

Arthropod communities in warm and cool grass riparian buffers and their influence on natural enemies in adjacent crops



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ABSTRACT

Riparian buffers of native warm season (WSG) or non-native cool season (CSG) species are commonly planted along margins of crop fields as part of the USDA Conservation Reserve Program. The soil, water and wildlife enhancement values of these buffers are well researched and documented. However, their conservation value for biological control is largely unknown. In this study, we examined and compared arthropod communities in WSG and CSG buffers and focused specifically on their influence on natural enemy populations in adjacent crops. Plant diversity measurements and relative estimates of epigeal and canopy-dwelling arthropods using pitfall trapping and sticky cards were recorded in 29 buffers of each grass type and adjoining crop fields during two years in Maryland. We predicted that the structurally more diverse and less stressed WSG buffers are more suitable for enhancing arthropod biodiversity and provide greater conservation value for natural enemies. Results demonstrated that the composition and relative abundances of most epigeal and canopy-dwelling taxa in both grass buffers corresponded with the composition and relative abundances of those taxa in neighboring crops, suggesting population linkage and movement of taxa between buffer and crop habitats. However, warm and cool season grasses in riparian buffers were inhabited by dissimilar arthropod communities in terms of taxa richness, abundance and composition, which in turn influenced differently the beneficial arthropod communities in adjacent crops. Contrary to our hypothesis, cool season grasses supported greater abundances of most beneficial arthropods in buffers and also enhanced their populations in adjacent crop fields, especially early in the growing season. Beneficial taxa responses were likely linked to differences in the early season phenology of the grass types. Although WSG buffers are green and actively growing during the summer, CSG grasses break dormancy earlier in the spring and provide higher quality food for many arthropod taxa that serve as prey and hosts for predators and parasitoids. Given this early season advantage, the addition of perennial flowering forbs to the CSG mixes is suggested to enhance their conservation value by improving structural complexity and providing floral resources to support natural enemy populations.

1. Introduction

The Conservation Reserve Program (CRP), implemented by the United States Department of Agriculture (USDA) Farm Service Agency (FSA), re-establishes valuable grassland to improve water quality, prevent soil erosion, and replace lost wildlife habitat (USDA, 2012a, 2012b). The program offers incentive payments to encourage landowners to protect environmentally sensitive areas by converting highly erodible cropland to riparian habitats. Land enrolled in the program remains out of crop production usually 10–15 years. As of September 2016, 9.55 million ha were enrolled in CRP, and a recent initiative now provides cost-share to landowners to establish buffer habitats that are

friendly to pollinator taxa (USDA, 2012a, 2012b). This is the first CRP practice that is specifically designed to benefit arthropods.

A riparian buffer bordering crop fields is one of several conservation practices available to landowners under the CRP. These buffers contain strips of permanent vegetation that are generally planted to protect environmentally sensitive areas from contiguous land management practices. Riparian buffers improve water quality by filtering nutrients and trapping sediment, provide refuge for the maintenance of biological diversity, and help preserve the natural hydrology of waterways (Naiman and Decamps, 1997; Lovell and Sullivan, 2006; Johnson et al., 2016).

In 2014, nearly 18,875 ha of land were enrolled in CRP as riparian

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buffers in Maryland (EWG, 2015). Seventy percent of riparian buffers are herbaceous filter strips planted along field edges of arable land and greater than 90% are located on the Eastern Shore of Maryland (USDA FSA, 2013). Riparian buffers (hereafter, referred to as grass buffers) are planted with warm season (WSG) or cool season (CSG) grass species, and often seeded with a mix of legumes and perennial flowering forbs. WSG buffers include one or more of the following native prairie species: switchgrass (*Panicum virgatum*), big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), and Indian grass (*Sorghastrum nutans*) (Tjaden and Weber, 1998). Warm season grasses break dormancy by late spring, grow during summer months, set seed in the fall, and go dormant during the fall after a freeze. Warm season grasses have deep root systems, are drought tolerant, and can remain green during high temperatures. Although WSG buffers are encouraged by the CRP to perpetuate native species, approximately two-thirds of grass buffers in Maryland are planted with non-native CSG species, primarily orchardgrass (*Dactylis glomerata*), red fescue (*Festuca rubra*), and sheep fescue (*Festuca ovina*) (Tjaden and Weber, 1998; Lynn, 2003). Cool season grasses break dormancy when soil temperatures are just above freezing and start growth earlier in the spring than WSGs. Cool season grasses set seed in early summer, thrive during cool temperatures and rainfall from early spring to summer, and then taper off or go completely dormant during hot, dry summer months. If moisture is adequate, they resume growth in the fall. Landowners prefer CSG over WSG buffers because they are less expensive, easier and quicker to establish, less laborious to maintain, and often create a more aesthetic habitat.

Research directed at demonstrating environmental benefits of CRP plantings has focused primarily on their potential to contribute to soil organic carbon and nitrogen pools (Munson et al., 2012; O'Connell et al., 2016; Whisler et al., 2016), as well as provide habitat for birds (McCoy et al., 2001; Coppedge et al., 2004; Blank, 2010) and mammals (Phillips et al., 2004; Kamler et al., 2007; Stanley, 2010). Consequently, few studies have quantified effects of different grasses in CRP lands on insects and other arthropods. Research conducted to evaluate impacts of CRP on arthropods have mainly focused on their potential to enhance communities of butterflies (Reeder et al., 2005; Davros et al., 2006; Dollar et al., 2013, 2014), crop pests (Phillips et al., 1991; Carroll et al., 1993; Mowry et al., 1995; Lefko et al., 1998), and to provide arthropod prey for grassland birds (McIntyre and Thompson, 2003; Benson et al., 2007). As such, there is a significant gap in our understanding of arthropod community responses to riparian grass buffers, especially with respect to their conservation value for arthropod natural enemies (French et al., 1998).

Several reviews have shown that uncultivated habitats neighboring crops can help sustain populations of natural enemies of agricultural pests by providing alternative food sources, floral resources, prey or hosts, overwintering sites and refuge (Landis et al., 2000; Maudsley, 2000; Sunderland and Samu, 2000; Marshall and Moonen, 2002). Most insect predators overwinter in these neighboring habitats because they provide a more favorable microclimate during winters than sparsely vegetated crop fields (Luff, 1966; Thomas et al., 1991; Landis et al., 2000). Structural parameters of the overwintering vegetation can influence natural enemy survival. For example, winter survival of carabid beetles, important predators in many cropping systems (Kromp, 1999; Melnychuk et al., 2003; Witmer et al., 2003), is positively correlated with vegetation height (Dennis et al., 1994), successional age (Frank and Reichhart, 2004), number of grass tussocks, and leaf litter depth (Thomas et al., 1992a) of non-crop habitats. Other predators and parasitoids are known to also overwinter in non-crop habitats (Landis and Haas, 1992; Bruck and Lewis, 1998; Tscharnke et al., 2002), including mymarid wasps (Corbett and Rosenheim, 1996), lady beetles (Bianchi and van der Werf, 2003), rove beetles (Frank and Reichhart, 2004), and spiders (Lemke and Poehling, 2002; Pywell et al., 2005). In general, overall arthropod diversity increases within crops when fields are bordering uncultivated habitats with favorable overwintering conditions (Dennis and Fry, 1992).

Tussock-forming grasses, such as switchgrass, are particularly favorable for overwintering arthropods because they are structurally diverse and provide microclimates that favor their survival (Luff, 1966; Dennis and Fry, 1992; Thomas et al., 1992b; Dennis et al., 1994). Grasses that grow in tussocks harbor greater abundance and species richness of arthropods than grasses that cover the habitat more uniformly (Dennis et al., 1998; Collins et al., 2003). Additionally, McIntyre and Thompson (2003) found greater densities of arachnids, coleopterans, orthopterans, and lepidopterans in native WSG prairie than in mixed and non-native grasses. In general, native grasses are expected to harbor co-evolved specialist and invasive generalist taxa, while generalist arthropods are predicted to more common in introduced plant species (Strong et al., 1984; Lankau et al., 2004). Additionally, WSG buffers are mixed more often with flowering forbs than CSG buffers, and mixed plantings are expected to provide more alternative food sources and have greater impact on reproductive rates of natural enemies (Baggen and Gurr, 1998).

Arthropod richness and abundance are also influenced by cultural practices used to manage landscape vegetation. For example, arthropod community diversity tends to be greater in moderately to frequently disturbed habitats (DiGiulio et al., 2001). This is relevant as WSG and CSG buffers are generally managed differently. Cool season grass buffers are mowed annually during the fall but the hay is not removed, whereas WSG buffers are subjected to fewer disturbances, usually a light tilling (with a tandem disk harrow) or controlled burning every 3–4 years. Benson et al. (2007) found that arthropod abundance and biomass were greater within disked compared to undisked portions of fields. The disking decreased the cover of grasses, litter and standing dead vegetation but resulted in greater plant species richness within the riparian grassland. However, cool season grasses may become less favorable for arthropod communities as the summer passes due to a decline in grass quality. These grasses become stressed during hot and dry conditions, whereas warm season grasses remain green and actively grow throughout summer months.

