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Increased area of a highly suitable host crop increases herbivore pressure in intensified agricultural landscapes

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Abstract
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Keywords
Agricultural intensification, Landscape simplification, Crop pest, Conservation biological control, Ecosystem services

Disciplines
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Comments
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Increased area of a highly suitable host crop increases herbivore pressure in intensified agricultural landscapes

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ABSTRACT

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1. Introduction

The conversion of natural habitats for agricultural use leads to dramatic changes to landscape structure impacting both natural and agricultural biota and ecosystems (Matson et al., 1997; Sala et al., 2000; Tilman et al., 2001; Foley et al., 2005). As agricultural expansion/intensification progresses, landscape complexity declines, culminating in highly simplified systems with very little natural or semi-natural habitat and domination by a small number of crop species (Matson et al., 1997; Tilman et al., 2001; Tscharntke et al., 2005). Landscape simplification, and in particular the loss of natural and semi-natural habitats, has been found to negatively affect the diversity and abundance of beneficial natural enemies in agricultural fields (see reviews in Landis et al., 2000; Bianchi et al., 2006; Chaplin-Kramer et al., 2011). The loss of natural enemies can in turn result in the disruption of the biological control of important crop pests (Landis et al., 2000; Bianchi et al., 2006; Chaplin-Kramer et al., 2011), potentially compromising the sustainability of agricultural systems (Tscharntke et al., 2005). Studies on landscape simplification have most often focused on impacts on natural-enemy communities (Bianchi et al., 2006; Chaplin-Kramer et al., 2011). When studies quantify pest abundance, a common assumption is that any difference in pest density across landscapes is the indirect result of a change in the impact of natural enemies.

However, pest herbivores can also respond directly to landscape changes associated with landscape simplification. For example, populations of pest species that alternate between different host plant species during a season may increase on crop hosts if the alternate host found in natural or semi-natural habitats increases in abundance. Under these conditions, pest density can be higher in complex versus simplified landscapes. Examples include studies showing increased colonization or abundance of host-alternating aphids (cereal aphids in wheat and soybean aphid in soybean) in crops embedded in complex landscapes containing higher densities
of alternative host plants (Thies et al., 2005; Bahai et al., 2010; Ragsdale et al., 2011), and higher abundance of generalist herbivores in alfalfa fields in more diverse landscapes (Jensen and Fahrig, 1997). Alternatively, a small but growing number of studies have shown that landscape simplification may drive increases in pest populations as a result of associated increases in the area of a suitable crop at the landscape scale (reviewed in Veres et al., 2013). This aligns with both theoretical and empirical work suggesting that herbivore incidence, abundance, and density tend to increase with increases in the area or connectivity of their host plant populations (Hanski. 1998; Connors et al., 2000; van Nouhuys, 2005). Examples from agricultural systems include studies showing that increasing landscape area or connectivity of a preferred crop increased the incidence and abundance of northern and western corn rootworms (Diabrotica virgifera and Diabrotica barberi) in corn (Beckler et al., 2004; O’Rourke et al., 2011) and the abundance of lygus in cotton (Carriere et al., 2012).

Clearly, landscape structure can influence both pest and enemy diversity and abundance within agricultural systems suggesting that effective pest management requires a landscape perspective (Tscharnkte et al., 2007). Indeed, advanced Integrated Pest Management (IPM) systems that consider habitat manipulation and biological controls with a regional orientation, offer more durable solutions for individual farmers and society (Brewer and Goodell, 2012). However, as outlined above, responses to landscape structure are often complex and system dependent such that effective management requires detailed understanding of the responses of the target species or functional groups involved to various aspects of landscape change and simplification (Tscharrntke et al., 2005, 2007). Furthermore, even within a given agroecosystem, landscape effects may vary regionally as cropping patterns, abiotic conditions or biological communities change (O’Rourke et al., 2011; Thies et al., 2011), yet cross-regional assessments of the importance of landscape composition for pest versus enemy dynamics remain uncommon.

