Seed predation increases with ground beetle diversity in a Wisconsin (USA) potato agroecosystem

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A B S T R A C T
Agri-environmental schemes (AES) are hypothesized to enhance biodiversity and ecosystem services in agroecosystems. We investigated how non-crop habitats in one AES influence seed-eating ground beetles (Coleoptera: Carabidae) and post-dispersal weed seed predation, an ecosystem service provided by these beetles. We found that the abundance of beetles was higher in the non-crop habitats than within the crop fields. Species diversity (measured by Simpson’s D), however, was greater in crop fields than in non-crop habitats. In addition, beetle assemblages were distinct between the crop and non-crop habitats possibly due to differences in the frequency and intensity of disturbance between crop and non-crop habitats. Seed predation by small predators (mainly ground beetles) was greater in the non-crop habitat than within the potato field. Moreover, we found a positive association between seed predation and beetle diversity both within the crop and in the non-crop habitat which provides evidence of a relationship between biodiversity and ecosystem services. Yet, differences in species assemblages suggest that species identity also affects rates of seed predation.

1. Introduction

The expansion of modern, intensive agriculture is one of the greatest threats to biodiversity worldwide (Benton et al., 2003; Tilman et al., 2001). The loss of insect diversity is especially pertinent in agroecosystems as insects provide a variety of ecosystem services vital to farming (Isaacs et al., 2009). These include pest suppression (Nicholls and Altieri, 2004), pollination (Kearns et al., 1998; Kremen et al., 2002), weed seed predation (Heggenstaller et al., 2006; Honek et al., 2003; Kromp, 1999), and decomposition (Klein, 1989). Losey and Vaughan (2006) estimate the annual value of pest control and crop pollination attributed to wild insects in the U.S. at $4.5 and $3.1 billion, respectively. Because of the value of biodiversity in agroecosystems, agricultural practices that favor the conservation of farmland biodiversity should be encouraged (Butler et al., 2007).

To counteract the potentially negative impacts of agriculture on biodiversity, governments and conservation organizations encourage the implementation of agri-environmental schemes (AES). AES include financial incentives for farm management practices that preserve non-crop habitat on farms, increase habitat heterogeneity or enhance biodiversity (Benton et al., 2003; Fischer et al., 2006; Merckx et al., 2009). Local availability of non-crop habitats is especially important in modern monocropped agroecosystems that are otherwise void of resources necessary for the survival and persistence of beneficial insects (Tscharntke et al., 2005). By increasing natural habitat in the local landscape it is expected that insect diversity and abundance will increase and, in turn, ecosystem services will be enhanced (Kremen et al., 2002; Morandin and Winston, 2006; Tsitsilas et al., 2006).

Although previous studies have shown a positive influence of AES within managed, non-crop habitats (e.g., Steffan-Dewenter et al., 2002; Thomas, 1990), few have investigated how AES influence within-crop arthropod communities and the ecosystem processes they provide (but see Collins et al., 2002). The objective of this study was to investigate how the management strategies of one AES, the Wisconsin Healthy Grown® potato program, influences granivorous ground beetle communities and post-dispersal weed seed predation within the crop itself as well as in the adjacent perennial habitat managed for conservation purposes. Weed pressure is a serious and expensive problem for farmers, requiring greater inputs annually than the control of insect pests (Marshall et al., 2003). Post-dispersal weed seed predation by arthropods can have a significant influence on weed populations in agroecosystems (O’Rourke et al., 2006). Specifically, ground beetles (Coleoptera: Carabidae) have been shown to be effective and important seed predators in agricultural habitats (Holland, 2002; Honek et al., 2006). Thus, by adopting management practices that enhance ground beetle populations in crop fields, farmers may be able to reduce their herbicide inputs as a result of the ecosystem services provided by these beetles.
In this study we examined if perennial non-crop habitats associated with an AES increase the diversity and abundance of ground beetle seed predators. We then measured how seed predation by small (<1.25 cm) and large (>1.25 cm) predators varied as a function of location (within potato fields versus in the adjacent non-crop habitat) and the type of non-crop habitat adjacent to the potato field, including oak savanna, grassy field margins, and oak woodland. These habitats are targets of conservation under the Healthy Grown® AES and are common in the Wisconsin potato agroecosystem (Werlinger and Gratton, 2008; Zedler et al., 2009). Previous studies have shown that beneficial insect communities are enhanced by the presence of perennial habitat (Bianchi et al., 2006), insects move between crop and non-crop habitats (Wratten et al., 2003), and a more diverse beetle assemblage should be able to consume a more diverse selection of seeds (Menalled et al., 2001). Therefore, we hypothesized that (1) the abundance and diversity of ground beetles would be greater in perennial non-crop habitats than within potato fields, (2) post-dispersal weed seed predation would be greater in perennial non-crop habitats than within potato fields, and (3) seed predation and ground beetle diversity would be positively correlated as a more diverse assemblage of beetles will be more functionally diverse, resulting in overall greater predation.