Riparian grass buffers have the potential to support diverse communities of natural enemies and serve as corridors for their movement into neighboring crops. However, the conservation biological control value of these non-crop habitats is largely unknown. In this study, we examined the arthropod communities in CRP grass buffers and focused specifically on their influence on arthropod natural enemies in adjacent crops. To test our hypothesis that WSGs are more suitable for enhancing arthropod biodiversity thereby providing greater conservation value for arthropod natural enemies, we addressed the following questions: (1) do WSG buffers harbor greater numbers and diversity of arthropods than CSG buffers, and (2) do crops adjacent to WSG buffers have greater numbers and diversity of arthropod natural enemies than crops adjacent to CSG buffers?

2. Methods

2.1. Study system

Study sites, distributed among 15 typical grain farms chosen from a list of CRP participating landowners in Caroline, Talbot, and Queen Anne's counties on the Eastern Shore of Maryland, were sampled over two years. Land use across these counties is very similar (Fig. S1), with less than 12% developed land in 2006 and a total 2010 population of 118,646 (Fry et al., 2011; U.S. Census Bureau, 2010). Farmland, mostly row-crop agriculture and pasture on coastal plain sandy soils, comprised 58% of Caroline, 57% of Talbot, and 60% of Queen Anne's county in 2006 (Fry et al., 2011). This is interspersed by upland forest blocks and woody wetlands (Fig. S1, 2006 Caroline: 14% forest, 15% woody wetland; 2006 Talbot: 12% forest, 13% woody wetland; 2006 Queen Anne's: 12% forest, 14% woody wetland) (Fry et al., 2011). Sites were separated by > 2 km and surrounded by this similar landscape. At each site, warm or cool season grasses buffers, maintained for a

minimum of three years, measured greater than 6 m wide and 200 m long. The entire length of each buffer was adjoined to a forested area (generally leading to a wetland or stream) on the opposite side from the crop field. Seven WSG and CSG buffers adjacent to corn fields (*Zea mays* subsp. *mays*) were sampled in 2003; whereas 13 WSG and 7 CSG buffers adjacent to corn, and 9 WSG and 15 CSG buffers adjacent to soybeans (*Glycine max*) were sampled in 2004. Crop fields ranged in size from 10 to 32 ha and were conventionally managed. With the exception of fungicide-treated seed and herbicides used at planting, no other pesticides were applied during the crop cycle at each site. Each buffer-field combination served as a replicate within each year.

2.2. Sampling layout

Three transects at least 75 m apart from one another and perpendicular to the edge of each buffer-field interface were established at each site and sampled at three locations: one in the buffer and two in the crop. The buffer site was located 6 m from the crop-buffer interface or half the width of buffers for those less than 12 m wide. Sampling sites in the crop were established at 6 m (near) and 46 m (far) from the buffer/crop interface, to evaluate possible distance effects in a logistically feasible manner. A sticky card and pitfall trap were placed at each sampling location for a 7-day period during the first week of June and July in both years.

2.3. Vegetation measurements

The average height and vertical density of the buffer vegetation around each sampling site was measured using a Robel pole (Robel et al., 1970) in areas where the vegetation had not been physically disturbed by wildlife activity. Vertical density measurements were taken in four cardinal directions and recorded as the highest obstructed point on the Robel pole visible at a height and distance of 1 and 4 m, respectively. A 1 m² frame was placed in the same general area to examine non-overlapping canopy coverage. Percent cover of grass and forb species, standing dead grass, bare-ground and litter was estimated using plants rooted within the frame. Forbs that occupied more than 5% of the frame area were identified to species. Measurements were recorded in August of 2004 and averaged over all sampling sites per buffer-field replicate.

2.4. Arthropod sampling methods

Pitfall traps were used to measure the community diversity and abundance of epigeal arthropods. Traps consisted of 355 mL plastic cups containing approximately 60 mL of ethylene glycol and were embedded in the ground with the top level with the soil surface. A 30 cm square plastic cover supported by three carriage bolts was placed approximately 2 cm above each cup to prevent weather and wildlife interference. After each sampling period, cups were brought back to the laboratory, vacuum-filtered and rinsed over fine organdy cloth to remove the ethylene glycol. Captured invertebrates were stored in 70% ethanol.

Yellow sticky cards (7.5 cm × 12.5 cm, Olson Products, Inc.) were used to measure the relative abundance of aerially active arthropods within the crop and buffer canopy. Cards were attached to bamboo poles using wooden clothespins. In corn, cards were positioned at canopy level during whorl stages and then at ear level after anthesis. In soybeans, cards were positioned at the height of the uppermost foliage. Cards in grass buffers were placed at the same level as in adjacent crops. One side of the card was exposed and faced the crop-buffer interface. On each collection date, cards were placed into clear plastic resealable bags, brought back to the laboratory, and frozen until they could be processed. Arthropods in each pitfall and sticky card sample were viewed under a stereomicroscope, identified and counted to the order or family level.

2.5. Statistical analyses

Samples were pooled across transects for each sampling site and within each buffer-field replicate. Taxa were assigned to one of four trophic groups (saprovores, herbivores, predators, or parasitoids) based on the primary ecological function of most members in each taxonomic group. We characterized the composition and diversity of arthropod communities in the buffer and crop habitats by the percentage of individuals in each trophic group, number of taxa (richness), total number of individual arthropods captured (abundance), and the Shannon and Simpson indices (Magurran 2004). Both indices provide a mathematical measure of taxa diversity, but the Simpson index gives more weight to common or abundant dominant taxa and provides a different measurement of taxa evenness.

A mixed model ANOVA (SAS Institute, 1997) tested for main and interaction effects of buffer type and sampling month on each community-related and buffer vegetation variable. Before analysis, data were tested for normality and homogenous variance using the Shapiro-Wilk *W* test, Spearman's rank correlation, and by examining residual plots. Data transformations and grouping of variance were performed as necessary. For each analysis, sampling month was modeled as a repeated measure, and year and farm were treated as random factors. For crop analyses, preliminary analyses revealed no significant interaction effect of sampling location (6 m or 46 m) with buffer type, so data for all sampling locations were averaged across transects for each buffer-field replicate. Significant effects among means were separated by using Tukey's adjustment for pair-wise comparisons ($P \leq 0.05$).

Redundancy analysis (RDA, CANOCO 5, Microcomputer Power) was used to detect patterns in abundances of arthropod taxa in the whole community in relation to buffer grass type (ter Braak and Smilauer, 2002). Four interaction terms consisting of combinations of buffer type (CSG and WSG) and sampling month (June and July) were coded as categorical explanatory variables. Crop was coded as a covariate because of its possible influence on the adjacent buffer. The interaction of year (2003 and 2004) and month was also coded as a covariable. RDA was also used to identify patterns and analyze beneficial arthropod communities in corn and soybean fields bordering cool and warm season buffers. In separate analyses by crop, combinations of buffer type and sampling month were set as explanatory variables; and the interaction of year and month designated as a covariable. In all analyses, raw data were $\log(x + 1)$ transformed to stabilize variance and reduce the influence of dominant taxa on the ordination.

To assess statistical significance of the relationship between community data and the explanatory variables, Monte Carlo permutation testing was performed in CANOCO to determine the significance of the first ordination axis and all axes together. Permutations were restricted within each combination of crop, year and sampling month. For each analysis, the relationship between taxa scores and centroids (groups of samples) of explanatory variables was represented in an ordination biplot. The diagram displayed the pattern of individual taxa abundance and the variance explained by each explanatory variable. The scaling option focused on the correlation of response taxa and their association with the explanatory variables. The most abundant taxa, as represented on the RDA biplot, were individually analyzed by the mixed model ANOVA using the same fixed and random factors as described above. All main and interaction means (\pm SE) reported were computed from the untransformed data.

3. Results

3.1. Vegetative characteristics of the grass buffers

The composition of grass species and structural diversity varied widely among the 29 buffers of each grass type sampled during both years (Table S1). The dominant plant species in order of abundance included orchardgrass, red fescue and foxtail in CSG buffers, and big

bluestem, little bluestem and switchgrass in WSG buffers. The vegetation in WSG was significantly taller (199.1 ± 7.1 cm; $F_{1,46} = 294.5$, $P < 0.001$) and had higher vertical density (75.0 ± 5.8 cm; $F_{1,52} = 10.9$, $P = 0.002$), compared to the average height (82.4 ± 2.8 cm) and vertical density (41.3 ± 2.8 cm) in CSG vegetation. The CSG vegetation consisted of more standing dead grass and litter present on the soil surface. The percentage of all herbaceous flowering plants and shrubs (total forbs) was significantly higher in WSG buffers ($F_{1,97} = 4.9$, $P = 0.029$), indicating greater plant biodiversity. In particular, there were significantly more perennial flowers (asters, coreopsis and goldenrods) associated with the WSG ($F_{1,97} = 22.1$, $P > 0.001$).