We used a large-scale stratified sampling approach to examine the influence of two components of landscape simplification (declining cover of the dominant natural/semi-natural habitat, grassland, and increasing cover of a highly suitable focal crop, wheat) on variation in infestation by a dominant pest of wheat (Cephus cinctus Norton; Hymenoptera: Cephidae), as well as parasitism of this pest by its dominant natural enemies (the parasitoid wasps Bracon cephi (Gahan) and B. lissogaster Muesebeck; Hymenoptera: Braconidae) across six regions in the northern Great Plains of North America. C. cinctus is the most important pest of wheat in the northern Great Plains (Morrill and Kushnak, 1996; Shanower and Waters, 2006), with economic losses estimated at 250–350 million USD per year (Beres et al., 2011b; Fulbright et al., 2011). Damage to wheat occurs because larvae feed by mining internally within the stem and cause stem lodging when feeding is complete and the larva prepares for overwintering and dia-pause by girdling (cutting) the stem base to form a protected chamber near the soil surface. Area-wide or landscape-level management approaches may improve management of C. cinctus, which has proven recalcitrant to classical small-scale pest management approaches focused on sampling, decision-making and control tactics applied to individual fields.

The presence of C. cinctus in grass species commonly found in natural and semi-natural grassland habitats e.g., in rangelands and restored grassland in set aside programs such as the United States Department of Agriculture’s (USDA) Conservation Reserve Program, has also long been documented (Ainslie, 1920; Cridde, 1922; Youtie and Johnson, 1988). Indeed, C. cinctus is thought to have evolved in native grasslands, where it prefers large-stemmed native wheat and rye grasses, and then spread into wheat crops as large areas of grassland were converted by European settlers to cropland, especially wheat (Cridde, 1915, 1922; Morrill and Kushnak, 1996). Wheat is highly suitable host for C. cinctus due to its larger stem diameter, compared with many small–stemmed native grasses (Cridde, 1922; Ainslie, 1929; Perez-Mendoza et al., 2006). C. cinctus is also known to attack many introduced weedy and forage grasses (Cridde, 1915; Farstad, 1940; Perez-Mendoza et al., 2006). Adult C. cinctus are relatively weak fliers, and generally oviposit in the nearest suitable host stem, but can move up to 800 m if suitable oviposition sites are not present at sites where adults eclose (Cridde, 1922). Oviposition preference can be influenced by a number of factors including plant developmental stage, stem diameter and plant volatiles (Ainslie, 1920; Holmes and Peterson, 1960; Buteler and Weaver, 2012).

Two native parasitoid wasps, B. cephi (Gahan) and Bracon lissogaster Muesebeck (Hymenoptera: Braconidae) attack C. cinctus (Morrill et al., 1998). In wheat crops, these two species represent the only important insect natural enemies of C. cinctus, with B. cephi generally dominating (Runyon et al., 2002). These beneficial enemies can reach high densities and reduce economic damage by C. cinctus (Morrill et al., 1998; Buteler et al., 2008), but populations are highly variable across wheat fields and regions (Shanower and Waters, 2006) and causes of their population fluctuations are not well understood. The only documented host of the braconid parasitoids is C. cinctus, which is attacked during the larval stage regardless of whether host plants are crop or non-crop grasses.

Natural and semi-natural habitat often provide important resources for natural enemies including nectar, alternative hosts, and refuges from disturbance (see reviews in Landsis et al., 2000; Bianchi et al., 2006; Chaplin-Kramer et al., 2011). Grassland provision of alternative hosts and refuges from disturbance may be particularly important for the parasitoids in our study system. Early maturation of wheat due to warm dry conditions is thought to negatively influence B. cephi, which is bivoltine, by preventing it from completing its second generation before wheat is harvested (Holmes et al., 1963). Thus, later maturing grasses, which are also attacked by C. cinctus, could serve as important refuges for B. cephi under such conditions (Cridde, 1922, 1924). In contrast, its host C. cinctus is univoltine, and thus better synchronized with wheat growth and development. Furthermore, parasitoids, tend to over-winter at a higher location within wheat stems where they initially attack larvae, and thus are potentially negatively influenced by cutting and threshing operations during harvest (Beres et al., 2011a). In contrast, unparasitized C. cinctus larvae move to the base of the stem after feeding is complete, overwintering just above the root crown, in either wheat or grasses, where they largely escape the disturbance caused by harvest or mowing. Thus, natural and semi-natural grassland habitats may serve as important sources of either C. cinctus or its natural enemies moving into wheat. However, based on differences in natural history between the two trophic levels, we predicted the positive influence of grassland habitat would be greater for the parasitoids, which are more susceptible to the lack of available hosts in wheat associated with early maturation as well as increased disturbance–related mortality in crops, compared with their herbivorous hosts. In contrast, we expected that C. cinctus may benefit equally, or even more, from increased cover of a suitable host crop, wheat, compared with grassland, due to higher resource availability (e.g., stem density) within crops.

