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Colonization dynamics of agroecosystem spider assemblages after snow-melt in Quebec (Canada)

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Abstract. Spiders are important generalist predators in agroecosystems, yet early season colonization is poorly understood, especially in northern regions. We investigated colonization patterns of spiders in agricultural fields after snow-melt in four cornfields in southwestern Quebec (Canada). Paired pitfall traps were associated with two drift fences to obtain data about immigration to and emigration from the fields and were placed at increasing distances from a deciduous forest border. Control traps were placed four meters inside the forest. Seventy-four species were collected, dominated by Linyphiidae and Lycosidae. Most of the fauna was already active during the first weeks of collection, and early season assemblages differed from late season assemblages. A significant ecotone effect was found for spider abundance, species richness and species composition. This study stresses the importance of early season spider activity in agroecosystems, and this context is relevant to a period of colonization by the dominant, active spider species.

Keywords: Agroecosystems, early season assemblage composition, dispersal, Linyphiidae, Lycosidae

Generalist arthropod predators, including spiders, are important biocontrol agents in agroecosystems (Riechert & Lawrence 1997; Symondson et al. 2002; Stiling & Cornelissen 2005) and, when seen as a species assemblage, can exert top-down effects on many agricultural pests (Riechert & Bishop 1990; Carter & Rypstra 1995). Their efficiency as pest control agents is, however, influenced by several factors including intra-guild predation (Balfour et al. 2003), cannibalism (Buddle et al. 2003), prey preference (Harmon & Andow 2004; Toft 2005) and colonization of agricultural habitats (Hibbert & Buddle 2008; Sackett et al. 2009).

Many generalist arthropod predators spend the winter in non-cultivated marginal habitats before colonizing fields in spring (Alderweireldt 1989; Thomas & Marshall 1999; Maloney et al. 2003). While marginal habitats are known to increase the diversity and abundance of generalist arthropod predators in fields (Halaj et al. 2000; Landis et al. 2000; Lemke & Poehling 2002; Schmidt et al. 2008; Sackett et al. 2009), few quantitative studies have estimated the proportions of arthropods using marginal habitats as shelters to spend the winter (Pywell et al. 2005). There is also evidence that dominant species in agricultural fields (e.g., agrobiont species: Luczak 1979; Samu & Szinetàr 2002) show synchronization with habitat changes and disturbances. In other words, species of ecological importance may spend most of their lives within disturbed habitats such as agroecosystems (e.g., linyphiids in desert agroecosystems: Gavish-Regev et al. 2008; Pluess et al. 2010) and make little use of marginal habitats as overwintering shelters (Sunderland & Samu 2000).

Early colonization dynamics of arthropod predators can be especially important in northern systems where the snow cover is extensive and active movement of predators into agricultural fields during the spring can only occur after snow-melt. Spiders are among the first predators to colonize agricultural fields (Maloney et al. 2003) and prey on numerous pest insects (Young & Edwards 1990; Pfannenstiel 2008). However, at northern latitudes, most studies of spider colonization of agroecosystems have focused on the summer season, when spider abundance is high (e.g., Hibbert & Buddle 2008; Sackett et al. 2008, 2009). This can bias our understanding of the way colonization proceeds in northern countries where certain taxa remain active and forage under the snow layer (e.g., Lycosidae and Lyniphiidae, Aitchison 1984 a, b).

To date, few studies have investigated early season dynamics and spider movement after snow-melt (Juen et al. 2003). Since spiders usually move into the field sooner than pests or specialist predators (Agnew & Smith 1989; Young & Edwards 1990; Marc et al. 1999), early colonization could help maintain a steady population of generalist arthropod predators, thus maximizing their affect on pests. Furthermore, early season colonization dynamics can differ greatly from those observed in late season studies: with the exception of the Linyphidae, most spider species disperse aerially while in immature stages when they can easily be lifted by air currents (Dean & Sterling 1985). Spiders usually overwinter either as adults or penultimates (Aitchison 1984a; Foelix 1996), suggesting that the cursorial mode of colonization could prevail over ballooning after snow-melt. Even though linyphiids are capable of ballooning at all stages, atmospheric conditions are unlikely to be favorable for aerial field colonization during early season. Hibbert & Buddle (2008) have also stressed the importance of cursorial movement over ballooning for short-distance colonization of cornfields.

We tested how distance to a forest-field ecotone, direction of movement and sampling week affected cornfield spider assemblages after snow-melt in southwestern Québec (Canada). The objectives of the research were to determine how spider abundance, species richness and assemblages varied temporally after snow-melt, and to compare spider abundance, species richness and assemblages as the distance to a non-managed forest border increased.

METHODS

Site description.—The study area was located adjacent to the Morgan Arboretum (Sainte Anne de Bellevue, 45.42°N, 73.95°W, Quebec, Canada). The experiment was established on four cornfields (*Zea mays*) with similar soil characteristics

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operated by the Macdonald campus farm, McGill University. These fields were on a corn-alfalfa rotation and managed using reduced tillage practices. Corn residues were left on the soil after harvesting during the previous year, and no insecticides were sprayed during the course of our study. All fields were adjacent to the Morgan Arboretum, a 254 ha deciduous reserve dominated by *Acer saccharum*, *A. rubrum* and *Fagus grandifola*. One of the studied fields was divided in two because of its large area (> 12 ha) compared to the three other fields (3 ha each). This allowed for five separate sites (i.e., five replicates) for experimentation.

