

# Analysis of the insect community in a stored-maize facility

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Maize samples were obtained at two depths [0–30 cm (top sample) and 30–60 cm (bottom sample) from the maize surface] at 19–28 locations from a naturally infested maize storage facility in Wisconsin, USA. Based on identification of insects in stored-maize samples from 13 weekly sampling events, four topics were addressed: (i) the seasonal fluctuation in the insect community; (ii) ordination analysis was conducted to examine the association among insect taxa and to determine their distribution along abiotic and geographic gradients; (iii) the demographic characteristics of insect communities in maize samples with high abundance of either *Plodia interpunctella* (*Plodia* samples) or *Sitophilus zeamais* (*Sitophilus* samples); and (iv) to what extent natural enemies were spatially associated with their prey species. We identified a total of 18 different taxa, composed of adults and larvae of 14 determined species, and others identified to genus, family or order. Insect density was significantly higher in top samples compared to bottom samples, and the insect taxa occurred more frequently in top samples compared to bottom samples. In the ordination analysis, the three explanatory variables accounting for eastern, northern and vertical position of maize samples explained the largest part of the total variance. There was a gradual time trend with some of the insect species mainly occurring early or late in the monitoring period. Moisture content of the maize was the weakest of the significant explanatory variables, while temperature in the grain mass did not explain a significant part of the total variance. *Plodia* samples and *Sitophilus* samples had significantly different spatial distribution patterns and had markedly different insect species composition. *Plodia* samples were characterized by low abundance of all granivores and fungivores, except *P. interpunctella*. Conversely, *Sitophilus* samples had high abundance of *T. castaneum*, *A. advena*, and *C. ferrugineus*. Consequently, *Sitophilus* samples seemed to comprise more diverse insect communities than *Plodia* samples. Natural enemies were not significantly associated with their most common hosts. In a highly homogeneous habitat (stored maize), we demonstrated that stored-product insect species had significantly different distribution patterns mainly along geographic gradients. Stochasticity of the initial infestation process or interspecific competition are two of the possible explanations for the spatial segregation of stored-product insects, and the spatial segregation of insects on the same trophic level may have profound implications for the understanding of how these ecosystems develop over time and thereby how integrated pest management strategies are implemented to control insect pest populations.

**Key words:** interspecific competition; postharvest ecology; spatial distribution; stored-product insects.

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## Introduction

A community is characterized by its species diversity, primary and secondary productivity, food webs, stability, patchiness in terms of microhabitats, and distribution of species in both time and space. Sinha (1995) described agroecosystems with particular reference to the stored-grain ecosystem and indicated that insect communities in stored grain ecosystems may be considered: (i) highly uniform with a homogenous distribution of an almost unlimited food source; (ii) temporal, because they only exist for as long as the grain is stored; (iii) subjected to high level of human

disturbance; (iv) well-defined physical units (such as buildings) with few connections to the surroundings (ventilation ducts, windows, doors, etc.) and hardly any internal physical barriers; (v) a fairly stable diurnal and seasonal microclimate, and (vi) having negligible flow of energy. Surveys of storage ecosystems in North America (Barak & Harein 1981; Storey *et al.* 1983; Arbogast & Mullen 1988; Arbogast & Throne 1997)

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Received 18 November 2002, Accepted 6 August 2003.

have shown that stored-product insect communities are represented by species on several trophic levels, including granivores, fungivores, omnivores, and natural enemies. The factors triggering an initial infestation in a storage ecosystem are not well understood, nor is it clear how environmental and insect demographic factors influence the spatial distribution of insects on a community level in stored grain, and how the spatial distribution patterns of these insects change during a storage period of several months.

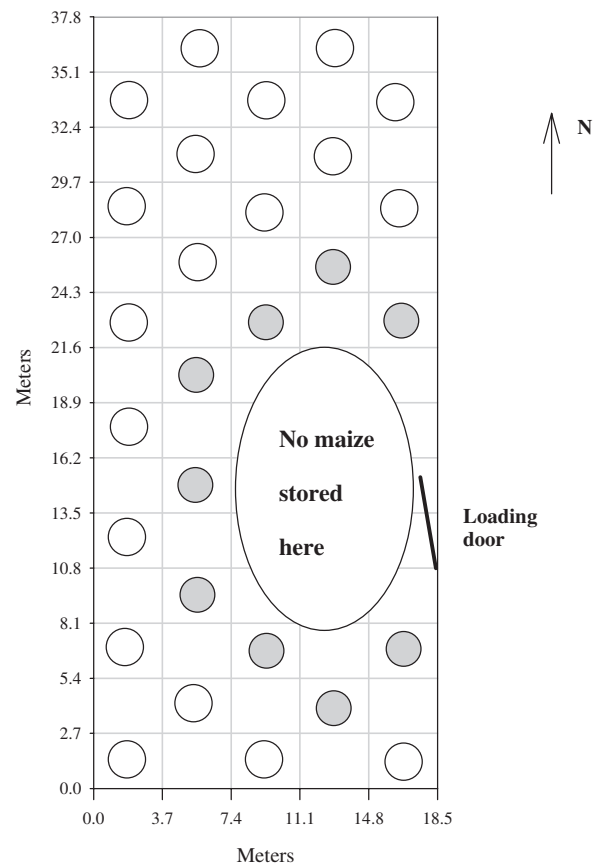
The physical environment can play an important role in the establishment of insect populations in grain masses. Small differences in temperature and grain moisture content have been shown to have a substantial impact on development time, mortality, and fecundity of both stored-product moths (Savov 1973; Bell 1975; Subramanyam & Hagstrum 1993) and beetles (Longstaff 1981; Jacob & Fleming 1990; Throne 1994) in North America. Behavioral experiments of *Cryptolestes ferrugineus* (Steph) showed positive orientation towards regions in stored grain with comparatively preferable moisture content (Loschiavo 1983) and temperature (Flinn & Hagstrum 1998). Also, when *Tribolium castaneum* (Hbst.) individuals were offered a temperature gradient from 22 to 36°C they tended to stay longest in the region with 30°C (Flinn & Hagstrum 1998). Toews and Phillips (2002) conducted trapping studies with *C. ferrugineus* in experimental silos containing wheat and showed that beetles were caught more abundantly with probe traps when the temperature was either lower or above the optimum growth conditions. The results by Toews and Phillips (2002) suggested that *C. ferrugineus* individuals moved more (probably due to dispersal) when the beetles were under unfavorable temperature conditions. Although these studies reveal important information about the ability of individual stored-product insect species to respond to abiotic conditions in controlled environments, the response pattern may become substantially more complicated in a real storage system with multiple insect species from several trophic levels involved.