3.2. Epigeal communities in grass buffers

Pitfall traps captured 46,625 individuals in WSG and CSG buffers belonging to over 100 families, 13 insect orders and 7 additional arthropod classes. Of the total, saprovores were the most abundant trophic group (65.9%), followed by predators (17.1%), herbivores (15.8%) and parasitoids (1.2%). Springtails (Collembola), sowbugs (Isopoda), and soil mites (Acarina) were the most abundant saprovores, together comprising 59.0% of epigeal arthropods collected in pitfall traps. Multiple species of ants (Formicidae), spiders (Araneida, primarily Lycosidae), ground beetles (Carabidae), and rove beetles (Staphylinidae) were the most abundant epigeal predators found in buffers, comprising 15.4% of total arthropods captured. Insect herbivores and parasitoids were the least abundant arthropods active at ground level, mainly including crickets (Gryllidae), immature leafhoppers (Cicadellidae) and plant bugs (Miridae), scelionid wasps (Scelionidae) and humpbacked flies (Phoridae).

The taxa richness and total abundance of the epigeal communities were not affected by the buffer grass type or interaction effect with sampling month. The number of taxa and total abundance of epigeal arthropods per pitfall trap averaged 15.5 ± 0.60 and 167.1 ± 18.9 in CSG buffers, compared to means of 14.2 ± 0.48 and 164.0 ± 14.3 in WSG buffers, respectively. However, the overall number of taxa captured significantly declined in both buffer communities as the season progressed ($F_{1,89} = 7.6$, $P = 0.008$). Analysis of the Shannon indices indicated a significant effect of buffer type on community diversity, but differences varied with sampling month (interaction: $F_{1,89} = 4.7$, $P = 0.032$). Taxa diversity increased in CSG buffers during the two months and was overall higher in contrast to declining diversity in WSG buffers. The Simpson index showed a similar interaction trend, but differences were not statistically significant ($P = 0.097$).

The epigeal abundance data were further subjected to RDA to analyze the taxa-specific relationship explained by the interaction of buffer type and sampling month. The ordination biplot in Fig. 1 displays the weighted abundances of 17 epigeal taxa which had variances most explained by the explanatory variables. Year, month and adjacent crop explained 18.4% of the total variance in taxa data. After removal of the covariable effects, the two axes explained 4.57% of the variation in the epigeal taxa data and 100% of the fitted data due to buffer type and month ($P = 0.004$, Monte-Carlo permutations). The pattern of taxa vectors relative to the explanatory variables shows clear differences between CSG (right side) and WSG (left side) buffers, mainly captured by the first axis, which accounted for 79.6% of the explained variance. Densities of sowbugs, crickets, centipedes (Chilopoda), and slugs were more abundant in CSG buffers, while springtails, ants, humpbacked flies, leafhopper nymphs, and scelionid wasps were more abundant in WSG buffers. Of these taxa, ANOVA results showed significantly higher densities (56% higher, mean 1.29 ± 0.26) of centipedes ($F_{1,89} = 10.08$, $P = 0.002$) and (38% higher densities, mean 21.4 ± 6.81) of sowbugs ($F_{1,89} = 6.3$, $P = 0.014$) per pitfall trap in CSG buffers. Trap captures of crickets, slugs, carabid beetles, various dipteran and lepidopteran larvae, big-eyed bugs, and several families of hymenopteran parasitoids were consistently higher in CSG buffers, but

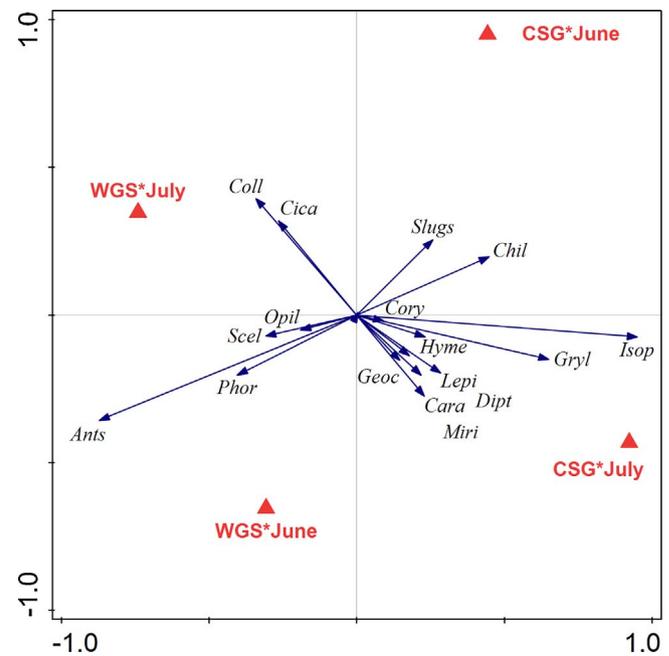


Fig. 1. RDA biplot illustrating the relationship between explanatory variables (buffer type and sampling month) and abundances of taxa in epigeal communities in cool season (CSG) and warm season (WSG) grass riparian buffers. The two axes explained 4.57% of the variation in the epigeal taxa data and 100% of the fitted data due to buffer type and month ($P < 0.001$, Monte-Carlo permutations). The taxa with greater than 2% of their variance explained are included: *Form* = Formicidae (ants), *Phor* = Phoridae (humpbacked flies), *Scel* = Scelionidae (parasitoid wasps), *Opil* = Opiliones (harvestmen), *Coll* = Collembola (springtails), *Cica* = Cicadellidae (leafhoppers), *Agro* = Agriolimacidae (slugs), *Chil* = Chilopoda (centipedes), *Cory* = Chilopoda (centipedes), *Cory* = Corylophidae (minute fungus beetles), *Hyme* = Hymenoptera (misc. wasps), *Isop* = Isopoda (sowbugs), *Gryl* = Gryllidae (crickets), *Lepi* = Lepidoptera (misc. larvae), *Dipt* = Diptera (higher taxa larvae), *Geoc* = Geocoridae (big-eyed bugs), *Cara* = Carabidae (ground beetles), and *Miri* = Miridae (plant bugs).

not statistically different from captures in WSG buffers. Densities in WSG buffers were significantly higher for ants, averaging 16.9 ± 2.98 compared to 8.2 ± 2.19 per trap in CSG buffers ($F_{1,89} = 8.0$, $P = 0.006$); for scelionid wasps, averaging 2.04 ± 0.31 compared to 1.27 ± 0.32 per trap in CSG buffers ($F_{1,89} = 3.9$, $P = 0.052$); and for humpbacked flies, averaging 1.11 ± 0.27 compared to 0.39 ± 0.15 per trap in CSG buffers ($F_{1,89} = 11.5$, $P = 0.001$). Of the 22 taxa not displayed in the biplot, their abundances were generally similar and not influenced by grass buffer type. Means, standard errors, and ANOVA statistics of all major epigeal taxa by buffer type are given in Table S2.

3.3. Canopy-dwelling communities in grass buffers

Sticky cards captured 51,478 individuals in WSG and CSG buffers belonging to 48 arthropod taxa, of which herbivores were the most abundant trophic group (68.0% of total), followed by parasitoids (19.1%), saprovores (10.1%), and predators (2.8%). Thrips (Thripidae), grass flies (Chloropidae), leafhoppers (Cicadellidae), aphids (Aphididae) and plant hoppers (Delphacidae, Flatidae, Cixiidae) accounted for 66.2% of the total number of individuals recorded. Eleven families of parasitic wasps were represented in the canopy-dwelling community, of which scelionid wasps, fairyflies (Mymaridae) and trichogrammatid wasps were the predominant taxa. Dipteran families (Phoridae, Tachinidae) with parasitic fly species were less abundant overall, but consistently captured on more than 70% of the sticky cards. Saprovores taxa consisted mainly of minute black scavenger flies (Scatopsidae), dark-winged fungus gnats (Sciariidae), non-biting midge flies (Chironomidae), picture-winged flies (Ulidiidae), and several families of fungivorous beetles, in order of abundance. Hoverflies (Syrphidae) and long-legged flies (Dolichopodidae) were the most

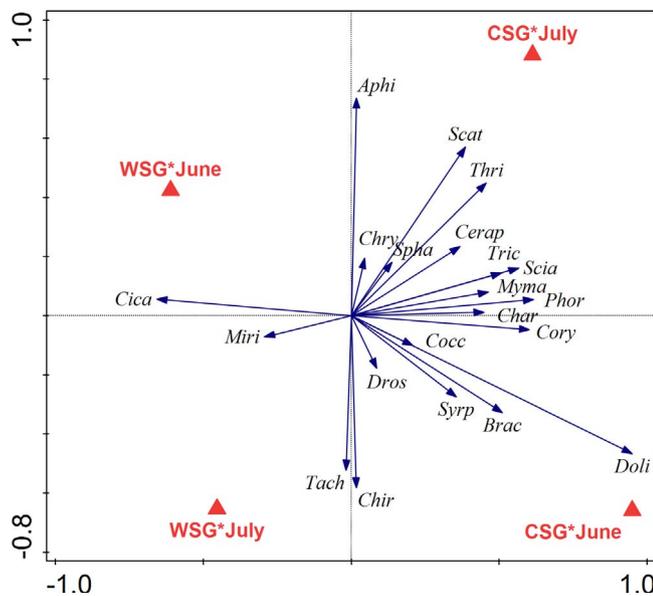


Fig. 2. RDA biplot illustrating the relationship between explanatory variables (buffer type and sampling month) and abundances of taxa in canopy-dwelling communities in cool season (CSG) and warm season (WSG) grass riparian buffers. The two axes explained 5.4% of the variation in the taxa data and 100% of the fitted data due to buffer type and month ($P < 0.001$, Monte-Carlo permutations). The taxa with greater than 2% of their variance explained are included: *Cica* = Cicadellidae (leafhoppers), *Miri* = Miridae (plant bugs), *Aphi* = Aphididae (aphids), *Chry* = Chrysomelidae (flea beetles), *Scat* = Scatopsidae (scavenger flies), *Spha* = Sphaeroceridae (small dung flies), *Thri* = Thripidae (thrips), *Cerap* = Ceraphronidae (parasitoid wasps), *Tric* = Trichogrammatidae (parasitoid wasps), *Scia* = Sciaridae (fungus flies), *Myma* = Mymaridae (fairlyflies), *Phor* = Phoridae (humpbacked flies), *Char* = Charipidae (alloxystine wasps), *Cory* = Corylophidae (minute fungus beetles), *Cocc* = Coccinellidae (lady beetles), *Doli* = Dolichopodidae (long-legged flies), *Brac* = Braconidae (braconid wasps), *Syrp* = Syrphidae (hoverflies), *Dros* = Drosophilidae (pomace flies), and *Chir* = Chironomidae (midges).

