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Carbon and nitrogen stable isotope ratios differ among invertebrates from field crops, forage crops, and non-cropped land uses[1]

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Abstract: Stable isotopes are an important tool for studying invertebrate food webs and movement of invertebrates in farmland. However, stable isotope values of farmland invertebrates have been reported for only a few crop types, and rarely for other land uses within farmland. We compared $\delta^{13}C$ and $\delta^{15}N$ of invertebrates captured in corn, soybean, hay, and hedgerows in eastern Ontario, Canada. $\delta^{13}C$ was significantly lower in invertebrates captured in hay and hedgerows than in invertebrates captured in soybean and corn, but was not different between invertebrates captured in corn and soybean. This suggests invertebrates may be moving between crop fields during the growing season, using alternative food sources within crop fields, or retaining $\delta^{13}C$ values from the previous year. When all invertebrates were examined together, $\delta^{15}N$ was significantly higher in invertebrates captured in manured corn than in those captured in soybeans, hedgerows, or manured or unmanured hay, but there was no difference between invertebrates captured in manured or unmanured corn. However, spiders from manured corn had significantly higher $\delta^{15}N$ than those from unmanured corn. Spiders had less variable $\delta^{15}N$ than other taxa in this study, because they occupy a single trophic level. This may make spiders more suitable for detecting changes in fertilization regimes. By demonstrating how invertebrate $\delta^{13}C$ and $\delta^{15}N$ vary with land use, this study will contribute to the understanding of agricultural food webs and of responses of invertebrates to land use change.
Keywords: agriculture, carbon, fencerow, insects, nitrogen, stable isotope.

Résumé : Les isotopes stables sont un outil important pour étudier les réseaux trophiques et les déplacements des invertébrés dans les terres agricoles. Cependant, on retrouve dans la littérature des valeurs d'isotopes stables d'invertébrés seulement pour quelques types de culture et très peu pour d'autres utilisations du sol en milieu agricole. Nous avons comparé les valeurs de $\delta^{13}C$ et $\delta^{15}N$ mesurées chez des invertébrés capturés dans des champs de maïs, de soja, de foin et dans des haies dans l'est de l'Ontario, Canada. Les valeurs de $\delta^{13}C$ étaient significativement plus faibles chez les invertébrés capturés dans le foin et dans des haies que chez ceux capturés dans le soja et le maïs, mais ces valeurs ne différaient pas entre les invertébrés capturés dans le maïs et le soja. Cela que suggère que soit les invertébrés se déplacent entre les champs durant la saison de croissance, soit ils utilisent des sources alternatives de nourriture au sein du champ, ou qu'ils conservent leurs valeurs de $\delta^{13}C$ de l'année précédente. Lorsque tous les invertébrés étaient examinés ensemble, les valeurs de $\delta^{15}N$ étaient significativement plus élevées chez les invertébrés capturés dans les champs de maïs amendés avec du fumier que chez ceux capturés dans le soja, les haies ou les champs de foin amendés ou non avec du fumier, mais il n'y avait pas de différence entre les invertébrés capturés dans les champs de maïs amendés ou non. Par contre, les araignées provenant de champs de maïs amendés avec du fumier avaient des valeurs de $\delta^{15}N$ significativement plus élevées que celles provenant de champs de maïs non amendés. Les valeurs de $\delta^{15}N$ des araignées étaient moins variables que celles des autres taxons de cette étude puisque les araignées occupent un seul niveau trophique. Ainsi, celles-ci pourraient constituer le taxon le plus approprié pour détecter des changements dans les régimes de fertilisation. En démontrant comment les valeurs de $\delta^{13}C$ et $\delta^{15}N$ varient avec le type d'utilisation du sol, cette étude contribue à une meilleure compréhension des réseaux trophiques en milieu agricole et des réponses des invertébrés aux changements dans le type d'utilisation du sol.
Mots-clés : agriculture, azote, carbone, haie-clôture, insectes, isotope stable.

Nomenclature: Gleason, 1963; Hitchcock & Chase, 1971.

Introduction

Stable isotope studies can be used to trace carbon sources in farmland food webs by taking advantage of the different $^{13}C/^{12}C$ ratios of C4 and C3 plants. Due to their different photosynthetic pathways, C4 plants, such as corn (*Zea mays*) and warm-season grasses, are enriched in ^{13}C compared to C3 plants, which include most other plants, trees, and cool-season grasses (DeNiro & Epstein, 1978). This gives C4 plants a higher $^{13}C/^{12}C$ ratio, measured as $\delta^{13}C$ (see Methods). Values of $\delta^{13}C$ change little between trophic levels (DeNiro & Epstein, 1978;

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McCutchan *et al*., 2003), so $\delta^{13}C$ can be used to distinguish between consumers using a C4 carbon source from those using a C3 carbon source (DeNiro & Epstein, 1978; Ostrom, Colunga-Garcia & Gage, 1997; Gould *et al*., 2002; Prasifka, Heinz & Winemiller, 2004; Gratton & Forbes, 2006; Vialatte *et al*., 2006).

$\delta^{13}C$ can also be used to track movement of invertebrates among farmland land uses. When an organism switches from feeding on C3 carbon sources to feeding on C4 carbon sources, it takes some time for the switch to be fully reflected in its $\delta^{13}C$ value (Ostrom, Colunga-Garcia & Gage, 1997; Prasifka, Heinz & Winemiller, 2004; Albers, Schaefer & Scheu, 2006; Gratton & Forbes, 2006; Vialatte *et al*., 2006). Therefore, an invertebrate $\delta^{13}C$ value distinctly different from that of the dominant local vegetation suggests a recent move from a different habitat (complete diet switch), whereas an intermediate value can be interpreted either as a less recent move (complete diet switch partially assimilated) or as regular movements between habitats, resulting in a mixed diet (Gratton & Forbes, 2006). Such a diet switch may be associated with a change in developmental stage if larvae and adults forage on different carbon sources (Gould *et al*., 2002).

To accurately reconstruct food webs or track movement of invertebrates, it is necessary to have isotope values of all important food sources (Lubetkin & Simenstad, 2004; Phillips, Newsome & Gregg, 2005). However, most farmland studies have focused on only a few crop types. For example, we could find only one field study that reported isotope values for invertebrates in soybeans (*Glycine max*) (Haubert *et al*., 2009) and only one study that reported isotope values for farmland invertebrates in non-crop habitat (Latendresse, 2004). Hedgerows and fencerows provide important habitat for invertebrates, birds, and mammals in farmland (Baudry, Bunce & Burel, 2000; Jobin, Choiniere & Belanger, 2001; Jobin *et al*., 2004), and since these habitats are dominated by C3 plants in temperate latitudes, it should be possible to distinguish between invertebrates from hedgerows and those from cornfields.