In the present study we sampled insects in a commercial maize storage facility for 13 consecutive weeks and we used the data to: (i) determine the seasonal fluctuation in the demographic composition of the insect community; (ii) conduct ordination analysis to examine the association of insect taxa and to determine their distribution over time and along abiotic and geographic gradients; (iii) describe demographic characteristics of insect communities in maize samples with high abundance of either *Plodia interpunctella* (Hbn) (*Plodia* samples) or *Sitophilus zeamais* (Motsch) (*Sitophilus* samples); and (iv) to examine at what extent natural enemies were spatially associated with their prey species.

## Methods

### Maize samples

A maize storage facility in Madison, Wisconsin, USA with dimensions of 18.5 m (width) × 37.8 m (length) × 5 m (height) and a total capacity of approximately 1800 T was sampled weekly from 1 July to 30 September 1992 (13 consecutive weeks) (Fig. 1). A grid of 70 equal-sized plots of 2.7 m × 3.7 m was established. The original intention had been to sample every second sampling plot in the storage facility, however, the facility was only partially filled with shelled dent maize, and no maize was stored in the area closest to the loading door on the east side. In addition, maize was gradually removed by the manager, so for the part of the facility with stored maize, the maize surface was initially about 2 m from the ceiling when this study began, and as maize was removed by the owner during the course of this study the maize surface was about 3 m from the ceiling by the time the study was completed. A total of 28 sampling plots was initially



**Fig. 1.** Outline of the grid of sampling plots in the maize storage facility used in the study, Madison, Wisconsin. The pattern in circles represents the difference in number of weekly samples obtained from each plot. The loading door was located in the southeastern part of the storage facility. (○), sampled during 13 weeks; (◐), sampled during 1–3 weeks in July.

sampled, and after 3 weeks, 19 sampling plots were sampled for the remaining 11 weeks. The maize had been harvested and mechanically dried to 12–14% moisture content at the end of 1991. Weekly samples of maize were obtained from the center of each sampling plot using a specially fabricated cylindrical cup sampler, which removed 1140 mL maize with each application. For each sampling plot, maize samples were obtained at depths of 0–30 cm (top sample) and 30–60 cm (bottom sample) from the maize surface. Maize samples were returned to the laboratory where insects were sifted out and identified. The granivore, *P. interpunctella*, was identified as larva, or unsexed adult, granivorous beetle larvae were not identified further, while all other insect taxa were unsexed adults. A paired *t*-test was used to compare insect species composition of top and bottom samples.

Temperature was recorded with a digital thermometer (Cole-Palmer Instrument Company, Chicago, IL, USA) at the time of sampling in top and bottom maize samples. Moisture content was determined bi-weekly for top and bottom maize samples using a Steinlite digital moisture meter (Seedburo Equipment Company, Chicago, IL, USA).

### Ordination

Ordination techniques in CANOCO (canonical community ordination) (Ter Braak 1992) for Windows version 4.02 were used to examine the association of insect

taxa and to determine their distribution over time and along abiotic and geographic gradients. Comprehensive descriptions of the ordination techniques used are available in Jongman *et al.* (1995) and Ter Braak 1987, 1994, 1996). The choice of appropriate direct ordination analysis mainly depends on the total variance in the dataset, and as Jongman *et al.* (1995) pointed out, ordination techniques based on unimodal response curves are more general than ordination techniques based on linear models. Canonical correspondence analysis is based on unimodal response curves and is described in detail by Ter Braak (1987), and this direct ordination technique was used with equal weight to all insect group and samples (no down-weighting).

The canonical correspondence analysis was conducted with monthly mean counts of granivores (eight taxa) and fungivores (four taxa) (Table 1) as response variables (predators and parasitoids were excluded). The monthly mean counts of insect taxa were  $\text{Log}_{10}(x + 1)$  transformed before conducting the canonical correspondence analysis. Using monthly means, the canonical correspondence analysis was based upon: 27 top and 27 bottom samples in July, and 19 top and 19 bottom samples in each of August and September (total of 130 maize samples). We used the canonical correspondence analysis to determine to what extent monthly means of insect taxa were significantly associated with the following explanatory variables (names in parentheses): (i) vertical position of samples, with 1 = top samples and 2 = bottom samples (position);