Sampling method.—Distance of colonization into the field was assessed by placing paired pitfall traps at 0, 4, 8, 16, and 100 m from the forest-field ecotone plus a control trap 4 m inside the forest border. One study site was not large enough to install a trap at 100 m; the trap was thus set at half the width of the field (54 m). Since no significant differences in abundance ($\chi^2_1 = 1.64$, $P = 0.2$) and species richness ($\chi^2_1 = 0.06$, $P = 0.8$) were found, these traps were grouped with 100 m traps for subsequent analyses. Paired traps were set at least 10 m apart from each other and spaced perpendicular to each other instead of in a linear transect, and traps within each replicates were located at least 200 m apart. To obtain data about immigration to and emigration from the field, we used two drift fences arranged in a "V" shape perpendicular to the forest border and containing a pitfall trap at the center of each fence. Traps facing the field center were counted as movement from the field into the forest, and traps facing the forest border were counted as movement into the field. The drift fence consisted in a 75 long × 15 cm high piece of aluminum flashing embedded 5 cm deep in the ground. The pitfall traps were plastic cups (6 cm diameter×6 cm height) filled with 1 cm of propylene glycol diluted 3:1 with water. Each trap was covered with a 15 × 15 cm plastic roof maintained about 5 cm above ground in order to avoid flooding by rain. The total trapping effort was therefore 60 pitfall traps (2 drift fences × 6 distances × 5 replicates).

Snow cover was extensive during the 2008 winter, since over 370 cm of snow precipitation was recorded (Environment Canada 2011). Snow-melt happened quickly, and no snow patches were observed in the field after the second week of collection. Traps were installed on 16 April 2008, immediately after snow-melt in the fields, and were collected weekly from 22 April until 2 July 2008, with a total of seven collection dates. Ecotone and field traps were removed from 7 May to 23 May for tillage-seeding period and from 6 June to 17 June for mid-season herbicide spraying. Forest traps were kept active during field disturbances and collected on 23 May (Week 5) and 17 June (Week 9) in order to see how spider abundance and species richness were affected by these disturbances. All adults collected were identified to species using Paquin & Dupérré (2003), and nomenclature followed Platnick (2011). Voucher specimens were deposited in McGill University's Lyman Entomological Museum (Ste. Anne de Bellevue, Quebec, Canada).

Statistical analyses.—We used Generalized Estimating Equations (GEE) with Poisson error and a log link to test the effects of distance, direction of traps and sampling week in R version 2.10.1 (R Development Core Team 2009) for Macintosh with the package geepack (Højsgaard et al. 2005). Response variables included spider abundance, abundance of the two most common families and the three most common species. Raw species richness was positively correlated with spider abundance (Spearman $\rho = 0.91$, $P < 0.0001$), and we therefore only present abundance data. Individual traps were set as the repeated measure, and we used an exchangeable correlation structure since sampling events were not equally interspersed due to tillage and herbicide spraying events. Number of sampling days was used as an offset variable to correct for sampling effort. Because of small sample size, only two-way interactions were considered. Species richness was estimated for distance, direction of colonization and sampling week with the non-parametric estimators Chao 2, Jacknife 1, Jacknife 2 and Bootstrap using EstimateS version 8.2 for Macintosh (Colwell 2009). These estimators perform well in case of high occurrence of rare species and are less dependent on sample size (Magurran 2004).

To assess the effect of sampling week and distance to border (continuous variables) on spider assemblage composition, we used non-metric multi-dimensional scaling (NMDS) ordinations with the package vegan (Oksanen et al. 2010). NMDS is a non-parametric technique that does not require linear relationships between variables (McCune & Grace 2002). Singletons and doubletons were excluded from the dataset, and abundances were $\log_{10}$ (abundance+1) transformed to decrease the influence of common species. NMDS that was run on raw abundance data showed substantially similar results and did not improve the fit of the analysis. We therefore only present results for log-transformed data. In order to minimize stress, data were pooled per distance and direction to observe sampling week effect on assemblage composition and pooled per sampling week and direction in order to observe distance effect. We ran a preliminary six-dimensional analysis to determine the optimal number of dimensions in order to minimize stress [parameters: Bray-Curtis distance measure, random starting configuration based on the time of the day, 500 iterations maximum (McCune & Grace 2002)]. We re-ran the NMDS using the same parameters as above, but altered the number of dimensions as recommended by the preliminary run and used the graph data from the initial run for starting coordinates (McCune & Grace 2002). To further analyze if differences in species composition could be observed between distance and sampling week, we used PERMANOVA (Anderson 2001, function adonis in Vegan). PERMANOVA is a non-parametric technique that assesses distance between groups based on a dissimilarity matrix (Anderson 2001) and can handle continuous predictors. We used Bray-Curtis distance to correspond with NMDS metrics and performed the permutation tests within replicates to conserve the structure of the data (n = 5000 permutations). Multiple comparisons between distances and sampling weeks were performed using the software PAST version 2.11 for Windows (Hammer et al. 2001).