Nitrogen has been used in farmland stable isotope studies to investigate trophic levels of invertebrates (McNabb, Halaj & Wise, 2001; Albers, Schaefer & Scheu, 2006; Wise, Moldenhauer & Halaj, 2006) and to track fertilizer type (Bateman, Kelly & Jickells, 2005; Choi *et al*., 2006; Rogers, 2008). All consumers become enriched in $^{15}N/^{14}N$ with respect to their diet (DeNiro & Epstein, 1981), so herbivores have higher $^{15}N/^{14}N$ ratios (measured as $\delta^{15}N$, see Methods) than the plants they consume, and in turn, predators have higher $\delta^{15}N$ than herbivores (McCutchan *et al*., 2003). This allows trophic levels of herbivores and predators to be compared using $\delta^{15}N$. Animal manure is also enriched in $\delta^{15}N$ with respect to the animal's diet (Steele & Daniel, 1978), and fresh manure typically has values of $\delta^{15}N$ above 8‰ (Wassenaar, 1995; Choi *et al*., 2002; Vitòria *et al*., 2004). Artificial nitrogen fertilizer has lower $\delta^{15}N$, typically between –2 and 2‰ (Wassenaar, 1995; Vitòria *et al*., 2004). This difference is conserved in crops grown under different fertilizer regimes (Choi, Ro & Hobbie, 2003; Choi *et al*., 2006), and has been used to differentiate between organic and conventional crops (Bateman, Kelly & Woolfe, 2007; Rogers, 2008). Unfertilized plants typically show a $\delta^{15}N$ close to that of the local soil, which averages 5‰, whereas legumes, which actively fix nitrogen, have a $\delta^{15}N$ close to that of air at 0‰. Therefore, different $\delta^{15}N$ of leguminous crops, non-leguminous crops, and unfertilized semi-natural vegetation could be used to assign invertebrates to different farmland land uses.

Our objective was to find out if we could use carbon and nitrogen stable isotopes to distinguish among invertebrates captured within crop fields (corn and soybean), hayfields, and hedgerows. We made the following predictions, which should hold true both among and within invertebrate taxa: 1) $\delta^{13}C$ would be most enriched in invertebrates captured in corn and would be lower in invertebrates captured in soybean, hedgerows, and hay. 2) $\delta^{15}N$ would be enriched in invertebrates captured in fields treated with manure compared to fields treated with artificial fertilizers, unfertilized fields, fields planted with leguminous crops, or hedgerows. 3) Despite the variation in $\delta^{15}N$ values of plants under different fertilizer regimes, we should still be able to detect $\delta^{15}N$ enrichment in invertebrates at higher trophic levels. 4) Invertebrates captured in edges between hedgerows and crop fields would show intermediate $\delta^{13}C$ and $\delta^{15}N$ values, due to movement across the boundary. The ability to identify invertebrates from these different land uses will help in tracking movement of invertebrates in farmland, and in better defining farmland food webs.

Methods

The study was carried out between 2006 and 2008 in eastern Ontario, Canada, on farms located between the towns of Navan (45° 25' 15.68" N, 75° 25' 36.28" W) and Embrun (45° 16' 26.29" N, 75° 16' 30.04" W). This is an area dominated by arable and dairy farming. The most common crops are field corn, soybean, and wheat (*Triticum* spp.), but hayfields are also common, especially on dairy farms. Tillage practices vary widely from no-till to conventional till. Fertilization practices also vary, with dairy farmers using manure on their fields more frequently than do farmers not involved in animal production. Thirteen sites were used in this study, where a site is a single continuous hedgerow and the adjoining fields. A single site can represent a hedgerow and fields owned by a single farmer or, more often, a hedgerow and fields owned by 2 or more farmers. Hedgerows were selected to avoid deep ditches or areas of permanent water.

This study was part of a larger project examining reproductive success of sparrows breeding in hedgerows, so invertebrate sampling was centred on active sparrow nests. Between 1 and 16 nests were found at each site. Invertebrates were sampled using pitfall traps, sweep netting, hand collection, and a D-Vac (model 122, D-Vac Company, Ventura, California, USA). Sampling methods differed between years. In 2006, pitfall traps consisted of a glass jar placed in a hole in the ground such that the top of the jar was level with the ground surface. Traps were one-third filled with denatured ethanol, and were in place for 24 h. At each nest, 4 traps were placed in the field on one side of the nest, 4 were placed at the interface of the field and the hedgerow (edge traps), 2 were placed in the hedgerow, and 2 were placed in the adjoining field (Figure 1). Edge traps were placed in bare soil, as close as possible to the edge of the hedgerow vegetation. Upon collection, traps were sealed and returned to the lab. The contents of each trap were passed through a 1-mm sieve and rinsed in water. Invertebrates were removed, and stored in a –20 °C freezer. Sweep netting was used in hedgerows to collect additional invertebrates. One observer walked 20 paces along the hedgerow, passing the net through the vegetation at each step. The contents of the net were transferred to a jar of denatured alcohol, returned to the lab, and processed as for pitfall traps. Finally, observers searched leaves and trunks of hedgerow bushes within 20 m of the nest for caterpillars and other invertebrates. These were transferred to a jar of denatured alcohol, returned to the lab, and processed as for pitfall traps. In 2006, invertebrate sampling occurred between 26 May and 26 July.

In 2007 and 2008, pitfall traps consisted of plastic cups placed in holes in the ground such that the top of each cup was level with the ground surface. Traps were one-third filled with water, with a drop of soap added to break the water tension, and were in place for 3 d. Trap layout was similar to 2006, but 8 more traps were used at each nest (Figure 1). Upon collection, the contents of the trap were transferred to a Ziploc bag and returned to the lab. The contents of each trap were passed through a 1-mm sieve and rinsed with water. Invertebrates were transferred to a vial of denatured ethanol until further processing. A D-Vac (Dietrick, Schlinger & van den Bosch, 1959) was also used to collect invertebrates in hedgerows, crop fields,

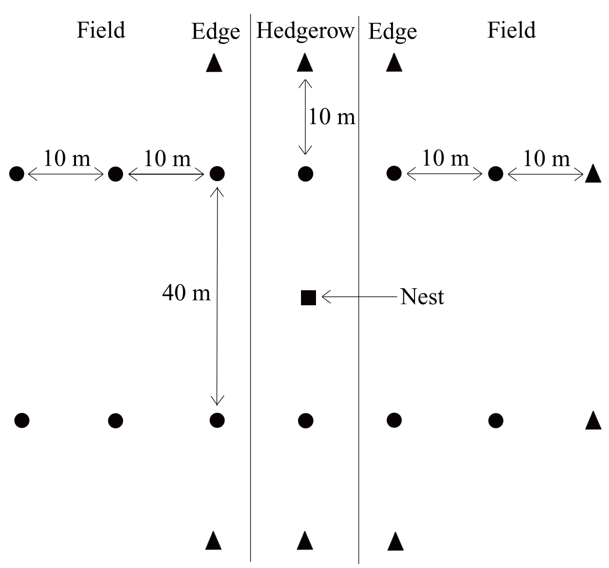

FIGURE 1. Pitfall trap layout, showing a single nest site with 4 hedgerow traps, 8 edge traps (at the borderline between hedgerow and field), and 8 traps in the adjacent fields. Dots represent pitfall trap locations used in all years (2006–2008), triangles represent pitfall trap locations used only in 2007 and 2008.

and hayfields. In the hedgerow and in soybean, a 340-mm diameter funnel was used on the D-Vac. A single sample was collected by placing the sampling funnel vertically over the vegetation and pressing it to the ground for 5 s in each of 3 places within a 2-m^2 area. Where corn was being sampled, a narrower, 100-mm diameter funnel was used, and the collector passed the funnel directly over the plants from top to bottom, walking along the row as necessary until 20 s of sampling was completed. In each case, the contents of the net were then transferred to a jar of denatured alcohol. D-Vac sampling was carried out twice in the hedgerow, within 20 m of the nest, and twice in each adjacent field. Invertebrate sampling was carried out between 30 May and 1 August in 2007 and between 24 May and 18 July in 2008.