abundant predators captured on sticky cards, followed by fireflies (Lampyridae), minute pirate bugs (Anthocoridae), and lady beetles (Coccinellidae).

The community of arthropods captured on sticky cards was consistently more diverse than the epigeal community. Taxa richness was significantly higher in CSG buffers (27.1 ± 0.73 taxa per card) than in WSG buffers (23.7 ± 0.74 taxa per card) ($F_{1,88} = 9.9$, $P = 0.008$). However, there were no statistical differences between buffer types in overall abundance or community diversity based on both diversity indices.

RDA results revealed distinct differences in abundances of the canopy-dwelling arthropods captured on sticky cards in CSG buffers compared to those in WSG buffers (Monte-Carlo permutations, $P < 0.004$, Fig. 2). Twenty-one percent of the total variance in taxa data was explained by the covariables year, sampling month and adjacent crop. Of the remaining variance, the two axes explained 5.4% of the total variation in taxa abundances and 100% of the fitted taxa data due to the interaction between buffer type and month. Twenty-seven taxa were not included in ordination biplot (Fig. 2) because the explanatory variables accounted for less than 2% of their variances. These taxa were either rare in abundance or captures were highly variable. For example, scelionid wasps were the most abundant parasitoid taxa, particularly in June with densities averaging 15.92 ± 4.02 and 6.94 ± 0.77 and WSG and CSG buffers, respectively. However, ANOVA results showed no statistical significant effects due to the high variance. Eighteen of the 21 taxa displayed in the biplot were mostly explained by axis 1, indicating the main effect of buffer type. Captures of thrips and plant hoppers were higher per sticky card in CSG buffers compared to WSG buffers, but differences were not statistically significant. In contrast, leafhoppers were strongly associated with WSG buffers, with

mean captures of 17.69 ± 2.41 compared to 10.59 ± 1.27 in CSG buffers ($F_{1,88} = 7.8$, $P = 0.007$). With the exception of the scelionid parasitoids mentioned above, captures of parasitoids in the families of Mymaridae, Trichogrammatidae, Ceraphronidae, and Braconidae, humpbacked flies, hoverflies, long-legged flies, and lady beetles were significantly higher in CSG buffers, particularly during June. Pooled together, these beneficial taxa averaged 21.2 ± 1.62 per sticky card compared to 13.4 ± 1.36 in WSG buffers ($F_{1,88} = 20.5$, $P < 0.001$). The second axis of the biplot largely accounted for the variances and abundances of aphids, tachinid flies, and midges, each significantly influenced by the buffer type, but differences depended on the sampling month. Aphid populations significantly increased from June to July in both buffer types, but the rate of increase was significantly higher in CSG buffers (interaction: $F_{1,88} = 11.2$, $P = 0.001$). Overall captures of aphids averaged 7.2 ± 1.42 and 4.6 ± 0.67 and CSG and WSG buffers, respectively. The taxa of tachinid flies probably included some species of calliphorid and sarcophagid flies, many of which are parasitic, due to the difficulty in identifying these calypterate flies stuck to sticky cards. Their abundance was highest during June in CSG buffers, but then lower than abundance in WSG buffers in July (interaction: $F_{1,88} = 4.6$, $P = 0.036$). Means, standard errors, and ANOVA statistics of all major canopy-dwelling taxa by buffer type are given in Table S3.

3.4. Beneficial epigeal communities in crops adjacent to grass buffers

The number of taxa and diversity measurements were slightly higher in traps near the field edge (6 m) than further into the field; however, interaction effects of distance and buffer type were not significant, so we averaged the captures at the six sampling sites within each crop field to provide an overall assessment of the epigeal community. In general, the composition of surface-dwelling arthropods in soybean and corn fields bordering grass buffers was similar, with saprovores (sowbugs, springtails, and soil mites) accounting for 62–67% of the arthropods captured in pitfall traps. Herbivores (primarily crickets) were more abundant in soybean fields, comprising 21% of the community compared to 14% in corn fields. In both crops, predators (spiders, ants, ground beetles, centipedes, rove beetles, and other minor predators) represented 15–17% of the community, while scelionid wasps and humpbacked flies were the only parasitoids captured in pitfall traps in appreciable numbers ($< 2\%$). In corn, the bordering buffer type had significant effects on taxa richness ($F_{1,120} = 16.5$, $P < 0.001$), total abundance ($F_{1,120} = 5.4$, $P = 0.022$), diversity ($F_{1,120} = 16.5$, $P < 0.001$), and taxa evenness ($F_{1,120} = 15.9$, $P < 0.001$) of the epigeal communities. The number of taxa and total abundance averaged 13.6 ± 1.98 and 203.9 ± 22.0 in corn fields next to CSG buffers compared to 10.7 ± 0.49 and 119.4 ± 14.9 in corn fields next to WSG buffers. However, community diversity and taxa evenness were significantly higher in fields bordering WSG buffers. In soybean fields, buffer type had no significant effect on taxa richness, total abundance, community diversity or taxa evenness.

All arthropods captured in pitfall traps were identified and recorded; however, the main focus for sampling adjacent crops was to assess the influence of bordering buffer types on abundances of beneficial taxa. RDA analysis of each crop did not capture enough variance of the beneficial taxa data to detect a significant pattern influenced by buffer type. ANOVA results indicated significant effects of buffer type on carabid beetle abundance, but differences varied with crop and sampling month. Beetle abundance was significantly higher in corn fields next to WSG buffers during June (5.86 ± 1.98) compared to trap captures in fields next to CSG buffers (2.18 ± 0.60), but the difference reversed during July when overall abundance was 62% higher in fields next to CSG buffers (interaction: $F_{1,48} = 5.2$, $P = 0.027$). In soybeans, ground beetles were consistently more abundant over the sampling period in fields associated with CSG buffers, averaging 16.6 ± 6.97 compared to 5.87 ± 1.60 per trap in fields next to WSG buffers ($F_{1,20} = 4.5$, $P = 0.046$). Abundance differences between buffer types

of other beneficial arthropods, including spiders, rove beetles, scelionid wasps, centipedes, and humpbacked flies in order of abundance, were mixed and not statistically significant. Pooled over beneficial arthropods in both crops, pitfall trap captures averaged 25.7 ± 3.14 and 19.5 ± 1.79 in fields next to CSG and WSG buffers, respectively. This overall difference was near significant ($F_{1,169} = 3.82$, $P = 0.052$). Means, standard errors, and ANOVA statistics of all major epigeal taxa by crop are given in Table S4.

3.5. Beneficial canopy-dwelling communities in crops adjacent to grass buffers

There was greater dissimilarity in the trophic composition of foliage-dwelling arthropods between crop systems than observed in the epigeal communities. Collectively, 45.5% and 87.2% of arthropods captured on sticky cards in corn and soybean fields belonged to taxa that are primarily herbivores. The major herbivores included chloropid flies, thrips, leafhoppers, planthoppers, whiteflies, and aphids. In contrast, saprovores (mainly fungivorous beetles and several dipteran families) were more numerous in corn than in soybean, accounting for 27.6% and 5.5% of the community, respectively. Of the remaining community, beneficial taxa were more abundant in corn, particularly the parasitoids. Hymenopteran parasitoids (mymarid, trichogrammatid, scelionid, braconid, encyrtid, and ceraphronid wasps), tachinid flies, and humpbacked flies were the most common parasitoids, comprising 22.8% and 6.3% of the overall community in corn and soybean fields, respectively. Long-legged flies, minute pirate bugs, syrphid flies, and lady beetles were the dominant predators, but accounted for only 1–4% of the total community as a combined trophic group. Grass buffer type had no significant effect on taxa richness, total abundance, diversity or taxa evenness of the aerial community in corn, although there was a significant decline in total abundance over sampling months ($F_{1,113} = 6.3$, $P = 0.013$). In soybeans, taxa richness and total abundance was significantly influenced by buffer type (number of taxa: $F_{1,53} = 6.7$, $P = 0.012$; abundance: $F_{1,53} = 10.5$, $P = 0.002$). The number of taxa and total abundance averaged 24.3 ± 0.85 and 324.5 ± 22.8 in soybean fields bordering CSG buffers compared to 21.4 ± 0.80 and to 281.2 ± 17.9 in fields bordering WSG buffers.