**Table 1** Occurrence of identified insect taxa in top and bottom maize samples

Taxon	Order: Family	Type	Top samples		Bottom samples	
			Weeks	Mean(SE)	Weeks	Mean (SE)
<i>Plodia interpunctella</i> (Hbn.) [L]	Lepidoptera: Pyralidae	G	13	0.32 (0.02)	13	0.16 (0.01)
<i>Sitophilus zeamais</i> Motsch. [A]	Coleoptera: Curculionidae	G	13	0.27 (0.02)	13	0.21 (0.02)
<i>Lathridius minutus</i> (L) [A]	Coleoptera: Lathridiidae	F	12	0.13 (0.01)	12	0.07 (0.01)
<i>Tribolium castaneum</i> (Hbst) [A]	Coleoptera: Tenebrionidae	G	13	0.12 (0.01)	13	0.07 (0.01)
<i>Ahasverus advena</i> (Waltl) [A]	Coleoptera: Silvanidae	F	13	0.12 (0.01)	13	0.12 (0.01)
<i>Nemapogon granella</i> (L) [A]	Lepidoptera: Tineidae	G	11	0.05 (0.01)	6	0.01 (0.00)
<i>Cryptolestes ferrugineus</i> (Steph.) [A]	Coleoptera: Laemophoeidae	G	13	0.09 (0.01)	11	0.06 (0.01)
<i>Plodia interpunctella</i> [A]β	Lepidoptera: Pyralidae	G	11	0.04 (0.00)	3	0.00 (0.00)
<i>Typhaea stercorea</i> (L) [A]	Coleoptera: Mycetophagidae	F	13	0.04 (0.00)	12	0.04 (0.01)
Beetle larvae [L]	Coleoptera	G	6	0.01 (0.00)	3	0.01 (0.00)
<i>Oryzaephilus surinamensis</i> (L) [A]	Coleoptera: Cucujidae	G	6	0.01 (0.00)	4	0.00 (0.00)
<i>Carpophilus</i> sp. [A]	Coleoptera: Nitidulidae	F	3	0.00 (0.00)	3	0.00 (0.00)
<b>Not included in the ordination analysis</b>						
<i>Dermestes lardarius</i> L. [A]	Coleoptera: Dermestidae	O	3	0.01 (0.00)	4	0.01 (0.00)
Diptera [A]	Diptera	O	6	0.01 (0.00)	5	0.01 (0.00)
<i>Anisopteromalus calandrae</i> H. [A]	Hymenoptera: Pteromalidae	P	11	0.17 (0.02)	11	0.11 (0.02)
Hymenoptera [A]	Hymenoptera	P	9	0.04 (0.01)	9	0.02 (0.00)
<i>Lyctocoris campestris</i> (F) [A]	Heteroptera: Anthracoridae	Pr	9	0.05 (0.01)	2	0.01 (0.00)
<i>Bracon hebetor</i> Say [A]	Hymenoptera: Braconidae	P	9	0.04 (0.01)	4	0.01 (0.00)

Insect taxa from top (0–30 cm from surface) and bottom (30–60 cm from surface) maize samples. '[A]', adults; '[L]', larvae. Insect taxa were grouped into 'Types' with: 'G', granivore; 'F', fungivore; 'O', Omnivore; 'P', parasitoid; and 'Pr', predator. 'Weeks' refer to the number of weeks in which the insect taxon was found in maize samples.

(ii) east–west coordinates of plots (measured in meters) (easting); (iii) north–south coordinates of plots (measured in meters) (northing); (iv) monthly mean grain temperature ( $^{\circ}\text{C}$ ) per sample (temperature); (v) monthly mean moisture content (%) per sample (moisture); and (vi) a discrete time-variable ranging from 1 to 3 (months) was used to account for the variation of consecutive monthly means. The significance of explanatory variables was determined using 199 unrestricted permutations in a Monte Carlo test. In the joint plot ordination analysis of insect taxa and maize samples, the axes units were presented in standard deviations. Due to apparent indications of auto-correlation among explanatory variables, partial canonical correspondence analyses were conducted in which the strength of an explanatory variable was examined after removing the effects of other explanatory variables. We also conducted partial canonical correspondence analyses to determine the significance of explanatory variables after removing the effects of two geographic variables (northing and easting).

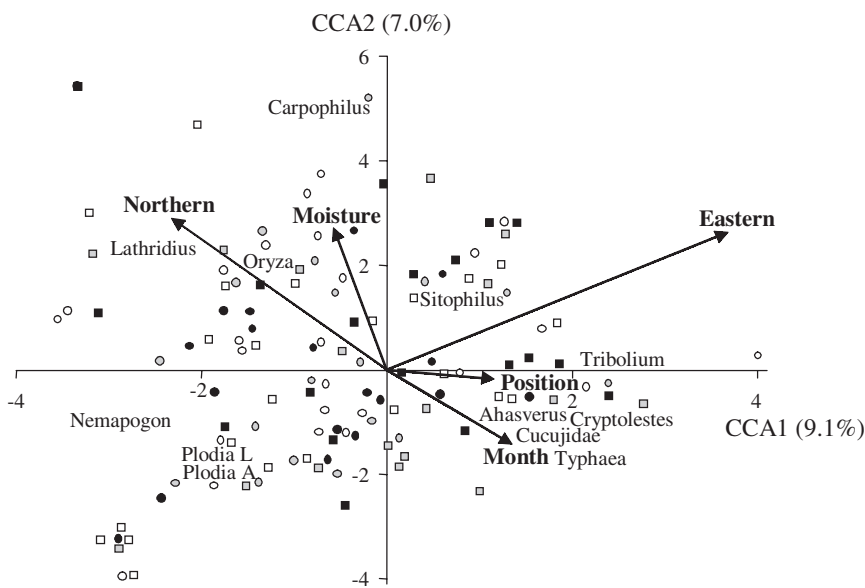
We used canonical correspondence analysis to characterize the insect composition of maize samples with comparatively high abundance of the two principal granivores: *P. interpunctella* and *S. zeamais*. The position of weekly maize samples in the canonical correspondence analysis was used to group the maize samples into ‘*Sitophilus* samples’ or ‘*Plodia* samples’: weekly maize samples that were located along the positive side of both principal axes, CCA1 and CCA2 (Fig. 2), were considered *Sitophilus* samples, while weekly maize samples that were located along the negative side of both principal axes, CCA1 and CCA2, were considered *Plodia* samples. A third sample group represented the remaining grain samples. The means per maize sample

of grain temperature, grain moisture, and geographic position were estimated for these three groups of samples. Four demographic characteristics (means per maize sample) were also used to describe *Plodia* samples and *Sitophilus* samples, but these were not included in the ordination analysis: (i) species diversity was measured according to the Shannon-Weaver function (diversity) (Southwood 1987); (ii) proportion of most abundant insect taxon of total number of insects per sample (dominance); (iii) number of insect taxa per sample (taxa); and (iv) total sum of insect individuals per sample (density). PROC MIXED (SAS 8.01; SAS Institute 1999) was used to conduct a one-way analysis of variance (ANOVA) with contrasts of the spatial, abiotic, and demographic characteristics of *Plodia* samples, *Sitophilus* samples, and the remaining samples. The same one-way ANOVA was used to compare the mean abundance of natural enemies in *Plodia* samples, *Sitophilus* samples with the mean of natural enemies in the remaining samples.