Five taxa were selected for analysis, due to their trophic level, their abundance in samples, and their expected importance in sparrow diet. These were true spiders (Araneae, n = 171 samples analyzed, carnivorous, abundant in pitfall trap, D-Vac, and sweep net samples, important in nestling sparrow diets), ground beetles (Carabidae, n = 167, various diets including herbivorous and carnivorous, abundant in pitfall traps), crickets (Ensifera, n = 26, omnivorous, fairly abundant in pitfall traps), hoppers (Auchenorrhyncha, n = 55, herbivorous, fairly abundant in pitfall trap, D-Vac, and sweep net samples), and caterpillars (Lepidoptera larvae, n = 35, herbivorous, very important in nestling sparrow diets). This coarse level of taxonomic resolution reflects selection of food items by larger insectivorous predators, like songbirds. The contents of each trap were sorted under a microscope, and individuals of the focal taxa were removed for isotope sampling. When individuals from one trap were not numerous or large enough for isotope sampling, individuals from different traps from the same field at the same nest were combined. This sometimes resulted in individuals from different species being combined into a single sample. Once isolated, each sample was either freeze-dried (2006) or oven-dried at 60 °C for at least 48 h until dry (2007, 2008). Samples were then crushed into a fine powder, and approximately 1 mg was weighed into a tin capsule.

In order to assess $\delta^{13}C$ and $\delta^{15}N$ of local plants, we collected plant samples around 41 sparrow nests. Plant samples were taken from the hedgerow and from the adjacent fields in late July or early August. Corn and soybean samples were collected by walking approximately 20 m into the field and collecting a leaf from the top of each of 2 plants, at least 20 m apart. Hay samples were collected by walking approximately 20 m into the hay and taking a sample of each plant species within a 1-m radius. This was repeated at 2 sampling points, at least 20 m apart. Plant surveys were conducted in hedgerows to determine the dominant herbaceous plant types. A 100-m transect was laid out parallel to the hedgerow and centred on a sparrow nest. Plant species that were estimated to cover more than 70% of the hedgerow along the transect were sampled. Samples were collected by taking the top leaves of 2 individual plants at least 20 m apart. At each nest, samples of each plant species were combined to make one sample. Samples were shredded by hand, and approximately 1 g of material was weighed into a container and oven dried at

60 °C for at least 48 h until dry. Samples were then crushed into a fine powder, and approximately 1 mg was weighed into a tin capsule.

Samples and standards were loaded into an elemental analyzer (Vario EL III, Elementar Analysen systeme, Hanav, Germany), which was interfaced to an isotope ratio mass spectrometer (Conflo II and Delta XP Plus Advantage, ThermoFinnigan, Bremen, Germany). Standards used were C-51 Nicotiamide (0.07, –22.95), C-52 mix of ammonium sulphate and sucrose (16.58, –11.94), C-54 caffeine (–16.61, –34.46), blind standard C-55: glutamic acid (–3.98, –28.53) for carbon, and air for nitrogen. The data are reported in delta notation, defined as $\delta = (R_{sample} - R_{standard})/R_{standard}) \times 1000$, where R is the ratio of the abundance of the heavy to the light isotope. All samples were analyzed at the Hatch Laboratories at the University of Ottawa.

We used nested linear mixed effects models to analyze the data (Pinheiro *et al.*, 2009). Mixed effects models enabled us to account for the nested structure of the sampling design, where the location of each sample was within a specific field or section of hedgerow (Figure 2), at a specific nest and within a specific site. If these random effects are not considered, the assumption of independence is violated, since in many cases multiple invertebrates of the same taxa were sampled within the same field, and at the same site.

Prediction 1, that δ^{13}C would be most enriched in invertebrates captured in corn and would be lower in invertebrates captured in soybean, hedgerows, and hay, was tested by comparing δ^{13}C among different trapping locations, both among and within taxa. δ^{13}C was frequently non-normal, in which case it was log- or square-root–transformed to improve normality. Prediction 2, that δ^{15}N would be enriched in invertebrates captured in fields treated with manure compared to fields treated with artificial fertilizers or unfertilized, hedgerows, or fields planted with leguminous crops, was tested in 2 parts. First, we tested for differences in δ^{15}N within spiders and ground beetles captured in corn and hay fields known to have been manured since the end of the previous growing season (manured) and corn and hay fields known not to have been treated with manure since the end of the previous growing season (unmanured). Only corn and hay fields were included in this analysis because soybean fields used in this study were not commonly manured. Ground beetles and spiders were the only taxa captured in high enough numbers to perform the analysis. Second, we compared δ^{15}N among all different trapping locations, among taxa. Prediction 3, that despite the variation in δ^{15}N values of plants under different fertilizer regimes, δ^{15}N should still be enriched in invertebrates at higher trophic levels, was tested by comparing δ^{15}N among taxa, while controlling for trapping location. Prediction 4, that invertebrates captured in edges between hedgerows and crop fields would show intermediate δ^{13}C and δ^{15}N values, due to movement across the boundary, was tested within spiders and ground beetles only, due to sample size restrictions. The analysis was repeated separately for corn, soybean, and hay. In each case, we compared δ^{13}C and δ^{15}N for fields, edges, and hedgerows bordered on at least one side by the relevant crop.

In all analyses, possible random effects were date, nest (nest at which sample was collected), field or hedgerow (where each field or section of hedgerow sampled was given a unique code; Figure 2), and site. Site represents a single, continuous hedgerow and all the fields connected to it. Date was included to account for seasonal differences; for example, δ^{13}C values of invertebrates might be expected to change as corn grows and increases in biomass. Nest was included to account for both temporal and spatial proximity of samples taken at each individual nest. Including field or hedgerow section as a random variable accounts for the spatial proximity of samples, as well as for variation in management of fields and hedgerows over time. Including site as a random variable accounts for the spatial proximity of fields, and for shared management over time. Year was not included, as preliminary analysis showed no effect of year on isotope values. For each taxon, we first averaged data within the taxon from trapping locations at the same nest (*i.e.*, if 2 spiders were sampled from the same cornfield at the same nest, the values were averaged for further analysis). Fewer data were available for hoppers and crickets, so when these taxa were analyzed

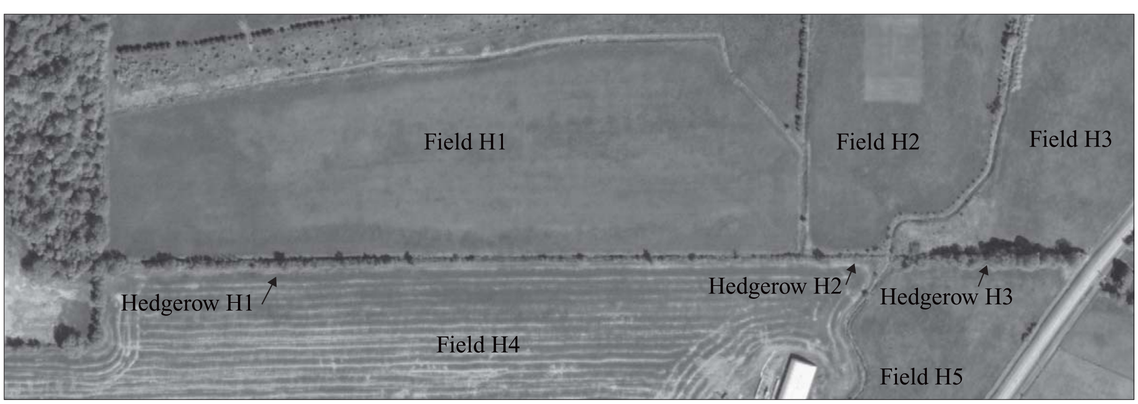

FIGURE 2. Aerial photograph of site H, showing how the fields and hedgerow were divided up for analysis. Each site consisted of one hedgerow and all the adjoining fields. Hedgerows were divided into sections, such that each section adjoined only 2 fields.

individually, data were averaged within each field or section of hedgerow. Due to the small sample size, caterpillars were only included in the analysis of prediction 1. The sample sizes for each taxon in each trapping location can be found in Appendix I. Degrees of freedom were calculated following Pinheiro and Bates (2000).

