

## Transgenes Sustain Epigeal Insect Biodiversity in Diversified Vegetable Farm Systems

T. W. LESLIE,<sup>1</sup> G. A. HOHEISEL,<sup>2</sup> D. J. BIDDINGER, J. R. ROHR, AND S. J. FLEISCHER

501 ASI Building, The Pennsylvania State University, University Park, PA 16802

---

Environ. Entomol. 36(1): 234–244 (2007)

**ABSTRACT** Many ecological studies have focused on the effects of transgenes in field crops, but few have considered multiple transgenes in diversified vegetable systems. We compared the epigeal, or soil surface-dwelling, communities of Coleoptera and Formicidae between transgenic and isoline vegetable systems consisting of sweet corn, potato, and acorn squash, with transgenic cultivars expressing Cry1 (A)b, Cry3, or viral coat proteins. Vegetables were grown in replicated split plots over 2 yr with integrated pest management (IPM) standards defining insecticide use patterns. More than 77.6% of 11,925 insects from 1,512 pitfall traps were identified to species, and activity density was used to compare dominance distribution, species richness, and community composition. Measures of epigeal biodiversity were always equal in transgenic vegetables, which required fewer insecticide applications than their near isolines. There were no differences in species richness between transgenic and isoline treatments at the farm system and individual crop level. Dominance distributions were also similar between transgenic and isoline farming systems. Crop type, and not genotype, had a significant influence on Carabidae and Staphylinidae community composition in the first year, but there were no treatment effects in the second year, possibly because of homogenizing effects of crop rotations. Communities were more influenced by crop type, and possibly crop rotation, than by genotype. The heterogeneity of crops and rotations in diversified vegetable farms seems to aid in preserving epigeal biodiversity, which may be supplemented by reductions in insecticide use associated with transgenic cultivars.

**KEY WORDS** biodiversity, Carabidae, genetically modified crops, nontarget effects, Staphylinidae

---

Agriculture, which covers roughly one half of usable land on the planet, inevitably affects biodiversity, and its expansion and/or intensification could further impact biodiversity and ecosystem services (Stoate et al. 2001, Tilman et al. 2001, 2002). This has become a concern reflected in international policy; in 2002, 190 countries committed to the goals of the Convention on Biological Diversity that proposed to reduce the rate of biodiversity loss by 2010 (Balmford et al. 2005). Managing agricultural pests and maximizing crop yields, while simultaneously minimizing the effects to nontarget organisms, has become an important challenge in modern farm management (Green et al. 2005).

The influence of pest management on nontarget communities has drawn much attention with the increased development and use of transgenic crops. Many have looked specifically at monocultures of field crops using experimental designs intended to isolate the effect of introduced transgenes (Sisterson et al.

2004, Dively 2005, Whitehouse et al. 2005). Some, typically dealing with herbicide tolerant crops (but also see Cattaneo et al. 2006 for a recent example including insect-resistant cotton), have used a farm systems approach where differences in chemical inputs as a result of the introduction of transgenics are inherently expressed as part of the experimental design (Squire et al. 2003). However, no studies have considered diversified vegetable farm systems, which include different insecticide use patterns tied to integrated pest management (IPM) practices than are common in modern agriculture. To understand the effect of transgenic crops on biodiversity, more studies are needed that incorporate pest management changes that occur when using transgenic crops (e.g., changes in pesticide use patterns), while still representing common farm system practices (e.g., crop rotations).

Invertebrates comprise a large part of the biodiversity in agroecosystems, and the adoption of transgenic crops could influence invertebrate diversity (Angle 1994, Groot and Dicke 2002). Indirect effects on nontargets, including reduction of bees, butterflies, and weed seed-eating carabids, were present with adoption of certain herbicide-tolerant field crops in Great Britain (Brooks et al. 2003, Haughton et al. 2003). In

---

<sup>1</sup> Corresponding author: Department of Entomology, 501 ASI Building, Pennsylvania State University, University Park, PA 16802 (e-mail: twl117@psu.edu).

<sup>2</sup> Current address: CAHRNS/Extension, 1121 Dudley Avenue, Washington State University, Prosser, WA 99350.

contrast, 11 large ecotoxicology experiments showed little or no detrimental effects of insecticidal transgenic cultivars of field crops on insect diversity and abundance (Naranjo et al. 2005). Riddick et al. (2000) found no differences in coccinellid, formicid, or epigeal carabid populations in transgenic and nontransgenic potato farming systems that included foliar insecticide treatments timed with IPM thresholds. The epigeal, or soil surface-dwelling, invertebrate community is often included in ecological analyses because of their contribution to ecosystem functions [e.g., regulation of invertebrate herbivores (Asteraki 1993, Clark et al. 1994) and weed seed banks (Hartke et al. 1998, Tooley and Brust 2002)], ease of collection, and high capture rate of species and individuals, which can increase the power of statistical analyses (Duelli et al. 1999). Additionally, epigeal taxa can be good bio-indicators of varying habitat features or farm management systems (e.g., Carabidae: Carcamo et al. 1995, Ellsbury et al. 1998, Holland and Luff 2000, Thorbek and Bilde 2004; Staphylinidae: Lassau et al. 2005; Formicidae: Andersen and Majer 2004).

At least three transgenic vegetable crops with insecticidal proteins, or with gene constructs that influence insect-transmitted plant pathogens, have been commercially considered or are being introduced into northeastern U.S. agroecosystems. These include (1) sweet corn expressing the Cry1(A)b protein that protects against several lepidopterans, (2) potatoes that express the Cry3 protein aimed primarily against *Leptinotarsa decemlineata*, and (3) acorn squash (*Cucurbita* spp.) that express viral coat proteins that protect against several aphid-transmitted viruses. In diversified fresh market farms in the northeastern United States, all three crops often occur on the same farm, in agroecosystems comprised of a complex mosaic of small fields or even multiple crops within a field. Although the transgenic potato cultivars were recently removed from commercial application, they could be reintroduced; the acorn squash cultivars are commercially available and commonly grown in some areas, and the sweet corn cultivars seem to be slowly gaining in adoption rates. These complex and constantly changing agroecosystems contain a greater variety of food resources and refuges, which should allow organisms to partition resources both temporally and spatially, permitting a larger complex of species to exist (Root 1973, Anderson 2000, Landis et al. 2000).

Here, we compare the diversity of soil surface-dwelling beetles and ants within diversified transgenic and nontransgenic vegetable farming systems that followed current IPM standards for insecticide use patterns. We use species richness and dominance distribution comparisons and direct gradient ordination analyses to examine the influence of transgenic vegetable cultivars on epigeal beetle and ant diversity. We hypothesized that transgenic and nontransgenic farm systems would require different pest management inputs, which would result in differences in biodiversity. Furthermore, we expected that these differences would depend on crop type.

## Materials and Methods

**Experimental Design.** We grew vegetables in a split plot design at the Russel E. Larson Experimental Farm in Rock Springs, PA, in 2001 and 2002. Two "genotype" main plots—consisting of all transgenic or all isoline (identical line without transgenes) cultivars—were replicated three times. In 2001, each main plot was split among three crops: sweet corn, acorn squash, and potatoes. In 2002, each main plot was split among two crops: sweet corn and potatoes (because of crop failure, acorn squash was not grown). Cultivars (isoline and transgenic, respectively) consisted of 'Jackpot' and 'BC 0801' expressing the Cry1Ab  $\delta$  endotoxin for sweet corn, 'Taybelle' and 'Taybelle PM' expressing plant viral coat proteins for acorn squash, and 'Superior' and 'New Leaf Superior' expressing the Cry 3A  $\delta$  endotoxin for potatoes.