In order to identify agrobiont species, we used Indicator Species Analysis with the package labdsv (Roberts 2010) (function indval) on the ten most abundant species in field traps. Indicator Species Analysis compares the distribution of a given species within a group of samples to a random generation of the group (Dufrene & Legendre 1997). Traps were grouped into three habitats (forest, ecotone and field)

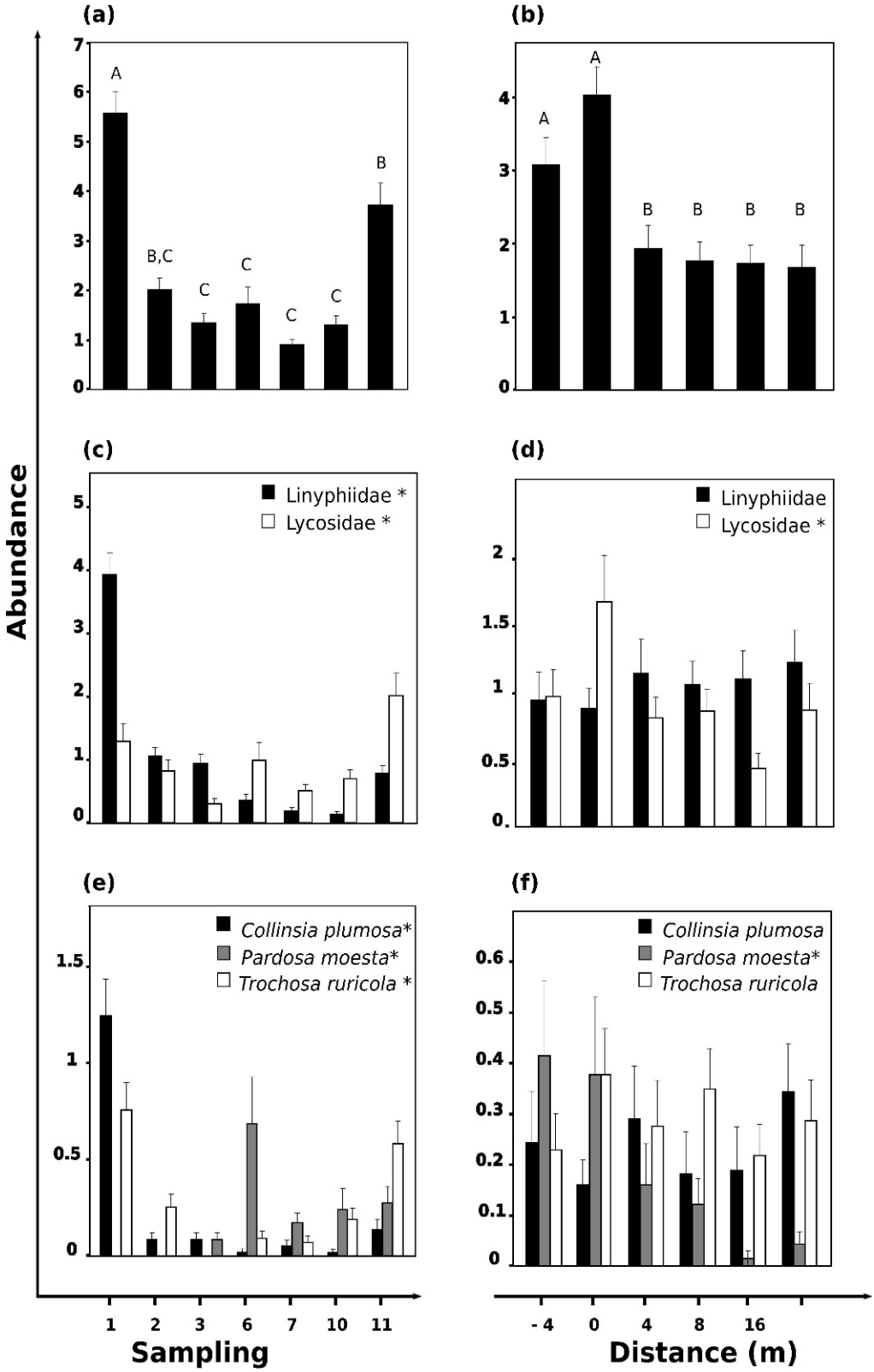

Figure 1a–f.—Mean spider abundance (+SE) in function of sampling week and distance to the forest-field ecotone. Letters indicate significantly different means at alpha = 0.05. Effects of sampling week and distance on total abundance (a, b) on dominant families (c, d) and on dominant species (e, f).

Table 1.—Species richness and richness estimators in function of sampling week (a), distance from the forest-field ecotone (b), and direction of colonization (c) (mean ± SD).

(a)

Sampling week	1	2	3	6	7	10	11
Raw species richness	20 ± 3.8	19 ± 3.8	17 ± 3.6	16 ± 3.6	10 ± 2.9	11 ± 3.1	28 ± 4.4
Chao 2	28.8 ± 7.3	29.4 ± 11.4	20.8 ± 6.3	24.2 ± 6.6	17.6 ± 3.8	22.9 ± 8	41.6 ± 8.6
Jacknife 1	27.9 ± 2.3	25.7 ± 2.9	19.7 ± 2.1	22.6 ± 2.8	16.6 ± 2.1	20.8 ± 2.7	38 ± 3.9
Jacknife 2	29.4 ± 5.4	28 ± 7.4	20.9 ± 4.9	24.6 ± 6.6	17.9 ± 5.3	22.5 ± 6.5	42.1 ± 8.9
Bootstrap	25.1 ± 2.2	22.5 ± 3	17.7 ± 2	19.4 ± 2.8	14.3 ± 2.3	18.1 ± 2.7	32.8 ± 3.9

(b)