RDA analysis revealed a significant pattern in the beneficial arthropod community in corn fields related to the bordering grass buffer (Fig. 3). Year and sampling month accounted for 38.9% of the total variance in taxa data. The two ordination axes explained 4.3% of the variation in aerial taxa data and 100% of fitted taxa data, and permutation testing indicated a significant relationship ($P = 0.004$). Twelve of the 15 most abundant natural enemies are depicted in Fig. 3 by taxa arrows directed toward the right side of the ordination plot, indicating that their variances were largely influenced by the adjacent CSG buffers and taxa abundances were higher in corn fields next to these buffers. Sticky card captures of most beneficial taxa were significantly higher during June, particularly in fields bordering CSG buffers. Abundance of hoverflies in corn fields bordering CSG buffers was significantly higher in June (7.55 ± 3.40) compared to fields bordering WSG buffers (2.21 ± 1.08), but overall numbers declined markedly in July (interaction effect: $F_{1,57} = 4.2$, $P = 0.044$). Lady beetles and braconid wasps also were significantly more abundant in corn fields bordering CSG buffers ($F_{1,57} = 4.6$, $P = 0.036$ and $F_{1,57} = 6.9$, $P = 0.010$, respectively). Two exceptions were the predatory minute pirate bugs and trichogrammatid wasps which were consistently higher in abundance in cornfields bordering WSG buffers, but only captures of the parasitoid wasps were significantly higher compared to fields bordering CSG buffers ($F_{1,57} = 4.4$, $P = 0.040$). With the exception of trichogrammatid wasps, all other parasitoid taxa were collectively more abundant in corn fields bordering CSG buffers ($F_{1,113} = 4.50$, $P = 0.036$). Specifically, the biplot revealed higher populations of scelionid wasps and tachinid flies in corn fields bordering CSG buffers in June and higher populations of braconid, ceraphronid and mymarid wasps in July.

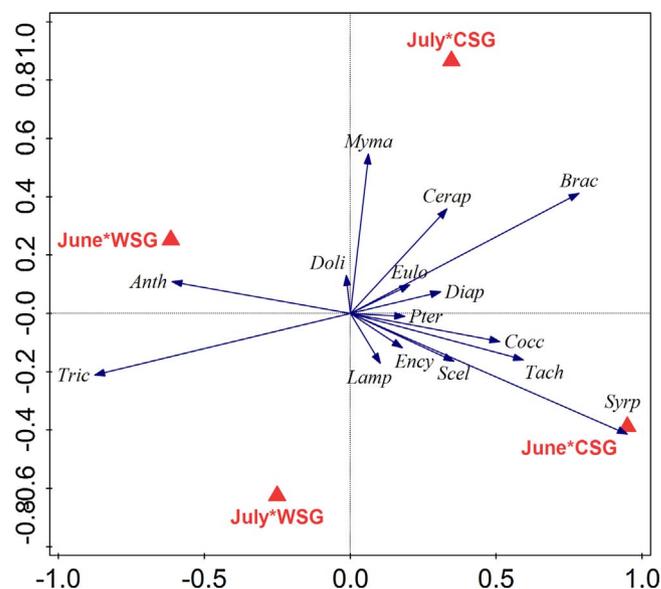


Fig. 3. RDA biplot illustrating the relationship between explanatory variables (buffer type and sampling month) and abundances of beneficial taxa in canopy-dwelling communities in corn fields bordering cool season (CSG) and warm season (WSG) grass riparian buffers. The two axes explained 4.3% of the variation in the taxa data and 100% of the fitted data due to buffer type and month ($P < 0.004$, Monte-Carlo permutations). The taxa with greater than 2% of their variance explained are included: *Tric* = Trichogrammatidae (parasitoid wasps), *Anth* = Anthocoridae (pirate bugs), *Doli* = Dolichopodidae (long-legged flies), *Myma* = Mymaridae (fairyflies), *Cera* = Ceraphronidae (parasitoid wasps), *Eulo* = Eulophidae (parasitoid wasps), *Brac* = Braconidae (braconid wasps), *Diap* = Diapriidae (parasitoid wasps), *Pter* = Pteromalidae (parasitoid wasps), *Cocc* = Coccinellidae (lady beetles), *Tach* = Tachinidae (tachinid flies), *Syrp* = Syrphidae (hoverflies), *Scel* = Scelionidae (parasitoid wasps), *Ency* = Encyrtidae (encyrtid wasps), and *Lamp* = Lampyridae (fireflies).

The canopy-dwelling community of beneficial arthropods in soybean fields was also influenced by the bordering grass buffers, but there was more similarity in abundances of individual taxa between grass types than those observed in cornfields. The overall community response explained by the interaction of buffer type and sampling month is depicted in Fig. 4 by the weighted abundances of 13 beneficial taxa. Year and sampling month accounted for 8.3% of the total variance in taxa data. The first two ordination axes explained 6.6% of the variation in taxa data and 100.0% of fitted data due to the interaction of buffer type and sampling month. Monte Carlo permutation testing was nearly significant for the first axis ($P = 0.058$) and significant for all canonical axes together ($P = 0.028$). Seven of the 13 beneficial taxa were numerically more abundant in soybean fields bordering CSG buffers, with variance of hoverflies and trichogrammatid wasps explained primarily by first axis. Sticky card captures of trichogrammatid wasps showed an opposite effect from that observed in corn fields, whereas these parasitoids were 50% more abundant in soybean fields bordering CSG buffers ($F_{1,27} = 4.6$, $P = 0.042$). Similar to hoverfly abundance in corn fields during June, these natural enemies were also consistently higher in soybean fields, but the difference between bordering CSG buffers was not statistically significant. Overall abundances of all predators and parasitoids per sticky card averaged 2.8 ± 0.38 and 16.5 ± 1.49 in soybean fields bordering CSG buffers, compared to 2.1 ± 0.27 and 14.7 ± 1.02 in soybean fields bordering WSG buffers, respectively. Means, standard errors, and ANOVA statistics of the major canopy-dwelling beneficial taxa by crop are given in Table S5.

4. Discussion

This study determined that WSG and CSG riparian buffers were inhabited by dissimilar epigeal and canopy-dwelling communities of arthropods measured as taxa richness, total taxa abundance and

Lankau et al., 2004). However, we found that CSG buffers supported canopy-dwelling communities with higher taxa richness of herbivores, saprovores, and beneficial arthropods.

Differences in nutrition and palatability of leaf tissue between grass types may influence the abundance of herbivores and also possibly saprovores that feed primarily on plant litter. Cool season grasses are generally higher in quality than WSG grasses and contain less silica (Cid et al., 1989; Tschamtko and Greiler, 1995). Silica, an effective feeding deterrent against chewing insects, causes increased abrasiveness and reduced digestion efficiency (Massey et al., 2006). In general, digestibility of WSG grasses is poor due to higher fiber and lignin concentrations compared with introduced temperate grass species at comparable growth stages (Wilson, 1994; Moore and Jung, 2001). The leaf toughness reduces herbivore feeding, and also decreases the nutritional content of leaves (Johnson et al., 2009). Despite lower plant quality, many species of leafhoppers are successful specialists on switchgrass and bluestem species (Holguin et al., 2010), having co-evolved on these native grasses. Therefore, the higher numbers of cicadellid leafhoppers in warm season grasses may be explained by specialist species; however, since we identified leafhoppers to the family level, it was not possible to separate specialists and generalists by species. Over time, many exotic plants have become equally susceptible to a diverse assemblage of native herbivores (Maron and Villà, 2001; Agrawal and Kotanen, 2003; Wolfe et al., 2004; Cripps et al., 2006). For example, orchardgrass was introduced in 1760 (Sullivan, 1992), allowing extended time for native herbivores to become tolerant to its natural defenses and subsequently exploit it as a food source. In addition, Koricheva et al. (2000) observed fewer cicadellid leafhoppers in more diverse grassland plots with higher biomass and percent cover compared to less biomass monocultures (Koricheva et al., 2000). Greater numbers of aphids, scatopsid scavenger flies, and sciarid fungus gnats were observed in the CSG buffers, which may have provided prey resources for natural enemies.

