method (pitfalls, sweeping, or bee bowls); agricultural function (potential beneficial {predator, parasitoid, pollinator}, potential pest {herbivorous}, or agriculturally neutral {detritivorous}); habitat type (wetland, agricultural land, habitat edges); and type of agricultural land (RC = row crop, P = pasture), in the years 2016 (16) and 2017 (17).

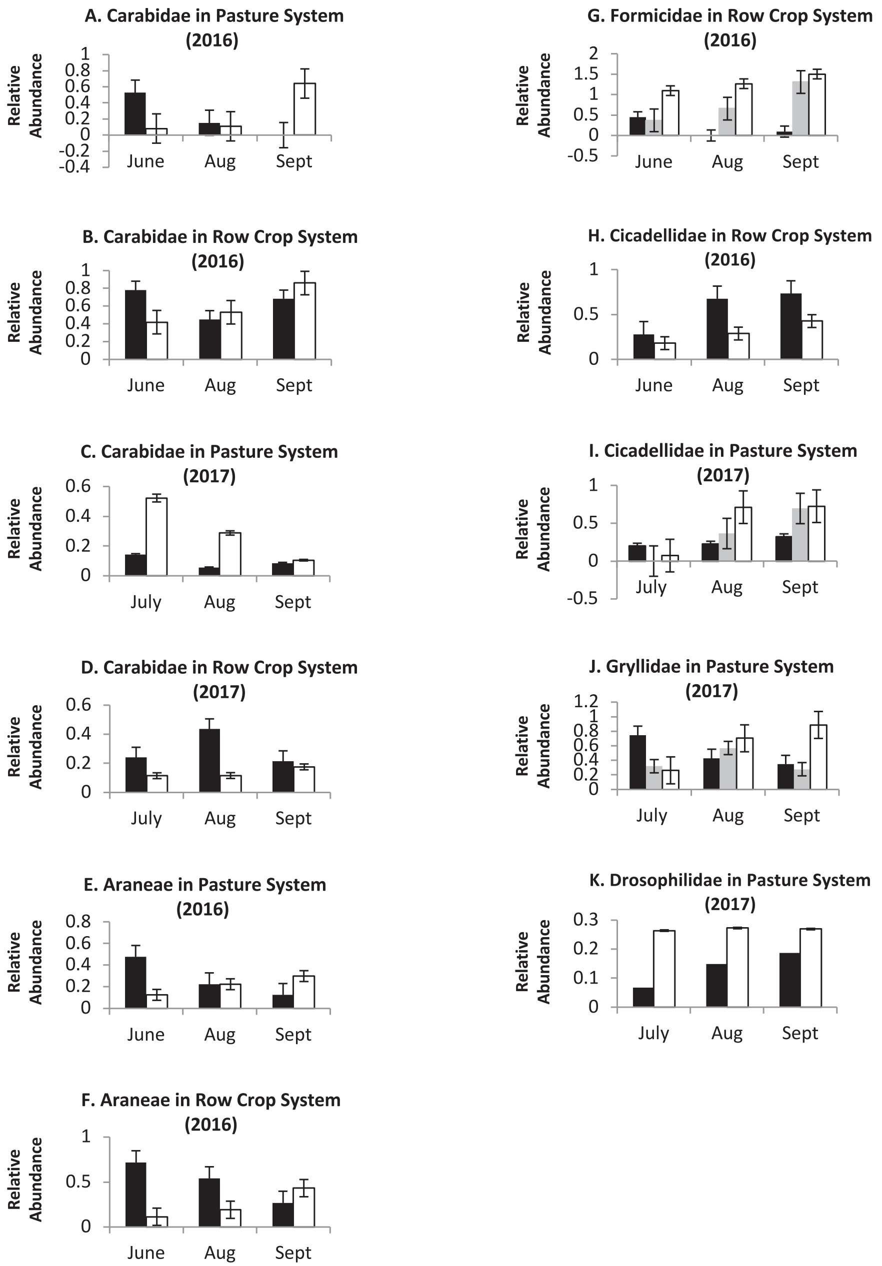

Fig. 1. Relative abundances (log (x+1)/sample) of common transient arthropods (A–D, Carabidae; E and F, Araneae; G, Formicidae; H and I, Cicadellidae; J, Gryllidae; K, Drosophilidae) in row crop-wet meadow and/or pasture-alluvial swamp systems, over the summers of 2016 or 2017. In every case, a statistically significant ($P < 0.05$)

Similarly, in 2016, pitfall sampling indicated that large numbers of ground-dwelling spiders initially occurred in the wetlands, both the alluvial swamp and the wet meadow, whereas few occurred in the agricultural lands, either the pasture grassland or the soybean field. As the season progressed, spider numbers in the wetlands declined while numbers in the paired agricultural lands increased (both interaction terms, $P \leq 0.02$; Fig. 1E, F). In 2017, however, ground-dwelling spiders exhibited either generalist or specialist behaviors, depending on the complex (Table 2). A final predaceous insect group affected by habitat juxtaposition were the ants in the wet-meadow and row-crop complex; here the ants were most abundant in the soybean field throughout the season (habitat effect, $P < 0.0001$; Fig. 1G), but numbers in the wetland edge tended to increase over the season, suggesting some movement of ants toward the wetland (interaction, $P = 0.006$).