2. Materials and methods

2.1. Study system and design

This study was conducted in Adams County in central Wisconsin, USA (43.86, −89.73) on commercial potato farms participating in the Wisconsin Healthy Grown® program. The Healthy Grown® program is a third party certified eco-label focused on whole farm management (Zedler et al., 2009). Whole farm management includes requirements for crop management as well as non-crop habitat management. Within the crop field this includes the use of reduced toxicity chemicals and the overall reduction of chemical applications. Non-crop habitat management includes the restoration of native, perennial habitat such as oak savanna and prairie within the farm landscape (Sexson, 2006), typically adjacent to the crop field. In return for producing an environmentally friendly product, farmers hope to receive a premium price for their potatoes in the market.

We selected 15 fields (sites), each of which consisted of an irrigated potato field and the perennial non-crop habitat immediately adjacent to the field. Potato fields ranged from 20 to 79 ha (mean 36.1 ± 4.9) and non-crop habitats ranged from 0.9 to 87 ha (mean 12.2 ± 6.0). The non-crop habitats included (1) unmanaged oak woodland, (2) restored/managed oak savanna, and (3) grassy field margins (n = 15 fields, 5 of each potato/non-crop combination). Oak woodland (unmanaged) and grassy field margins (regularly mowed) are common habitats in central Wisconsin and oak savanna, which is actively managed through thinning and burning, is a conservation target under the ecosystem component of the Wisconsin Healthy Grown® program. The vegetation of non-crop habitats was surveyed by Nye (2008). Oak woodland and oak savanna sites were dominated by Hill’s oak (Quercus ellipsoidalis) and black oak (Quercus velutina). Oak woodlands were characterized by a relatively dense canopy (>70%) and low dominance of exotic plant species in the understory. Grassly field margins were mainly dominated by exotic grass and forb species, although some sites were planted with alfalfa (Medicago sativa) as a forage crop. A single transect was established running 50 m into the crop field and 50 m into the non-crop habitat. Four by eight meter plots were set along this transect at 10 and 50 m from the edge into the potato field and non-crop habitat with the longer axis parallel to the crop/non-crop interface.