Distance (m)	−4	0	4	8	16	100
Raw species richness	35.5 ± 3.7	40 ± 4.5	22 ± 3.9	16 ± 3.6	15 ± 3.5	16 ± 3.6
Chao 2	20.6 ± 2.1	64.2 ± 5.6	47.6 ± 5	34.71 ± 3.3	39.1 ± 4.4	35.5 ± 3.7
Jacknife 1	22.1 ± 4.8	46.2 ± 3.8	28.9 ± 2.7	22 ± 2.3	20.8 ± 2.5	20.6 ± 2.1
Jacknife 2	18.1 ± 2	48.7 ± 8.5	31.4 ± 6.3	23 ± 5.5	22.8 ± 6	22.1 ± 4.8
Bootstrap	30.1 ± 2.9	41.2 ± 3.4	25.3 ± 2.6	19.7 ± 2.3	18.2 ± 2.7	18.1 ± 2

(c)

Direction	Forest-field	Field-forest
Raw species richness	46 ± 4.4	41 ± 4.6
Chao 2	55 ± 7.5	48.7 ± 6
Jacknife 1	57 ± 4	52 ± 3.7
Jacknife 2	61.6 ± 9.3	55 ± 8.6
Bootstrap	50.5 ± 3.9	46.4 ± 3.7

and three sampling periods (early season (weeks 1 through 3), post-tillage (week 6 and 7) and post-herbicide (week 10 and 11)).

RESULTS

We collected a total of 1076 individuals representing 74 species and 14 families. Of these, 25% were immature spiders and could not be identified to species level. Singletons and doubletons represented more than 50% of all captured species and the most commonly collected families were Linyphiidae (444 individuals), Lycosidae (435 individuals) and Thomisidae (103 individuals). The three most abundant species were the wolf spiders *Trochosa ruricola* (De Geer 1778) (121 individuals), *Pardosa moesta* Banks 1892 (114 individuals) and the linyphiid *Collinsia plumosa* (Emerton 1882) (97 individuals).

Spider abundance and species richness.—No effects of direction were found for all tested models ($P > 0.1$). Even during field disturbance weeks, no effect was reported for forest traps ($P > 0.1$). For the total abundance model, significant effects were found for distance ($\chi^2_5 = 78.1$, $P < 0.0001$) and sampling week ($\chi^2_6 = 286.6$, $P < 0.0001$) and a significant distance × sampling week interaction was reported ($\chi^2_{30} = 126.8$, $P < 0.0001$). Spider abundance was highest during the first and last week of collection, while species richness remained stable across sampling weeks except for the last collection date (Fig. 1a, Table 1a). Spider abundance and species richness decreased as distance to the forest-field ecotone increased (Fig. 1b, Table 2b). Overall, abundance and species richness were highest at the ecotone and 4 m inside the forest, whereas field traps had similar abundances and species richness. Despite the interaction between sampling week and distance, the shape of the distance effect was relatively similar across all sampling weeks, with the exception of weeks 1 and 7 (Fig. 2). Similarly to spider abundance, direction of colonization did not affect spider estimated species richness (Table 1c).

Table 2.—*P*-values for multiple comparisons of sampling week (a) and distance (b) effects on spider assemblages using PERMANOVA. * indicates significant *P*-value at alpha = 0.05.

(a)

	Sampling week						
	1	2	3	6	7	10	11
1	-	-	-	-	-	-	-
2	0.0083*	-	-	-	-	-	-
3	0.0078*	0.47	-	-	-	-	-
6	0.0077*	0.0072*	0.0096*	-	-	-	-
7	0.0062*	0.008*	0.0065*	0.35	-	-	-
10	0.0084*	0.0099*	0.0092*	0.41	0.22	-	-
11	0.0078*	0.0078*	0.0082*	0.017*	0.0082*	0.24	-

(b)

	Distance (m)				
	−4	0	8	16	100
−4	-	-	-	-	-
0	0.052	-	-	-	-
8	0.0089*	0.70	-	-	-
16	0.0019*	0.24	0.58	-	-
100	0.0039*	0.62	0.64	0.65	-

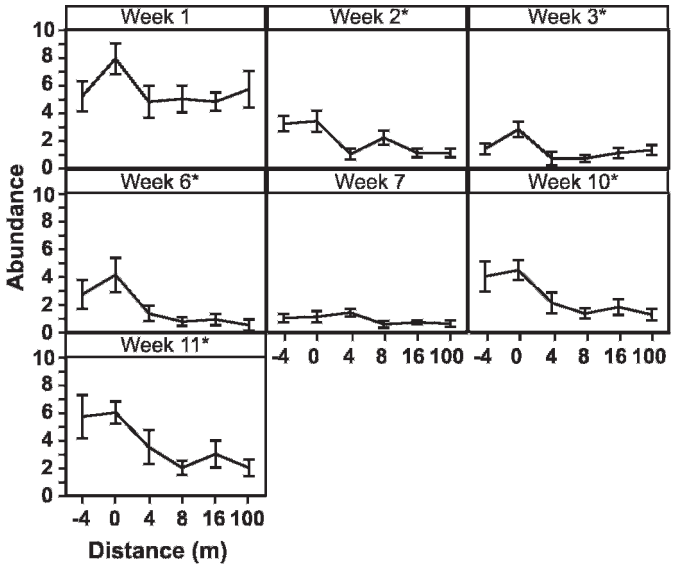

Figure 2.—Mean spider abundance (± SE) in function of sampling week and distance to the forest-field ecotone.* indicates significant P-value at alpha = 0.05.