2. Materials and methods

2.1. Sampling design

We sampled C. cinctus and its natural enemies across the major wheat growing regions where it has been historically most prevalent and economically damaging in the USA (Fulbright et al., 2011). In total we sampled 127 fields (77 spring and durum wheat and
50 winter wheat) spanning six regions across three states, Montana (MT), North Dakota (ND) and South Dakota (SD) (Fig. 1). Our study regions were defined based on the United States Environmental Protection Agency’s (EPA) Level IV ecoregional classifications for the contiguous United States (US Environmental Protection Agency, 2013). For the larger ecoregions, a defined study region encompassed the entire EPA level IV classification (e.g., region 1 = EPA ecoregion 42o, North Central Brown Glaciated Plains; region 4 = EPA ecoregion 43a, Missouri Plateau). In other cases, smaller contiguous ecoregional areas with similar cropping systems were merged (region 2 = EPA regions 42l, j and k; region 3 = EPA ecoregion 46d, g, h, i, and j; region 5 = EPA ecoregions 42a, b, c; Region 6 = EPA ecoregions 42f, 43f).

Sampled wheat fields (sites) were selected to represent a gradient in landscape complexity within each region (based on the USDA-National Agricultural Statistics Service Cropland Data Layer, see Section 2.3) from those with a high proportion of natural habitat cover (grassland) to those dominated by annual cropping systems (Table 1). Additional criteria were that sites were a minimum of 10 km apart, and accessible by four-wheel drive vehicle. We aimed to sample 10 or more fields per region with those with either more wheat cover, or a greater total area, sampled more intensively (Fig. 1, Table 1). Samples collected from three sites in region six were not processed due to loss or damage during storage.

In each study field, we collected wheat stems along a 90 m transect, starting at the center point along a field edge and working towards the field center. Approximately 20 wheat stems were collected every 10 m along this transect (total of 200 stems sampled per field). This has been found to be an adequate sample size for quantifying infestation and parasitism, even at relatively low population densities (Cárcamo et al., 2007). Wheat was sampled as close to harvest as possible from July 22 to August 18, 2010, starting with the western-most sites where wheat matures earliest and moving east. The growth stage (i.e., zedos stage (Zadoks et al., 1974)) of

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**Fig. 1.** Map of sampled wheat fields across six regions and three states, Montana (MT), North Dakota (ND) and South Dakota (SD), in the north-central USA. Points representing sampled fields are scaled by the percent infestation of wheat stems by *C. cinctus* (top panel) and parasitism of this pest by native parasitoid wasps (bottom panel).
wheat in sampled fields did not significantly differ across regions ($F_{5,121} = 1.80, P = 0.1184$). Collected wheat stems were placed into perforated plastic sleeves for protection and brought back to the laboratory where they were removed from sleeves and stored until processed. In total we processed samples from 127 fields (77 spring and durum wheat; 50 winter wheat) spanning six regions (Table 1).

### 2.2. Sample processing

To quantify the presence of *C. cinctus* and its parasitoids, sampled stems were dissected lengthwise. Evidence of *C. cinctus* presence within a stem included the presence of characteristic frass left behind by feeding larvae or direct observation of larvae (dead or alive). Evidence of *Bracon* spp. parasitoids included parasitoid larvae feeding externally on the sawfly larva or the presence of characteristic parasitoid cocoons and/or exit holes within the stems. Because the two *Bracon* species are difficult to distinguish morphologically in the larval and pupal phases (Runyon et al., 2001), they were not distinguished in sample counts.

Wheat stem sawfly infestation levels were calculated by dividing the number of sawfly-infested stems (i.e., those containing any evidence of larvae) by the total number of stems sampled per field. Parasitism was calculated as the number of stems that contained evidence of parasitoids divided by the total number of *C. cinctus* infested stems per site, and was calculated only for sites where *C. cinctus* was present. The wheat type, spring wheat or winter wheat (*Triticum aestivum* L.) or durum wheat (*Triticum durum* Desf.), and whether wheat stems were solid (the trait associated with resistance to the *C. cinctus* (Berzonsky et al., 2003)) or hollow, was also noted for each field. Few durum wheat fields were sampled ($n = 18$ fields across three regions) and infestation and parasitism values for these fields did not significantly differ from those in spring wheat within regions where durum occurred ($P > 0.1$ in all cases), thus these types were combined for analysis.

