ORIGINAL CONTRIBUTION

Spatial and numerical relationships of arthropod communities associated with key pests of maize

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Abstract

Pest management largely focuses on managing individual pest species with little concern for the diverse communities that co-occur with key pests and potentially shape their population dynamics. During anthesis, we described the foliar arthropod communities on 53 maize farms throughout the region of eastern South Dakota. The resulting communities were examined for trends in local associations in the abundances of taxa with key pests in the system (rootworms [*Diabrotica* spp.], European corn borers [*Ostrinia nubilalis*], aphids and Western bean cutworm [*Striacosta albicosta*]) using regression analyses. Regional spatial clustering in the abundances of key pests with members of the community was explored using Moran's I test statistic. The distributions of rootworms and European corn borer were mapped. A total of 37 185 arthropods representing at least 91 taxa were collected in South Dakota maize; there was an average of 5.06 predators and 8.29 herbivores found per plant. Key pests were never found at economically threatening levels (with one exception for *Diabrotica*). Numerous species were consistently numerically associated with each of the key pests across the farms during anthesis. Occasionally, these pests shared species with which they were locally associated with; for example, coccinellid egg abundances were predictive of the abundances of all key pest species except rootworm adults. Spatial analysis across the region suggested that species co-occurred with key pests based on local characteristics surrounding the fields, rather than as a result of regional characteristics. Exceptions were documented; namely aphids and Western bean cutworms that spatially clustered with a handful of other members of the community. The results of the study point out that the abundances of key pests of maize were interconnected through indirect associations in the abundances of other members of the community. These associations may be useful for manipulating maize agroecosystems to minimize the effects of maize pests.

Introduction

The relative abundance and composition of biological communities affect the stability and invasibility of habitats (Tilman 1996; Emery and Gross 2007; Gilbert et al. 2009), a topic of particular interest to land managers charged with managing pests (Van Emden and Williams 1974). Natural regulation of dominant species comes about through direct competitive interactions with a focal species (Denno et al. 2000; Mayer et al. 2002; Wielgoss et al. 2012) or through biotic resistance to a species' growth imposed by processes like predation (Symondson et al. 2002; Cardinale et al. 2003). Often, pest management decisions are

focused on regulating a single outbreak species within an arthropod community, with little attention paid to other members of the community that may play a role in the outbreak species' success. A good example of this is the arthropod community of maize fields in the United States.

In spite of the value of maize production and the economic costs associated with insect pests in this crop, the arthropod community of maize arguably remains poorly understood. In North America, the European corn borer (*Ostrinia nubilalis* Hübner; Lepidoptera: Crambidae) (Mason et al. 1996) and the corn rootworm complex (*Diabrotica* spp., especially *D. virgifera virgifera* LeConte; Coleoptera: Chrysomelidae) (Gray et al. 2009) are consistently the dominant pests of untreated maize fields. Their management conservatively costs farmers $3.2 billion every year (approximately $123 in technology fees per ha on approximately 26 million ha of Bt maize seed in 2013; (NASS 2013) and J.G.L. unpublished data), primarily through the prophylactic use of Bt hybrids treated with systemic neonicotinoid insecticides. Western bean cutworm (*Striacosta albicosta* (Smith) (Catangui and Berg 2006; Michel et al. 2010) and corn leaf aphids (Carena and Glogoza 2004) are two other pests of concern in this region, but less is known about their distribution and impacts on yield. Although aspects of maize arthropod communities have been studied (Bhatti et al. 2005a,b; Dively 2005; Ahmad et al. 2006; Lundgren and Fergen 2010), there remains a poor knowledge of the diversity of insects associated with major pest species. Rather, focus has been given to identifying and studying dominant interactions of species with key maize pests (e.g., primary parasitoids or predators of European corn borer (Andow 1990; Phoofolo et al. 2001), corn rootworms (Toepfer et al. 2009) and corn leaf aphid (Elliott et al. 2002; Park and Obrycki 2004)). Furthermore, the cropping conditions, collection procedures and focal organisms vary among studies, and this challenges cross-study comparisons throughout a region or across regions. This lack of resolution of arthropod communities in maize is understandable, because describing these communities necessitates consistent, labour-intensive sampling procedures implemented many times across a geographic region, and subsequent identification of a breadth of infrequently collected species. Nevertheless, the resulting relative abundances of insects within a community could have important implications for pest management.