Main plots were 61 by 30.5 m (0.186 ha) and subplots were 20.3 by 30.5 m (0.062 ha), for a total of 1.116 ha (2.76 acres) in vegetable crops; in addition, we established mowed alfalfa/grass borders around all main plots, resulting in a 1.22-ha (3 acre) experimental field with drip irrigation per year. The experiment was planted in spring of 2001 after an alfalfa crop. In 2002, the sweet corn was rotated after potatoes, and potatoes after the acorn squash, while keeping the transgenic or isoline cultivars within their respective "genotype" main plots. The sweet corn and potatoes were planted with a 0.30-m seed spacing totaling 100 plants/row or 2,600 plants/corn subplot (0.76 m row spacing) and 1,900 plants/potato subplot (0.91 m row spacing). The acorn squash was planted in plastic mulch, was drip-irrigated, and was spaced at 1.22 m, for a total of 25 plants/row or 275 plants/subplot (1.83 m row spacing). Planting dates were 8 May (potatoes), 31 May (sweet corn), and 6 June (acorn squash) in 2001 and 13 May (potatoes) and 28 May (sweet corn) in 2002.

We monitored for pests within subplots twice a week by scouting 10 plants/subplot in all crops and using sweep nets in potatoes. We also established and serviced traps baited with pheromones (Hercon Environmental, Emigsville, PA) to monitor corn earworm, European corn borer, and fall armyworm. In both transgenic and isoline mainplots, insecticides were applied when the average pest population among all replicates of a main plot treatment for that crop reached predetermined thresholds described in Foster and Flood (1995). Based on standard potato production practices, imidacloprid was applied at planting (without pest monitoring) in the isoline plots. All insecticides were applied at the midpoint of the labeled rate range. Applications of fungicides (in potatoes) and herbicides (in all crops) did not vary among treatments and are described in Hoheisel (2002).

**Insect Collection and Identification.** In both 2001 and 2002, we placed six pitfall traps in each subplot. The pitfall traps, 14.1 cm deep with 10.9 cm ID, were inserted flush with the ground and contained small collection cups (5.5 cm deep, 8.2 cm ID) filled with ethylene glycol. Inverted funnels, made from 2-liter soda bottles, fit inside the rim of the plastic container.

**Table 1.** Insecticide applications used on isoline and transgenic vegetable cultivars in diversified Pennsylvania farm plots during 2001 and 2002

Year	Genotype	Crop	Target species	Product	
2001	Isoline	Sweet corn	<i>Delia platura</i> (Meigen) <i>Helicoverpa zea</i> (Boddie) <i>Helicoverpa zea</i> (Boddie)	Diazinon + lindane <sup>a</sup> Lambda-cyhalothrin <sup>b</sup> Lambda-cyhalothrin	
		Potato	<i>Leptinotarsa decemlineata</i> (Say) <i>Empoasca fabae</i> (Harris)	Imidacloprid <sup>c</sup> Cyfluthrin <sup>d</sup>	
		Acorn squash	<i>Acalymma vittata</i> (Fabricius) <i>Anasa tristis</i> (DeGeer)	Cyfluthrin Cyfluthrin	
	Transgenic	Sweet corn	<i>D. platura</i> <i>Popilia japonica</i> Newman	Diazinon + lindane Lambda-cyhalothrin	
		Potato	<i>E. fabae</i> <i>E. fabae</i> Aphididae	Esfenvalerate <sup>e</sup> Cyfluthrin Oxamy <sup>f</sup>	
		Acorn squash	<i>A. vittata</i>	Cyfluthrin	
	2002	Isoline	Sweet corn	<i>Helicoverpa zea</i> (Boddie) <i>Helicoverpa zea</i> (Boddie)	Lambda-cyhalothrin Lambda-cyhalothrin
			Potato	<i>Leptinotarsa decemlineata</i> (Say) <i>Empoasca fabae</i> (Harris)	Imidacloprid Cyfluthrin
		Transgenic	Potato	<i>E. fabae</i> <i>E. fabae</i>	Cyfluthrin Cyfluthrin

Insecticide use was based on common preventative measures (at-planting applications) and pest threshold scouting.

<sup>a</sup> Germate Plus, Trace Chemical LLC, Perkins, IL, 15% AI (diazinon), 25% AI (lindane), 2.23 g/kg seed.

<sup>b</sup> Warrior, Syngenta Crop Protection, Greensboro, NC, 11.4% AI, 222 ml/ha.

<sup>c</sup> Admire 2F, Bayer CropScience, Research Triangle Park, NC, 21.4% AI, 950 ml/ha.

<sup>d</sup> Baythroid, Bayer CropScience, Research Triangle Park, NC, 25% AI, 117 ml/ha.

<sup>e</sup> Asana XL, E. I. Dupont, Wilmington, DE, 585 ml/ha.

<sup>f</sup> Vydate L, E. I. Dupont, Wilmington, DE, 4677 ml/ha.

The funnels and their placement within the pitfall trap provided a barrier between the collection container and small mammals (Morrill et al. 1990). Between trapping periods, the traps were closed with a plastic lid.

Three pitfall traps per subplot were open at any given time. In 2001, we opened three traps early in each week for 24 h, and the other three pitfall traps later in the same week also for 24 h. Because of decreased labor availability in 2002, three pitfall traps were opened for 48 h once a week and were alternated weekly with the other three traps. For both years, all data were recorded as no./48 h/wk. Therefore, for each week, we recorded data from 54 traps (3 traps × 3 crops × 6 main plots). The collection period (late June to late August) lasted for 8 wk in 2001 and 9 wk in 2002.

We emptied pitfall traps onto a 420- $\mu$ m (0.004 cm) sieve and sorted out all ants (only in 2001) and beetles. Insects were preserved in 70% ethanol. R. Davidson and R. Andow (Carnegie Museum of Natural History, Pittsburgh, PA) identified or confirmed identifications of Buprestidae, Cerambycidae, Carabidae, and Cicindelidae. R. Hoebeke of Cornell University identified most of the 2001 Staphylinidae. All additional taxonomic work was done by D. Biddinger (Coleoptera) and G. Hoheisel (Formicidae) of the Pennsylvania State University. Voucher specimens are currently being held in the Fleischer Laboratory, Department of Entomology, Pennsylvania State University.

**Data Analysis.** We compared epigeal biodiversity between transgenic and isoline cultivars at the farm system level, where all crops were combined for transgenic or isoline cultivars, and individual crop level using multivariate analyses and measures of species richness and

evenness to investigate effects of treatment variables (i.e., crop, genotype, and crop × genotype interactions) on community composition. We estimated species richness with rarefaction curves (Gotelli and Colwell 2001) using EstimateS 7.5 (Colwell 2005). Samples were randomly reordered 50 times and standardized to the number of individuals caught. Rarefaction curves were developed for all specimens, and for Carabidae separately, because all carabids were identified to species level. Significance was determined by nonoverlapping confidence intervals. We examined the dominance distribution of the Carabidae and Staphylinidae communities, the two most abundant families, between years and treatments with rank abundance curves. Percent of total abundance was used to determine the most dominant species, those representing >1% of total abundance.