### 2.3. Quantifying landscape structure

The latitude and longitude of each sampled wheat field were recorded using a handheld GPS unit (Garmin® GPS V). Coordinates were then imported into an ArcGIS 10.1 (ESRI, 2010) database and mapped using ArcMap. A grid layer containing 2010 land cover data (USDA, National Agricultural Statistics Service Cropland Data Layer 2010; http://nassgeodata.gmu.edu/CropScape/) was added to the ArcGIS data base. Land cover was extracted in buffers surrounding each field at radii of 250 m, 5 km, and 20 km (local, landscape and regional scales respectively). The 250 m buffer was chosen to capture variation at the local field level (typical crop fields range from 200 to 1600 m in width). The 5000 m buffer was chosen to reflect variation, above the individual field level, yet within the range of landscape response typical of flying insects (Chaplin-Kramer et al., 2011); initial analyses validated that this was the most predictive scale of landscape response in our system. Finally, the 20 km scale was chosen to reflect regional variation in land cover potentially influencing longer term buildup of insect populations. Within each buffer zone, the proportion of area in wheat (the preferred crop host of *C. cinctus*) and grassland (the dominant natural habitat in the northern Plains) was calculated for each sampling point, for local and landscape scales. Wheat habitat included three land cover classes (winter wheat, spring wheat and durum wheat). Grassland habitat was defined by the Grassland/herbaceous cover class which encompasses grass dominated habitats such as natural mixed grass prairie as well as semi-natural grasslands, such as those in the USDA Conservation Reserve Program, pastures and hay meadows. At the regional scale, there was some overlap in buffers surrounding individual sampling points, thus cumulative cover was calculated for all the area included in 20 km buffers for all sites within a given region.

### 2.4. Statistical analyses

Generalized linear models (binomial distribution, logit link) were run in JMP 10 (SAS Institute Inc., 1989–2013) to investigate the influence of region, wheat characteristics (wheat type and stem type, defined below), habitat composition and additional covariates on the proportion of *C. cinctus* infested wheat stems and proportion parasitism in focal wheat fields. Initial variables included in the model for *C. cinctus* infestation were: region, proportion grassland cover and proportion wheat cover at the local (250 m radius) and landscape (5 km radius) scales, wheat type (spring wheat or winter wheat), stem type (hollow or solid) and the interactions between the local and landscape composition variables and region. A similar initial model was run for parasitism, with the addition of host density (proportion of stems infested by *C. cinctus*) as a covariate in the initial model. Overdispersion tests and intervals were specified due to significant overdispersion in the data for both models (SAS Institute Inc., 2010). Full models were simplified to the best fit model by removing the least significant predictor variables until no further increases in model fit (i.e. reductions in corrected quasi-Akaaike information criterion values, qAICc) were observed. Contrasts were used to compare proportion infestation and parasitism among regions following an overall significant region effect in the main model (SAS Institute Inc., 2010).

Because region was a dominant factor in generalized linear models predicting both *C. cinctus* infestation, and its parasitism by native *Bracon* spp., we carried out further analyses to explore potential causes of this regional variation. Specifically, we explored correlations between major climatic and landscape composition variables

### Table 1

Summary of field types sampled, means of major climatic variables, ranges for local and landscape habitat composition variables (250 m and 5 km radius) and sum for regional habitat composition (20 km) variables across the six study regions.

<table>
<thead>
<tr>
<th>Region</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
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<tbody>
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<td>Number of fields</td>
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<td>28</td>
<td>28</td>
<td>28</td>
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<td>28</td>
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<tr>
<td>Winter wheat</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
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<tr>
<td>Spring wheat</td>
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<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
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<tr>
<td>Mean annual precipitation (cm)</td>
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<td>Mean annual maximum temperature (°C)</td>
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<td>Local % grassland cover (min–max)</td>
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<td>0–55.50</td>
<td>0–55.50</td>
<td>0–55.50</td>
<td>0–55.50</td>
<td>0–55.50</td>
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<tr>
<td>Local % wheat cover (min–max)</td>
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<td>14.05–92.69</td>
<td>14.05–92.69</td>
<td>14.05–92.69</td>
<td>14.05–92.69</td>
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<tr>
<td>Landscape % grassland cover (min–max)</td>
<td>6.30–68.38</td>
<td>6.30–68.38</td>
<td>6.30–68.38</td>
<td>6.30–68.38</td>
<td>6.30–68.38</td>
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<tr>
<td>Landscape % wheat cover (min–max)</td>
<td>12.28–52.90</td>
<td>12.28–52.90</td>
<td>12.28–52.90</td>
<td>12.28–52.90</td>
<td>12.28–52.90</td>
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</tr>
<tr>
<td>Regional % grassland cover (sum)</td>
<td>42.20</td>
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and C. cinctus infestation and parasitism across regions. Climatic variables included long-term averages (1981–2010) in precipitation and maximum temperature extracted for each sampling point based on maps obtained from the USDA-NRCS National Geospatial Data Gateway at http://datagateway.nrcs.usda.gov (Daly et al., 2002). We also calculated growing degree days for the period during which C. cinctus and parasitoids were developing or actively flying (March 1–July 31, 2010), using a 50 °F base, as this could have an important influence on emergence time and activity during oviposition. Values were extracted for each site based on modeled maps obtained from the US degree-day map calculator at http://uspest.org/cgi-bin/usmapmaker.pl (Coop, 2010). Regional means were calculated for all variables. The landscape composition variables were regional totals (pooled across all sites in a region) in proportional cover of grassland and wheat at the 20 km radius scale. We then calculated Pearson’s correlations between each of these environmental/landscape variables (precipitation, growing degree days, regional grassland and wheat cover) and regional means for both proportion C. cinctus infestation and proportion parasitism.