Here, we created an extensive database of the foliar maize arthropod communities across a large geographic region (eastern South Dakota, approximately 95 000 km^2) to determine which species within the foliar maize arthropod community cluster together in their abundance, particularly with respect to the key pests European corn borers and corn rootworms. The maize arthropod community on the western edge of the US Corn Belt has never been systematically characterized. We also chart the abundance and distributions of these pests within non-Bt maize fields (treated with at most a low rate of insecticidal seed treatment) across the surveyed region. The results may provide opportunities for using insect communities to maintain key pests of maize at subeconomic levels.

Material and Methods

Field survey

A group of 53 study sites was selected in South Dakota, east of the Missouri River, where most maize is produced in the state. Twenty-eight of these sites were sampled in 2010, and the other 25 sites were sampled in 2011 (the sample sites are presented in figs 2 and 3). In each year, at least 1.6 km separated study sites. Requirements for inclusion in the study were that the fields were at least 4 ha in size and planted with non-Bt maize. Ideally, the fields received no insecticides; this requirement was relaxed due to the rising use of insecticides in our region (Fausti et al. 2012), and as such some of the fields received an insecticidal seed treatment of clothianidin or thiamethoxam at the rate of 0.25 mg active ingredient per kernel. Sampling occurred within 10 d of maize anthesis at all sites, which occurred between 21 July through 11 August 2010 and 2 August through 11 August 2011. This stage consistently harbours the most diverse and abundant arthropod community in maize fields (J.G.L, personal observation), as well as life stages of the predominant pests of maize (Wright and Laing 1980; Darnell et al. 2000; Campbell and Meinke 2006). Fifty plants were randomly selected and destructively sampled at each site. Maize plants were collected at least 8 m from the field margin, severed at the soil line and carefully moved to the field margin. Here, the plants were dissected on a white cotton sheet, and all arthropods on or in the plant were identified to the lowest taxonomic unit possible under field conditions. Arthropods were identified as predators or herbivores to the lowest taxonomic level possible in the field (see Tables S1 and S2). The numbers of each taxon and numbers of predators and herbivores per plant were subsequently tabulated in a database. Pests were considered as having 'low

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447

abundance' at a site if fewer than 0.1 insects per plant were found.

Mapping pest distributions

GPS coordinates and associated arthropod density for all sampled sites in each year were imported and mapped in ArcMap (ArcGIS 10.1, ESRI, Redlands, CA). A continuous raster surface for arthropod densities was then generated by interpolating between sampling points using an inverse distance weighted (IDW) technique, with the IDW tool in the ArcGIS toolbox.

Data analyses

To help interpret the results, pests were considered at 'low densities' at a site when they were fewer than one insect per 10 plants. The Chao I metric (S) was used to predict how many species were expected from each plot, given the community assemblage. This metric is measured as:

$$S = S_{obs} + F_1^2/2F_2$$

where S_{obs} = observed number of species, F_1 = the number of singletons and F_2 = the number of doubletons collected in a sample. Rarefaction analysis provided the number of species that were expected as specimens accumulated from sampling. The rarefaction curve was generated using the program Analytic Rarefaction 1.3.

We used forward stepwise regression models to determine whether there were numerical correlations between specific community members and key pests. Pests were categorized as corn rootworms (adults of *D. virgifera, D. barberi, and D. undecimpunctata*), European corn borer (eggs, larvae, pupae), aphids (all species combined) and Western bean cutworm (eggs, larvae). Criteria to add and remove species from the model was $P = 0.15$. Resulting species that had significant regression coefficients were considered to be numerically tied to a particular pest complex. The regression analyses were conducted using Systat 13 (Systat Software Inc., Chicago, IL).

Spatial cluster analysis was first run on ordinal level groups of the herbivores and predators. Data sets from 2010 and 2011 had to be analysed separately, because the analyses relied on nearest neighbours for estimating clustering coefficients. Specifically, pairwise correlations in spatial clustering between arthropod orders were tested using bivariate Moran's I tests. When significant results were obtained at the ordinal level ($\alpha = 0.10$), additional tests were run to see which taxa were responsible for the pattern. Spatial clustering

analyses were conducted using Open GeoDa (Arizona State University, Tucson, AZ).