We performed redundancy analyses (RDA) using CANOCO 4.5 (ter Braak and Šmilauer 2002) to determine associations between species and treatment variables (crop, genotype, and crop × genotype interactions) for Carabidae and Staphylinidae. RDA is a form of direct gradient analysis, or constrained ordination, where the ordination of the species data are constrained by the axes determined by the treatment variables (Lepš and Šmilauer 2003). Because the experimental design had two levels of variability (genotype = whole plot; crop type = split plot) we used a split plot restriction in our analysis. Treatment variables were assessed using Monte Carlo simulations with 999 iterations and forward stepwise selection. Abundance data were Hellinger-transformed (Legendre and Gallagher 2001), centered, and standardized. Species scores were divided by the SD after axes extraction. Bi-plot diagrams of the ordination results

**Table 2. Coleoptera and Formicidae identified from Pennsylvania diversified vegetable farm plots in 2001 and 2002 (excluding Carabidae and Staphylinidae; see Tables 2 and 3)**

Anthicidae <i>Anthicus cervinus</i> LaF. A. species 1-3 <i>A. thomasi</i> Pic. <i>Notoxus anchora</i> Hentz <i>Tomoderus constrictus</i> (Say)	Cleridae <i>Enoclerus rosmarus</i> (Say)	Lathrididae <i>Melanophthalma cavicollis</i> Mannerhelm M. species 1-3
Bruchidae	Coccinellidae <i>Coccinella septempunctata</i> L. <i>Coleomegilla maculata</i> DeGeer <i>Harmonia axyridis</i> Pallas <i>Hippodamia convergens</i> Guerin <i>H. parenthesis</i> (Say) <i>Psyllobora vigintimaculata</i> (Say) <i>Scymnus americanus</i> Mulsant	Languriidae <i>Toramus pulchellus</i> (LeConte)
Byrrhidae <i>Curimopsis</i> species 1 <i>C. strigosa</i> (Melsh.)	Corylophidae <i>Molamba lunata</i> (LeConte) <i>Sericoderus obscurus</i> LeConte S. species 1	Mycetophagidae <i>Litargus balteatus</i> LeConte <i>Typhaea stercorea</i> L.
Byturidae <i>Byturus griseus</i> (Jayne)	Cryptophagidae <i>Anchicera ephippiata</i> Zimmermann A. species 1 <i>Atomaria pumilio</i> Casey A. species 1 Species 1-4	Nitidulidae <i>Carpophilus humeralis</i> (F.) <i>C. lugubris</i> Murray <i>C. sayi</i> Parsons <i>Glischrochilus fasciatus</i> (Olivier) <i>G. quadrisignatus</i> (Say) <i>Stelidota geminata</i> (Say)
Cantharidae <i>Cantharis scitulus</i> Say	Cucujidae <i>Telephanus velox</i> Haldemann	Phalacridae <i>Acylopus ergoti</i> Casey <i>A. piceus</i> Casey <i>Phalacrus</i> species 1 <i>Stilbus apicalis</i> (Melsh.) S. species 1
Cerambycidae <i>Elaphidion incertum</i> Newman	Curculionidae	Ptiliidae <i>Ptilinus</i> species 1
Chrysomelidae <i>Acalymma vittata</i> (F.) <i>Aphthona nigricutis</i> Foundras <i>Chaetocnema confinis</i> Crotch <i>C. cribrifrons</i> LeConte <i>C. denticulata</i> (Illiger) <i>C. minuta</i> (Melsh.) <i>C. pulicaria</i> Melsh. <i>Diabrotica barberi</i> Smith & Lawr. <i>D. undecimpunctata howardi</i> Barber <i>D. virgifera</i> Le Conte <i>Disonycha xanthomelas</i> (Dalmar) <i>Epitrix cucumeris</i> (Harris) <i>E. fuscula</i> Crotch <i>E. hirtipennis</i> (Melsh.) <i>E. humeralis</i> Drury E. species 1-2 <i>Leptinotarsa decemlineata</i> (Say) <i>Psylliodes punctulata</i> Melsh. P. species 1 <i>Phyllotreta ramosa</i> (Crotch) <i>Systema frontalis</i> (Forster)	Elateridae <i>Aeolus dorsalis</i> (Say) <i>Conoderus lividus</i> (DeGeer)	Ptilodactylidae <i>Anchytarsus bicolor</i> (Melsh.) <i>Ptilodactyla</i> species 1
Cicindellidae <i>Cicindela punctulata</i> Olivier	Formicidae <i>Camponotus</i> <i>Formica</i> <i>Lasius</i> <i>Myrmica</i> <i>Prenolepis imparis</i> (Say) <i>Solenopsis</i> <i>Tetramorium</i>	Scarabaeidae <i>Ataenius spretulus</i> (Haldeman) <i>Onthophagus</i> species 1 <i>Phyllophaga fraterna</i> Harris <i>Popillia japonica</i> Newman <i>Serica sericea</i> (Illiger)
Clambidae <i>Clambus</i> species 1	Histeridae <i>Phelister subrotundus</i> Say <i>Saprinus assimilis</i> (Paykull)	Scolytidae
	Hydrophilidae <i>Cercyon connivens</i> Fall	Silphidae <i>Silpha americana</i> L.
	Lampyridae <i>Photinus pyralis</i> (L.)	Throscidae <i>Aulonothroscus convergens</i> Horn

were generated using CanoDraw (ter Braak and Šmilauer 2002).

## Results

**Insecticide Inputs.** Transgenic and isoline crops received different insecticide treatments based on commonly used preventative measures, such as at planting applications and pest threshold scouting. The isoline cultivars received 11 insecticide applications, whereas the transgenic cultivars received 8 applications, primarily because of the efficiency of the transgenic cultivars at protecting against major pests. Insecticide use information is detailed in Table 1.

**Insect Collection and Taxonomic Resolution.** A total of 11,925 beetle and ant specimens were collected

in 1,512 pitfall traps over both years. Activity density rates were fairly consistent between years because 864 traps accumulated 6,750 specimens (7.8 specimens/trap/48 h) in 2001 and 648 traps accumulated 5,175 specimens (7.9 specimens/trap/48 h) in 2002. Carabidae and Staphylinidae represented more than one half of all specimens collected, with 4,261 and 2,677 specimens, respectively. All other Coleoptera totaled 2,885 specimens, and Formicidae (collected only in 2001) totaled 2,102 specimens.

Coleoptera consisted of a diverse array of species belonging to 32 families (Tables 2 and 3, Carabidae; Table 4, Staphylinidae); 77.6% of specimens were identified to the species/morphospecies level, including all Carabidae (Table 3), which consisted of 47 species. Ninety-four percent of the Staphylinidae were identified to species or genus level (Table 4),

**Table 3.** Carabidae species identified from Pennsylvania diversified vegetable farm plots in 2001 and 2002

<i>Agonum cupripenne</i> (Say)	<i>Elaphropus anceps</i> (LeConte)
<i>A. muelleri</i> (Herbst)	<i>Harpalus affinis</i> (Shrank)
<i>A. placidum</i> (Say)	<i>H. caliginosus</i> Fabricius
<i>A. punctiforme</i> (Say)	<i>H. compar</i> LeConte
<i>Amara aenea</i> DeGeer	<i>H. erythropus</i> DeJean
<i>A. familiaris</i> (Duftschmid)	<i>H. faunus</i> Say
<i>A. impuncticollis</i> (Say)	<i>H. herbivagus</i> Say
<i>A. littoralis</i> Mannerheim	<i>H. longicollis</i> LeConte
<i>A. species 1</i>	<i>H. pensylvanicus</i> (DeGeer)
<i>Anisodactylus sanctaerucis</i> Fabricius	<i>H. rubripes</i> (Duftschmid)
<i>Bembidion affine</i> Say	<i>Lebia viridis</i> Say
<i>B. impotens</i> Casey	<i>Microlestes linearis</i> (LeConte)
<i>B. obtusum</i> Audinet-Serville	<i>Notiobia terminata</i> (Say)
<i>B. patrule</i> Dejean	<i>Notiophilus ceneus</i> (Herbst)
<i>B. quadrimaculatum oppositum</i> Say	<i>Patrobus longicornis</i> (Say)
<i>B. rapidum</i> (LeConte)	<i>Poecilus chalcites</i> (Say)
<i>B. vicolor</i> (LeConte)	<i>P. lucublandus</i> (Say)
<i>Bradycellus rupestris</i> (Say)	<i>Pterostichus melanarius</i> (Illiger)
<i>Calathus gregarius</i> (Say)	<i>Scarites quadriceps</i> Chaudoir
<i>Chlaenius tricolor tricolor</i> Dejean	<i>Stenolophus comma</i> (Fabricius)
<i>Clicina impressifrons</i> LeConte	<i>S. ochropezus</i> (Say)
<i>Cymindis limbata</i> Dejean	<i>S. species 1</i>
<i>Dicaeolus elongatus</i> Bonelli	<i>Trechus quadristriatus</i> (Schrank)
<i>Dyschirius globulosus</i> Say	

representing at least 30 species. Formicidae consisted of seven genera, which also are included in Table 2.