## Results

### Seasonal variation

A total of 18 insect taxa were identified in 257 top and 257 bottom maize samples collected during 13 consecutive weeks, and they included eight granivores (six determined to species, one of which was collected as larvae and adults; and one a conglomerate of beetle larvae), four fungivores (three identified species and one determined to genus), one predatory species, three species of parasitic Hymenoptera (two identified to species and one undetermined hymenopteran species), one omnivorous beetle species, and a group of fly adults



**Fig. 2.** Canonical correspondence analysis of the 18 insect taxa (Table 1) in top and bottom maize samples. Significant explanatory variables were in order of importance: east–western position of sampling plots (easting), north–southern position of eastern position of vegetation plots (northing), the difference between top and bottom maize samples (position), seasonal variation (month), and moisture content of maize samples (moisture). Axes are in units of standard deviations, and percentages represent the amount of the total variation explained by these axes. (○), July (top samples); (●), August (top samples); (□), July (bottom samples); (■), August (bottom samples); (●), September (top samples).

that were not classified trophic level (diptera) (Table 1). Mean sample abundance of insect taxa was significantly higher ( $T_{17} = 3.82$ ,  $P = 0.01$ ) and the different insect taxa were significantly more frequent in the weekly sampling events of top samples compared to bottom samples ( $T_{17} = 2.90$ ,  $P = 0.01$ ) [e.g. *P.interpunctella* adults, *Nemapogon granella* (L), *Lyctocoris campestris* (F), and *Bracon hebetor* Say]. *P.interpunctella* larvae and *S. zeamais* adults were the most abundant insect taxa in both top and bottom samples, and together with *Ahas-versus advena* (Waltl) they occurred in all weekly samples. Twelve of the encountered insect taxa were represented by less than 10 individuals in the entire study.

Table 2 summarizes the occurrence of insect taxa and abiotic conditions in samples during the 13 weeks of sampling. The main seasonal trends were: (i) the number of uninfested samples declined over time; (ii) the grain temperature peaked around mid-August, while the grain moisture content generally showed a gradual increase; (iii) the number of insect taxa and insect density in maize samples increased over time; and (iv) the Shannon index of diversity and the level dominance remained fairly stable over time.

### Ordination

The principal ordination axes in an initial detrended correspondence analysis (not shown) were both about five standard deviations long, which suggested that direct gradient analysis based on unimodal response curves would be more appropriate than methods based on linear response curves. The principal ordination axes in the initial detrended correspondence analysis

explained 23.2% of the total variance, which was about twice the variance explained by the two principal ordination axes in the canonical correspondence analysis (16.1% in Fig. 2). Hence, the combination of five significant explanatory variables included in the ordination accounted for about two-thirds of the variance to be explained in a two-dimensional space. The tested explanatory variables were selected individually by order of importance and are briefly described below.

The east–west location of sample plots (easting) was the explanatory variable that explained most of the total variance ( $F = 9.94$ ,  $P = 0.01$ ). Comparing the most abundant insect taxa, *P.interpunctella*, *Oryzaephilus surinamensis* (L), and *Lathridius minutus* (L) were mainly found in samples from the western part of the storage facility (negatively correlated with the variable easting), while *S. zeamais*, *T.castaneum*, and *C.ferrugineus* mainly occurred in the eastern part of the storage facility. The second most important explanatory variable, north–south location of sample plots ( $F = 7.09$ ,  $P = 0.01$ ). *O.surinamensis*, and *L.minutus* mainly occurred in the northern part of the storage facility, while *C.ferrugineus* mainly occurred in the southern part of the storage facility. The explanatory variable, accounting for the vertical position of maize samples, position, was the third most important variable ( $F = 3.32$ ,  $P = 0.01$ ), which suggested that there was a significant difference in occurrence of insect taxa in top and bottom samples. Insect taxa located in the left part of Fig. 2 were mainly associated with top samples, while insect taxa to the right were mainly associated with bottom samples. The time variable, month, accounting for the variation in insect occurrence throughout the monitoring period, was the fourth most important

**Table 2** Summary of sampling results during 13 weeks in a maize storage facility

Date	Samples		Temperature (°C)	Moisture(%)	Taxa		Density		Shannon	Dominance
	Total	Non inf.	Mean (SE)	Min–Max	Min–Max	Total	Mean (SE)	Max	Mean (SE)	Mean (SE)
1 July	54	14			2.11 (0.28)	14	4.87 (0.89)	32	0.521 (0.08)	0.506 (0.05)
8 July	42	9	16.5–24.1	10.8–13.6	1.81 (0.26)	13	3.93 (0.76)	20	0.437 (0.08)	0.569 (0.06)
15 July	38	16	17.0–22.0		1.55 (0.36)	14	5.50 (2.90)	109	0.347 (0.09)	0.440 (0.07)
22 July	38	13	17.0–21.2	10.3–13.9	1.71 (0.35)	9	6.25 (1.91)	43	0.480 (0.10)	0.315 (0.06)
29 July	38	16	17.6–24.5		1.84 (0.36)	19	6.21 (3.08)	117	0.467 (0.10)	0.373 (0.06)
5 Aug	38	8	17.7–25.7	11.2–14.3	2.76 (0.48)	20	10.47 (2.66)	63	0.553 (0.10)	0.569 (0.06)
12 Aug	38	10	18.3–27.6		2.18 (0.37)	18	8.34 (2.47)	68	0.488 (0.09)	0.519 (0.06)
19 Aug	38	7	17.5–28.0	11.5–14.2	2.53 (0.44)	22	12.89 (5.41)	161	0.522 (0.09)	0.602 (0.06)
26 Aug	38	9	18.3–26.6		2.18 (0.40)	17	8.18 (2.89)	77	0.479 (0.09)	0.545 (0.06)
2 Sept	38	5	17.8–24.6	11.1–14.3	3.97 (0.57)	21	13.63 (3.87)	120	0.909 (0.12)	0.489 (0.05)
9 Sept	38	9	17.6–23.0		2.76 (0.58)	20	10.45 (3.71)	110	0.575 (0.11)	0.518 (0.06)
16 Sept	38	7	11.3–14.4		3.05 (0.47)	19	9.00 (2.20)	54	0.689 (0.11)	0.526 (0.06)
23 Sept	38	7	14.3–22.2		3.03 (0.56)	19	13.66 (4.17)	120	0.597 (0.11)	0.575 (0.06)