At the family level, GEE analysis revealed significant family × distance ($\chi^2_5 = 14.3$, $P < 0.05$) and family × sampling week ($\chi^2_6 = 82.9$, $P < 0.0001$) interactions. Linyphiids were most abundant during the first week of collection and decreased steadily afterwards while lycosids showed the opposite pattern, and distance to the ecotone only affected lycosids ($\chi^2_5 = 12.4$, $P < 0.05$; Fig. 1c, d). At the species level, we also found evidence of species specific responses to the distance gradient and sampling week as the interaction terms with species were significant (distance × species: $\chi^2_{10} = 32$, $P < 0.0005$; sampling week × species: $\chi^2_{12} = 34053$, $P < 0.0001$). Only *P. moesta* was absent from the early season data set and had increased abundance as sampling went on (Fig. 1e). *Collinsia plumosa* appeared mostly during the first week of collection, whereas *T. ruricola* had high abundance on the first and last weeks of collection. *Pardosa moesta* was also the only dominant species to show a strong distance effect ($\chi^2_5 = 21.9$, $P < 0.001$), with a preference for forest and ecotone habitats and lower abundance in remote field traps (Fig. 1f).

Spider assemblage composition.—PERMANOVA on spider assemblages indicated a significant effect of sampling week ($F_{1,33} = 8.09$, $R^2 = 0.19$, $P < 0.001$). NMDS ordination provided a two-dimensional solution that minimized stress after 105 iterations (final stress = 6.75). The three first weeks of collection showed a clear separation from later collection dates on axis 1, while later season assemblages showed strong overlap (Fig. 3a). Multiple comparisons of PERMANOVA results on sampling weeks confirmed this trend and indicated that the first week of collection differed significantly from all other sampling weeks ($P < 0.01$; Table 2a). Weeks 2 and 3 had similar assemblage composition as well as weeks 6, 7, 10 and 11. We hereafter refer to early season period for the three first weeks of collection, post-tillage period for weeks 6 and 7 and post-herbicide period for weeks 10 and 11.

Distance to the ecotone also significantly affected spider assemblages ($F_{1,28} = 2.27$, $R^2 = 0.075$, $P < 0.021$). The NMDS ordination produced a two-dimensional solution that minimized stress after 115 iterations (final stress = 5.75). Spider assemblages were distinct between the forest border and field traps, but showed overlap between ecotone and field habitats (Fig. 3b). Multiple comparisons of distances with PERMANOVA results showed a similar trend: the ecotone was similar to both field and forest habitats, while the forest and the field differed significantly ($P < 0.01$) (Table 2b).

Species that were frequently collected in field traps also had high relative abundance during the early season (first three weeks of collection) (Table 3a). Indicator species analysis did not show any species with significant affinity for the field habitat, as most species were equally associated with the ecotone and the field.

DISCUSSION

Our results indicate that spiders were active immediately after snow-melt and were frequently collected in field traps in the early spring. The forest and ecotone habitats had distinct spider assemblages, but some overlap was shown between ecotone and field habitats (Fig. 3b). This could mean that a significant proportion of the spider diversity used field habitats as shelters during the winter and mitigates the influence of surrounding non-crop habitats as sources for field colonization (Alderweireldt 1989; Thomas & Marshall 1999; Maloney et al. 2003).

The most abundant species were active quickly after snow-melt (Table 3): over 300 spiders were collected during the very first week of sampling, which represents a third of our sample size. Out of the 74 species collected, 29 were first collected during early season. Linyphiidae and Lycosidae composed most of the early spider assemblage, and two of the most common species (*T. ruricola* and *C. plumosa*) had high activity density during this period. NMDS ordination and PERMANOVA on sampling weeks confirmed that early season assemblages differed significantly from the later season. In short, the early season was composed of few species with high abundance compared to later season assemblages (Table 1a, Fig. 1a).

These results show that the dominant species and families were those active early after snow-melt and with high affinity for the field environment. Indeed, the life history of some species may be such that they spend their entire lives within disturbed habitats such as agroecosystems (Samu & Szinetàr 2002; Gavish-Regev et al. 2008; Pluess et al. 2010).According to Samu & Szinetàr (2002), the agrobiont community is typically represented by "less than 10 species making up 60 to 90% of the whole spider community". In our case, the ten most abundant species formed 68% of the field assemblage (Table 2). These species had high activity density during early season (over 50% of these species were captured during this period, except for *P. moesta*) and were frequently collected in field traps. Three species (*Pardosa moesta*, *Trochosa terricola* and *Diplostyla concolor*) were unlikely to be agrobiont species, since their indicator species value was low in the field habitat (Table 3). The rest of the agrobiont assemblage had equal indicator value in field and ecotone habitats, but this could be due to low sample size. To confirm whether these species effectively use field habitats during the winter, sampling techniques enabling spider collection under snow (Paquin