**Species Richness.** There were no significant differences in rarefied species richness estimates of all taxa between isoline and transgenic cultivars at the farm system or crop level in either year (Figs. 1 and 2). Although the transgenic treatments exhibited higher species richness in all instances except sweet corn in 2002, the 95% CIs were always overlapping (data not shown). There was a trend of lower species richness in 2002; however, comparison of all taxa between years is not possible because of the removal of acorn squash from the fields and because no formicid taxa were included in the 2002 analyses.

Carabidae had no differences in rarefied species richness estimates at the farm system or crop level for

either year (Figs. 3 and 4). As in the all taxa analyses, species richness estimates were always higher in the transgenic treatments except for corn in 2002, but the 95% CIs were overlapping in all instances (data not shown). Carabidae species richness estimates were consistently lower in 2002. At the farm system level, this may be caused by the removal of acorn squash from the experiment; however, direct comparisons can be made for sweet corn and potato at the crop level. In sweet corn, rarefied estimates at 300 individuals resulted in 17–23 species for 2001 but only 13–14 species in 2002 (Fig. 4). For potato, rarefied estimates at 300 individuals resulted in 16–19 species for 2001 and 15–16 species in 2002.

**Dominance Distribution.** Dominance distributions of the Carabidae community were highly skewed because of the extremely high abundance of a single species, *Pterostichus melanarius* (Illiger), which accounted for 73.5% of all carabids. Of 47 carabid species, only 7 species accounted for >1% of the total abundance at the farm systems level (for both years combined), whereas all other carabid species combined accounted for 8.1% of total abundance. In addition to *P. melanarius*, five species were among the most abundant in both years: *Poecilus chalcites* (Say), *Harpalus affinis* (Shrank), *Harpalus pensylvanicus* (DeGeer), *Anisodactylus sanctaerucis* Fabricius, and *Poecilus lucublandus* (Say). The order of dominance varied between years; however, *P. melanarius* was always the most dominant species (Fig. 5).

Staphylinidae displayed a skewed dominance distribution as well, although the most abundant species was not consistent between years (Fig. 6). In 2001, *Dinaraea angustula* (Gyllenhal) was the most dominant species and accounted for 55% of the total abundance. In 2002, the Staphylinidae community exhibited a more even distribution, and *Hoplandria lateralis* (Melsheimer) was the most dominant species, representing 38.4% of the total abundance. In addition to *D. angustula* and *H. lateralis*, *Strigota ambigua* (Erichson) was among the three most abundant species in both years. The rank abundance of the remaining species was similar in both years.

**Genotype and Crop Influence on Community Composition.** An RDA of the 2001 Carabidae data revealed that there were differences in community composition associated with crop type (Fig. 7a). Potato significantly differentiated from the other crops ( $F = 3.75$ ,  $P = 0.002$ ) and explained 21.4% of the unconstrained species variation and 60.2% of the constrained species variation ( $\lambda_1 = 0.21$ ). Of the most influential species, *P. melanarius* was highly associated with potato. The remaining species were more highly associated with sweet corn and acorn squash. In 2001, genotype (isoline versus transgenic) did not have significant effects ( $F = 1.19$ ,  $P = 0.808$ ) on Carabidae community composition, although *Agonum muelleri* (Herbst) and *Elaphropus anceps* (LeConte) were collected more often in transgenic plots, whereas *A. sanctaerucis* and *P. lucublandus* were found more often in isoline plots (Fig. 7a). No significant treatment effects caused by crop ( $F = 1.12$ ,  $P = 0.096$ ) or genotype ( $F =$

**Table 4.** Staphylinidae species identified from Pennsylvania diversified vegetable farm plots in 2001 and 2002

<i>Acylophorus</i> species 1	<i>Neohypnus</i> spp.
<i>Aleochara curtula</i> (Gavenhorst)	<i>Paederus littoratus</i>
<i>A. gracilicornis</i> Bernhauer	Gravenhorst
<i>A. verna</i> Say	<i>Philonthus concinnus</i>
<i>Anotylus</i> species 1	(Gravenhorst)
<i>A. tetracarlinatus</i> Block	<i>P. debilis</i> (Gravenhorst)
<i>Astenus longiusculus</i> Mannerheim	<i>P. species 1</i>
<i>Belonuchus rufipennis</i> (Fabricius)	<i>Platystethus</i> species 1
<i>Dinaraea angustula</i> (Gyllenhal)	<i>Scaphisoma convexum</i> Say
<i>Falagria dissecta</i> Erichson	<i>S. suturale</i> LeConte
<i>Gabrieus nigritulus</i> (Gravenhorst)	<i>Senistoderus rubripennis</i>
<i>Hoplandria lateralis</i> (Melsheimer)	(LeConte)
<i>Lobrathium collare</i> Erichson	<i>Stenus</i> species 1
<i>Neobisnius sobrinus</i> (Erichson)	<i>Strigota ambigua</i>
<i>Neohypnus obscurus complex</i> (Erichson)	(Erichson)
	<i>Tachinus fimbriatus</i>
	Gravenhorst
	<i>Tachyporus nitidulus</i>
	(Fabricius)
	<i>Tinotus</i> species 1

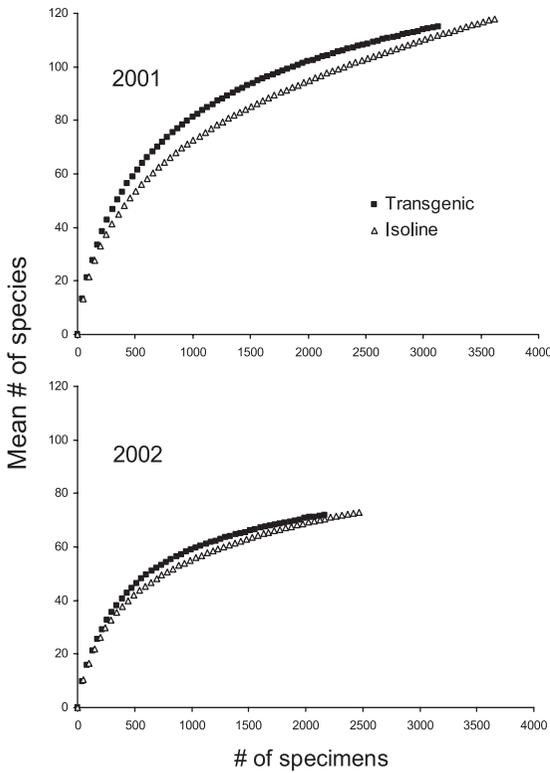


Fig. 1. Species rarefaction curves for epigeal beetles and ants found in transgenic and isoline diversified vegetable farm systems consisting of sweet corn, potatoes, and acorn squash in 2001 and sweet corn and potatoes in 2002 (based on 50 permutations of data). Expected number of species is plotted against number of individuals. 95% CIs (data not shown) are overlapping for all transgenic versus isoline comparisons.