The first step in model building was to test for significance of random effects (Zuur *et al.*, 2009). For each analysis, we built models with all combinations of nested random effects (no random effects [*i.e.*, linear model], nest, field, site, field nested in site, and nest nested in site, with and without date). We then tested for the most parsimonious model using AIC_c. Model validity was checked using residual analysis. If visual inspection of residual graphs showed that assumptions were not being met, we either altered the variance structure or considered the next best model, as appropriate. Altering the variance structure enabled us to relax the assumption of homogeneity of variances, by allowing the variance to change with levels of the dependent or random variables (Pinheiro & Bates, 2000). Once the most parsimonious model was selected, we tested for significance of the model and levels of fixed variables.

All analyses were carried out in R (R Development Core Team, 2010), and results are presented as mean ± SE unless otherwise stated.

Results

PREDICTION 1: CARBON VALUES

We predicted that $\delta^{13}C$ would be most enriched in invertebrates captured in corn, and lower in invertebrates captured in soybean, hedgerows, and hay. $\delta^{13}C$ varied widely among and within invertebrate taxa (Figure 3). However, there were significant differences in $\delta^{13}C$ among trapping locations, once taxa were controlled for (Table I). As predicted, $\delta^{13}C$ was lower in invertebrates captured in hay and in hedgerows than those captured in corn (Figure 4). However, contrary to our prediction, $\delta^{13}C$ values of invertebrates captured in corn were not significantly different from those captured in soybean. Invertebrates captured in corn had lower $\delta^{13}C$ than corn plants, while invertebrates captured in soybean, hedgerow, and hayfields had higher $\delta^{13}C$ than dominant plants in these habitats (Table II).

Within taxa, spiders and ground beetles captured in corn and soybean had significantly higher $\delta^{13}C$ than those captured in hedgerows and hay (Table III; Figure 5a, 6a). Values of $\delta^{13}C$ of crickets captured in corn, soybean

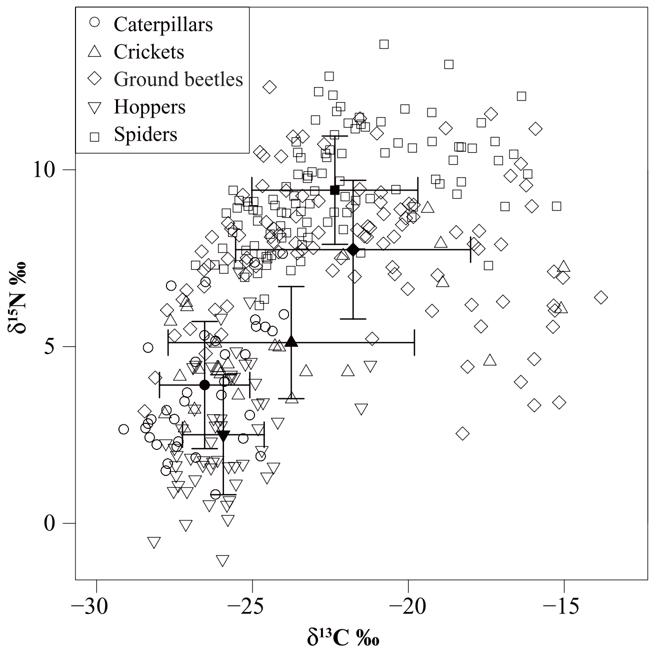

FIGURE 3. $\delta^{13}C$ and $\delta^{15}N$ values for caterpillars (circles), crickets (triangles), ground beetles (diamonds), hoppers (downward triangles), and spiders (squares). Filled symbols show means ± 1 SD.

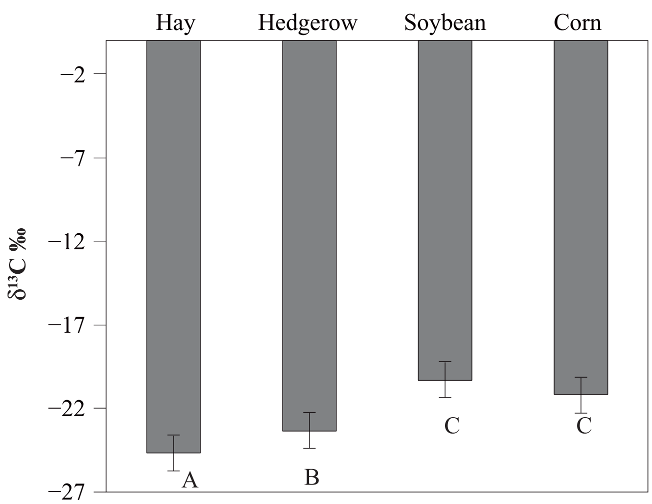

FIGURE 4. Mean values of $\delta^{13}C$ for all trap locations, once taxon is controlled (± 1 SE). Means with the same letter are not significantly different ($P < 0.05$).

TABLE I. Results of mixed effects models showing differences in carbon and nitrogen stable isotopes among taxa (spiders, ground beetles, crickets, hoppers, and caterpillars) captured in different trapping locations (corn, soybean, hedgerow, hay).

Dependent variable	Random effects	Stratification variable[1]	Fixed effects	*F* for fixed effects	df for fixed effects	*P* for fixed effects
$\delta^{13}C$	Date, field	Species	Taxa	54.33	271	< 0.0001
			Trapping location	26.71	271	< 0.0001
$\delta^{15}N$	Date, nest		Taxa	222.58	267	< 0.0001
			Trapping location	14.14	267	< 0.0001

[1]Models including a variance function allow for heterogeneity among levels of the stratification variable.

and hedgerows were highly variable, and there was no significant difference among land uses (Figure 7). Hoppers captured in hedgerows had significantly higher $\delta^{13}C$ than those captured in hay, but there was no significant difference among hoppers captured in corn and in other trapping locations (Figure 7). $\delta^{13}C$ values of hoppers captured in corn were variable but much lower than those of the corn plants (Table II). The 2 lowest values of $\delta^{13}C$ of hoppers from corn came from 2 cornfields on the only organic farm included in this study. These fields were extremely weedy (J. Girard, pers. observ.), which may have diluted the $\delta^{13}C$ of the corn plants. If these 2 values are excluded, $\delta^{13}C$ for hoppers captured in corn is significantly greater than that of hoppers captured in hedgerows or hayfields ($\delta^{13}C$ –24.05 ± 2.19, $F_{2, 24} = 9.24$, $P = 0.001$).

TABLE II. Ranges of $\delta^{13}C$ and $\delta^{15}N$ of plants from different land covers adjacent to sparrow nests.