Results

Arthropod community

In sum, we collected and identified 37 185 arthropods in maize fields during anthesis. This community consisted of 91 OTUs (Operational Taxonomic Units, likely >91 species) of arthropods on South Dakota maize plants, representing four Classes (Gastropoda, Diplopoda, Arachnida and Insecta), and 19 Orders (Stylommatophora, Julida, Opiliones, Acari, Arachnida, Collembola, Coleoptera, Diptera, Dermaptera, Ephemeroptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Odonata, Orthoptera, Psocoptera, Trichoptera and Thysanoptera) (Tables S1 and S2). The number of species discovered is likely an underestimate, because we did not identify Araneae, Staphylinidae, Formicidae, Miridae, etc. to species level. There was a mean ($\pm$SEM) of 14.03 ± 1.35 arthropods per plant, of which 5.06 ± 0.35 were mostly predaceous and 8.29 ± 0.35 were mostly herbivorous. The remainder were either saprophagous, fungivorous or had unknown feeding behaviour. At the common planting rate for our region of 81 500 plants per ha, this extrapolates out to approximately 1 144 000 arthropods per ha, of which 412 000 are predatory. The mean ($\pm$SEM) number of species collected per field was 28.19 ± 0.80, which is 67% of the Chao I predicted number of species (41.58 ± 1.64). The rarefaction analysis of the entire community (cross-locations) suggests that we collected the complete foliar community at this stage of the growing season (the upper asymptote approached 106 species) (fig. 1).

Corn rootworms (Coleoptera)

Diabrotica barberi Smith & Lawrence (Northern corn rootworm) adults were the most frequently collected rootworm species encountered at the field sites (Table S1; fig. 2). Although the pest was found at many sites, the Northern corn rootworm was not abundant. Maximum abundances were 1.34 and 1.58 beetles per plant in 2010 and 2011, respectively. Twenty and 14 sites had low pest abundance in 2010 and 2011, respectively (low pest abundance equates to fewer than one insect per 10 plants). In 2010, Western corn rootworms were consistently at low abundance on the infested plants throughout the region. One infested location (Hanson County; 43.657, 97.755 lat
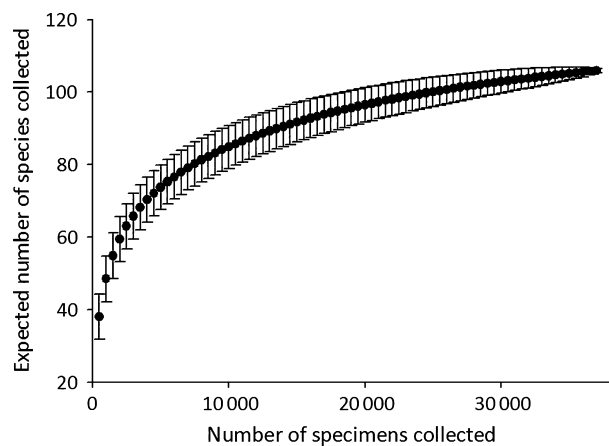
Fig. 1 Rarefaction analysis of the total foliar arthropod community collected from maize during anthesis. Expected number of species collected was based on actual data collected from 53 maize farms during 2010 and 2011 in eastern South Dakota, USA. Error bars represent upper and lower 95% confidence intervals.

Fig. 2 Corn rootworm densities collected in eastern South Dakota, USA in 2010 and 2011. All samples were collected during anthesis, and sample sites are indicated by open circles.

and long) in 2011 had high Western corn rootworm densities (6.9 beetles per plant), but the rest of the sites had fewer than 0.16 rootworms per plant. Southern corn rootworms were found only in 2010 at roughly half of the sites, but this pest was never abundant (maximum infestation was 0.12 beetles per plant).

European corn borers and Western bean cutworm (Lepidoptera)