0.53,  $P = 0.902$ ) on Carabidae community composition were found in 2002 (data not shown).

An RDA of the Staphylinidae data yielded results that were similar to that for Carabidae. Crop type had a significant influence on Staphylinidae community composition (Fig. 7b) in 2001. Potato significantly differentiated from the other crops ( $F = 4.72$ ,  $P = 0.002$ ) and explained 24% of the unconstrained species variation ( $\lambda_1 = 0.24$ ). Seven of the nine most influential species had higher activity densities in transgenic management; however, genotype ( $F = 2.31$ ,  $P = 0.092$ ) did not have a significant effect on Staphylinidae community composition. In 2002, crop ( $F = 2.19$ ,  $P = 0.058$ ) and genotype ( $F = 0.98$ ,  $P = 0.69$ ) had no significant effect on Staphylinidae community composition (data not shown).

**Discussion**

Insecticidal transgenic crops have the ability to reduce the number of insecticide applications in transgenic versus conventional farm systems (Lynch et al. 1999, Qaim et al. 2003, Hutchison et al. 2004). Many

studies have documented negative effects of insecticides on nontarget invertebrates, including decreases in species richness or abundance of important predators, such as carabids (Los and Allen 1983, Teodorescu & Cogalniceanu 2005). Duan et al. (2004) compared transgenic and nontransgenic potato management on nontarget communities and found a significant decrease in spider abundance caused by permethrin but not transgenic management. In laboratory trials, Mullin et al. (2006) found no detrimental effect of *Bt* pollen fed to carabids, but documented high levels of mortality caused by neonicotinoid seed treatments. These trends suggest a possible difference in biodiversity between transgenic and nontransgenic management regimens as typified by a dose- or frequency-dependent response. Because of a high degree of target specificity and possibility for insecticide reductions, certain *Bt*-transgenic crops may be important in sustaining biodiversity on agricultural lands and an important component of IPM systems using biological control (Musser and Shelton 2003, Romeis et al. 2006).

In this study, transgenic and isoline diversified vegetable crops, consisting of sweet corn, potato, and acorn squash, required different insecticide inputs based on IPM pest thresholds and normal management procedures. Over 2 yr, transgenic crops received fewer insecticide applications than the isoline crops (isoline = 11; transgenic = 8). This difference was

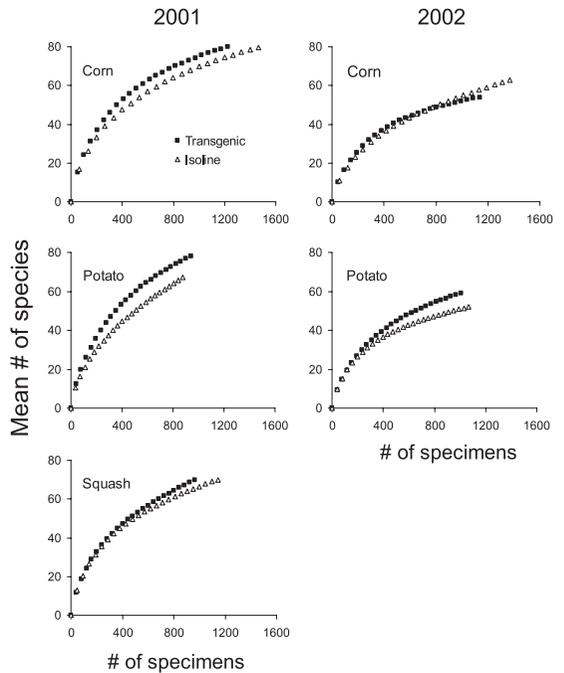


Fig. 2. Species rarefaction curves for epigeal beetles and ants found in transgenic and isoline sweet corn, potato, and acorn squash in 2001 and sweet corn and potatoes in 2002 (based on 50 permutations of data). Expected number of species is plotted against number of individuals. 95% CIs (data not shown) are overlapping for all transgenic versus isoline comparisons.

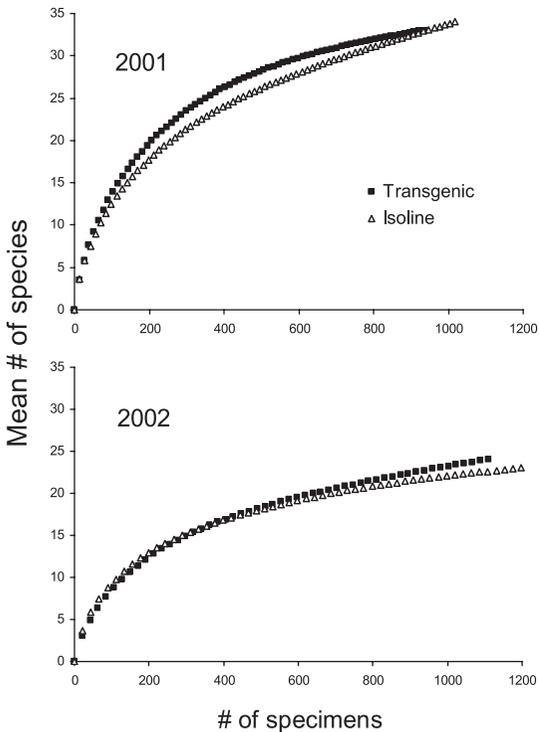


Fig. 3. Species rarefaction curves for Carabidae found in transgenic and isoline diversified vegetable farm systems consisting of sweet corn, potatoes, and acorn squash in 2001 and sweet corn and potatoes in 2002 (based on 50 permutations of data). Expected number of species is plotted against number of individuals. 95% CIs (data not shown) are overlapping for all transgenic versus isoline comparisons.

primarily because of the ability of the transgenic cultivars to effectively control the target pests, in that transgenic sweet corn and transgenic potatoes required no insecticide applications for lepidopteran pests or Colorado potato beetle, respectively. Conversely, the isoline cultivars received insecticide inputs in the form of a preventative at planting neonicotinoid application in potatoes or responsive pyrethroid applications during the reproductive stage of sweet corn. There were instances where the greater selectivity of the transgenic system increased the number of foliar insecticide applications. For example, transgenic potatoes did not control *Empoasca fabae* (Harris), whereas imidacloprid at planting did early in the season, resulting in more foliar sprays directed at *E. fabae* in transgenic than isoline potatoes.

Despite differences in insecticide inputs, there were no detectable differences in species richness (Figs. 1–4) between transgenic and isoline treatments, whereas crop type had the only significant effect on biodiversity by altering community composition (Fig. 7). In almost all cases, transgenic treatments had higher species richness estimates; however, these differences were not significantly different (Figs. 1–4). There was evidence of a decrease in species richness from 2001 to 2002 for carabids in sweet

corn and potatoes (Fig. 4). This may be a result of the increase in management intensity on our study site, such as soil tillage and insecticide applications, compared with the previous conditions of the uniform alfalfa stand in 2000. Interestingly, the decrease in carabid species richness from 2001 to 2002 seemed to be caused by the loss of rare species, because the dominant species composition was similar between years (Fig. 5).