'Date', the first day in the sampling week; 'Total', the total number of samples per week; 'Non. Inf.', the number of maize samples in which no insects were found. For temperature and grain moisture content, the minimum and maximum are presented. 'Taxa', mean number per maize sample and total number of insect taxa from that week; 'Density', mean and maximum number of insect individuals per sample; 'Shannon', mean index of diversity per sample (Shannon-Weaver Function [Southwood 1987]), and 'Dominance', mean proportion of most abundant insect taxon of total number of insects per sample.

explanatory variable ( $F = 3.40$ ,  $P = 0.01$ ), and *L. minutus*, and *O. surinamensis* occurred mainly in the beginning of the monitoring period, while *C. ferrugineus*, *Typhaea stercorea* (L.), and *Ahasverus advena* (Waltl) predominated in the last part of the monitoring period. The two most important granivores, *S. zeamais* and *P. interpunctella*, were unrelated with the time variable, which suggests that they were similarly abundant throughout the monitoring period. The variable representing moisture content of the stored maize, moisture, was the fifth most important explanatory variable ( $F = 2.81$ ,  $P = 0.01$ ), and an unknown *Carpophilus* species was mainly found in samples with high moisture content, while the two main fungivores (*T. stercorea*, and *A. advena*) had a negative association with moisture content in the maize. *S. zeamais* showed a slight positive association with the explanatory variable accounting for the maize moisture content, while *P. interpunctella* was unrelated with this variable. The explanatory variable, temperature, did not explain a significant part of the total variance ( $P > 0.05$ ).

### Partial canonical correspondence analyses

From the small angles between several of the explanatory variables in Fig. 2, we suspected that auto-correlation of the explanatory variables attributed to their statistical significance. For instance, it was not clear whether: (i) there was a significant difference between bottom and top maize samples because of a vertical difference in grain moisture content; (ii) certain insect taxa were more abundant in the eastern part of the storage facility because the grain moisture content was comparatively higher there; or (iii) there was a significant monthly time trend, because the insects mainly immigrated into the storage facility in either the northern or southern part. The partial canonical correspondence analyses we conducted showed that the explanatory variable: (i) easting was still significant after removing the effect of moisture and position ( $F = 7.25$ ,  $P = 0.01$ ); (ii) month was still significant after removing the effect of northing ( $F = 5.20$ ,  $P = 0.01$ ); (iii) northing was still significant after removing the effect of month ( $F = 2.24$ ,  $P = 0.01$ ); (iv) moisture was still significant after removing the effect of easting and position ( $F = 1.76$ ,  $P = 0.02$ ), and (v) position was still significant after removing the effect of easting and moisture ( $F = 6.50$ ,  $P = 0.01$ ). Consequently, the apparent auto-correlation of explanatory variables in Fig. 2 was mainly related to the restriction of visualizing the ordination analysis in a two-dimensional space.

### *Plodia* and *Sitophilus* samples

Samples located in the upper right part of Fig. 2 were considered *Sitophilus* samples (21 samples), while

samples in the lower left part were considered *Plodia* samples (39 samples), while ‘other samples’ represents the remaining samples (70 samples). Characteristics of *Plodia* and *Sitophilus* samples and other samples are summarized in Table 3. There was a significant difference in the eastern position of the three groups of samples ( $F_{2,127} = 15.70$ ,  $P < 0.01$ ), and *Plodia* samples were characterized by being located significantly more to the east than *Sitophilus* samples ( $F_{1,127} = 20.66$ ,  $P < 0.01$ ) and other samples ( $F_{1,127} = 25.40$ ,  $P < 0.01$ ). There was no significant difference in the northern position of the three groups of samples ( $F_{2,127} = 2.81$ ,  $P = 0.06$ ). The temperature was significantly lower in *Plodia* samples compared to other samples ( $F_{1,127} = 7.63$ ,  $P = 0.01$ ), but there was no significant difference in the temperatures of *Plodia* samples and *Sitophilus* samples ( $F_{1,127} = 1.38$ ,  $P = 0.24$ ). The moisture content of the grain was significantly lower in *Plodia* samples compared to both other samples ( $F_{1,127} = 5.40$ ,  $P = 0.02$ ) and *Sitophilus* samples ( $F_{1,127} = 7.64$ ,  $P = 0.06$ ), but there was no significant difference in the temperatures of *Sitophilus* samples and other samples ( $F_{1,127} = 1.30$ ,  $P = 0.26$ ). The level of dominance varied significantly among the three groups of samples ( $F_{2,127} = 12.49$ ,  $P < 0.01$ ) with a significantly higher level of dominance in *Sitophilus* samples ( $F_{1,127} = 16.42$ ,  $P < 0.01$ ) and *Plodia* samples ( $F_{1,127} = 15.81$ ,  $P < 0.01$ ) compared to other samples. There was no significant difference in: position (top or bottom) of the three groups of samples ( $F_{2,127} = 1.75$ ,  $P = 0.18$ ); monthly