With the exception of scelionid parasitoids, for which we observed no difference in sticky card abundances between the buffers, sticky card captures of the major beneficial taxa were significantly higher in CSG buffers, particularly during June. This was unexpected because WSG buffers contained a higher mix of flowering forbs that usually attract a greater arthropod fauna and provide food resources for many arthropod natural enemies (Baggen and Gurr, 1998). In a study comparing mixed species prairie, mixed species forb, and single species buffers, the diverse mixed plant treatments exhibited higher natural enemy abundances compared to most of the simpler buffer treatments, including switchgrass (*P. virgatum* L.) alone (Gill et al., 2014). While more similar across the treatments, diverse buffers also performed well for supporting natural enemy diversity (Gill et al., 2014). Parasitoids represented a large portion of the natural enemy community captured within buffers (60% and 49% in 2010 and 2011, respectively) (Gill et al., 2014). Parasitoids represented a much smaller proportion of the natural enemies captured in this study; however, methodological sampling differences (sticky cards versus vacuum sampling) likely explain this difference. Given the high percentage of parasitoids within the natural enemy abundances, parasitoids likely responded to buffer treatments. However, where Gill et al. (2014) observed higher abundances in more diverse buffers, we observed higher abundances in the less diverse CSG buffers. Because Gill et al. (2014) present natural enemies as one category we cannot compare whether the same families of parasitoid were driving the response. Both syrphid and dolichopodid predatory flies exhibited seasonal variations in their abundances, with syrphids declining from June to July, and dolichopodids increasing from June to July. Another study comparing prairie mix, switchgrass, and corn biofuel crops observed similar seasonal phenology for these groups (Gardiner et al., 2010). This study also resulted in an interaction between sampling time and treatment similar to the month by buffer interaction shown here. Syrphids did not exhibit a clear trend with all biofuel crop treatments exhibiting the highest captures at some point in

the season (Gardiner et al., 2010). In our study, more syrphids were captured in CSG buffers than WSG buffers in June, with no differences in July. In general, dolichopodids were more abundant in the mixed prairie and switchgrass fields in comparison to corn, but switchgrass approached corn later in the season (Gardiner et al., 2010). In our study, more dolichopodids were captured in CSG buffers at both time points than in WSG buffers. These groups are abundant in row crop agriculture and grasslands and respond to plant community treatments, but the relationship between plant community and predatory fly abundance remains unclear.

Our observed higher taxa richness and abundance in CSG buffers may relate to the phenology and growth patterns of the cool season grasses. Orchardgrass and fescues probably favor earlier colonization of herbivores and natural enemies because they break dormancy and “green-up” much earlier than warm season grasses in the spring. Coupled with higher food quality, this allows for faster buildup of herbivore populations that serve as prey and hosts for predators and parasitoids, thus resulting in earlier establishment and subsequently higher abundance of natural enemies in CSG buffers. In particular, aphids were significantly more abundant in CSG buffers, providing available prey and hosts of many predatory and parasitic insects.

The type of riparian grass buffer significantly influenced arthropod communities in adjacent crop fields. In corn fields, taxa richness and abundance of epigeal arthropods were significantly higher in CSG buffers; however, community diversity and taxa evenness were higher in fields bordering WSG buffers. Carabid beetles are important epigeal predators of slugs and lepidopteran pests of corn, and they exhibited the only significant response related to the bordering buffer type. Beetle abundance was significantly higher in cornfields next to WSG buffers during June, but this trend reversed during July when overall abundance was 62% higher in cornfields next to CSG buffers. In soybeans, pitfall captures of ground beetles were 66% higher during both months in fields associated with CSG buffers compared to densities in fields next to WSG buffers.

In general, there was greater dissimilarity in the trophic composition of canopy-dwelling arthropods in corn and soybean fields than differences observed in epigeal communities. Although this was not reflected in overall measures of taxa richness, abundance or diversity in corn, we observed significantly higher taxa richness and abundance in soybean fields next to CSG buffers. Sticky card captures of herbivores and most parasitoid taxa comprised a greater proportion of the communities in both crops. A few beneficial taxa showed mixed responses to bordering buffer type that were dependent on the crop. For instance, trichogrammatid wasps were 64% more abundant in corn fields bordering WSG buffers, but abundance was significantly higher in soybean fields bordering CSG buffers during both sampling months. Unlike trichogrammatids, corn bordered by CSG buffers exhibited higher coccinellid lady beetle and braconid wasp abundances, and in some months higher numbers of braconid, ceraphronid, mymarid, and scelionid wasps. Altogether, total abundances of predators and parasitoids were consistently higher in soybean crop fields bordering CSG buffers.

Natural enemy abundances frequently increase in response to landscape complexity and habitat diversity (Bianchi et al., 2006; Gardiner et al., 2010; Gill et al., 2014). A review of 24 studies revealed that in 74% of the cases landscape complexity increased natural enemies, and in 45% of the cases complexity reduced pest density (Bianchi et al., 2006). Landscapes included wooded habitats as well as herbaceous habitats, with similar responses for both habitat types (Bianchi et al., 2006). Often, herbaceous habitats and buffers evaluated for conservation biological control are comprised of specific flowering plants with a history of use for enhancing natural enemies (Fiedler et al., 2008). Other commonly studied flowering plants include those that provide resources for pollinators (Wratten et al., 2012). In our study, flowering plants (including legumes, forbs, and shrubs) comprised approximately 20% of the WSG buffers, and 11% of the CSG buffers. Most studies attempting to improve natural enemy and

pollinator abundances include a much higher percentage of flowering plants in their buffer treatments. For example, Gill et al. (2014) designed their diverse buffer treatments to contain between 64 and 75% flowering species relative to grasses [e.g., big and little bluestems, switchgrass, Indian grass]. The switchgrass and mixed prairie biofuel plantings examined in Gardiner et al. (2010) contained native grasses, sedges, and forbs as well as common weedy and invasive species, averaging 27 species in switchgrass fields and 34.6 in mixed prairie; both types of field were diverse and contained flowering plant species. Therefore, the abundance of flowering plant species and plant diversity in the grass buffers examined here may have been insufficient to attract the natural enemies commonly targeted by flowering buffer strips. In addition, landscape level effects may have impacted our results.

The spatial distribution of non-crop habitat at the landscape scale impacts natural enemy abundances in crop and non-crop habitat (Bianchi et al., 2006). Both the dispersal ability of the specific natural enemies as well as the habitat connectivity and landscape patchiness impact natural enemy and pest abundances (Bianchi et al., 2006). This experiment was conducted in an area with relatively intensive agriculture, which represented around 60% of the land cover in the surrounding areas. While larger scale landscape effects were outside the scope of this study, they would play a role in the species that were present and responding to our smaller scale buffer strips. Further research is needed to examine the influence of small and large-scale landscape composition on riparian buffer communities.

5. Conclusions

Riparian grass buffers are important habitats in the agricultural landscape to provide overwintering shelter and food for many arthropods and serve as corridors for arthropod movement into crop fields. This study demonstrated that the composition and relative abundances of most epigeal and canopy-dwelling taxa in crop fields corresponded with the composition and relative abundances of those taxa in neighboring grass buffers, suggesting population linkage and movement of taxa between buffer and crop habitats. Contrary to our hypothesis, non-native CSG buffers supported greater taxa richness (canopy and epigeal community) of arthropods in the riparian buffer, had positive influences on many natural enemy taxa in adjacent crop fields, especially early in the growing season, and would seemingly provide greater biological control conservation value than WSG buffers. Beneficial arthropod responses were likely linked to differences in contrasting early season phenologies of the two grass types. Although structurally less diverse and often stressed during the summer, cool season grasses provide more food resources in terms of prey and host for natural enemies to build up during the early growing season than warm season grasses.

The general policy in CRP planning for riparian buffers has been to encourage the planting of warm season grasses mixed with flowering forbs. CSG buffers are usually mixed with legumes and fewer flowering forbs. Given the early season advantage of the cool season grasses as a better habitat for natural enemy recruitment, the addition of perennial flowering forbs to the mixes may be an effective way to enhance their conservation value by improving structural complexity and providing a greater assortment of pollen and nectar as food sources to support natural enemy populations. Many natural enemies emerging from overwintered stages in the spring require nectar and pollen sources to maintain their longevity and egg laying ability and thus their effectiveness in controlling pests. With the current focus on conservation practices throughout the Mid-Atlantic US, this study highlights the opportunity to better plan and manage riparian grass buffers in ways that enhance arthropod natural enemies. However, further research is necessary to investigate management practices to achieve this goal and specifically to find perennial flowering forbs that provide floral resources during the critical spring period and successfully compete in mixes of both grass types. The added biological control benefits of

riparian buffers will ultimately provide landowners and farmers with additional incentive for maintaining conservation habitats within arable lands.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.agee.2018.01.019>.