Although the second generation of the European corn borer was frequently collected (Table S1; fig. 3), their densities were uniformly low across the region. In 2010, larvae reached a maximum density of 0.58 larvae per plant. Thirteen infested sites had low abundance of larvae per plant. In 2011, only one of the infested sites had more than 0.1 larvae per plant (0.16 larvae per plant). Similarly, corn borer pupae and egg masses were not abundant throughout the region; pupae exceeded 0.1 per plant at only one infested site (0.14 pupae per plant in 2011), and eggs were never so abundant. Western bean cutworm larvae were infrequently collected in 2010 (Table S1) and were relatively abundant (0.49 larvae per plant) only at one site (McPherson County; 45.798 and 99.511, lat and long). In 2011, larvae were more frequently collected (17 locations), but were seldom abundant. Two locations had relatively high abundance (0.98 and 0.82 larvae per plant at Deuel [44.574, 96.561] and McPherson [45.775, 99.449] Counties, respectively). Other caterpillars were almost never abundant; an
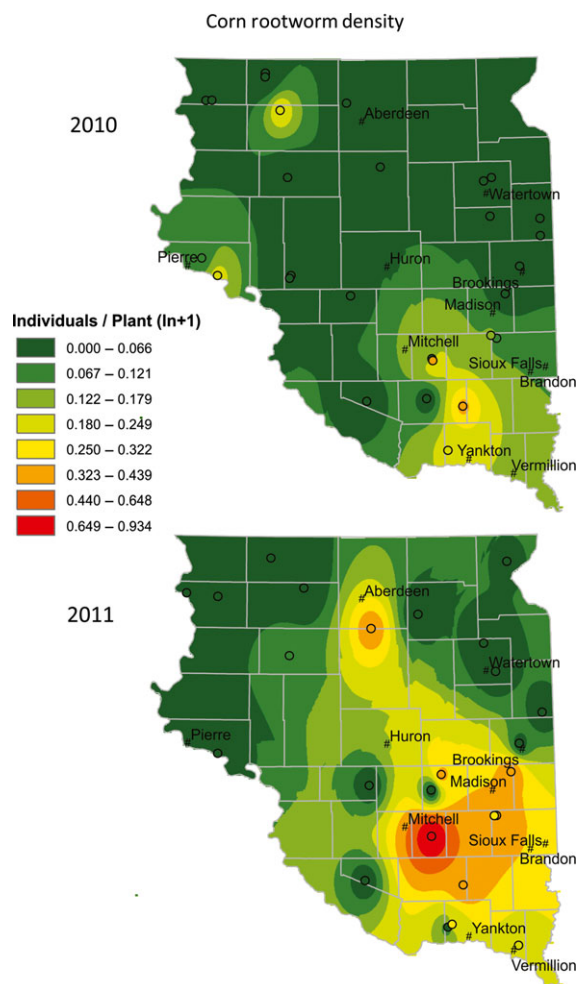
exception is that one location had 0.16 corn earworms (*Helicoverpa zea* [Boddie]) per plant.

Aphids (Hemiptera) and thrips (Thysanoptera)

Aphids and thrips were the most numerous herbivores in our system. Corn leaf aphids were rarely found in the experiment (found in only three fields, and with a maximum of 0.42 aphids per plant), although other undetermined aphid species were nearly always encountered. Occasionally, these aphids were abundant (much more so in 2010); a maximum of 52 aphids per plant were found in Brown County (45.605, 98.633; lat, long); 29 aphids per plant were found in a field in Minnehaha County (43.805, 97.071; lat, long). Many infested fields (10 and 22 fields in 2010 and 2011) had low aphid
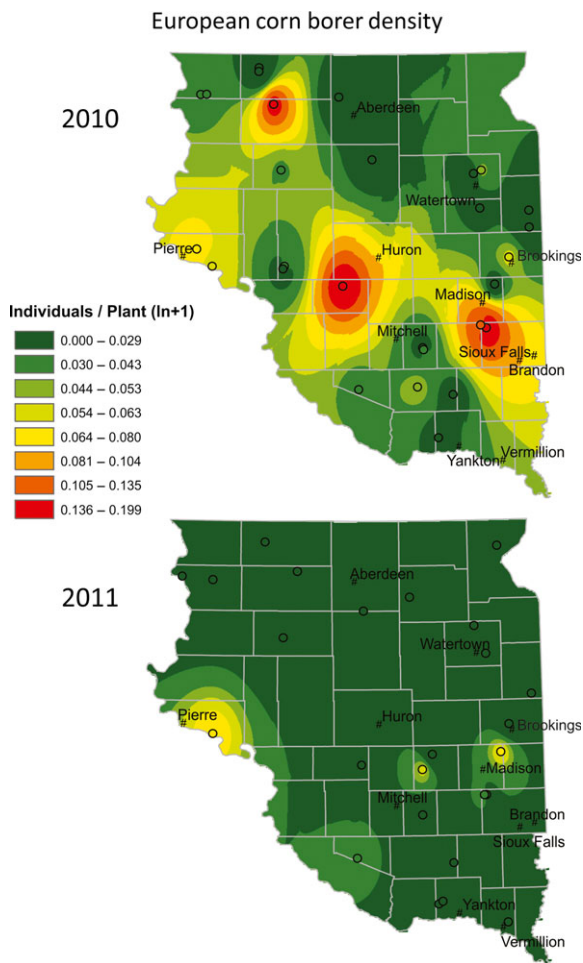
European corn borer density

Fig. 3 European corn borer densities collected in eastern South Dakota, USA in 2010 and 2011. All samples were collected during anthesis, and sample sites are indicated by open circles.

abundance (<1 aphid per plant). Thrips were by far the most abundant and frequently encountered herbivores; thrips were found in every field, usually (23 and 14 sites in 2010 and 2011, respectively) at a density of more than two thrips per plant.

