



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



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ABSTRACT

Landscape simplification associated with agricultural intensification has important effects on economically important arthropods. The declining cover of natural and semi-natural habitats, in particular, has been shown to reduce natural-enemy attack of crop pests, but also in some cases reduced crop colonization by such pests. In this study, we examined the influence of changes in two elements of landscape composition, natural grassland cover and cover of a highly suitable crop host, on infestation by a generalist insect pest in wheat, and parasitism of this pest by its dominant natural enemies. Surprisingly, we found no significant influences of increasing natural grassland habitat, at either local or landscape scales, on infestation by the wheat stem sawfly, *Cephus cinctus*, or parasitism of this pest by the native parasitoid wasps, *Bracon cephi* and *Bracon lissogaster*. In contrast, we found significant increases in levels of *C. cinctus* infestation with increasing wheat cover at the landscape scale. This pattern was consistent across six study regions spanning three states in the northern Great Plains of North America, despite large differences in cropping systems and pest population densities across regions. Regional variation in pest infestation was best explained by long-term averages in precipitation, with higher *C. cinctus* infestation rates found in drier regions. Results suggest that landscape-mediated variation in pest pressure in this system is better explained by a direct response of pest insects to increasing cover of a highly suitable crop rather than an indirect response via reductions in natural enemies as natural habitat declines. The implication is that habitat diversification at the landscape scale could play a role in suppressing agricultural pest populations via reductions in area of suitable crop hosts.

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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

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of alternative host plants (Thies et al., 2005; Bahlai et al., 2010; Ragsdale et al., 2011), and higher abundance of generalist herbivores in alfalfa fields in more diverse landscapes (Jonsen 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; Connor 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 (Tscharrntke 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 diapause 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; Criddle, 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 (Criddle, 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 (Criddle, 1922; Ainslie, 1929; Perez-Mendoza et al., 2006). *C. cinctus* is also known to attack many introduced weedy and forage grasses (Criddle, 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 (Criddle, 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 Landis et al., 2000; Bianchi et al., 2006; Chaplin-Kramer et al., 2011). Grassland provisioning 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 (Criddle, 1922, 1924). In contrast, its host *C. cinctus* is univoltine, and thus better synchronized with wheat growth and development. Furthermore, parasitoids, tend to overwinter 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

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