2.2. Ground beetle abundance and diversity

To measure ground beetle abundance and diversity we sampled the community using pitfall traps consisting of two nested plastic cups (∼0.5 L) set into the ground and filled with 100 mL of 0.4% propylene glycol. The upper cup was replaced each collection round. The lower cup was left in the ground over the entire field season and covered with a Petri dish to prevent capture during non-trapping weeks. In order to prevent vertebrate disturbance/accidental capture each trap was covered with 1.25-cm hardware cloth held down with plastic garden stakes and metal bolts. Plastic covers (30 cm diameter) were staked 10 cm above the traps to prevent rainfall and irrigation water from entering the cups. Within each plot, 3 pitfall traps were left open for 1-week intervals four times over the growing season from June 11–20, July 2–9, July 23–30, and August 13–20, 2007. Upon collection, samples from each individual plot were combined into a single vial of alcohol, resulting in a single sample per plot per sampling round (n = 60 samples). For the final statistical analysis the 10 and 50 m plots were combined so that the sample unit was location (crop or non-crop habitat) within site (n = 30). Ground beetles were identified to species using Laroche and Lariviere (2003), Lindroth (1961, 1963, 1966, 1968, 1969), and verified by a specialist. Voucher specimens were deposited at the University of Wisconsin Insect Research Collection in Madison, WI. Based on a search of the literature, each species was designated as seed-eaters or non-seed-eaters (Forbes, 1883; Goldschmidt and Toft, 1997; Holland, 2002; Honek et al., 2003; Honek and Jarosik, 2000; Honek and Martinkova, 2001; Laroche, 1990; Lindroth, 1961, 1963, 1966, 1968, 1969) and only designated seed-eaters (hereafter “ground beetles” or “beetles”) were used for further analyses presented in this paper (Appendix A). Abundance was calculated as the sum of all specimens collected over the four sample rounds in each plot. We used Simpson’s D (1 − Σpi2), where pi is the proportion of the abundance of a sample comprised of species i as an index of species diversity. Simpson’s D, unlike species richness and the Shannon’s H’, is not influenced by the abundance of organisms and is thus useful when comparing samples from habitats that vary in species abundance (Lande et al., 2000).

2.3. Post-dispersal weed seed predation

In order to measure rates of seed predation, we set seed cards in each of four plots at our 15 sites adapting the methods of O'Rourke et al. (2006). Seed cards were made from 7 cm × 7 cm cards of sandpaper (3M™ 80 grit aluminum oxide) and transported to the field in coin envelopes. Fifty seeds of a single weed species were attached to each card using a fine layer of glue (Elmer’s® Glue-All™ Multi-Purpose Glue). Four weed species including Setaria faberi (giants foxtail), Ambrosia trifida (giant ragweed), Abutilon theophrasti (velvetleaf), and Amaranthus retroflexus (pigweed) were used. These species are common in our study area and are of economic importance (Jed Colquhoun, pers. comm.). They also represent a diversity of seed shape and size, from 1 mm (pigweed) to 2 mm (giant foxtail) to 3 mm (velvetleaf) to 10 mm (ragweed), which allowed us to examine seed predation over a range of weed seed size diversity. Since seed preference varies by beetle size (Honek et al., 2007) we expected that different beetles would eat different seeds.

Seed cards were constructed for each species (n = 3 cards/spp × 4 spp × 4 plots/site × 15 sites × 4 sample rounds = 2880 cards total). Seed cards of each species at all plots were assigned to three treatments: (1) open, (2) closed, and (3) large-predator enclosure. “Open” cards were staked to the ground under an elevated plastic cover. This treatment allowed open access to the seeds by all seed predators (large and small). “Closed” cards were enclosed in a 1-mm cloth mesh bag and then covered with a 1.25-cm hardware cloth cage. This treatment accounted for random seed loss in the...
absence of predators associated with handling and transport of seed cards. Cards in the final treatment, “large-predator enclosure”, were placed under 1.25-cm hardware cloth cages to measure predation by small predators only (<1.25 cm, i.e., ground beetles). This enclosure allowed beetles and other small predators to access the seed cards but prevented larger seed predators from eating the seeds. The number of seeds on each card was counted before and after field exposure. All beetles sampled in this study were small enough to fit through the 1.25-cm wire mesh cages as each pitfall trap was covered with a piece of this same mesh. Larger seed-eating ground beetle species are not known to be present in our study system (Werling, 2009). We left the cards in the field for 1-week intervals repeated four times over the growing season from June 11–20, July 2–9, July 23–30, and August 13–20, 2007.