Land cover	Min $\delta^{13}C$	Max $\delta^{13}C$	Min $\delta^{15}N$	Max $\delta^{15}N$	*n*	Number of species
Corn unmanured	–13.18	–11.66	1.01	17.10	13	1
Corn manured	–13.53	–11.67	1.82	19.88	21	1
Hay unmanured	–30.57	–28.23	–0.86	2.54	11	6
Hay C_4[1] unmanured	–11.20	–10.82	7.80	10.25	2	2
Hay manured	–29.75	–27.59	–1.31	13.31	15	6
Hedgerow	–32.08	–25.62	–1.46	7.55	103	26
Hedgerow C_4[1]	–12.39	–11.23	1.07	3.96	5	4
soybean	–30.64	–27.75	–0.96	3.02	16	1

[1] C_4 plants collected from within C_3 dominated land cover types.

PREDICTION 2: NITROGEN, FERTILIZER REGIME, AND PLANT TYPE.

We predicted that $\delta^{15}N$ would be enriched in invertebrates captured in fields treated with manure compared to fields treated with artificial fertilizers,

TABLE III. Results of models testing differences in carbon stable isotopes among trapping locations for 4 different taxa of invertebrates.

Taxa	Model type[1]	Random effects	Weights	Fixed effects	*F*	df	*P*
Spiders	lmem	Site, date		Location (corn, soybean, hay, hedgerow)	15.16	94	< 0.0001
Ground beetles	lmem	Field	Location	Location (corn, soybean, hay, hedgerow)	5.74	56	0.002
Crickets	lmem	Site		Location (corn, soybean, hedgerow)	3.42	10	0.07
Hoppers	gls		Location	Location (corn, hay, hedgerow)	4.20	26	0.03

[1]Model types were linear mixed effects models (lmem) and generalized least squares (gls).

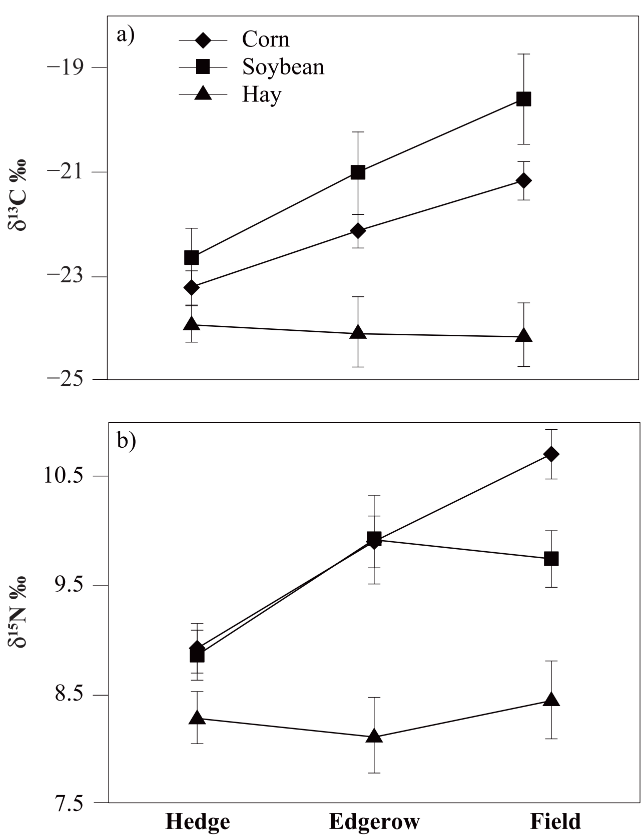

FIGURE 5. Mean a) $\delta^{13}C$ values (± 1 SE) and b) $\delta^{15}N$ values (± 1 SE) for spiders captured in different trap locations. Hedgerow values include only hedgerows adjacent to the specified crop.

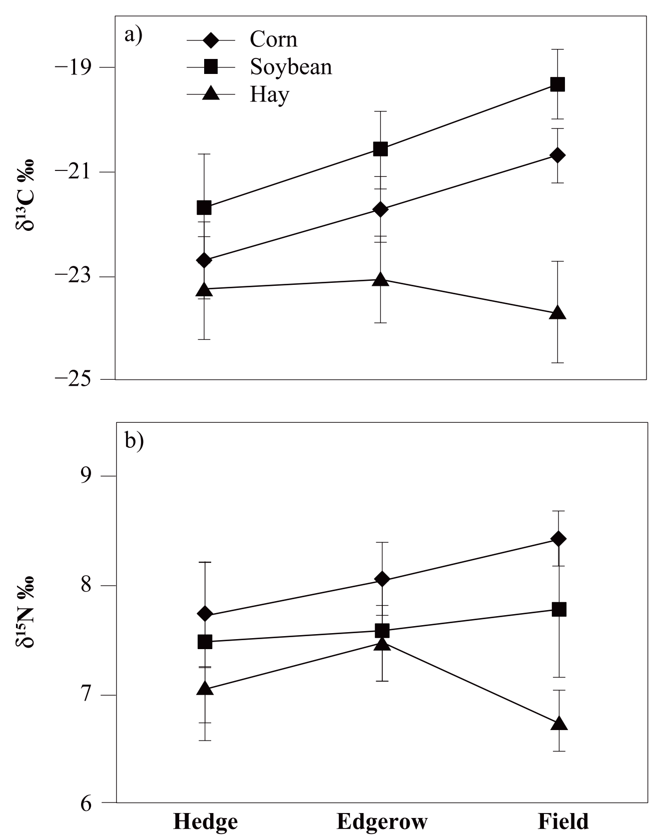

FIGURE 6. Mean a) $\delta^{13}C$ values (± 1 SE) and b) $\delta^{15}N$ values (± 1 SE) for ground beetles captured in different trap locations. Hedgerow values include only hedgerows adjacent to the specified crop.

unfertilized fields, fields planted with leguminous crops, or hedgerows. In agreement with our prediction, mean $\delta^{15}N$ of spiders from manured corn was higher than for spiders from unmanured corn (Table IV, manured corn: $\delta^{15}N = 11.01 \pm 0.23$; unmanured corn: $\delta^{15}N = 9.65 \pm 0.52$). However, ground beetles did not show a significant difference in $\delta^{15}N$ values between manured and unmanured cornfields (Table V, manured corn: $\delta^{15}N = 8.80 \pm 0.30$; unmanured corn: $\delta^{15}N = 8.06 \pm 0.35$). In contrast with our prediction, neither spiders nor ground beetles showed significant differences in mean $\delta^{15}N$ between manured and unmanured hayfields (spiders in manured hay: $\delta^{15}N = 8.77 \pm 0.58$; unmanured hay: $\delta^{15}N = 8.62 \pm 0.77$; ground beetles in manured hay: $\delta^{15}N = 6.85 \pm 0.70$; unmanured hay: $\delta^{15}N = 6.36 \pm 0.31$).