Predators

In order of abundance, *Chrysoperla* eggs (53 sites), *Orius insidiosus* Say (adults and nymphs) (53 fields), *Glischrochilus quadrisignatus* Reitter (Picnic beetles) (51 fields) and the consolidated taxa 'lady beetle larvae' (44 sites) and 'spiders' (48 sites) were the most commonly encountered and abundant predators found (Table S2). A general linear model did not reveal any correlations between predator taxa and the ratio of *Chrysoperla* larvae to eggs ($F_{41, 11} = 1.35$, $P = 0.31$),

suggesting that intraguild predation was not the cause for the diminished lacewing larval populations. A simple linear regression of *Orius insidiosus* adult and thrips abundances per farm found a significant, positive correlation between these two taxa ($F_{1, 51} = 3.87$, $P = 0.05$).

Regression correlations of insect abundance with key pests

The forward stepwise regression analyses revealed several numerical correlations between species and the key pests within individual fields: corn rootworms (all three species), European corn borers (eggs, larvae, pupae), aphids (all species) and Western bean cutworms (eggs and larvae). The forward stepwise regression model searching for species whose abundances were strongly correlated with rootworms included 12 taxa ($R^2 = 0.95$, constant coefficient = 0.34, $F_{13, 39} = 52.98$, $P < 0.001$). Of these, all 12 taxa had significant ($\alpha = 0.05$) coefficients: Chrysomelid sp. 1 (coefficient = 46.04, $P < 0.001$), Collembola (19.10, <0.001), Diptera larva (−1.03, <0.001), *Helicoverpa zea* (6.68, <0.001), Pentatomid nymph (5.71, <0.001), Psocoptera (23.40, 0.04), Trichoptera (−180.87, <0.001), unknown beetle larva (10.52, <0.001), *Coleomegilla maculata* (−7.09, 0.001), *Harmonia axyridis* (−18.77, 0.008), lacewing egg (−0.07, 0.02) and Formicidae (−3.29, <0.001). European corn borer abundance was well predicted by the forward stepwise regression model, which included 15 taxa ($R^2 = 0.93$, constant coefficient = −0.008, $F_{15, 35} = 31.99$, $P < 0.001$). All 15 taxa were significantly associated with corn borer abundance: Elateridae (16.34, <0.001), *Helicoverpa zea* (1.09, <0.001), Heteroptera nymph (0.88, 0.001), trombidiid mite (0.07, <0.001), slug (−18.64, 0.001), Psocoptera (−4.61, 0.003), unknown beetle (−14.04, 0.02), unknown beetle larva (1.04, 0.02), coccinellid eggs (0.26, <0.001), coccinellid pupa (1.06, <0.001), Dermaptera (−19.80, <0.001), *Hippodamia convergens* (coefficient = 7.31, $P < 0.001$), Syrphidae adult (42.82, <0.001) and Syrphidae larva (−4.03, <0.001). Aphid abundance was well described by the forward stepwise regression model that included 11 taxa ($R^2 = 0.97$, coefficient = −0.53, $F_{11, 41} = 123.55$, $P < 0.001$). All 11 taxa included in the model had significant coefficients: little brown beetle #2 (153.33, <0.001), *Trichoplusia ni* (−175.06, <0.001), tortoise beetle (coefficient = 211.28, $P < 0.001$), *Coccinella septempunctata* (157.26, <0.001), coccinellid eggs (9.99, <0.001), coccinellid pupa (22.92, <0.001), *Orius insidiosus* nymph (−1.63, <0.001), *Scymnus rubricaudus*

(18.77, <0.001), spider egg cluster (18.87, <0.001), syrphid adult (1398.38, <0.001), unidentified carabid beetle (214.58, 0.003). Western bean cutworm abundance was also well predicted by the forward stepwise regression model, which included 13 taxa (R^2 = 0.96, coefficient = 0.006, $F_{13, 39}$ = 32.48, $P < 0.001$). Of these, eight taxa had significant coefficients: Membracidae (48.58, <0.001), Pseudococcidae (32.54, <0.001), *Trichoplusia ni* (−2.56, 0.005), *Chrysoperla* sp. (3.59, <0.001), coccinellid eggs (−0.11, 0.02), *Cycloneda munda* (coefficient = −4.29, P = 0.04), lacewing egg (0.03, <0.001) and syrphid larva (5.99, <0.001).