Some herbivorous insects also were affected by the juxtaposition of wetland and agricultural habitats, although in inconsistent ways. In 2016 sweep net samples, cicadellid leafhoppers initially had low population levels overall and then increased over the season (sample date, $P < 0.0001$), with levels being higher in the wetland (habitat, $P = 0.0005$). However, leafhopper numbers surged in the interior of the soybean field into late summer, perhaps resulting from migration from the wetlands (interaction, $P = 0.03$; Fig. 1H). In 2017, leafhopper patterns reversed, with more occurring in the grassland pasture than the adjacent alluvial swamp, but as the season progressed numbers increased in the wetland edge habitat (interaction, $P < 0.0001$; Fig. 1I). Gryllidae crickets appeared to move from the alluvial swamp into the adjacent pasture (interaction, $P = 0.0001$; Fig. 1J). Drosophilidae vinegar flies appeared to move from the pasture into the alluvial swamp (interaction, $P = 0.0002$; Fig. 1K). For other habitat/year combinations, the leafhoppers, crickets, and vinegar flies exhibited either specialist or generalist tendencies (Table 2).

Exclusion studies. There were no significant differences in arthropod abundances or plant biomass between the partial and open treatments in either the corn or soybean studies, suggesting that cage effects were not significant; thus, these 2 treatments were combined as "open habitat" to contrast with the full exclusion cages. Fewer carabid beetles were collected in the exclusion cages than the open habitat ($P < 0.01$), indicating that the exclusion cages met the goal of reducing the numbers of those predators in both the corn and soybean studies. However, the cages did not effectively exclude spiders ($P > 0.05$). We did not detect any cascading trophic effects of carabid beetle predation because herbivorous arthropod numbers and plant biomass (above or below ground) did not differ between treatments, in either the corn or soybean fields.

←

interaction existed between habitat types and time, suggesting transient movement between habitats. Data from wetland, wetland edge, and agricultural land habitats are indicated by black, gray, and white bars, respectively. Y-axes sometimes include negative values where error bars (SE) extended into negative ranges. (Nontransient common taxa are listed in Table 1.)

Discussion

We found strong ecological interactions between the wetlands and the agricultural land in our study, with pronounced movements of several common arthropods between the 2 kinds of habitat. Movements of carabid beetles and spiders were especially dramatic and consistent. These organisms constitute 2 of the largest and most abundant predatory taxa in the ecosystems and, thus, are likely among the most ecologically important arthropods that occurred. Carabid beetles and spiders have been identified as playing important roles in the biological control of crop pests elsewhere (Bomford and Vernon 2005, Duelli and Obrist 2003, Holland and Luff 2000, Madeira et al. 2016), although in our system, we could not verify significant effects of these predators on herbivorous insects or any indirect effects on plant growth (it should be noted that pests overall did not seem to be a major problem during our studies). We found weaker and less consistent movements of potential plant pests (i.e., herbivorous arthropods) between the wetlands and the agricultural land and, thus, the presence of the wetlands did not appear to have any major deleterious effects on crop production.

Our use of family-level classification requires that results be viewed cautiously; some responses at the genus level may have remained undetected, and all genera within a family may have occurred and gone undetected. Furthermore, our process of winnowing taxa may underestimate some landscape-level impacts of the juxtaposition of wetlands with agricultural lands. As discussed by Duelli et al. (1999), ground-dwelling arthropods will have different levels of mobility in habitats of variable vegetation. Although generalist taxa occurring with equal frequency in both wetland and agricultural lands may suggest that the juxtaposition is irrelevant, it is alternatively possible that the juxtaposition of habitats boosted population levels in both habitats (i.e., if the wetlands had not been present, populations in the agricultural lands might have been lower, and vice versa). As previous studies have shown, these abundances may be due more to the range of adaptability of the organisms rather than the actual habitats present specifically (Duelli et al. 1999). Additionally, although specialist taxa may strongly prefer 1 habitat over the other, most were still present in the nonpreferred habitat, meaning that some wetland specialist individuals may “bleed” into adjacent agricultural lands and perhaps have ecological impacts there. Finally, the occurrence of edge-habitat specialists (Table 2) may represent an impact of wetland-agricultural land juxtaposition, although it is not clear that the involvement of a wetland in creating the edge habitat was crucial (i.e., any kind of edge habitat may suffice). As described with different habitat types by Duelli and Obrist (2003), Holland and Luff (2000), and Madeira et al. (2016), wetlands, as natural habitats adjacent to crop lands, may serve as compensatory habitat for common species in the area, allowing for higher abundances to develop. In some years and some types of crop lands, transient groups acted as either generalists and/or specialists, suggesting that habitat ecotones function in complex ways. For example, Altieri and Nicholls (2003) found that soil compositions influenced plant-pest interactions. Despite these caveats, our study suggests that broad ecological connections likely exist between wetlands and croplands in terms of the arthropod fauna.

Our case study provides insight into a previously undocumented ecosystem service offered by wetlands, providing a source of beneficial arthropods to agriculture that should be more fully explored across a variety of agricultural settings. By acting as a refuge habitat to arthropods, wetlands may allow more resilient ecosystems to develop with possible benefits to biocontrol for agriculture (Brinson and Malvárez 2002, Duelli and Obrist 2003). Globally, wetlands are valued for serving as ecotones between land and water, and for contributing to mosaic-like, diverse landscapes (Denny 1994). Many studies have already highlighted the positive impact wetlands have on nearby ecosystems, by contributing to higher biodiversity, nutrient and sediment retention and cycling, and for improving water quality (Brinson and Malvárez 2002, Denny 1994, Heimlich et al. 1998, Steven and Gramling 2011). The possibility that wetlands may provide benefits in terms of pest control adds to this list. However, more study will be required to determine if it is the mere presence of natural habitat, regardless of type (e.g., forest, grassland, wetland), that contributes to higher arthropod abundances (Duelli et al. 1999, Duelli and Obrist 2003) or if wetlands instead provide unique conditions that favor certain key taxa, as described by Madeira et al. (2016).

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