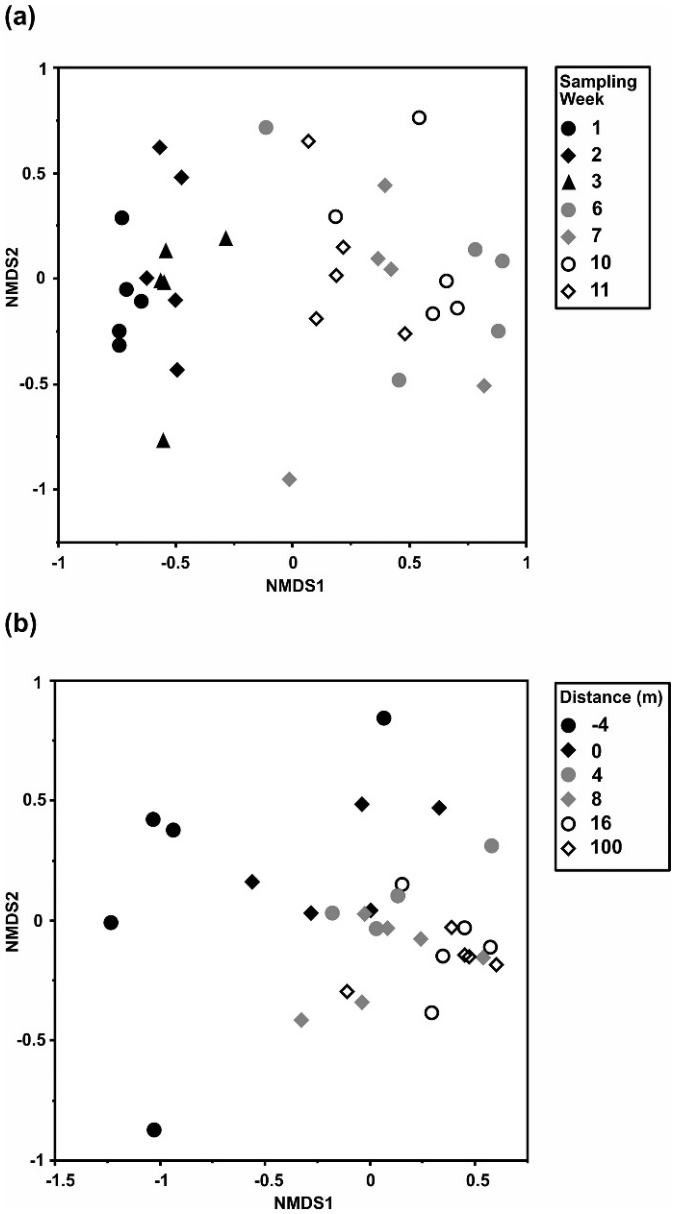

Figure 3a, b.—NMDS ordinations based on log-transformed abundance data of 35 spider species depicting spider assemblage composition in function of sampling period (a) and distance (b). Data points represent pooled samples (n = 35 for sampling week, n = 30 for distance).

2004) could provide useful information on the identity and life cycles of agrobiont spiders.

Species richness and spider abundance were both highest in the forest and ecotone habitats compared to the field. Analysis of spider assemblages at the different distances from the ecotone indicated that the ecotone was similar to the field and forest habitats. These results are confirmed by several studies on terrestrial arthropods that have documented similar increases in abundance and species richness at the ecotone compared to the two adjacent habitats (Helle & Muona 1985; Jökimaki et al. 1998; Pearce et al. 2005a; Öberg & Ekbom 2006). This effect can be explained by the fact that species that are usually present in only one of the two habitats may meet in the overlapping ecotone (Samu et al.1999). More recent studies confirmed this fact and showed the positive influence of landscape heterogeneity and high degree of perennial crops in the surrounding landscape on spider abundance and species richness (Clough et al. 2005; Schmidt et al. 2005; Öberg et al. 2007, 2008; Gavish-Regev et al. 2008; Pluess et al. 2008, 2010). This is also supported by Juen & Traugott (2004), where spider assemblages in a small field (~ 0.3 ha) had little within-field variation, whereas the ecotone was distinct from other sampled habitats.

The modalities of field colonization are likely to differ depending on families or even between species. Lycosid abundance decreased with distance, while linyphiids did not (Fig. 1d). Species such as *T. ruricola*, however, were abundant irrespective of distance, and *P. moesta* was highly affected by this variable (Fig. 1f). It is unlikely that this pattern was caused by aerial dispersal for lycosids, since ballooning mostly occurs at immature stages in this family (Dean & Sterling 1985; Pearce et al. 2005b) and they use cursorial dispersal as their main mode of agroecosystem colonization (Luczak 1979; Weyman et al. 2002). An early ballooning event from the surrounding landscape cannot be ruled out for linyphiids (Gavish-Regev et al. 2008). However, in temperate countries, major ballooning events occur mainly after crop senescence rather than in the spring (Sunderland & Topping 1993; Topping & Sunderland 1994). Contrary to Lemke & Poehling (2002) where linyphiid densities were low after winter in the absence of adjacent sown weed strips, in our case linyphiid densities were high immediately after snow-melt. In an experiment conducted in the same cornfields, Hibbert & Buddle (2008) showed that field colonization occurred primarily through cursorial dispersal. We also frequently encountered active linyphiid webs after snow-melt, suggesting that linyphiids were already present in the field before snow-melt (Royauté, personal observation).

Particular attention can be given to the wolf-spider *T. ruricola*, the most abundant species in field traps. This large-size lycosid typically feeds on aphids, collembolans and dipterans (Kielty et al. 1999) and originated from Eurasia. It was recently introduced in the New World, potentially via the Paleartic (Platnick 1993) and was first documented in North America by Edwards (1993) then by Lalongé et al. (1997) for Canada. This species is very similar in morphology to the native species *T. terricola* (Thorell 1856), but has slightly different habitat preferences. *Trochosa terricola* is abundant in forest areas, moist meadows and forest borders, whereas *T. ruricola* inhabits more disturbed areas such as vegetable gardens or arable fields (Edwards 1993). There is limited evidence that *T. ruricola* can displace the native species, especially in perennial crops such as vineyards (Lalongé et. al. 1997; Bolduc et al. 2005). In the present context, however, *T. ruricola* showed little overlap with *T. terricola*'s habitat choice since the latter was largely absent in field traps (Appendix 1). The presence of a species showing such affinity for field habitats could therefore represent a selective advantage in this particular system.