**Table 3** Mean (SE) characteristics of *Plodia* and *Sitophilus* samples compared to other samples

Variable	Sample group		
	<i>Plodia</i>	<i>Sitophilus</i>	Other
Number	39	21	70
Position	1.38 (0.08)	1.62 (0.11)	1.53 (0.06)
Eastern	4.04 (0.72)	9.96 (1.21)	8.88 (0.57)
Northern	18.17 (1.85)	26.04 (2.75)	21.21 (1.58)
Temperature (°C)	18.85 (0.21)	19.37 (0.22)	19.75 (0.23)
Moisture (%)	12.53 (0.13)	13.07 (0.14)	12.86 (0.09)
Month	1.92 (0.14)	2.00 (0.20)	1.81 (0.10)
Taxa	5.72 (0.63)	5.43 (0.96)	5.26 (0.50)
Dominance	0.60 (0.04)	0.64 (0.05)	0.42 (0.02)
Density	5.47 (0.91)	8.99 (2.59)	10.13 (2.37)
Shannon	1.14 (0.10)	1.11 (0.13)	1.22 (0.07)

‘*Plodia*’, a group of 39 samples located in the lower left part of Fig. 2; ‘*Sitophilus*’, a group of 21 samples located in the upper right part of Fig. 2; ‘Other’, the remaining 70 samples from the analysis. ‘Position’, the mean vertical position (1 = top samples and 2 = bottom samples); ‘Eastern’ and ‘Northern’, the east–west and north–south coordinates (m) (see Fig. 1); ‘Temperature’ (°C), mean temperature; ‘Moisture (%)’, mean moisture content; ‘Month’, mean monthly score, as each sample was given a monthly score with July = 1, August = 2, and September = 3; ‘Taxa’, mean number of insect taxa; ‘Dominance’, mean proportion of most abundant insect taxon of total number of insects; ‘Density’, mean total sum of insect individuals per sample; ‘Shannon’, Shannon index of diversity (Shannon–Weaver Function [Southwood 1987]).

occurrence of samples ( $F_{2,127} = 0.48, P = 0.62$ ); number of taxa in samples ( $F_{2,127} = 0.26, P = 0.77$ ), density of insects in samples ( $F_{2,127} = 1.12, P = 0.33$ ), and Shannon diversity index of samples ( $F_{2,127} = 1.18, P = 0.31$ ) of the three sample groups. The mean abundance of granivores and fungivores in other samples and *Plodia* and *Sitophilus* samples is summarized in Fig. 3. Interestingly, *Plodia* samples were characterized by lower abundance of all granivores and fungivores, except *P.interpunctella* and *N.granella*, than the mean in all samples. Consequently, the insect community in *Plodia* samples was highly dominated by *P.interpunctella*. In *Sitophilus* samples, the abundance of *T.castaneum*, *A.advena*, and *C.ferrugineus* was higher than the overall mean in samples, which suggests that the insect populations in *Sitophilus* samples was more heterogeneous than in *Plodia* samples.

The abundance of natural enemies in all samples and *Plodia* and *Sitophilus* samples is summarized in Fig. 4. There was no significant difference in the abundance of *L.campestris* ( $F_{2,127} = 0.56, P = 0.57$ ), *A.calandreae* ( $F_{2,127} = 0.18, P = 0.83$ ), and *B.hebetor* ( $F_{2,127} = 1.47, P = 0.23$ ) among the three sample groups.

### Discussion

Ordination provides powerful analytical tools for spatial, temporal, and ecologic analyses of stored-product insect communities, and this approach is used to quan-

tity the distribution of organisms along geographic, environmental, demographic, and abiotic gradients. Several studies have used ordination techniques to outline biophysiological patterns in stored-grain to describe: (i) changes in physical characteristics of damaged grain as a consequence of arthropod infestations (Sinha *et al.* 1969b; Imura & Sinha 1989); (ii) composition analysis of mites, fungi and insects in stored grain (Sinha *et al.* 1969a; Sinha 1977; Sinha *et al.* 1979; White & Sinha 1980).

### Occurrence of insects

In this study, we analysed a naturally infested maize facility in which both emigration and immigration of insects likely occurred and was unaccounted for by our work. There was a considerable level of human disturbance of the stored grain (gradual removal of maize from the storage facility) and likely variation in ambient climate conditions during the sampling period. Despite these sources of environmental instability, we found that the two main granivores, *P.interpunctella* and *S.zeamais*, were abundant throughout the monitoring period and that 10 insect taxa out of the 18 encountered insect taxa were identified in at least 10 of the weekly sampling events. Therefore, a fairly high insect diversity was observed throughout the monitoring period. The species composition of samples in this study was similar to those found in other surveys of insects in stored maize facilities in North America (Barak & Harein