3. Results

Grassland prairie is the dominant natural habitat in the Northern Great Plains, and as such the proportion of grassland cover at a 5 km radius was highly positively correlated with total natural/semi-natural habitat cover ($r = 0.98, P < 0.0001$) the recommended metric for quantifying landscape complexity (Chaplin-Kramer et al., 2011). Since our study insects are restricted to feeding on grasses, the proportion of area in grassland is an appropriate measure of potential available natural habitat. As is often found in landscape studies, the amount of natural/semi-natural habitat (proportion grassland cover at the 5 km scale) was inversely correlated with the proportion of cultivated land (all crops, $r = −0.77, P < 0.0001$) as well as with the proportion of wheat ($r = −0.76, P < 0.0001$) in our study. Wheat and grassland cover were similarly inversely correlated at the local scale ($r = −0.57, P < 0.0001$). Local and landscape composition metrics were also somewhat correlated (proportion wheat cover at the 250 m and 5 km scales: $r = 0.35, P < 0.0001$; proportion grassland cover at the 250 m and 5 km scales: $r = 0.62, P < 0.0001$; proportion wheat 250 m with grassland 5 km: $r = −0.38, P < 0.0001$; proportion grassland 250 m with wheat 5 km: $r = −0.51, P < 0.0001$).

Although we found moderately strong correlations among some landscape variables, variance inflation factors (VIF) for each landscape predictor included in our initial statistical models were ≤5, well below the level (10) considered to be problematic from the perspective of multicollinearity (Montgomery et al., 2001).

Three significant predictor variables were retained in our best fit model for C. cinctus infestation: region, wheat type and proportion wheat cover (5 km radius). On the whole, winter wheat fields were attacked significantly more than spring wheat fields (Table 2; mean ± SE percent infestation, spring wheat, 13.84 ± 2.37, winter wheat, 44.33 ± 5.39). Winter wheat is primarily grown in region 1, in central Montana, where infestation was highest (Figs. 1 and 2). However wheat type had a significant effect on C. cinctus infestation levels independent of region, which was included in the final, best fit, statistical model (Table 2). We found significant regional differences in the proportion of wheat stems infested by C. cinctus (Fig. 2, Table 2). Region one, in north central Montana, had double or higher levels of C. cinctus infestation than any other region, followed by fields in southwestern ND and northwestern SD; infestations generally declined in the eastern and southern most regions sampled, regions four and six (Fig. 2, Table 2). C. cinctus infestation was consistently and significantly positively related to wheat cover at the landscape (5 km radius) scale (Table 2, Fig. 3). There were no significant interaction between local and landscape composition
metrics (wheat or grassland cover) and region ($P>0.5$ in all cases), and all interaction terms were excluded from the best fit model (Table 2).

Region was the only significant predictor of variation in proportion parasitism retained in the best fit model (Table 2). We found the lowest levels of parasitism in region one, where *C. cinctus* infestation was highest. Region five, comprised mostly of sites in southwestern North Dakota, with the second highest levels of *C. cinctus* infestation, had the highest observed levels of parasitism averaging 48% (Figs. 1 and 2, Table 2). Even in regions four and six, where *C. cinctus* infestation levels were very low (ranging from 0.5% to 5%) we detected average levels of parasitism (35% and 20% respectively) far exceeding those observed in region 1. Thus regional host densities are not clearly related to levels of parasitism. In contrast to expectations, neither local nor landscape-scale grassland cover were important predictors of parasitism levels (i.e., they were not retained in the best fit model).