Spatial clustering of arthropods across the region

There were no consistent trends in the spatial clustering of species with key pests of maize and predatory taxa across study years. In 2010, areas of low aphid populations were clustered with areas of high picnic beetle (coefficient = −0.039 ± 0.013, $P < 0.001$) and *Coleomegilla maculata* adults (coefficient = −0.031 ± 0.013, $P < 0.10$). Also in 2010, areas of low Western bean cutworm populations were clustered with areas of high spider (coefficient = −0.043 ± 0.016, $P < 0.05$), spider egg sack (coefficient = −0.034 ± 0.019, $P < 0.10$) and *Phalangium opilio* (coefficient = −0.043 ± 0.016, $P < 0.10$) populations. The only significant herbivore–predator clustering in 2011 involved thrips and lacewing eggs; these two groups were positively correlated with each other (coefficient = 0.081 ± 0.044, $P < 0.10$). There were also negative correlations between thrips and Syrphidae and Predatory Hemiptera in 2011, but individual taxa in these broader groups were not significantly correlated with thrips. *Orius insidiosus* adults and nymphs both had a negative coefficient, but were not significantly associated ($P < 0.15$).

Key pests had regional, spatial correlations with some herbivorous taxa in the maize system, but none of these patterns were consistent between study years. The only instance of significant spatial correlations between key pests and other herbivores in 2010 was between Western bean cutworm and herbivorous beetles. Specifically, cutworm populations were negatively correlated with the chrysomelid beetle with a red prothorax (Criocerinae; nr *Oulema* sp.) (−0.024 ± 0.011; $P < 0.05$) and corn flea beetles (−0.035 ± 0.017; $P < 0.05$). In 2011, Western bean cutworms were only significantly correlated with Orthoptera, specifically with grasshoppers (−0.08 ± 0.030; $P < 0.05$). Also in 2011, aphids were significantly spatially correlated with herbivorous Coleoptera. Aphid densities were negatively correlated with tortoise beetles (−0.05 ± 0.017; $P < 0.01$) and flea

beetles (−0.069 ± 0.023; $P < 0.01$). Thrips were significantly correlated spatially with herbivorous Hemiptera, Orthoptera and Lepidoptera in 2011. In the herbivorous Hemiptera, Hemiptera nymphs (−0.062 ± 0.034; $P < 0.10$), Fulgoroidea (−0.078 ± 0.037; $P < 0.05$), pentatomidae nymph (−0.093 ± 0.047; $P < 0.10$), Pentatomidae egg masses (−0.075 ± 0.036; $P < 0.05$), grasshoppers (−0.066 ± 0.031; $P < 0.05$) and long-horned grasshopper (0.051 ± 0.024; $P < 0.05$), *Helicoverpa zea* larvae (0.092 ± 0.039; $P < 0.05$), green caterpillar (−0.083 ± 0.039; $P < 0.05$), unknown caterpillars (−0.076 ± 0.040; $P < 0.1$), but the spatial distributions of individual taxa within these orders were not significantly correlated with thrips ($P > 0.05$). None of the key pests were significantly spatially clustered with one another at a regional scale ($P > 0.10$).

Discussion

Key pests of maize were consistently low in these non-Bt maize fields that were untreated or treated with a minimum dose of neonicotinoid seed treatment at planting (Table S1). Recent evidence suggests that high adoption of Bt technology has resulted in area-wide suppression of at least one maize pest, European corn borer, throughout much of the Corn Belt of the USA (Hutchison et al. 2010). Our data support this pattern on the western edge of maize production in North America (fig. 3), but is in direct contrast to reports developed 10 year ago in southeast South Dakota that showed fairly high densities of corn borers (up to 80% of stalks infested; Catangui and Berg 2006). Rootworm adults were also at low levels in our study in all except for one site (fig. 2). This highly infested and untreated field had been continually planted with maize for many years in a row, allowing the accumulation of high rootworm populations. Northern corn rootworm was the most abundant rootworm species throughout much of the study range, confirming earlier reports in similar regions (Krysan 1986). The consistently sparse adult rootworm populations could also be the result of area-wide suppression by adoption of Bt maize targeting this pest. Also, local crop rotation patterns may explain the lower rootworm adult numbers (Pikul et al. 2005; Schroeder et al. 2005), although we do not have site histories for each of these farms at this point. Rootworm adult populations have been shown to be correlated with subsequent year's larval populations and root damage (Tollefson 1975), making our sampling approach a meaningful metric for producers. Aphids averaged only three per plant, largely driven by a few population hotspots (hence the high variance