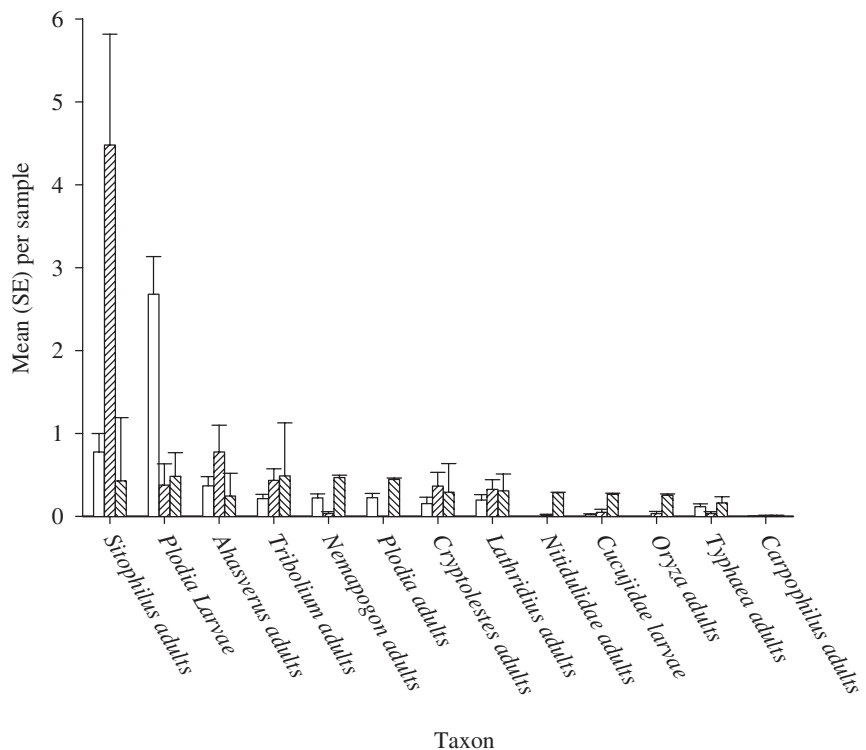
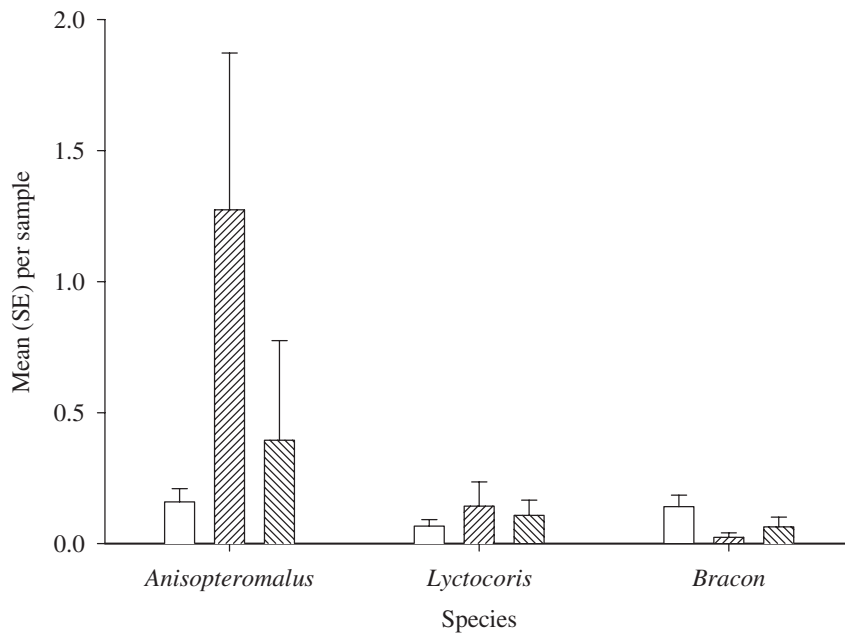


Fig. 3. Mean (SE) abundance of granivores and fungivores in ‘*Plodia* samples’ ( $n = 39$ ), ‘*Sitophilus* samples’ ( $n = 21$ ), and other samples ( $n = 70$ ). *Plodia* samples and *Sitophilus* samples represented grain samples in the lower left part and the upper right part of Fig. 2, respectively. (□), *Plodia* samples ( $n = 39$ ); (▨), *Sitophilus* samples ( $n = 21$ ); (■), other samples ( $n = 70$ ).



**Fig. 4.** Mean (SE) abundance of natural enemies in 'Plodia samples' ( $n = 39$ ), 'Sitophilus samples' ( $n = 21$ ), and other samples ( $n = 70$ ). Plodia samples and Sitophilus samples represented grain samples in the lower left part and the upper right part of Fig. 2, respectively. (□), Plodia samples ( $n = 39$ ); (▨), Sitophilus samples ( $n = 21$ ); (▩), other samples ( $n = 70$ ).

1981; Storey *et al.* 1983; Arbogast & Mullen 1988; Arbogast & Throne 1997).

#### Distribution of insect taxa along gradients

The canonical correspondence analysis revealed that over a 3-month storage period, the identified insect taxa were distributed significantly (positively or negatively correlated) along most of the examined explanatory variables, and the implications of this are briefly summarized below.

##### Vertical gradient

We found a significant difference in insect distribution obtained from top and bottom samples. Hagstrum *et al.* (1998) compared catches with probe traps of four important storage beetles, *C. ferrugineus*, *Rhyzopertha dominica* (F), *A. advena*, and *T. stercora* at the surface and 7.6 cm below the surface of stored wheat. Except for *R. dominica* trap catches, Hagstrum *et al.* (1998) obtained systematically higher catches near the grain surface compared to further into the grain mass. Despite the observed quantitative difference between insect communities in top and bottom samples, all insect taxa were either most abundant in top samples or equally abundant in top and bottom maize samples. Thus, adequate qualitative information about the presence of insect species could have been obtained from top samples alone.

##### Horizontal gradients

Despite the many factors affecting the stability of the environment inside the maize storage facility, granivores were clearly spatially segregated with: (i) *S. zeamais* and *T. castaneum* being most abundant in the eastern part of the storage facility; (ii) *P. interpunctella* occurring predominantly in the western part of the storage facility; and (iii) *O. surinamensis* mainly associated with the north-western part of the storage facility.

The spatial segregation pattern of granivores persisted throughout the monitoring period, and it seems reasonable to assume that stochasticity during the initial infestation process, at least partially, is responsible for the spatial segregation of granivores. However, during the fourth weekly sampling event as many as 117 *S. zeamais* individuals were identified in a single maize sample, while 16 maize samples from the same week did not contain any insects. In general, temperature and grain moisture content were only weakly associated with this highly aggregated spatial distribution pattern of insect taxa. Hutchinson (1957) distinguished between the 'fundamental' and the 'realized' niche of a species, in which the fundamental niche represents the range along ecologic variables under which a species can survive, while the realized niche represents its actual distribution along these ecologic variables. Although all the grain in a storage facility is potentially susceptible to insect granivores, it is possible that interspecific competition and predation influenced the spatial and temporal distribution pattern of stored-product insects in the grain. Field studies documenting this type of spatial segregation in stored-product insect communities are scarce, but White and Sinha (1980) conducted multiple sampling of experimental bins containing stored wheat infested with different insect combinations of *T. castaneum*, *Rhyzopertha dominica* (F), *S. oryzae*, *C. ferrugineus*, and *O. surinamensis* during a 22-week



period. Using principal component analysis, they showed that, even in experimental storage facilities with low species diversity, there was a tendency of spatial segregation of some species while others tended to coexist.