Multivariate analyses of community composition indicated that crop type had the largest effect on Carabidae and Staphylinidae communities in 2001 (Fig. 7). The diversified farm plots were preceded by a uniform alfalfa crop in 2001. Therefore, epigeal beetle communities may have been defined by the different crops, which represent differences in vegetative architecture, soil manipulation, and pest management practices. These combined characteristics may have created habitat niches for various species as seen in Fig. 7. No treatment variables explained community composition in 2002. By 2002, crop rotations may have confounded any distinct community assemblages that were developing in 2001. Thus, crop rotation may act as a mechanism for species mixing in diversified, small-scale agroecosystems.

The carabid community was defined by species positively or negatively associating with potato (Fig. 7a). *P. melanarius* was the only species that seemed to prefer potato plots. Potato could be considered the most highly “disturbed” habitat because of the intense cultivation (i.e., hilling) of the soil and insecticide use in the isoline plots. *P. melanarius* thrives in highly disturbed habitats and may have found an interspecific

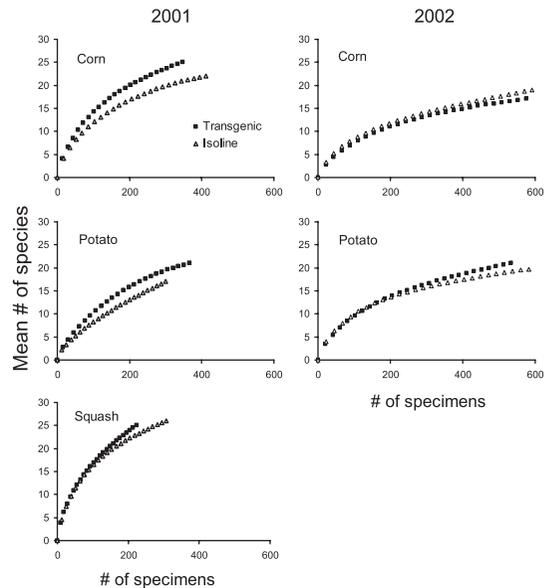


Fig. 4. Species rarefaction curves for Carabidae found in transgenic and isoline sweet corn, potato, and acorn squash in 2001 and sweet corn and potato in 2002 (based on 50 permutations of data). Expected number of species is plotted against number of individuals. 95% CIs (data not shown) are overlapping for all transgenic versus isoline comparisons.

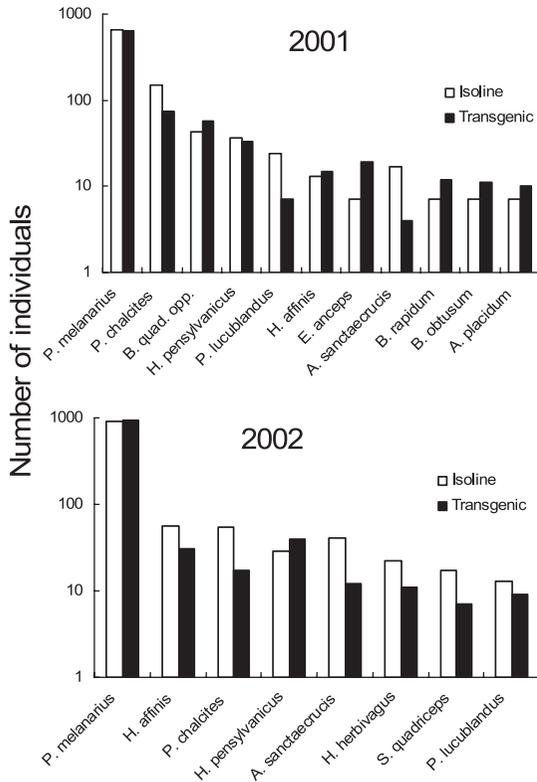


Fig. 5. Rank abundance (on a log<sub>10</sub> scale) of Carabidae in transgenic and isoline diversified farm systems in 2001 and 2002. Species shown represent at least 1% of total abundance.

competitive advantage in this crop type. The other influential carabid species were common in acorn squash and sweet corn. Acorn squash plots and early season sweet corn plots contained the most open environment, allowing weed invasion (not quantified) in which *A. sanctaerucis* and *H. pensylvanicus*, weed seed predators, may have found an important food resource. *Poecilus* spp. may have been attracted to the open foraging environments (Larochelle and Larivière 2003) of sweet corn and acorn squash, which could account for their higher abundances in these crops.

Species-level community analyses of Staphylinidae are rare. Our work showed at least 29 epigeal species existing in northeastern agroecosystems. An RDA of the staphylinid community indicated that species were separating out by those associated with potato and those associated with sweet corn and acorn squash. Of the most abundant species, *H. lateralis* and *S. ambigua* were found more often in potato, whereas *D. angustula* was associated more with sweet corn and acorn squash.

The dominance distributions of Carabidae (Fig. 5) and Staphylinidae (Fig. 6) were highly skewed. In an agricultural setting, many epigeal taxa such as carabids (Tonhasca 1993) and staphylinids (Byers et al. 2000) often exhibit a dominance structure in which only a few species comprise a large proportion of the total abundance. This disparity seems to

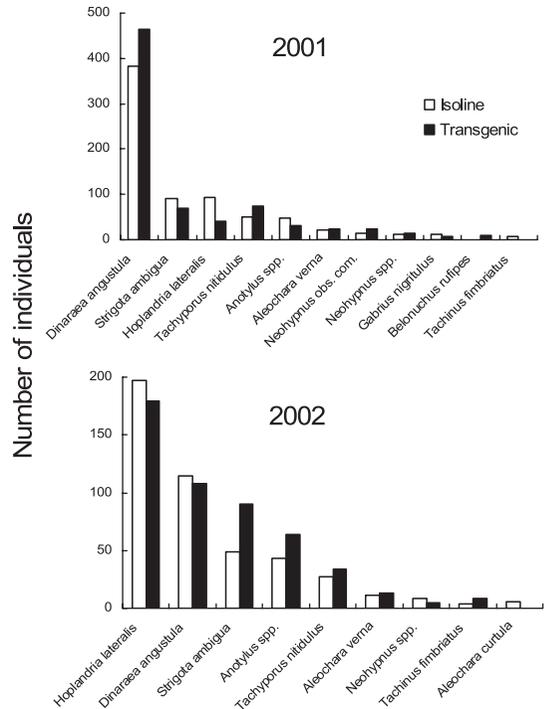


Fig. 6. Rank abundance of Staphylinidae in transgenic and isoline diversified farm systems in 2001 and 2002. Species shown represent at least 1% of total abundance.

increase with agricultural intensification and loss of natural habitat (Desender et al. 1994, Kromp 1999). Tonhasca (1993) likened these assemblage characteristics to those of early successional communities because of the frequent disturbance of the agricultural habitat. This may be especially evident in small, diversified vegetable farms because of high disturbance levels associated with annual crop rotations and a variety of intensive pest management techniques.

The skewed dominance structure was readily apparent for Carabidae, where one species, *P. melanarius*, accounted for 73.5% of all the specimens. *P. melanarius* is an introduced generalist predator that has thrived in disturbed environments and has the ability to out compete native species (Larochelle and Larivière 2003). Temporal niche partitioning may explain the success of the other dominant carabid species. *P. melanarius* is an autumn breeding species, whereas many of the other abundant generalist predators in this study (*Bembidion quadrimaculatum oppositum* Say, *P. chalcites*, and *P. lucublandus*) are spring breeding species. There is also evidence of temporal niche partitioning in another functional group: two well-known weed seed predators that were found in high abundance, *A. sanctaerucis* (spring breeder) and *H. pensylvanicus* (autumn breeder), have similar trophic roles, yet segregate temporally (Lundgren 2005).