The fact that the early season showed such a distinct colonization dynamics has several implications for spiders' role in agroecosystems. As suggested by Juen et al. (2003),

Table 3.—Ten most abundant species in field traps with their indicator species values (I.V.) by habitat (Forest, Ecotone and Field traps) and sampling period (ES: early season, PT: post-tillage, PH: post-herbicide). *P*-values were calculated for the class that had highest indicator value. Bold indicates species that do not belong to the agrobiont, * indicates significant P-value at alpha = 0.05.

			Habitat I.V.			Sampling period I.V.		
Species	Abundance in field traps	Relative abundance in ES (%)	Forest	Ecotone	Field	ES	PT	PH
A.fabra (Linyphiidae)	16	62.5	0.02	0.22	0.25	0.26	0.16	0.026
A.jacksoni (Linyphiidae)	17	76	0.06	0.29	0.16	0.42*	0.09	0.005
C. plumose (Linyphiidae)	76	87	0.005	0.5*	0.43	0.65*	0.06	0.02
D. concolor (Linyphiidae)	6	83	0.07	0.56*	0.033	0.4*	0.009	0.034
E. atra (Linyphiidae)	21	43	0.09	0.09	0.28	0.11	0.38*	0.02
I. flaveola (Linyphiidae)	51	98	0.04	0.47	0.41	0.72*	0	0.002
W. spiralis (Linyphiidae)	31	87	0	0.26	0.42	0.67*	0.67	0
P. moesta (Lycosidae)	22	0	0.61	0.2	0.031	0	0.33	0.53*
T. ruricola (Lycosidae)	80	54	0.14	0.44	0.31	0.39	0.46	0.05
T. terricola (Lycosidae)	10	60	0.07	0.36	0.054	0.33	0.07	0.008

spider species that are active early in the season can represent an important first line of defense against pests. Though many pests use non-crop habitats to spend the winter (Morishita 1992; Norris & Kogan 2005), some pests such as the European corn borer overwinter in corn stalks (Coll & Bottrell 1991). Given that the field habitat has no vertical structure after snow-melt, pest overwintering in the field could be more vulnerable to spiders even when still in a diapause state. Pfannenstiel (2008) showed that some families (Linyphiidae, Lycosidae) prey on lepidopteran eggs, and it is possible that spiders are capable of consuming prey that are in a diapause state. Alternatively, cannibalism and intraguild predation could be particularly important during the early season period since the diversity and density of prey may be low. Further investigations of species interaction during early season would be required to shed light on these questions.

Our results indicated that spiders were captured directly after snow-melt, forming an important potential natural enemy complex in early season, mostly composed of linyphiids and lycosids. The forest border and ecotone habitats had higher abundance and species richness than the field, but the ecotone showed overlap with field assemblages. The most abundant species were active quickly after snow-melt and were frequently collected in field traps. In this respect, early season was the period when most of the spider species of agronomical value were active, and early season could be important in facilitating high abundance of spiders in arable fields.

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Appendix 1.—Number of individuals collected per distance to border (−4, 0, 4, 8, 16, 100) and sampling period pooled for all replication (ES: Early Season, T: Tillage, PT: Post-Tillage, H: Herbicide spraying, PH: Post Herbicide). * indicates species belonging to the agrobiont.