There may be several explanations for the comparatively lower abundance of fungivorous and granivorous insect species in maize samples with dominating *P. interpunctella* infestations. *T. castaneum* is known as a potential predator of *P. interpunctella* progeny (Lecato & Flaherty 1973), so it is likely that ovipositing *P. interpunctella* females will try to avoid locations with high *T. castaneum* populations. In addition, secretion of oily droplets by phycitid stored-product larvae on the silk has been studied (Mossadegh 1978, 1980), and these oil droplets have been found to be repelling to conspecific larvae (Mudd & Corbet 1973; Mossadegh 1980), and, although we know of no studies supporting this hypothesis, it may be speculated that the same oil droplets are repelling to other granivorous and fungivorous insects as well.

### Abiotic gradients

Several studies of individual stored-product insect species under controlled conditions have demonstrated how they seem to respond to differences in abiotic conditions (Loschiavo 1983; Flinn & Hagstrum 1998; Toews & Phillips (2002). This analysis suggested that temperature and moisture content of the maize were only loosely associated with the distribution of the different insect taxa. The relationship between heat generation and insect infestations is important for the use of thermo-monitoring in bulk grain for detection of developing insect problems. Hagstrum *et al.* (1999) mentioned that *S. oryzae* may cause the temperature to increase in infested wheat. In the study described above, White and Sinha (1980) showed that the occurrence of both *T. castaneum* and *R. dominica* was positively correlated temperature and moisture content of the wheat. In our study with multiple insect species originating from natural infestations during several months of storage, we found no significant association of temperature with distribution of insects. Within the examined range of temperature we therefore find it unlikely that thermo-monitoring could have been used for detection of high insect densities. Moisture content explained a significant part of the total variance, but it seemed to affect the distribution of fungivores more than the distribution of granivores.

### Natural enemies

Presence of several naturally occurring parasitoids was documented. *A. calandrae* is a larval parasitoid of con-

cealed or internal-feeding stored-product beetles (Ryoo *et al.* 1996), and they are natural parasites on stored-product weevils (Williams & Floyd 1971). However, we found this parasitoid to be randomly distributed in the maize samples. Over an 8-year survey in a maize storage facility, Arbogast and Mullen (1988) found *S. zeamais* to be the only suitable host for this parasitoid, and *A. calandrae* was suggested to provide sufficient control of *S. zeamais* population if introduced early in the storage season (Arbogast & Mullen 1990). Although encountered in fairly low numbers, *A. calandrae* was present in 11 of the 13 sampling weeks, and *A. calandrae* was the only parasitoid that was positively associated with the occurrence of *S. zeamais*, *C. ferrugineus*, and *T. castaneum*. *B. hebetor* is a parasitoid of wandering late-instar larvae of pyralid moths. It has been estimated that 97% suppression of a *P. interpunctella* infestation can be obtained by releasing one 1-day-old *B. hebetor* female per 7.2 host larvae (Reinert & King 1971). Similar to *A. calandrae*, we found *B. hebetor* to be randomly distributed among maize samples, and it occurred in 9 of the 13 sampling weeks. *L. campestris* is a polyphagous predator of stored-product insects (Parajulee & Phillips 1995), and laboratory experiments suggested that it can feed on a wide range of species and age-sizes of preys (Parajulee & Phillips 1993). In this study, the abundance of *L. campestris* was not significantly associated with either *Plodia* samples or *Sitophilus* samples. Since this study did not include control sampling plots (without presence of natural enemies), it is not possible to determine the relative role of parasitoids and predators on the temporal and spatial population dynamics of granivores and fungivores.

### Conclusions

The following conclusions can be drawn from the present study:

- 1 The most abundant granivorous insects had significantly different spatial distribution patterns and these patterns remained constant throughout the monitoring period.
- 2 In the ordination analysis, temperature did not explain a significant part of the total variance, and grain moisture content was the weakest of the significant explanatory variables. This emphasizes that, compared to other examined explanatory variables, abiotic factors apparently had limited effect on the insects species' spatial distribution patterns.
- 3 *Plodia* samples were characterized by low abundance of all granivores and fungivores, except *P. interpunctella*. Conversely, *Sitophilus* samples had high abundance of *T. castaneum*, *A. advena*, and

*C. ferrugineus*. Consequently, *Sitophilus* samples seemed to comprise more diverse insect communities than *Plodia* samples.

- 4 Natural enemies were not significantly associated with their main hosts.
- 5 We used ordination analysis to determine that stored-product insect species had significantly different distribution patterns along geographic and abiotic gradients. Without knowing the process of infestation, we can only speculate about the reasons for the observed spatial segregation of the most abundant granivores. Based on the present analysis a set of laboratory experiments can be developed as we suspect that there may be important competition factors among *P. interpunctella* and *S. zeamais*, and that *S. zeamais* is more willing to share a microhabitat with fungivores and scavengers than *P. interpunctella*.

## Acknowledgements

We thank Dr James E. Throne for his critical review of a previous version of this manuscript. This research was supported in part by a grant from the USDA, Cooperative and State Research, Education and Extension Service in the Risk Avoidance and Mitigation Program, agreement no. 00-51101-9674. This manuscript was approved for publication by the Oklahoma Agricultural Experiment Station and supported by Agricultural Experiment Station project number OKL 02320.

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