References

- Agrawal, A.A., Kotanen, P.M., 2003. Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecol. Lett.* 6, 712–715.
- Baggen, L.R., Gurr, G.M., 1998. The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Biol. Control.* 11, 9–17.
- Beattie, A.J., 1985. *The Evolutionary Ecology of Ant-Plant Mutualisms*. Cambridge University Press, New York.
- Benson, T.J., Dinsmore, J.J., Hohman, W.L., 2007. Responses of plants and arthropods to burning and disking of riparian habitats. *J. Wildl. Manage.* 71, 1949–1957.
- Berg, R., 1975. Myrmecochorous plants in Australia and their dispersal by ants. *Aust. J. Bot.* 23, 475–508.
- Berg, M.P., Hemerik, L., 2004. Secondary succession of terrestrial isopod, centipede, and millipede communities in grasslands under restoration. *Biol. Fertil. Soils* 40, 163–170.
- Bianchi, F.J.J.A., van der Werf, W., 2003. The effect of the area and configuration of hibernation sites on the control of aphids by *Coccinella septempunctata* (Coleoptera: Coccinellidae) in agricultural landscapes: a simulation study. *Environ. Entomol.* 32, 1290–1304.
- Bianchi, F.J.J.A., van der Werf, W., 2004. Model evaluation of the function of prey in non-crop habitats for biological control by ladybeetles in agricultural landscapes. *Ecol. Modell.* 171, 177–193.
- Bianchi, F.J.J.A., Booi, C.J.H., Tschamntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity, and natural pest control. *Proc. R. Soc. B* 273, 1715–1727.
- Blank, P.J., 2010. *Bird Community Response to Herbaceous Buffers in Maryland*. U.S. Department of Agriculture, Natural Resources Conservation Service, Washington, DC Wildlife Insight 90.
- Bruck, D.J., Lewis, L.C., 1998. Influence of adjacent cornfield habitat, trap location, and trap height on capture numbers of predators and a parasitoid of the European corn borer (Lepidoptera: Pyralidae) in central Iowa. *Environ. Entomol.* 27, 1557–1562.
- Carroll, S.C., Rummel, D.R., Segarra, E., 1993. Overwintering by the boll weevil (Coleoptera: Curculionidae) conservation reserve program grasses on the Texas High Plains. *J. Econ. Entomol.* 86, 382–393.
- Chen, B., Wise, D.H., 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 80, 761–772.
- Cid, M.S., Detling, J.K., Brizuela, M.A., Whicker, A.D., 1989. Patterns in grass silification—response to grazing history and defoliation. *Oecologia* 80, 268–271.
- Collins, K.L., Boatman, N.D., Wilcox, A., Holland, J.M., 2003. Effects of different grass treatments used to create overwintering habitat for predatory arthropods on arable farmland. *Agric. Ecosyst. Environ.* 96, 59–67.
- Coppedge, B.R., Engle, D.M., Masters, R.E., Gregory, M.S., 2004. Predicting juniper encroachment and CRP effects on avian community dynamics in southern mixed-grass prairie, USA. *Biol. Conserv.* 115, 431–441.
- Corbett, A., Rosenheim, J.A., 1996. Impact of a natural enemy overwintering refuge and its interaction with the surrounding landscape. *Ecol. Entomol.* 21, 155–164.
- Cripps, M.G., Schwarzländer, M., McKenney, J.L., Hinz, H.L., Price, W.J., 2006. Biogeographic comparison of the arthropod herbivore communities associated with *Lepidium draba* in its native, expanded and introduced ranges. *J. Biogeogr.* 33, 2107–2119.
- Davros, N.M., Debinski, D.M., Reeder, K.F., Hohman, W.L., 2006. Butterflies and continuous conservation reserve program filter strips: landscape considerations. *Wildl. Soc. Bull.* 34, 936–943.
- Dennis, P., Fry, G.L.A., 1992. Field margins: can they enhance natural enemy population

- densities and general arthropod diversity on farmland? *Agric. Ecosyst. Environ.* 40, 95–115.
- Dennis, P., Thomas, M.B., Sotherton, N.W., 1994. Structural features of field boundaries which influence the overwintering densities of beneficial arthropod predators. *Appl. Ecol.* 31, 361–370.
- Dennis, P., Young, M.R., Gordon, L.J., 1998. Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed indigenous grasslands. *Ecol. Entomol.* 23, 253–264.
- DiGiulio, M., Edwards, P.J., Meister, E., 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Appl. Ecol.* 38, 310–319.
- Dollar, J.G., Riffell, S.K., Burger Jr., L.W., 2013. Effects of managing semi-natural grassland buffers on butterflies. *J. Insect Conserv.* 17, 577–590.
- Dollar, J.G., Riffell, S.K., Adams, H.L., Burger Jr., L.W., 2014. Evaluating butterflies as surrogates for birds and plants in semi-natural grassland buffers. *J. Insect Conserv.* 18, 171–178.
- EWG https://conservation.ewg.org/crp_practices.php?fips=00000*ionname=theUnitedStates.
- Fiedler, A.K., Landis, D.A., Wratten, S.D., 2008. Maximizing ecosystem services from conservation biological control: the role of habitat management. *Biol. Control* 45, 254–271.
- Frank, T., Reichhart, B., 2004. Staphylinidae and Carabidae overwintering in wheat and sown wildflower areas of different age. *Bull. Entomol. Res.* 94, 209–217.
- French, B.W., Elliott, N.C., Berberet, R.C., 1998. Reverting conservation reserve program lands to wheat and livestock production: effects on ground beetle (Coleoptera: Carabidae) assemblages. *Environ. Entomol.* 27, 1323–1335.
- Fry, J., Xian, G., Jin, S., Dewitz, J., Homer, C., Yang, L., Barnes, C., Herold, N., Wickham, J., 2011. Completion of the 2006 national land cover database for the conterminous United States. *PEARS* 77, 858–864.
- Gardiner, M.A., Tuell, J.K., Isaacs, R., Gibbs, J., Ascher, J.S., Landis, D.A., 2010. Implications of three biofuel crops for beneficial arthropods in agricultural landscapes. *Bioenergy Res.* 3, 6–19.
- Gerlach, A., Voigtländer, K., Heidger, C.M., 2009. Influences of the behaviour of epigeic arthropods (Diplopoda, Chilopoda, Carabidae) on the efficiency of pitfall trapping. *Soil Org.* 81, 773–790.
- Gill, K.A., Cox, R., O'Neal, M.E., 2014. Quality over quantity: buffer strips can be improved with select native plant species. *Environ. Entomol.* 43, 298–311.
- Harwood, J.D., Sunderland, K.D., Symondson, W.O.C., 2001. Living where the food is: web location by linyphiid spiders in relation to prey availability in winter wheat. *J. Appl. Ecol.* 38, 88–99.
- Holguin, C.M., Reay-Jones, F.P.F., Frederick, J.R., Adler, P.H., Chong, J.-H., Savereno, A., 2010. Insect diversity in switchgrass grown for biofuel in South Carolina. *J. Agric. Urban Entomol.* 27, 1–19.
- Honek, A., 1988. The effect of crop density and microclimate on pitfall catches of Carabidae, Staphylinidae (Coleoptera) and Lycosidae (Araneae) in cereal fields. *Pedobiologia* 32, 233–242.
- Jackson, R.R., Li, D., Barrion, A.T., Edwards, G.B., 1998. Prey-capture techniques and prey preferences of nine species of ant-eating jumping spiders (Araneae: Salticidae) from the Philippines. *N. Z. J. Zool.* 25, 249–272.
- Johnson, M.T.J., Smith, S.D., Rausher, M.D., 2009. Plant sex and the evolution of plant defenses against herbivores. *Proc. Natl. Acad. Sci. U. S. A.* 106, 18079–18084.
- Johnson, K.A., Dalzell, B.J., Donahue, M., Gourevitch, J., Johnson, D.L., Karlovitse, G.S., Keeler, B., Smith, J.T., 2016. Conservation Reserve Program (CRP) lands provide ecosystem service benefits that exceed land rental payment cost. *Ecosyst. Serv.* 18, 175–185.
- Kamler, J.F., Ballard, W.V., Wallace, M.C., Gipson, P.S., 2007. Diets of swift foxes (*Vulpes velox*) in continuous and fragmented prairie in northwest Texas. *Southwestern Nat.* 52, 504–510.
- Koricheva, J., Mulder, C.P.H., Schmid, B., Joshi, J., Huss-Danell, K., 2000. Numerical responses of different trophic groups of invertebrates to manipulations of plant diversity in grasslands. *Oecologia* 125, 271–282. Crossref, PubMed, Google Scholar.
- Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.* 74, 187–228.
- Landis, D.A., Haas, M.J., 1992. Influence of landscape structure on abundance and within-field distribution of European corn borer (Lepidoptera: Pyralidae) larval parasitoids in Michigan. *Environ. Entomol.* 21, 409–416.
- Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45, 175–201.
- Langelotto, G.A., Denno, R.F., 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139, 1–10.
- Lankau, R.A., Rogers, W.E., Siemann, E., 2004. Constraints on the utilization of the invasive Chinese tallow tree *Sapium sebiferum* by generalist native herbivores in coastal prairies. *Ecol. Entomol.* 29, 66–75.
- Lefko, S.A., Pedigo, L.P., Rice, M.E., Batchelor, W.D., 1998. Wireworm (Coleoptera: Elateridae) incidence and diversity in Iowa conservation reserve environments. *Environ. Entomol.* 27, 312–317.
- Lemke, A., Poehling, H.M., 2002. Sown weed strips in cereal fields: overwintering site and source habitat for *Oedothorax apicatus* (Blackwall) and *Erigone atra* (Blackwall) (Araneae: Erigonidae). *Agric. Ecosyst. Environ.* 90, 67–80.
- Lovell, S.T., Sullivan, W.C., 2006. Environmental benefits of conservation buffers in the United States: evidence, promise, and open questions. *Agric. Ecosyst. Environ.* 112, 249–260.
- Luff, M.L., 1966. The abundance and diversity of the beetle fauna of grass tussocks. *J. Anim. Ecol.* 35, 189–208.
- Lynn, A., 2003. Conservation Reserve Program: Establishing, Maintaining, and Managing Cool-season Grasses. USDA Natural Resources Conservation Service (NRCS), Maryland, pp. 1–6. Accessed 22 October 2016. http://www.talbotscd.com/pdf/CP21_cool.pdf.
- Maron, J.L., Vilà, M., 2001. When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses. *Oikos* 95, 361–373.
- Marshall, E.J.R., Mooney, A.C., 2002. Field margins in northern Europe: their functions and interactions with agriculture. *Agric. Ecosyst. Environ.* 89, 5–21.
- Massey, F.P., Ennos, A.R., Hartley, S.E., 2006. Silica in grasses as a defense against insect herbivores: contrasting effects on folivores and a phloem feeder. *J. Anim. Ecol.* 75, 595–603.
- Maudsley, M.J., 2000. A review of the ecology and conservation of hedgerow invertebrates in Britain. *J. Environ. Manage.* 60, 65–76.
- McCoy, T.D., Ryan, M.R., Burger Jr., L.W., Kurzejeski, E.W., 2001. Grassland bird conservation: CP1 v. CP2 plantings in conservation reserve program fields in Missouri. *Am. Midl. Nat.* 145, 1–17.
- McIntyre, N.E., Thompson, T.R., 2003. A comparison of conservation reserve program habitat plantings with respect to arthropod prey for grassland birds. *Am. Midl. Nat.* 150, 291–301.
- Mcnett, B.J., Rypstra, A.L., 2000. Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution. *Ecol. Entomol.* 25, 423–432.
- Melbourne, B.A., 1999. Bias in the effect of habitat structure on pitfall traps: an experimental evaluation. *Aust. J. Ecol.* 24, 228–239.
- Melnychuk, N.A., Olfert, O., Youngs, B., Gillott, C., 2003. Abundance and diversity of Carabidae (Coleoptera) in different farming systems. *Agric. Ecosyst. Environ.* 95, 69–72.
- Miyashita, T., Takeda, M., Shimazaki, A., 2003. Experimental evidence that aboveground predators are sustained by underground detritivores. *Oikos* 103, 31–36.
- Moore, K.J., Jung, H.-J.G., 2001. Lignin and fiber digestion. *J. Range Manage.* 54, 420–430.
- Mowry, T.M., Halbert, S.E., Pike, K.S., 1995. Russian wheat aphid (Homoptera: Aphididae) performance on perennial grasses. *J. Econ. Entomol.* 88, 635–639.
- Munson, S.M., Lauenroth, W.K., Burke, I.C., 2012. Soil carbon and nitrogen recovery on semi-arid conservation reserve program lands. *J. Arid Environ.* 79, 25–31.
- Naiman, R.J., Decamps, H., 1997. The ecology of interfaces: riparian zones. *Annu. Rev. Ecol. Evol. Syst.* 28, 621–658.
- O'Connell, J.L., Daniel, D.W., McMurry, S.T., Smith, L.M., 2016. Soil organic carbon in plays and adjacent prairies, cropland, and Conservation Reserve Program land of the High Plains, USA. *Soil Till. Res.* 156, 116–124.
- Phillips, I.D., Cobb, T.P., 2005. Effects of habitat structure and lid transparency on pitfall catches. *Environ. Entomol.* 34, 875–882.
- Phillips, S.A., Brown Jr., C.M., Cole, C.L., 1991. Weeping lovegrass, *Eragrostis curvula* (Schrad.) Nees von Esenbeck, as a harborage of arthropods on the Texas high plains. *Southwestern Nat.* 36, 49–53.
- Phillips, M.L., Clark, W.R., Nusser, S.M., Sovada, M.A., Greenwood, R.J., 2004. Analysis of predator movement in prairie landscapes with contrasting grassland composition. *J. Mammal* 85, 187–195.
- Porter, S.D., Savignano, D.A., 1990. Invasion of polygene ants decimates native ants and disrupts arthropod community. *Ecology* 71, 2095–2106.
- Pywell, R.F., James, I., Herbert, K.L., Meek, W.R., Carvell, C., Bell, D., Sparks, T.H., 2005. Determinants of overwintering habitat quality for beetles and spiders on arable farmland. *Biol. Conserv.* 123, 79–90.
- Reddy, M.V., Venkataiah, B., 1990. Seasonal abundance of soil-surface arthropods in relation to some meteorological and edaphic variables of the grassland and tree-planted areas in a tropical semi-arid savanna. *Int. J. Biometeorol.* 34, 49–59.
- Reeder, K.F., Debinski, D.M., Danielson, B.J., 2005. Factors affecting butterfly use of filter strips in Midwestern USA. *Agric. Ecosyst. Environ.* 109, 40–47.
- Reiss, K.Z., 2001. Using phylogenies to study convergence: the case of the ant-eating mammals. *Am. Zool.* 41, 507–525.
- Robel, R.L., Briggs, J.N., Dayton, A.D., Hulbert, L.C., 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *J. Range Manage.* 23, 295–297.
- SAS Institute, 1997. SAS Users Guide. SAS Institute, Cary, NC.
- Stanley, T.R., 2010. Land use and small mammal predation effects on shortgrass prairie birds. *J. Wildl. Manage.* 74, 1825–1843.
- Strong, D.R., Lawton, J.H., Southwood, R., 1984. Insects on Plants: Community Patterns and Mechanisms. Blackwell Scientific, Oxford, England.
- Sullivan, J., 1992. *Dactylis glomerata*. Fire Effects Information System, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). Available: <http://www.fs.fed.us/database/feis/> [2008, February 4].
- Sunderland, K., Samu, F., 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomol. Exp. Appl.* 95, 1–13.
- ter Braak, C.J.F., Smilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, New York, USA.
- Thomas, M.B., Wratten, S.D., Sotherton, N.W., 1991. Creation of 'island' habitats in farmland to manipulation populations of beneficial arthropods: predator densities and emigration. *Appl. Ecol.* 28, 906–917.
- Thomas, M.B., Sotherton, N.W., Coombes, D.S., Wratten, S.D., 1992a. Habitat factors influencing the distribution of polyphagous predatory insects between field boundaries. *Ann. Appl. Biol.* 120, 197–202.
- Thomas, M.B., Wratten, S.D., Sotherton, N.W., 1992b. Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *Appl. Ecol.* 29, 524–531.
- Tjaden, R.L., Weber, G.M., 1998. Riparian Buffer Management: Grasses for Riparian