Proportion of seed survivorship was calculated by dividing the number of seeds predated (initial count corrected for non-predation losses – post-exposure seed count) by the initial seed count on each card (corrected for non-predation losses as estimated from the closed control cards, using the overall average for the entire experiment of ~1%). Daily seed survivorship was calculated as the geometric mean (total survivorship = d, where d is total days of field exposure). Daily seed disappearance was then calculated as 1-daily survivorship. For cards in the large-predator enclosure treatment, this correction results in predation attributable to small predators only. To estimate predation by large predators only, daily seed disappearance on the open seed cards (which represents predation by both large and small predators) was corrected by subtracting daily seed disappearance from the large-predator enclosure cards on a plot by plot basis. Daily seed predation rate by small predators (x) was log10(x + 0.001) transformed to normalize variances. To examine if there were differences in the mean and variance of seed size taken in different habitats by different predator groups, we calculated the average seed size taken in each sampling location by summing the total number of seeds of each species multiplied by the average seed size for that species and finally dividing this by total seeds taken at a site. Average seed size taken was calculated separately for small predators (under the “large predator” excluders) and for large predators (as the difference between “open cages” and “large predator” excluders).

2.4. Statistical analyses

To examine differences in beetle abundance and diversity across habitat (i.e., grassy field margin, oak savanna restoration and oak woodland) and location (i.e., crop versus non-crop) we used a 2-way mixed model ANOVA with site as a random variable and, for analysis of predation by small predators, we also included weed species as a random variable. For all analyses seed predation data were averaged over the four collection dates and, for large predators, data were also averaged over the four species of weed seeds. The relationship between predation by small predators and ground beetle abundance and diversity was examined by analysis of covariance (ANCOVA) with crop/non-crop as a covariate. A homogeneous slope model was used as there were no statistical differences in the slope between crop and non-crop (location × abundance F1,19 = 0.012, p = 0.915, location × diversity F1,24 = 2.06, p = 0.164). Comparisons of crop and non-crop across habitat types were done using a priori planned contrasts. Differences in average seed size taken in crop and non-crop habitats by small and large predators were tested by ANOVA. All ANOVA and ANCOVA were performed in JMP 8.0.1 (SAS Institute, 2009). Simpson’s D was calculated using Primer 6.1.5 (Clarke and Warwick, 2001).

3. Results

3.1. Ground beetle abundance and diversity

We collected a total of 1689 specimens of seed-eating ground beetles representing 62 species (Appendix A). Overall the most abundant species collected were Synuchus impunctatus (n = 720), Amara convexa (n = 110), Harpalus pensylvanicus (n = 107), and Agonum placidum (n = 96). The most abundant species in the potato fields was A. placidum. In non-crop habitat types the most common species were Anisodactylus rusticus (grassy field margins), and S. impunctatus (oak woodland and oak savanna).

Ground beetle abundance was greater in perennial non-crop habitat than within potato fields (location, F1,12 = 32.3, p < 0.001, Fig. 1). Beetle abundance did not vary by habitat type (habit, F2,12 = 1.99, p = 0.18), and there was no interaction with location (location × habitat, F2,12 = 0.36, p = 0.70, Fig. 1). Species diversity was on average greater within the potato field than in the non-crop habitat (location, F1,12 = 1.10, p = 0.006, Fig. 2) but this pattern varied by habitat type (location × habitat, F2,12 = 15.9, p < 0.001, Fig. 2); the crop/non-crop difference was most evident at oak woodland sites but not at oak savanna or grassy field margin sites (Fig. 2).

Beele assemblages were distinct among potato fields, grassy field margins, and wooded habitats (ANOSIM, Global R = 0.724, p = 0.001, Fig. 3). Assemblages were most similar between oak woodland and oak savanna sites (R = 0.312, p = 0.05). This similarity was partly due to the presence of one very abundant species (S. impunctatus) in both habitats, but even when this species was
Table 1
Most abundant species (>90% of total abundance) collected by habitat type (top 10 species, highlighted in gray). Aside from oak savanna and oak woodland sites, very few species overlap across habitat types, consistent with the differences seen in Fig. 3.