There were no significant correlations between regional means for *C. cinctus* infestation or parasitism and any of our regional means of climate variables (GDD or temperature) or proportion grassland or wheat cover at the 20 km scale ($P \geq 0.1$ in all cases) with the exception of a negative relationship ($P=0.052$) between *C. cinctus* infestation and mean annual precipitation across regions (Fig. 4).

### 4. Discussion

We found consistent and significant increases in infestation levels of a dominant pest in wheat, *C. cinctus*, in response to increasing amounts of landscape-level wheat cover across six regions spanning the northern Great Plains of North America. In contrast, increasing areas of local or landscape-level natural habitat cover (grassland) had no effect on either *C. cinctus* infestation or parasitism of this pest by its natural enemies. Larger-scale variation in infestation was best explained by changes in precipitation across regions. Our results suggest that direct responses of insect pests to increasing cover of a highly suitable crop may be an important and often overlooked component of landscape simplification effects on crop pest dynamics.

#### 4.1. Pest response to landscape composition

Theoretical and empirical studies demonstrate that herbivore incidence, abundance and density often decline as the area or connectivity of habitat is reduced (Hanski, 1998; Connor et al., 2000; van Nouhuys, 2005). Habitat area and connectivity are in turn highly positively correlated with their landscape-level cover, which may often be the underlying driver of patch area and isolation effects (Fahrig, 2013). From an agricultural perspective, this leads to the prediction that pest populations should increase with increasing landscape cover of their predominant host crop, as has been found in a number of empirical studies (Veres et al., 2013). In further support of this prediction, we found that *C. cinctus* infestation levels in wheat increased with increases in wheat cover at the landscape (5 km radius) scale, with wheat cover ranging from 1% to 66%. An unexpected result of our study was finding that increases in natural habitat (grassland) cover had no effect on *C. cinctus* infestation when differences in wheat cover were taken into account. Furthermore, the reduction in *C. cinctus* infestation associated with lower wheat cover was not driven by changes in natural-enemy effectiveness inasmuch as we found no effect of local or landscape-scale habitat composition variables on parasitism rates. Instead our results suggest that landscape-associated reductions in pest density are more likely a direct result of reductions in the area, and therefore abundance, of a highly suitable crop in the landscape. Interestingly, this occurred despite the fact that natural and semi-natural grassland habitats also contain host plants that are highly suitable for our focal pest herbivore, i.e., it is not a specialist. Although *C. cinctus* can feed on a variety of grass species, and probably evolved in native grassland systems (Cridle, 1922; Ainslie, 1929) our results suggest that its populations are more strongly influenced by landscape-scale cultivated wheat cover than grassland cover in the study region. This is in accordance with the historical observation that *C. cinctus* emerged as a pest only after large portions of native prairie were converted to wheat cultivation (Cridle, 1915; Ainslie, 1929), as well as anecdotal evidence that *C. cinctus* infestation declines when wheat is rotated with crops that are not hosts, e.g., pulses and oilseeds.

Although we did not directly investigate the mechanisms that contribute to increase in pest infestation in wheat-dominated landscapes, wheat crops represent a potentially hyper-abundant resource, with densities of suitable host stems generally an order of magnitude greater than those observed in natural grassland habitats on an equal area basis (TA Rand, unpublished data). Wheat is also a particularly suitable host for *C. cinctus* due to its larger stem diameter, compared with many small-stemmed native grasses (Cridle, 1922; Ainslie, 1929; Perez-Mendoza et al., 2006). Thus increasing wheat cover at the landscape-scale increases resource availability, likely augmenting populations of *C. cinctus* and
creating large source populations that end up colonizing wheat crops in subsequent years.

Previous work has similarly shown that variation in densities of pest herbivores can be strongly positively linked to the abundance of highly attractive and suitable host crops across the landscape. Carriere et al. (2012) found that the density of Lygus hesperus in cotton, where it is a serious pest, was strongly positively associated with the landscape cover of seed alfalfa, due to high attractiveness and suitability of this crop as a host, and negatively correlated with the abundance of cotton, which supports lower Lygus densities and is relatively less attractive. Similar results have also been documented in work evaluating the influence of landscape-scale patterns in corn cover on insect pests of corn (Beckler et al., 2004; French et al., 2004; O’Rourke et al., 2011). O’Rourke et al. (2011) found increased densities of both the northern and western corn rootworms (Diabrotica spp.) with increasing corn area at the landscape scale. They suggest that the pattern likely reflects a combination of increased mortality during dispersal between corn fields and reduced fecundity in landscapes with less corn. Similarly, Beckler et al. (2004) found a positive relationship between the abundance of Diabrotica virgifera and the proximity of first year cornfields to areas of continuous corn, suggesting that inter-field distances are an important driver of landscape influences on pest dynamics. Reduced connectivity may be an additional mechanism underlying reduced C. cinctus infestation in landscapes with low wheat cover in our study. This hypothesis is supported by the observation that C. cinctus infestation is often higher at wheat field edges (Criddle, 1915; Nansen et al., 2005), suggesting they are unlikely to colonize areas distant from source populations.