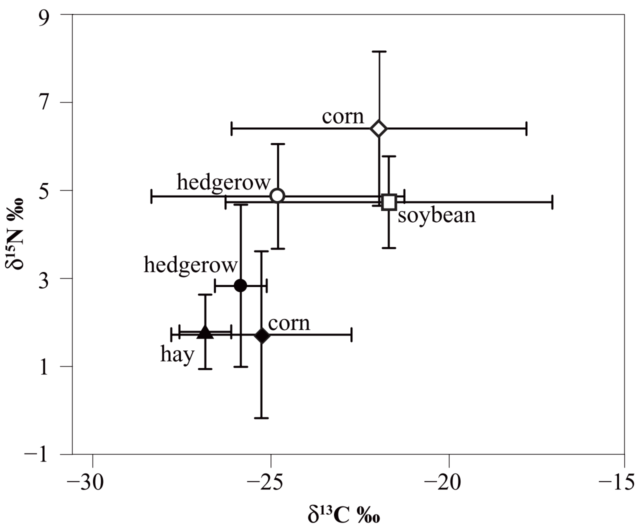

FIGURE 7. Mean $\delta^{13}C$ and $\delta^{15}N$ values (± 1 SD) for crickets (open symbols) and hoppers (filled symbols) captured in corn (diamond), hay (triangle), hedgerow (circle), and soybean (square).

When all invertebrates were analyzed together, the results partially agreed with our prediction, in that invertebrates captured in manured corn had significantly higher $\delta^{15}N$ than invertebrates captured in soybeans, hedgerows, or manured or unmanured hay (taxon: $F_{3,209} = 239.11$, $P < 0.0001$; trapping location: $F_{5,209} = 7.56$, $P < 0.0001$; Figure 8). However, there was no significant difference in $\delta^{15}N$ between invertebrates captured in manured and unmanured corn, or between invertebrates captured in manured and unmanured hay (Figure 8).

PREDICTION 3: NITROGEN AND TROPHIC LEVEL

There were significant differences in $\delta^{15}N$ among taxa, once trapping locations were controlled for (Table I). As predicted, the herbivorous hoppers and caterpillars had the lowest $\delta^{15}N$, while the spiders had the highest $\delta^{15}N$ (Figure 9). This suggests that once capture location was controlled for, the different fertilizer regimes and plant types did not obscure the basic trophic level increase in $\delta^{15}N$.

PREDICTION 4: VALUES OF $\delta^{13}C$ AND $\delta^{15}N$ IN EDGES

We predicted that $\delta^{13}C$ and $\delta^{15}N$ values of invertebrates captured in edges would be intermediate between values of invertebrates captured in the adjacent fields and hedgerows. Both spiders and ground beetles in corn and in soybean showed a tendency for this to be true for carbon, but it was only significant for spiders in corn (Table IV; Figure 5a). For spiders in soybean, $\delta^{13}C$ in the hedgerow was significantly lower than in the edge or the soybean, but there

TABLE IV. Results of models testing differences in carbon and nitrogen stable isotopes among trapping locations for spiders.

Dependent variable	Model type[1]	Random effects	Weights	Fixed effects	F	df	P
$\delta^{15}N$	lm			Manured corn, unmanured corn	7.09	28	0.01
$\delta^{15}N$	lm			Manured hay, unmanured hay	0.02	8	0.89
$\delta^{13}C$	lmem	Nest	Site	Corn, corn edge, hedgerow	16.26	56	< 0.0001
$\delta^{15}N$	lmem	Site		Corn, corn edge, hedgerow	14.59	88	< 0.0001
$\delta^{13}C$	lmem	Site		Soybean, soybean edge, hedgerow	6.76	38	0.003
$\delta^{15}N$	lmem	Field		Soybean, soybean edge, hedgerow	4.23	28	0.02
$\delta^{13}C$	lm			Hay, hay edge, hedgerow	0.28	45	0.75
$\delta^{15}N$	lm			Hay, hay edge, hedgerow	0.27	45	0.77

[1]Model types were linear mixed effects models (lmem) and linear models (lm).

TABLE V. Results of models testing differences in carbon and nitrogen stable isotopes among trapping locations for ground beetles.

Dependent variable	Model type[1]	Random effects	Fixed effects	F	df	P
$\delta^{15}N$	lm		Manured corn, unmanured corn	1.98	33	0.17
$\delta^{15}N$	lm		Manured hay, unmanured hay	0.41	10	0.54
$\delta^{13}C$	lmem	Site, date	Corn, corn edge, hedgerow	6.04	86	0.004
$\delta^{15}N$	lmem	Site, nest	Corn, corn edge, hedgerow	1.89	25	0.17
$\delta^{13}C$	lm		Soybean, soybean edge, hedgerow	1.96	39	0.15
$\delta^{15}N$	lmem	Site, nest	Soybean, soybean edge, hedgerow	0.25	21	0.78
$\delta^{13}C$	lmem	Field	Hay, hay edge, hedgerow	0.44	27	0.65
$\delta^{15}N$	lmem	Site	Hay, hay edge, hedgerow	0.98	39	0.38

[1]Model types were linear mixed effects models (lmem) and linear models (lm).

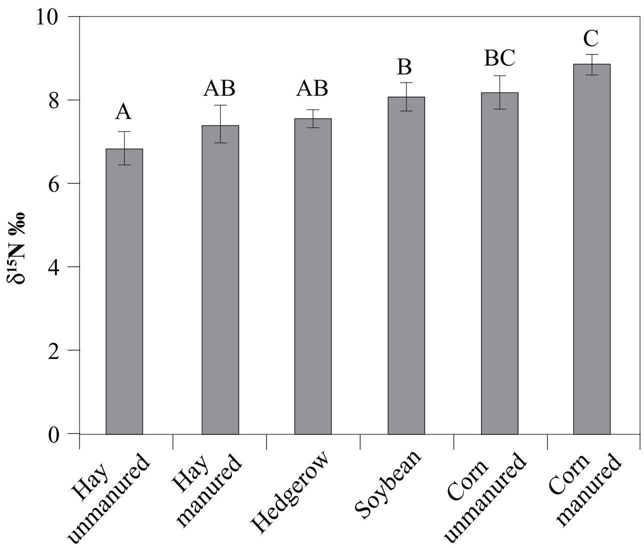

FIGURE 8. Mean $\delta^{15}N$ values for all trap locations, once taxon is controlled (± 1 SE). Means with the same letter are not significantly different ($P < 0.05$).

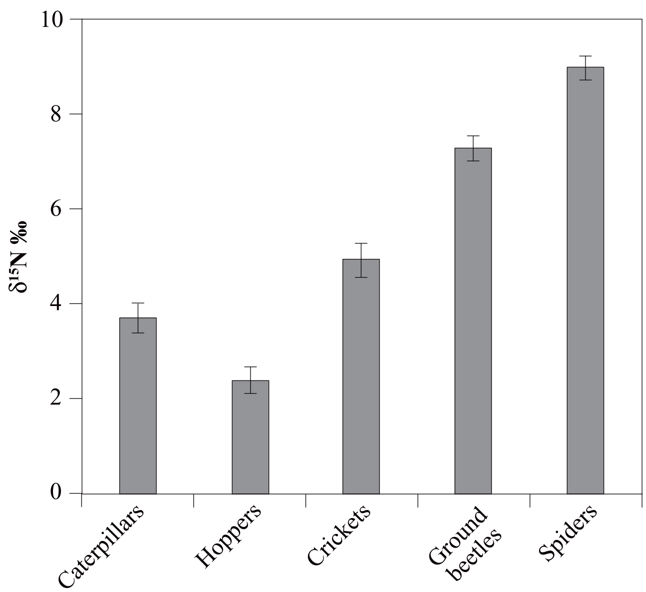

FIGURE 9. Mean $\delta^{15}N$ values for all taxa, once trap location is controlled (± 1 SE). Values were significantly different among all taxa ($P < 0.05$).

was no significant difference between edge and soybean. For ground beetles, there was a significant difference in $\delta^{13}C$ between corn and hedgerow, but not between corn and edge or between edge and hedgerow (Table V; Figure 6a).