<table>
<thead>
<tr>
<th>Species</th>
<th>Oak savanna</th>
<th>Oak woodland</th>
<th>Grassy field margin</th>
<th>Potato</th>
</tr>
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<tr>
<td>Synuchus impunctatus</td>
<td>166</td>
<td>551</td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Cyclothetales sodalis sodalis</td>
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<td>1</td>
<td></td>
<td>3</td>
</tr>
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<td>Pterostichus mutus</td>
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<td>2</td>
<td></td>
<td>3</td>
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<td>Harpalus providens</td>
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<td></td>
<td>1</td>
</tr>
<tr>
<td>Amara angustatoides</td>
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<td></td>
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<tr>
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<td>Amara oltosa</td>
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<td>5</td>
<td>3</td>
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<td>5</td>
<td>2</td>
<td>1</td>
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<td>2</td>
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<td>Harpalus compar</td>
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<tr>
<td>Poecilus chalotes</td>
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Fig. 1. Average abundance (number of beetles/plot over course of season) of granivorous carabids (+SE) in potato fields and adjacent non-crop habitats. Significance levels, determined by a priori contrasts are indicated by *(p < 0.05), ***(p < 0.01), and ****(p < 0.001). Abundance was greater in the non-crop habitats than within the potato fields (crop).

Fig. 2. Average diversity (1-Simpson’s D) of granivorous carabids (+SE) in potato fields and adjacent non-crop habitats. Significance levels, determined by a priori contrasts are indicated by ***(p < 0.01), ****(p < 0.001), and NS (p > 0.05). On average, diversity was greater within the potato field (crop) than in the non-crop habitat, although this difference varied by adjacent habitat type (location × habitat, p < 0.001).
Fig. 3. Non-metric multidimensional scaling (MDS) plot of between site resemblance (Bray-Curtis, square root-transformed beetle abundance). The distance between points (sites) within the plot is proportional to the degree of similarity between ground beetle assemblages at each site (closer points have more similar beetle assemblages than points further apart). The stress index is a measure of fit between the between site resemblance and the two-dimensional representation of the similarity matrix (<0.10 excellent fit, Clarke and Warwick, 2001).

Fig. 4. Mean predation (mean proportion seeds predated per day + SE) by small predators in potato fields and adjacent non-crop habitats. Significance levels, determined by a priori contrasts are indicated by *(p < 0.05), ***(p < 0.01), ****(p < 0.001), and NS (p > 0.05). On average, seed predation was greater in the non-crop habitat than within the potato field, although this difference varied by adjacent habitat type (location × habitat, p < 0.05).

Fig. 5. Seed predation by small predators (log10(proportion seeds predated per day)) versus (a) beetle abundance and (b) beetle diversity. When the effect of location (crop/non-crop) was included in the model, predation was not associated with beetle abundance but was positively associated with beetle diversity.

removed from the analysis these two habitats were still more similar to each other (R = 0.45, p = 0.03) than any other pairwise comparison between habitats. Of the top ten most abundant species from each habitat, five overlap between oak savanna and oak woodland, only two between oak savanna and potato field, oak woodland and potato field, grassy field margin and potato field, only one between grassy field margin and oak savanna, and none between grassy field margin and oak woodland (Table 1).

3.2. Post-dispersal weed seed predation

Seed predation by small predators (i.e., ground beetles) was on average greater in the perennial non-crop habitat than within the potato fields (location, F1,18 = 14.4, p = 0.001, Fig. 4) but this pattern varied as a function of habitat type (location × habitat, F2,18 = 4.37, p = 0.02, Fig. 4); the crop/non-crop difference was evident at oak savanna and grassy margin sites but not at oak woodland sites (Fig. 4). There was no difference in the average seed size taken in crop and off crop habitats for either small predators (location, F1,12 = 0.21, p = 0.66) or large predators (F1,12 = 1.17, p = 0.30). The average seed size taken by small predators was 3.26 ± 0.32 mm (mean ± SEM, n = 30) which was significantly smaller than the
initial seed size available \((4 \text{ mm}, \bar{z}_{20} = -2.27, p = 0.03)\) while the average seed size taken by large predators was \(4.47 \pm 0.20 \text{ mm}\) \((\text{mean} \pm \text{SEM}, n = 30)\) and significantly larger than the initial seed size available \((4 \text{ mm}, \bar{z}_{20} = 2.37, p = 0.02)\).