- Buffers and Wildlife Habitat Improvement. Fact Sheet 728, Maryland Cooperative extension, https://extension.umd.edu/sites/default/files/_docs/programs/riparianbuffers/FS728.pdf (Accessed 22 October 2016).
- Tscharntke, T., Greiler, H.J., 1995. Insect communities, grasses, and grasslands. *Annu. Rev. Entomol.* 40, 535–558.
- Tscharntke, T., Steffan-Dewenter, I., Kreuss, A., Thies, C., 2002. Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecol. Appl.* 12, 354–363.
- U.S. Census Bureau, 2010. Quick Facts. Accessed 14 September 2017. <https://www.census.gov/quickfacts/fact/table/US/PST045216>.
- USDA FSA, 2013. The Conservation Reserve Program: 45th Signup Results. USDA Farm Service Agency Accessed 12 October 2016. <http://www.fsa.usda.gov/Assets/USDA-FSA-Public/usdafiles/Conservation/PDF/su45state0913.pdf>.
- USDA, 2012a. Agriculture Secretary Vilsack Announces New Conservation Reserve Program Initiative to Restore Grasslands, Wetlands and Wildlife. News Release No. 0076.12 <http://www.usda.gov/wps/portal/usda/usdamediafb?contentid=2012/03/0076.xml&printable=true&contentidonly=true> (Accessed 12 November 2016).
- USDA, 2012b. National Agricultural Statistics Service, Washington, D.C. . https://www.agcensus.usda.gov/Publications/2012/Full_Report/Volume_1,_Chapter_2_County_Level/Maryland/.
- Whisler, K.M., Rowe, H.I., Dukes, J.S., 2016. Relationships among land use, soil texture, species richness, and soil carbon in Midwestern tallgrass prairie, CRP and crop lands. *Agric. Ecosyst. Environ.* 216, 237–246.
- Willson, M.F., Rice, B.L., Westoby, M., 1990. Seed dispersal spectra: a comparison of temperate plant communities. *J. Veg. Sci.* 1, 547–562.
- Wilson, J.R., 1994. Cell wall characteristics in relation to forage digestion by ruminants. *J. Agric. Sci.* 122, 173–182.
- Witmer, J.E., Hough-Goldstein, J.A., Pesek, J.D., 2003. Ground-dwelling and foliar arthropods in four cropping systems. *Environ. Entomol.* 32, 366–376.
- Wolfe, L.M., Elzinga, J.A., Biere, A., 2004. Increased susceptibility to enemies following introduction in the invasive plant *Silene latifolia*. *Ecol. Lett.* 7, 813–820.
- Wratten, S.D., Gillespie, M., Decourtye, A., Mader, E., Desneux, N., 2012. Pollinator habitat enhancement: benefits to other ecosystem services. *Agric. Ecosyst. Environ.* 159, 112–122.
- Youngs, L.C., 1983. Predaceous ants in biological control of insect pests of North America forests. *Bull. Entomol. Soc. Am.* 29, 47–50.