Overall our results, combined with the studies just described and conclusions from recent reviews (Veres et al., 2013) suggest that densities of pest herbivores can be strongly and positively linked to the abundance of a suitable host crop across the landscape, even if they can feed on alternative host plants in other habitat types. This suggests that crop diversification at the landscape scale could play a direct role in suppressing agricultural pest populations by reducing the cover of any one crop type, in addition to previously observed influences on natural enemies (Rusch et al., 2013a). However, these responses will depend on the biology of the crop pest species examined. For example in some cases herbivore density or damage has been found to be negatively related (Rici et al., 2009) or unrelated (Jensen and Fahrig, 1997; Thies et al., 2008) to the cover of their host crop species or more closely positively related to the cover of natural areas, such as woodland and grassland (Rusch et al., 2013b) at the landscape scale. In the case of C. cinctus, our results suggest that wheat fields are likely an important source habitat for this pest in the landscape while more natural grassland habitats appear to be relative sinks.

4.2. Consistent pest responses to landscape composition across regions

Studies examining regional variation in landscape effects on agricultural pests remain uncommon (but see Noma et al., 2010; O’Rourke et al., 2011; Thies et al., 2011). Landscape influences may vary regionally for a number reasons including shifting pest and enemy complexes, shifts in cropping systems or crop composition, or changes in the levels of landscape domination by agriculture across regions (O’Rourke et al., 2011; Thies et al., 2011). In contrast with the strong regional effects observed in other studies (O’Rourke et al., 2011; Thies et al., 2011), we found a consistent pattern of increased pest infestation associated with increasing landscape-scale cover of a highly suitable crop plant (wheat) across our six study regions, as indicated by the lack of a significant interaction between wheat cover and region (P = 0.97; all interaction terms were excluded from the best fit model). Our observed pattern of increasing pest pressure in response to increasing landscape domination by wheat was detected despite substantial regional variation in mean levels of pest infestation, cropping systems and climate (Table 1, Fig. 2). Nonetheless, much of the site level variability in pest pressure that we observed remains unexplained (e.g., the scatter in Fig. 3), and non-equilibrium dynamics are likely to play a key role. For example, extreme weather events, such as severe droughts, can cause crashes in C. cinctus populations (Criddle, 1915). Such events would be predicted to reset the clock such that pest populations are out of synchrony with resource availability, weakening the relationship between landscape wheat cover and infestation. This may be especially important at the pest’s range limits (which were not studied here) where climatic factors may be more important drivers of insect population dynamics than resource availability.

Similar to previous studies of other plant-insect interactions (O’Rourke et al., 2011; Thies et al., 2011), we observed large differences in average levels of pest pressure across study regions (Fig. 2). Wheat has long been a dominant crop across the Northern Plains, and the percentage of wheat acreage (at the 20km scale) was relatively similar across our study regions (Table 1). Furthermore, regional wheat cover was not significantly correlated with C. cinctus infestation at the regional scale. Thus, in contrast with results at the landscape scale, differences in wheat cover do not appear to be an important determinant of the regional variation in pest pressure. Instead, regional variation was best explained by differences in average precipitation, with a strong trend of increasing infestation in drier regions (Fig. 4), underscoring the potential importance of climate as a driver of larger-scale differences in pest pressure across regions. These results may help to explain the recent southward expansion of economic infestations of C. cinctus into the states of Nebraska and Colorado, large areas of which have been experiencing drier than normal conditions in recent years (http://droughtmonitor.unl.edu/). The mechanisms via which moisture might negatively influence C. cinctus have not, to our knowledge, been systematically investigated. Nevertheless, historical observations suggest that increased precipitation may have negative effects on larval survival and adult behavior. Direct negative effects can result from larvae “drowning” when excessive sap is created inside the wheat stem because of high summer precipitation (Seamans, 1945) or from adult females laying fewer eggs and moving less because of suboptimal levels of sunshine during the spring (Criddle, 1915). Indirect negative effects may result from the pest’s increased susceptibility to disease under moist conditions (Seamans, 1945).