presented in Table S1). These aphids may cause damage through direct physiological effects of feeding, but yield reductions appear to most often be attributed to fouling silks and anthers with honeydew (Everly 1960; Foott and Timmins 1973). A commonly reported threshold for corn leaf aphid is 50% of plants exceeding 100 aphids per plant (C. Krupke, Purdue University, pers. comm., although this depends especially on the water availability of the maize plant), and aphid populations in our study did not warrant treatment. Yield losses by Western bean cutworm are approximately 62 kg of grain per ha (3.7 bu per ac) for infestations of one larva per plant (Appel et al. 1993), and these insects never exceeded this density in our fields. The most consistently abundant herbivore in the maize system was thrips, likely grass thrips, *Anaphothrips obscurus* Müller (Corey et al. 1998). Thrips must be at very high densities to merit concern from farmers in our region, and we know of no reports of economic damage resulting from thrips in northern maize. Given the consistently low populations of key pests in untreated maize during this period of the growing season when most key pests are at important abundances, it begs the question of whether farmers in this region need to invest in prophylactic insecticidal seed traits on an annual basis.

Natural enemy communities represented a large component of the maize arthropod community. Two predator taxa that were represented on every farm were *Orius insidiosus* Say and *Chrysoperla* sp. eggs. *Orius insidiosus* is a major predator of thrips in many systems (Corey et al. 1998; Harwood et al. 2007), and we found that *O. insidiosus* adult (but not nymph) populations were significantly and positively associated with thrips abundance on these farms, reinforcing the idea that thrips presence at least partially explains the high densities of *O. insidiosus*. This species also is an important predator of European corn borer egg masses (Andow 1990; Phoofolo et al. 2001) and *Helicoverpa zea* eggs (Pfannenstiel and Yeargan 2002). A noteworthy pattern that we saw in this study and in others (Lundgren et al. 2013) is a disconnect between the numbers of *Chrysoperla* sp. eggs and larvae found in a particular field. Lacewing eggs consistently represented the most frequently collected predator OTU in our maize fields (they were four times more abundant than the next most abundant predator; Table S2), while lacewing larval populations represented on average only 3% of the egg abundance. Intraguild predation seems a plausible explanation for the deaths of lacewing eggs and neonates (Rosenheim et al. 1999), but exploratory analyses did not reveal any predator taxa with strong ties in abundances to either of these lacewing life

stages. Gut content analyses of predator stomachs may be useful for resolving why the young lacewings are disappearing. Another abundant predatory species was the picnic beetle, *Glischrochilus quadrisignatus*. This species frequents maize fields and consumes the larvae of European corn borers within their tunnels (McCoy and Brindley 1961; Carlson and Chiang 1973), but a linear regression of this beetle's abundance did not reveal any significant numerical relationship with the abundance of European corn borers. Lady beetles and spiders are frequently reported as visitors to pollen-shedding maize fields and were some of the most frequently collected predators in eastern South Dakota maize during anthesis. Many of the natural enemies found in this community consume maize pollen (Lundgren 2009), including *O. insidiosus* (Kiman and Yeargan 1985; Lundgren 2009), *Chrysoperla* sp. (Pilcher et al. 1997; Li et al. 2008) and lady beetles (Lundgren et al. 2004, 2005). Thus, by targeting the anthesis stage of the crop, we have likely recorded omnivorous species interested in pollen feeding. Finally, although the natural enemies found in the maize system are abundant, recent evidence suggests that these abundances fall far short of those found in natural systems (J. G. Lundgren, unpublished data), and increasing predator abundance has been shown to increase the strength of trophic interactions of predators with corn rootworm prey (Lundgren and Fergen 2014).