The most abundant Staphylinidae (*D. angustula*, *H. lateralis*, and *S. ambigua*) all belong to the subfamily

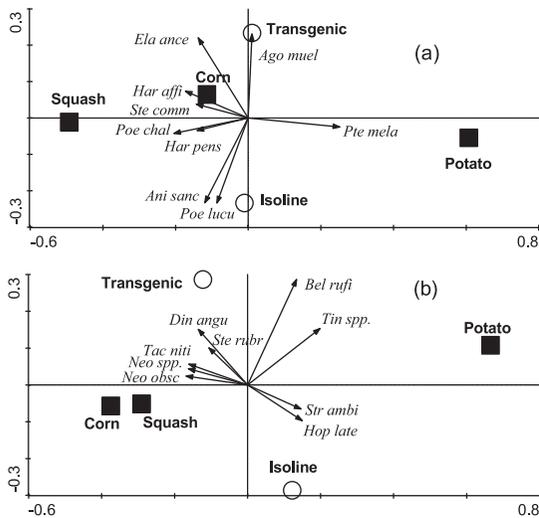


Fig. 7. Redundancy analysis of the most abundant (a) Carabidae and (b) Staphylinidae in relation to nominal treatment variables in 2001. For both families, potato ( $P = 0.002$ ) had a significant influence on community composition and is represented by the first (x-) axis (potato versus corn and squash). The second (y-) axis is represented by genotype (isoline versus transgenic). The nine most influential species are shown in each bi-plot. Species, shown as arrows, are denoted by the first three letters of the genus and the first four letters of the species (see Tables 3 and 4 for full names).

Aleocharinae, which, like many of the dominant carabid species, are considered generalist predators. The most dominant species shifted from *D. angustula* in 2001 to *H. lateralis* in 2002. This may indicate that *D. angustula* was better suited to the environment of the alfalfa crop in the years preceding the study, resulting in a carryover effect in 2001, or possibly, *H. lateralis* is better suited to deal with environmental disturbance and gradually surpassed *D. angustula* in dominance.

Biodiversity studies with invertebrates are often constrained because of the high number of species and corresponding difficulties with identification. Our work will help focus future epigeal coleopteran studies in agroecosystems by identifying, as a baseline, community members that are predominant in the Carabidae and Staphylinidae. We also provide a list of the seven formicid genera, including one species identification, collected during our study. While ants are primarily associated with tropical agroecosystems (Way and Khoo 1992), the large number of specimens found in diversified vegetable plots provides evidence that ants should be further studied in temperate agricultural systems to better define their role. This study also shows that northeastern U.S. agroecosystems are not sterile communities but contain a relatively high level of biodiversity.

This study indicates that implementing transgenic vegetable crops in diversified farm systems has little or no effect on species richness and dominance distribution of several dominant epigeal insect taxa. Additionally, genotype effects were not evident in

multivariate analyses of community composition for Carabidae and Staphylinidae. Instead, crop type was a better predictor of variation in species assemblages. In diversified farm systems, longer-term, larger-scale (e.g., approaching monoculture), or continuous-cropping studies may be needed to detect effects on biodiversity caused by the deployment of transgenic crops. However, at least in the short term, the heterogeneity of crops coupled with crop rotation patterns common to diversified vegetable farms in northeastern U.S. agroecosystems seems to aid in preserving epigeal biodiversity, which may be supplemented by reductions in insecticide use associated with transgenic crops.

### Acknowledgments

We thank R. Hoebeke (Cornell University), R. Davidson (Carnegie Museum of Natural History, Pittsburgh, PA), and R. Andow (CMNH, Pittsburgh, PA) for taxonomic help, S. Smiles, T. Grove, N. McPherson, D. Hay, and J. Walker for assistance in field work conducted during this study, and P. Blom for assistance in database management and museum curation techniques. Partial funding was provided by the USDA NRI Biotechnology Risk Assessment Research Grants Program, Grant 2002-33522-12719.

### References Cited

- Andersen, A. N., and Majer, J. D. 2004. Ants show the way down under: invertebrates as bioindicators in land management. *Front. Ecol. Environ.* 2: 291–298.
- Anderson, J. 2000. Food web functioning and ecosystem processes: problems and perceptions of scaling, pp. 3–24. *In* D. Coleman and P. Hendrix (eds.), *Invertebrates as webmasters in ecosystems*. CABI Publishers, New York.
- Angle, J. S. 1994. Release of transgenic plants: biodiversity and population-level considerations. *Mol. Ecol.* 3: 45–50.
- Asteraki, E. J. 1993. The potential of carabid beetles to control slugs in grass/clover swards. *Entomophaga* 38: 193–198.
- Balmford, A., P. Crane, A. Dobson, R. E. Green, and G. M. Mace. 2005. The 2010 challenge: data availability, information needs and extraterrestrial insights. *Phil. Trans. R. Soc. Lond. Biol.* 360: 221–228.
- Brooks, D. R., D. A. Bohan, G. T. Champion, et al. 2003. Invertebrate responses to the management of genetically modified herbicide-tolerant and conventional spring crops. I. Soil-surface-active invertebrates. *Phil. Trans. R. Soc. Lond. Biol.* 358: 1847–1862.
- Byers, R. A., G. M. Barker, R. L. Davidson, E. R. Hoebeke, and M. A. Sanderson. 2000. Richness and abundance of Carabidae and Staphylinidae in northeastern dairy pastures under intensive grazing. *Great Lakes Entomol.* 33: 81–105.
- Carcamo, H. A., J. K. Niemala, and J. R. Spence. 1995. Farming and ground beetles: effects of agronomic practice on populations and community structure. *Can Entomol.* 127: 123–140.
- Cattaneo, M. G., C. Yafuso, C. Schmidt, C. Huang, M. Rahman, C. Olson, C. Eilers-Kirk, B. J. Orr, S. E. Marsh, L. Antilla, P. Dutilleul, and Y. Carriere. 2006. Farm-scale evaluation of the impacts of transgenic cotton on biodiversity, pesticide use, and yield. *Proc. Nat. Acad. Sci. U.S.A.* 103: 7571–7576.