Cropping systems also vary across regions due to variation in climatic factors. Most notably, region one, which was the driest region with the highest C. cinctus infestations, was dominated by a wheat-fallow rotation system, with other crops being relatively rare. In all other regions that were sampled, wheat was grown in rotation with various alternative crops that are not hosts of C. cinctus, such as pulses (peas, lentils) and oilseeds (canola, sunflower). Here fallow land was rare. While it seems likely that differences in cropping systems contribute to the observed regional variation in C. cinctus, it was not possible to distinguish these effects from concomitant differences in rainfall and temperature.

4.3. Lack of enemy responses to landscape structure

Natural enemies often benefit from landscape-scale natural and semi-natural habitats, which provide important resources, including nectar, alternative hosts, and refuges from the disturbances related to cultivation (Landis et al., 2000; Bianchi et al., 2006). Furthermore, spatial effects are predicted to be stronger for organisms at higher trophic levels (Holt, 1996), and can have stronger effects on specialized insect natural enemies relative to their herbivorous
hosts (Kruess and Tscharntke, 1994, 2000; Thies et al., 2008). In contrast to these findings, we found that herbivores exhibited significant responses to landscape composition while natural enemies were not significantly influenced by either natural grassland cover or wheat cover at local (250 m) or landscape (5 km) scales. These results were unexpected, given our hypothesis that grasses could serve as an important refuge for the second generation of one of C. cinctus's natural enemies, which is unable to complete development in wheat when the crop matures early (Holmes et al., 1963). Furthermore, if wheat is now the dominant habitat for native natural enemies, as appears to be the case for their host C. cinctus, then theoretically they should be more strongly influenced by shifts in landscape-scale wheat abundance. The opposite was observed. Our results contrast with a number of studies demonstrating that landscape complexity is associated with increased rates of parasitism of crop pests (reviewed in Bianchi et al., 2006; Chaplin-Kramer et al., 2011), and once again point to the highly context and species-specific nature of landscape–insect interactions.

Overall, our results suggest that the parasitoids in our system are highly unresponsive to shifts in either local or landscape-scale habitat composition. Thus conservation of parasitoids in this case might be better focused on more traditional within-field management approaches to reduce disturbance to parasitoid populations. For example, increasing cutting height of the crop can leave parasitoids in the stubble of the field rather than removing them during harvest, and reduced or no-tillage practices can increase survivorship of overwintering parasitoids (Beres et al., 2011a). Both these practices have been proposed as a means to conserve natural enemies within wheat fields (Beres et al., 2011a).

We were unable to identify any factors explaining the spatial variability in parasitism in our system. Region was the only significant predictor of parasitism levels retained in our best fit model. Overall, parasitism was lowest in region one, which had the highest est pest infestation levels, and highest in region five, with second highest infestation levels (Figs. 1 and 2). Surprisingly, parasitoids were present and in some cases achieved relatively high levels of attack (up to 35% parasitism) even in regions with very low C. cinctus densities, e.g. regions four and six. However, none of the measured environmental correlates explained the regional variation in parasitism levels, suggesting that parasitoids are either responding to unmeasured large-scale variables, or perhaps are more influenced by local habitat characteristics than landscape or regional factors.

4.4. Management implications

Direct responses of pest insects to increases in the landscape-scale cover of their host plants represents one of the most parsimonious explanations for the greater pest infestations in simplified agricultural landscapes. Our study suggests that reducing the area of a highly suitable host crop can play a role in reducing insect pest populations in wheat. Crop diversification, for example by incorporating more non-host crops (e.g. peas or canola in our system) into the landscape, should contribute to the reduction in populations of important crop pests, such as C. cinctus. More broadly, our results and those of similar studies make clear that understanding the influence of shifting landscape-level patterns of crop diversity and dominance on pest and enemy populations will be important in ultimately managing agricultural landscapes to minimize pest damage (Landis et al., 2008; O’Rourke et al., 2011; Carriere et al., 2012; Rusch et al., 2013a; Vasseur et al., 2013). This shift from individual field-based pest management approaches to larger landscape or “area-wide” approaches, though challenging, has the potential to provide more sustainable and effective solutions to pest problems (Brewer and Goodell, 2012). Future studies addressing the relative importance of habitat type diversity or heterogeneity per se versus reductions in the abundance of particular crops in determining insect responses will be important in furthering our understanding of the mechanisms underlying the impacts of agricultural intensification, which will be critical to guiding management and incentive programs.

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