Our models revealed a number of herbivorous and predatory species whose abundances were predictive of the abundances of key pests on farms during this period of the growing season. Predators were commonly found to be good predictors of pest abundances, but this was particularly true of aphids. Eight of the 11 taxa that helped predict aphid densities were known aphidophagous predators, and nearly all had positive model coefficients, suggesting a positive numerical response to increasing aphid densities. While the voracity of aphidophagous predator guilds has been repeatedly documented in other systems (Conway et al. 2006; Costamagna and Landis 2006; Obrycki et al. 2009; Diehl et al. 2013), little work has been carried out to determine the importance of maize aphids in supporting predators in North America (but see Wright and Laing 1980). The abundances of some of these aphid predators were linked to the abundances of other key pests in the system. For example, coccinellid egg abundance was significantly predictive for all key pests except rootworm adults. In contrast, specific herbivore taxa were not commonly associated with multiple pests. Only two of 12 herbivorous taxa whose abundances were predictive of key

pests were predictive of more than one key pest; these exceptions were *Helicoverpa zea* populations which were predictive of corn rootworms and European corn borers, and *Trichoplusia ni* which were predictive of Western bean cutworm and aphids. In contrast, five (of 17) predator taxa that were predictive of the abundances of more than one key pest. An outcome of this analysis is that all key pests are connected through indirect linkages of shared connections with certain arthropods. This is not entirely surprising. These pests may function as shared prey for generalist predators (Cottrell and Yeargan 1998; Lundgren et al. 2004), and herbivores may be attracted to fields under similar conditions (e.g., drought-stressed plants are simultaneously attractive to multiple herbivores) (Mattson and Haack 1987; Tariq et al. 2012).

Species that co-occurred with key pests within individual fields (revealed by regression analysis and discussed above) seldom clustered together within a regional neighbourhood (as measured with the Moran's I test statistic). In landscape analysis, Moran's I tests for autocorrelation have been used to ensure that local fields included in landscape analysis are independent observations (Thies et al. 2008; Zaller et al. 2008; Meehan et al. 2011). The fact that there is a risk of autocorrelation in landscape analysis supports our findings that within a neighbourhood some key pests can be correlated with other members of the community. Of the key pests in the maize system, aphids and Western bean cutworm were the only species to demonstrate any spatial clustering with other members of the community. Aphids clustered with two predatory species in 2010 (picnic beetles and *C. maculata*) and with two herbivore species in 2011 (tortoise beetles and flea beetles; tortoise beetles were the only of these four taxa that were correlated with local aphid abundance). Cutworms clustered with spiders, harvestmen and two chrysomelids in 2010, and with grasshoppers in 2011. This demonstrates that a local community within maize fields is at least partially influenced by species and processes that occur within a neighbourhood. Processes such as climate, crop production patterns, etc. vary across a region, and this produces spatial clustering of species within maize fields. The resulting snapshot of the relative spatial clustering of specific taxa within a neighbourhood can be the outcome of common regional effects on multiple species, or it may be the neighbourhood-wide result of species' responses to the abundances of a particular member of the community (i.e. aphids and Western bean cutworms) (Legendre et al. 2002; Dormann et al. 2007). Regardless, establishing these

relationships, both in-field and across regions, can help identify key interactions worth exploring for pest management. Nevertheless, our results suggest that community constituency is shaped more frequently by more local processes than across broader spatial patterns in the region; a look at more proximal landscape features that contribute to maize community constituency may be worthwhile as an intermediate between regional and local patterns in community structure.

While this research clearly reveals patterns that are significant and supported across a wide breadth of farms, mechanisms for explaining these species interactions and whether these interactions can be manipulated for pest management remain important questions. It is clear that there is substantial interplay among species in the maize arthropod community, both locally and throughout a region. The complexities of these interactions merits attention using more sophisticated tools such as network analysis to determine how increases or decreases in populations of certain taxa will affect the management of key pests (Proulx et al. 2005). Also, these community 'snapshots' during anthesis may have very different and important interactions during other periods of the growing season. The Moran's I spatial clustering analysis suggests that regional trends surrounding a focal field may be an underlying characteristic that could influence when and where pest populations outbreak, and this warrants further attention. Finally, this research suggests that a 'pest-centric' view of pest management (basing management decisions solely on the density of pest species) may ignore important underlying causes for pest outbreaks that could be exploited to prevent outbreaks before they occur.

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454

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Herbivorous insects collected from maize fields of eastern South Dakota in 2010 and 2011.

Table S2. Predatory arthropods (mean ± SEM) collected from maize fields of eastern South Dakota in 2010 and 2011.