- Clark, M. S., J. M. Luna, N. D. Stone, and R. R. Youngman. 1994. Generalist predator consumption of armyworm (Lepidoptera: Noctuidae) and effect of predator removal on damage in no-till corn. *Environ. Entomol.* 23: 617–622.
- Colwell, R. K. 2005. EstimateS: statistical estimation of species richness and shared species from samples. Version 7.5 ([purl.oclc.org/estimates](http://purl.oclc.org/estimates)).
- Desender, K., M. Dufrene, and J.-P. Maelfait. 1994. Long term dynamics of carabid beetles in Belgium: a preliminary analysis on the influence of changing climate and land use by means of a database covering more than a century, pp. 247–252. *In* K. Desender, M. Dufrene, M. Loreau, M. L. Luff, and J.-P. Maelfait (eds.), *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Boston, MA.
- Dively, G. P. 2005. Impact of transgenic VIP3A x Cry1Ab Lepidopteran-resistant field corn on the non-target community. *Environ. Entomol.* 34: 1267–1291.
- Duan, J. J., G. Head, A. Jensen, and G. Reed. 2004. Effects of transgenic *Bacillus thuringiensis* potato and conventional insecticides for Colorado potato beetle (Coleoptera: Chrysomelidae) management on the abundance of ground-dwelling arthropods in Oregon potato ecosystems. *Environ. Entomol.* 33: 276–281.
- Duelli, P., M. K. Obrist, and D. R. Schmatz. 1999. Biodiversity evaluation in agricultural landscapes: above ground insects. *Agricult. Ecosys. Environ.* 74: 33–64.
- Ellsbury, M. M., J. E. Powell, F. Forcella, W. D. Woodson, S. A. Clay, and W. E. Riedell. 1998. Diversity and dominant species of ground beetle assemblages (Coleoptera: Carabidae) in crop rotation and chemical input systems for the Northern Great Plains. *Ann. Entomol. Soc. Am.* 91: 619–625.
- Foster, R., and B. Flood. 1995. *Vegetable insect management*. Meister Publishing, Willoughby, OH.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4: 379–391.
- Green, R. E., S. J. Cornell, J.P.W. Scharlemann, and A. Balmford. 2005. Farming and the fate of wild nature. *Science* 307: 550–555.
- Groot, A. T., and M. Dicke. 2002. Insect-resistant transgenic plants in a multitrophic context. *Plant J.* 31: 387–406.
- Hartke, A., F. A. Drummond, and M. Liebman. 1998. Seed feeding, seed caching, and burrowing behaviors of *Harpalus rufipes* De Geer larvae (Coleoptera: Carabidae) in the Maine potato agroecosystem. *Biol. Control* 13: 91–100.
- Haughton, A. J., G. T. Champion, C. Hawes, et al. 2003. Invertebrate responses to the management of genetically modified herbicide-tolerant spring crops. II. Within-field epigeal and aerial arthropods. *Phil. Trans. R. Soc. Lond. Biol.* 358: 1863–1877.
- Hoheisel, G.-A. 2002. Do transgenics affect the seasonal dynamics of Coccinellidae and diversity of Coleoptera and Formicidae on a diversified vegetable farm using IPM? MS thesis, The Pennsylvania State University, University Park, PA.
- Holland, J. M., and M. L. Luff. 2000. The effects of agricultural practices on Carabidae in temperate agroecosystems. *Integrat. Pest Manag. Rev.* 5: 109–129.
- Hutchison, W. D., B. Flood, and J. A. Wyman. 2004. Advances in United States sweet corn and snap bean insect pest management, pp. 247–278. *In* A. R. Horowitz and I. Ishaaya (eds.), *Insect pest management*. Springer, Berlin, Germany.
- Kromp, B. 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agricult. Ecosys. Environ.* 74: 187–228.
- Landis, D., S. Wratten, and G. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175–201.
- Larochelle, A., and M.-C. Larivière. 2003. A natural history of Carabidae (Coleoptera) of America north of Mexico. Pensoft Publishers, Sofia, Bulgaria.
- Lassau, S. A., D. F. Hochuli, C. Gerasimos, and C.A.M. Reid. 2005. Effects of habitat complexity on forest beetle diversity: do functional groups respond consistently? *Divers. Distributions* 11: 73–82.
- Legendre, P., and E. Gallagher. 2001. Ecologically meaningful transformations for ordination of species data. *Oecology* 129: 271–280.
- Lepš, J., and P. Šmilauer. 2003. *Multivariate analysis of ecological data using CANOCO*. University Press, Cambridge, MA.
- Los, L. M., and W. A. Allen. 1983. Abundance and diversity of adult Carabidae in insecticide-treated and untreated alfalfa fields. *Environ. Entomol.* 12: 1068–1072.
- Lundgren, J. G. 2005. Ground beetles as weed control agents: effects of farm management on granivory. *Am. Entomol.* 51: 224–226.
- Lynch, R. E., B. R. Wiseman, D. Plaisted, and D. Warnick. 1999. Evaluation of transgenic sweet corn hybrids expressing Cry1A(b) toxin for resistance to corn earworm and fall army worm (Lepidoptera: Noctuidae). *J. Econ. Entomol.* 92: 246–252.
- Morrill, W. L., D. G. Lester, and A. E. Wrona. 1990. Factors affecting efficacy of pitfall traps for beetles (Coleoptera: Carabidae and Tenebrionidae). *J. Entomol. Sci.* 25: 284–293.
- Mullin, C. A., M. C. Saunders, T. W. Leslie, D. J. Biddinger, and S. J. Fleischer. 2006. Toxic and behavioral effects to Carabidae of seed treatments used on Cry3Bb1- and Cry1Ab/c-protected corn. *Environ. Entomol.* 34: 1626–1636.
- Musser, F. R., and A. M. Shelton. 2003. *Bt* sweet corn and selective insecticides: impacts of pests and predators. *J. Econ. Entomol.* 96: 71–80.
- Naranjo, S. E., G. Head, and G. P. Dively. 2005. Field studies assessing arthropod non-target effects on Bt transgenic crops: introduction. *Environ. Entomol.* 34: 1178–1180.
- Qaim, M., J.E.J. Cap, and A. de Janvry. 2003. Agronomics and sustainability of transgenic cotton in Argentina. *AgBioForum* 6: 41–47.
- Riddick, E. W., G. Dively, and P. Barbosa. 2000. Season-long abundance of generalist predators in transgenic versus nontransgenic potato fields. *J. Entomol. Sci.* 35: 349–359.
- Romeis, J., M. Meissle, and F. Bigler. 2006. Transgenic crops expressing *Bacillus thuringiensis* toxins and biological control. *Nat. Biotech.* 24: 63–71.
- Root, R. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collard (*Brassica oleracea*). *Ecol. Monog.* 43: 95–124.
- Sisterson, M. S., R. W. Biggs, C. Olson, Y. Carriere, T. J. Dennehy, and B. E. Tabashnik. 2004. Arthropod abundance and diversity in Bt and non-Bt cotton fields. *Environ. Entomol.* 33: 921–929.
- Squire, G. R., D. R. Brooks, D. A. Bohan, et al. 2003. On the rationale and interpretation of the farm scale evaluations of genetically modified herbicide-tolerant crops. *Phil. Trans. R. Soc. Lond. Biol.* 358: 1779–1799.
- Stoate, C., N. D. Boatman, and R. J. Borralho. 2001. Ecological impacts of arable intensification in Europe. *J. Environ. Manag.* 63: 337–365.
- Teodorescu, I., and D. Cogalniceanu. 2005. Rapid assessment of species diversity changes after pesticide appli-

- cation in agricultural landscapes. *Appl. Ecol. Environ. Res.* 4: 55–62.
- ter Braak, C.J.F., and P. Šmilauer. 2002.** CANOCO reference manual and CanoDraw for Windows user's guide: software for canonical community ordination, 4.5 edition. Microcomputer Power, Ithaca, NY.
- Thorbeck, P., and T. Bilde. 2004.** Reduced numbers of generalist arthropod predators after crop management. *J. Appl. Ecol.* 41: 526–538.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001.** Forecasting agriculturally driven global environmental change. *Science* 292: 281–284.
- Tilman, D., K. G. Cassman, P. A. Matson, R. Naylor, and S. Polasky. 2002.** Agricultural sustainability and intensive production practices. *Nature (Lond.)* 418: 671–677.
- Tonhasca, A. Jr. 1993.** Carabid beetle assemblage under diversified agroecosystems. *Entomol. Exp. Appl.* 68: 279–285.
- Tooley, J., and G. E. Brust. 2002.** Weed seed predation by carabid beetles, pp. 215–230. *In* J. M. Holland (ed.), *The agroecology of Carabid beetles*. Intercept, Andover, UK.
- Way, M. J., and K. C. Khoo. 1992.** Role of ants in pest management. *Annu. Rev. Entomol.* 37: 479–503.
- Whitehouse, M.E.A., L. G. Wilson, and G. P. Fitt. 2005.** A comparison of arthropod communities in transgenic Bt and conventional cotton in Australia. *Environ. Entomol.* 34: 1224–1241.

*Received for publication 2 August 2006; accepted 3 November 2006.*

---