For nitrogen, the pattern was not as clear: spiders in corn showed a significant difference in values among hedgerow, edge, and field, but values were not significantly different in soybean, field, and edge (Table IV; Figure 5b). There was no significant difference in nitrogen values in ground beetles between hedgerow, edge, and field for either corn or soybean (Table V; Figure 6b).

Carbon and nitrogen values were not significantly different between hay, hay-edge, and hedgerows adjacent to hay for either taxon (Tables IV and V; Figures 5 and 6).

Discussion

This study is the first to report $\delta^{13}C$ and $\delta^{15}N$ values of invertebrates captured in hedgerows, and one of the first to report $\delta^{13}C$ and $\delta^{15}N$ values of invertebrates captured in soybean fields. We showed that invertebrates captured in hayfields and hedgerows have significantly lower $\delta^{13}C$ than invertebrates captured in soybean and corn fields. $\delta^{15}N$ was important in distinguishing different taxa, due to the different trophic levels they occupy, and in differentiating invertebrates captured in soybean fields, hayfields, and hedgerows from manured cornfields. $\delta^{15}N$ was higher in spiders from manured cornfields than spiders from unmanured cornfields, but there was no difference for spiders in manured and unmanured hayfields, or for ground beetles from either field type.

Although we only collected invertebrates at 10 m and 20 m into crop fields, both $\delta^{13}C$ and $\delta^{15}N$ values of spiders and ground beetles captured in corn were comparable with values obtained by Latendresse (2004), who sampled invertebrates up to 250 m from a corn–forest edge. In that study, field values of $\delta^{13}C$ stabilized within 5 m of the edge, so our values from invertebrates collected 10 m or 20 m into the field probably reflect $\delta^{13}C$ and $\delta^{15}N$ of field invertebrates accurately.

This study was carried out in the context of a larger study of insectivorous songbirds, and the level of taxonomy used here is fairly coarse, reflective of the level of selection of insectivorous vertebrates in farmland. Because invertebrates were grouped at the level of orders or suborders, different species were combined to make up of samples of each taxa in each cover type. Therefore, we can't say whether the invertebrate community differs among cover types in this study. Combining different species probably increases the variability of $\delta^{13}C$ and $\delta^{15}N$ in our samples. This is especially important for ground beetles, since foraging behaviour differs widely among species and between life-stage within the same species (reviewed in Goulet, 2003). For example, Birkhofer *et al*. (2010) show that different species of ground beetles, spiders, and rove beetles can each vary in $\delta^{15}N$ by approximately 2‰ within wheat fields. The additional variation introduced by combining species at each taxonomic level makes our analysis conservative, since differences among cover types appear despite pooling of species. Future studies at finer taxonomic resolution may well clarify some issues raised in this study.

CARBON VALUES

As we predicted, carbon values were lower in invertebrates captured in hedgerows and hayfields than those captured in corn. However, there was no significant difference in $\delta^{13}C$ between invertebrates captured in corn and soybean fields. We predicted that invertebrates from corn would have the highest $\delta^{13}C$ due to the high $\delta^{13}C$ value of corn. However, our results show that none of the invertebrates captured in corn and soybean fields fully reflected the $\delta^{13}C$ values of the dominant crops in their local area (Table II; Figures 4–7). Invertebrates captured in soybean, hedgerows, and hayfields tended to have higher

$\delta^{13}C$ than the dominant plants in the respective trapping locations. In contrast, invertebrates captured in corn had $\delta^{13}C$ much lower than the corn plants. Isotope values do tend to increase with trophic level, but the changes are typically small for carbon (*e.g.*, 0.5‰ per trophic level; McCutchan *et al.*, 2003). This might explain the relatively small differences between plant values and invertebrate values found in hedgerows and hayfields, but it can't explain the large differences found in soybeans and in corn. The largest difference between plants and invertebrates was found for hoppers in corn (Table II; Figure 7), despite hoppers being strict herbivores. This strongly suggests that the hoppers we captured in corn were not primarily feeding on corn plants, or had recently switched from another food source and had not yet incorporated the relatively high $\delta^{13}C$ value of corn into their tissues. In partial support of this, the 2 lowest $\delta^{13}C$ values of hoppers in corn came from 2 cornfields on the organic site. The extremely weedy nature of the organic fields would have provided hoppers feeding in cornfields abundant C3 carbon sources, which may have produced the low $\delta^{13}C$ values.

There are at least 3 reasons why invertebrates captured in crop fields did not fully reflect the $\delta^{13}C$ value of the local dominant crop plants: movement among different land uses, use of alternative food sources, and retention of previous years' $\delta^{13}C$ by overwintering invertebrates. Firstly, as suggested by Haubert *et al.* (2009), low $\delta^{13}C$ values of invertebrates from cornfields and high values of invertebrates from soybean fields might reflect movement of invertebrates among different agricultural land uses. Some species of ground beetles do move between crop fields during the growing season, while other species remain associated with a single field or with hedgerows (Frampton & Çilgi, 1995; Mauremooto *et al.*, 1995; Thomas *et al.*, 2001). Spiders disperse from permanent habitats into crop fields early in the growing season (reviewed by Marc, Canard & Ysnel, 1999), but little information is available about movements between crop fields during the growing season. However, spiders are very mobile, and can recolonize areas of local extinction within a few weeks (Holland, Winder & Perry, 2000; Wick & Freier, 2000), so movements between crop fields can occur. The different sowing and growing patterns of different crops compared to hedgerows and hayfields make it probable that herbivores also move between land uses during the growing season. For example, McNabb, Halaj, and Wise (2001) found that herbivores feeding on C3 plants (cucumbers and squash) had higher than expected $\delta^{13}C$ values and suggested that herbivores might be getting some carbon from C4 grasses outside their experimental plots. Laboratory studies have shown that when invertebrates are switched between diets with contrasting $\delta^{13}C$ values, it can take between several days to several weeks for the new carbon source to be fully reflected in the $\delta^{13}C$ value of the organism (Ostrom, Colunga-Garcia & Gage, 1997; Gratton & Forbes, 2006), so movement between different land uses could explain the observed similarity in $\delta^{13}C$ values of invertebrates captured in corn and soybean fields.

Secondly, the availability of alternative food sources within the crop fields could affect the $\delta^{13}C$ values of generalist foragers. For herbivores, this would take the form of C3 weeds (*e.g.*, alfalfa [*Medicago sativa*], clover [*Trifolium* spp.], dandelions [*Taraxacum* spp.], timothy grass [*Phleum pratense*]) and C4 weeds (primarily foxtail grasses [*Setaria* spp.] and sedges), both of which were found in the study fields (J. Girard, pers. observ.). For higher trophic levels, alternative food sources include detritivores living in the soil. Both spiders and ground beetles are known to feed on detritivores in agroecosystems (Wise, Snyder & Tuntibunpakul, 1999; Halaj & Wise, 2002). Crop residues take time to break down in the soil, so detritivores may have $\delta^{13}C$ values that reflect the previous crop, not the current one. For example, Albers, Schaefer, and Scheu (2006) found that 18 months after corn was planted in a field that had previously been planted only in C3 crops, small detritivores had incorporated less than 40% carbon from corn. The delay in the appearance of a new carbon value in the detritivore food chain may explain why carbon values of ground beetles and spiders were actually higher in soybean fields than in cornfields (Figure 5a and 6a).