There is a positive relationship \((R^2 = 0.23, p < 0.0001)\) between seed predation by small predators and beetle abundance \((\text{Fig. 5a})\). However, this relationship is entirely explained by the variation in beetle abundance between crop and non-crop habitat \((\text{Fig. 1})\). When location \((\text{crop}/\text{non-crop})\) was taken into account, seed predation by small predators was not associated with beetle abundance \((\text{ANCOVA}, \text{abundance}, F_{1,27} = 0.203, p = 0.66, \text{Fig. 5a})\) because abundance is always high in the non-crop and always low within the potato field. In contrast, predation increases with diversity in both the perennial non-crop habitat and potato fields \((\text{ANCOVA}, \text{location}, F_{1,27} = 50.8, p = 0.0001, \text{diversity: } F_{1,27} = 8.71, p = 0.0065, \text{Fig. 5b})\).

Seed predation by large predators was on average greater in the crop fields than in the non-crop habitats \((\text{location, } F_{1,12} = 19.9, p < 0.001, \text{Fig. 6a})\). Predation did not vary by habitat type \((\text{habitat, } F_{2,12} = 3.20, p = 0.08)\) or by location \((\text{crop}/\text{non-crop})\) as a function of habitat type \((\text{location} \times \text{habitat, } F_{2,12} = 2.07, p = 0.169, \text{Fig. 6b})\). Overall, predation by large predators was on average six times greater than predation by small predators in both the potato fields and the non-crop habitat.

### 4. Discussion

Conservation of non-crop habitats in agroecosystems is implemented in the anticipation that it will enhance biodiversity and ecosystem services. This study found that non-crop habitats in the Wisconsin potato agroecosystem have a greater abundance of seed-eating ground beetles and experience a higher rate of weed seed predation than potato fields. Beetle community assemblages were different between crop and non-crop habitats and between wooded non-crop habitats \((\text{oak woodland and oak savanna})\) and open non-crop habitats \((\text{grassy field margin})\). Beetle diversity, however, as indexed by Simpson’s \(D\), was greater within potato fields than in non-crop habitats. Although there was a positive relationship between beetle diversity and seed predation in both crop and non-crop habitats, beetle diversity was on average greater in the crop habitat where lower average predation was observed. These results suggest that diversity per se plays a less important role in provisioning this ecosystem service than does species composition or possibly the functional diversity of species \((\text{Straub and Snyder, 2006})\).

The clearest pattern that emerged from this study was the difference in beetle assemblage between crop and non-crop habitats. Beetle abundance was on average 6 times greater in non-crop habitats than within-crop fields \((\text{Fig. 1})\). The obvious explanation for the low abundance of beetles in the crop is that crop fields are highly disturbed habitats with low plant diversity, frequent cultivation, and occasional pesticide application, creating an inhospitable habitat for the establishment of stable beetle communities. In contrast, perennial habitat has greater plant structure and diversity and provides temporarily stable resources, allowing beetle communities to become established over time \((\text{Bianchi et al., 2006})\).

The crop/non-crop contrast is consistent with previous research investigating beneficial insects in agroecosystems \((\text{Pollard and Holland, 2006; Tsitsilas et al., 2006})\) and seed-eating ground beetles in particular \((\text{Menalled et al., 2001})\). While some of the non-crop habitats \((\text{e.g., grassy field margin and oak savanna})\) do experience varying levels of routine disturbance through mowing or prescribed burns \((\text{Zedler et al., 2009})\), the difference in frequency and intensity of disturbance with annually cultivated crop fields likely dictates the ability of beetle communities to persist.

These major differences between crop and non-crop habitats likely contribute to differences in beetle diversity. The Simpson’s index is sensitive to species dominance so an assemblage with an even distribution of individuals across species will have a higher \(D\) than an assemblage with a high abundance of a few common species and a low abundance of other species \((\text{Lande et al., 2000})\). On average, potato fields have a low abundance of many species resulting in a higher diversity index \((\text{greater evenness})\), compared to non-crop habitats which, on average, have a high abundance of a few common species and a low abundance of many rare species \((\text{greater dominance})\). Yet, overall species richness in non-crop habitats \((53 \text{ spp.})\) was higher than in the potato \((30 \text{ spp.})\), suggesting that beetle communities in the non-crop habitat have more species. Frequent agricultural disturbance may prevent species from ever becoming too common in potato fields resulting in relatively even \((\text{diverse})\) assemblages compared to non-crop habitats that become dominated by one or two species \((\text{e.g., S. impunctatus})\).

Another pattern that emerged from this study was the positive relationship between seed predation and beetle diversity. As diversity increased, seed predation increased. Since species assemblages are virtually non-overlapping between crop and non-crop habitats \((\text{Table 1 and Fig. 3})\), we suggest that these differences in species composition are associated with the differences in predation rates as well. Moreover, species assemblages found in non-crop habitats could be more functionally diverse \((\text{a feature not captured by the Simpson’s index})\), resulting in a higher level of seed predation. Functional diversity is a measure of the functional roles represented within a community, as compared to diversity per se which is the number of \((\text{potentially functionally redundant})\) species present. Previous research has shown the benefits of species identity and functional diversity in the provisioning of ecosystem services \((\text{Hoehn et al., 2008; Klein et al., 2003; Straub and Snyder, 2006})\). A more functionally diverse community will have a greater ability to perform diverse services.

In this study, seeds representing a diverse array of shape and size were used so as to allow the effects of predator diversity to be assayed. The lower predation rates observed in the crop may imply that the beetle assemblages present may be functionally less diverse, resulting in reduced capacity to effectively exploit the resources available. Yet the nature of potential functional differences between invertebrate consumers is not well understood. Our findings show that small predators on average consume seeds smaller \((3.26 \text{ mm})\) than presented on seed cards \((4 \text{ mm})\) and large predators are biased towards larger seeds \((4.47 \text{ mm})\). However, differences in mean seed size consumed do not vary as a function of location at a site. That is, invertebrate and vertebrate selection of
seed size is relatively consistent in both crop and non-crop areas at a site even though the intensity of predation is not. Thus, functional differences between assemblages of predators may be influenced by factors such as the rate of foraging in different habitats, and not necessarily on the ability to consume a seed.

This study shows that ground beetles play an important role in post-dispersal seed predation, an underlying mechanism of weed control (Heggenstaller et al., 2006), but their regulating services may only be realized in the non-crop habitat. This result is somewhat inconsistent with other studies which found that seed predation by invertebrates could be high within-crop fields (Honek et al., 2006; O’Rourke et al., 2006; Westerman et al., 2003). When predation rates by small predators are scaled up, our study found on average ∼1000 seeds/m²/day were consumed in the non-crop habitats, but only ∼200 seeds/m²/day were consumed within the potato field. Honek et al. (2003) found rates of 1000 seeds/m²/day consumed within annual crop fields which was positively correlated to beetle activity density. O’Rourke et al. (2006) found that within field seed predation rates varied depending on the crop type, suggesting that differences in crop plant structure and management practices (e.g., till versus no-till agriculture) influence invertebrate activity density and predation services. This suggests that shifting towards management strategies that cause less disturbance within the field might help increase populations of beneficial insects and the services they provide.

In addition to small predators, large predators may also be important seed-eaters. The experimental design used in this study allowed us to separate the effects of large versus small predators. Predation of seeds by large consumers (>1.25 cm) was significantly higher than small consumers and was higher within the crop field than in the non-crop habitat. Though we are not certain of the identity of large predators in this study, it is likely that they are mostly vertebrates (rodents) based on indirect visual evidence of rodent feces, chew marks, and a nest, and the fact that large seed-feeding invertebrates are not present in these habitats (Werling and Matt Ziehr. We thank the potato growers who allowed us to conduct research on their farms. Jed Colquhoun and Ed Luschei provided seeds for the predation study. We thank Paul Zedler and Randy Jackson for reading and commenting on earlier drafts. Peter Messer provided beetle identification and verification. Funding was provided by US Department of Agriculture National Research Initiatives grant number 2005-55101-16238 and UW Hatch grants to CG (WIS#04956 and 01415).

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.agee.2010.03.003.

References

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