One possible method for testing these 2 hypotheses is to analyze invertebrates in separate pieces, rather than as whole organisms. Different parts of an organism assimilate carbon isotopes at different speeds; for example, after a diet switch, the reproductive and fatty tissues of beetles reflect the new carbon source more quickly than do the hind wings (Gratton & Forbes, 2006). Therefore, an invertebrate that has recently moved between land uses will have different carbon values in different tissues, whereas an invertebrate that has a constant diet, even if it is composed of alternative food sources, will have similar carbon values in different tissues. Such further analysis was beyond the scope of this study.

A third explanation for the dissimilarity between invertebrate $\delta^{13}C$ values and the those of the dominant plants in capture locations is carryover of $\delta^{13}C$ values in overwintering invertebrates. An invertebrate that overwinters, either as an adult, larva, or egg, might reflect the $\delta^{13}C$ and/or $\delta^{15}N$ value of the habitat it (or its parent) used in the previous year. For example, the larval food source of adult moths can be determined using $\delta^{13}C$ (Gould *et al.*, 2002). If after emerging in the spring, an invertebrate is captured in a land cover type with a different dominant plant cover than that used for foraging prior to overwintering, it would show a $\delta^{13}C$ different from that expected based on its capture location. Given the strong corn–soybean rotation in the study area, this may explain why we could not differentiate between invertebrates captured in corn and soybean using $\delta^{13}C$.

Invertebrates captured in hedgerows and hayfields showed $\delta^{13}C$ values close to those expected for invertebrates using C3 plants as the primary food source. This may result from invertebrates in these less disturbed habitats moving around less than those in crop fields (either within or between seasons), or it may simply reflect the overall dominance of C3 plants in the area.

In our study, the main carbon sources provided by corn and by various C3 plants differed considerably in

$\delta^{13}C$ (Table II). However, $\delta^{13}C$ ranges of C3 and C4 plants do overlap (or very nearly so; Rounick & Winterbourn, 1986; O'Leary, 1988), so these differences may not be apparent in all systems. This method of using $\delta^{13}C$ to identify carbon source and therefore habitat of invertebrates (or other consumers) will only work where large differences in carbon sources exist.

Nitrogen, fertilizer regime, and plant type

We predicted that nitrogen values would be higher in manured fields compared to all other land uses. Nitrogen values were higher in invertebrates from manured cornfields than in invertebrates from soybean fields, hedgerows, or hayfields, and for spiders in manured and unmanured cornfields. However, this was not true for ground beetles in cornfields or for spiders or ground beetles in hayfields. Powell *et al*. (2005) found that corn plants took up 14–16% of available ^{15}N from manure in the year of manure application and 4–8% in the year after application. This additional uptake in years when corn or hay is not treated with manure may make detecting changes in fertilization using $\delta^{15}N$ more difficult. Spiders were less variable in $\delta^{15}N$ than ground beetles (Figures 3, 5, 6), probably because spiders are predatory, whereas ground beetles vary in trophic level (Lövei & Sunderland, 1996; Bennett & Hobson, 2009). This may make changes in fertilization regime easier to detect in spiders than in ground beetles.

Nitrogen and trophic level

As we predicted, $\delta^{15}N$ did reflect trophic levels of the different taxa sampled, with hoppers and caterpillars having the lowest $\delta^{15}N$ and spiders the highest $\delta^{15}N$, while the omnivorous crickets and ground beetles had intermediate values. Based on a trophic level $\delta^{15}N$ increase of 2.3‰ (McCutchan *et al*., 2003), spiders were 3 trophic levels higher than hoppers. Other agricultural food web studies have compared trophic levels of spiders and detritivorous collembola and found that spiders are between 2 and 3 trophic levels above collembola (McNabb, Halaj & Wise, 2001; Wise, Moldenhauer & Halaj, 2006). Ground beetles were less than one trophic level lower than spiders, suggesting that they are largely predatory in this system.

Values of $\delta^{13}C$ and $\delta^{15}N$ in edges

Our prediction that $\delta^{13}C$ and $\delta^{15}N$ values of invertebrates captured in edges would be intermediate between values of invertebrates captured in the adjacent fields and hedgerows was only partially supported. Although the prediction was supported for $\delta^{13}C$ and $\delta^{15}N$ values of spiders in corn, it was not supported for spiders in soybean, or for ground beetles in either corn or soybean.

Intermediate values of $\delta^{13}C$ and $\delta^{15}N$ in edges suggest a movement of invertebrates between hedgerow and field, but not necessarily between fields. If there were a direct movement of invertebrates between corn and soybean fields, one would expect that values of $\delta^{13}C$ and $\delta^{15}N$ for invertebrates in soybean edges would be higher (more similar to cornfields) than the values of invertebrates in soybean fields. This is shown only for $\delta^{15}N$ values of spiders (Figure 5b). Therefore, the edge values reported here do not strongly support direct movement of ground beetles and spiders between crop fields.

$\delta^{13}C$ and $\delta^{15}N$ were not significantly different between hay, hay-edge, and hedgerows adjacent to hay for any taxon. This is not surprising as both land uses were dominated by C3 plants, and there was no significant difference in $\delta^{15}N$ values between manured and unmanured hayfields, so a difference would not be expected.

We have shown that $\delta^{13}C$ and $\delta^{15}N$ can be used to distinguish between invertebrates captured in different agricultural land uses, even at a small spatial scale. In addition, $\delta^{15}N$ can distinguish between invertebrates at different trophic levels. The ability to distinguish between invertebrates from different agricultural land cover types will benefit research into food webs and land use change in farmland. However, further studies at finer taxonomic levels, together with laboratory studies into discrimination factors and foraging preferences, will be necessary to further investigate how changes in crop type are reflected in the isotope values of invertebrates.

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APPENDIX I. Sample sizes of each taxon in each trapping location. Where manure status is not given (corn - other or hay - other), we were not able to obtain enough information from the farmer to determine the fertilization regime of the field, and the field was excluded from the manure analysis.

Taxon	Trapping location	*n*
caterpillars	corn	3
caterpillars	hay	4
caterpillars	hedge	28
crickets	corn - manured	3
crickets	corn - not manured	2
crickets	corn - other	1
crickets	hay - not manured	2
crickets	hedge	14
crickets	soy	4
ground beetles	corn - manured	25
ground beetles	corn - not manured	10
ground beetles	corn - other	3
ground beetles	corn edge	33
ground beetles	hay - manured	6
ground beetles	hay - not manured	6
ground beetles	hay - other	6
ground beetles	hay edge	14
ground beetles	hedge	36
ground beetles	soy	13
ground beetles	soy edge	15
hoppers	corn - manured	4
hoppers	corn - not manured	2
hoppers	corn - other	1
hoppers	hay - manured	3
hoppers	hay - not manured	4
hoppers	hay - other	3
hoppers	hedge	36
hoppers	soy	2
spiders	corn - manured	23
spiders	corn - not manured	7
spiders	corn - other	3
spiders	corn edge	31
spiders	hay - manured	4
spiders	hay - not manured	6
spiders	hay - other	5
spiders	hay edge	15
spiders	hedge	49
spiders	soy	13
spiders	soy edge	15