	−4	0	4	8	16	100	ES	T	PT	H	PH	Total
Agelenidae												
Agelenopsis sp.	0	1	0	1	0	0	0	0	0	0	2	2
Corinnidae												
Phrurotimpus alarius (Hentz 1847)	3	0	0	0	0	0	0	0	1	0	2	3
Phrurotimpus borealis (Emerton 1911)	4	0	0	0	0	0	0	0	0	1	3	4
Scotinella divesta (Gertsch 1941)	0	1	0	0	0	0	0	0	0	0	1	1
Scotinella pugnata (Emerton 1890)	1	2	0	0	0	1	2	0	0	0	2	4
Clubionidae												
Clubiona abbotti L. Koch 1866	0	0	0	0	1	0	0	0	0	0	1	1
Clubiona bishopi Edwards 1958	1	0	0	0	0	0	0	1	0	0	0	1
Clubiona canadensis Emerton 1890	1	0	0	0	0	0	0	0	1	0	0	1
Clubiona riparia L. Koch 1866	0	3	0	0	0	0	0	0	1	0	2	3
Clubionidae sp.	2	1	0	0	1	0	3	0	1	0	0	4
Dictynidae												
Cicurina arcuata Keyserling 1887	2	0	0	0	0	0	1	0	0	0	1	2
Cicurina brevis (Emerton 1890)	4	0	2	1	0	0	7	0	0	0	0	7
Cicurina pallida Keyserling 1887	2	0	0	0	0	0	0	1	0	1	0	2
Emblyna sublata (Hentz 1850)	0	0	2	0	0	0	0	0	2	0	0	2
Gnaphosidae												
Drassylus socius Chamberlin 1922	0	1	0	0	0	0	0	0	0	0	1	1
Gnaphosa orites Chamberlin 1922	0	1	0	0	0	0	1	0	0	0	0	1
Micaria pulicaria (Sundevall 1831)	0	1	0	0	0	0	0	0	0	0	1	1
Zelotes fratris Chamberlin 1920	1	4	1	0	0	0	2	0	2	0	2	6
Gnaphosidae sp.	0	1	0	0	1	0	0	0	0	0	2	2
Hahniidae												
Neoantistea agilis (Keyserling 1887)	0	1	0	0	0	1	1	0	0	0	1	2
Neoantistea magna (Keyserling 1887)	0	0	2	0	0	0	0	0	0	0	2	2
Linyphiidae												
Agyneta sp.	0	1	0	0	0	0	1	0	0	0	0	1
Agyneta fabra (Keyserling 1886)*	1	3	5	1	4	6	13	0	2	0	5	20
Agyneta jacksoni Braendegaard 1937*	2	6	2	7	4	4	18	0	1	0	6	25
Agyneta unimaculata (Banks 1892)	0	1	3	0	0	2	6	0	0	0	0	6
Baryphyma trifrons affine (Schenkel 1930)	0	0	0	0	1	0	1	0	0	0	0	1
Batyphantes brevis (Emerton 1911)	0	1	0	0	0	0	1	0	0	0	0	1
Batyphantes pallidus (Banks 1892)	1	0	0	0	0	0	0	0	0	0	1	1
Centromerus cornupalpis (O. P.-Cambridge 1875)	20	2	1	1	1	1	23	2	1	0	0	26
Centromerus furcatus (Emerton 1882)	0	1	1	0	0	0	1	0	0	0	1	2
Centromerus persolutus (O. P.-Cambridge 1875)	1	0	1	0	0	0	1	0	1	0	0	2
Centromerus sylvicatus (Blackwall 1841)	1	1	0	0	0	0	2	0	0	0	0	2
Ceraticelus laetus (O. P.-Cambridge 1874)	1	0	0	0	0	1	0	0	1	1	0	2
Collinsia plumosa O.P.-Cambridge 1913*	1	20	12	22	22	20	84	0	4	0	9	97
Diplocephalus cristatus (Blackwall 1833)	4	1	0	1	1	0	6	0	0	1	0	7
Diplostyla concolor (Wider 1834)	2	8	2	3	0	1	13	0	2	0	1	16
Erigone atra Blackwall 1833*	2	2	7	3	9	2	9	0	2	0	14	25
Erigone autumnalis Emerton 1882	0	1	0	2	1	1	1	0	0	0	4	5
Erigone blaesa Crosby & Bishop 1928	0	0	0	0	0	1	1	0	0	0	0	1
Gnathonaroides pedalis (Emerton 1923)	0	0	0	0	0	1	1	0	0	0	0	1
Grammonata gentilis Banks 1898	0	0	0	0	0	3	2	0	1	0	0	3
Islandiana flaveola (Banks 1892)*	3	14	9	9	15	18	67	0	1	0	0	68
Lepthyphantes intricatus (Emerton 1911)	0	1	1	0	0	0	0	0	1	0	1	2
Meioneta amersaxatilis (Saaristo & Koponen 1998)	1	0	0	0	0	0	0	0	0	0	1	1
Neriene clathrata (Sundevall 1830)	2	2	0	0	0	0	3	0	1	0	0	4
Oedothorax sp.	0	0	1	0	0	0	1	0	0	0	0	1

Appendix 1.—Continued.

	−4	0	4	8	16	100	ES	T	PT	H	PH	Total
Oedothorax montifer (Emerton 1882)	0	0	0	0	1	0	1	0	0	0	0	1
Perregrinus deformis (Tanasevitch 1982)	1	2	1	1	1	0	5	1	0	0	0	6
Sciastes dubius (Hackman 1954)	1	0	0	0	0	0	0	1	0	0	0	1
Tenesselum formica (Emerton 1882)	0	0	0	1	1	2	0	0	0	0	4	4
Tenuiphantes zebra (Emerton 1882)	14	14	3	1	0	1	26	2	4	0	1	33
Vermontia thoracica (Emerton 1913)	1	0	0	0	0	0	1	0	0	0	0	1
Walckenaeria spiralis (Emerton 1882)*	0	6	5	5	12	9	31	0	6	0	0	37
Linyphiidae sp.	6	12	3	11	8	3	34	0	3	0	6	43
Liocranidae												
Agroeca ornata Banks 1892	1	0	0	0	0	0	0	1	0	0	0	1
Liocranidae sp.	1	0	0	0	0	0	0	0	0	0	1	1
Lycosidae												
Pardosa sp.	3	0	0	1	0	0	4	0	0	0	0	4
Pardosa modica (Blackwall 1846)	1	2	1	0	0	0	3	0	1	0	0	4
Pardosa moesta Banks 1892	60	32	11	5	4	2	0	15	48	18	33	114
Pardosa xerampilina (Keyserling 1877)	0	2	0	0	0	0	0	0	1	0	1	2
Pirata sp.	1	0	0	0	0	0	0	0	0	0	1	1
Pirata aspirans Chamberlin 1904	1	0	0	0	0	0	0	0	0	0	1	1
Pirata minutus Emerton 1885	3	5	1	0	1	0	0	0	0	0	10	10
Pirata piraticus (Clerck 1757)	0	0	0	0	1	0	0	0	0	0	1	1
Pirata zelotes Wallace & Exline 1978	1	0	0	0	0	0	0	0	0	0	1	1
Schizocosa communis (Emerton 1885)	1	0	2	0	1	0	0	0	3	1	0	4
Schizocosa crassipalpata Roewer 1951	0	3	0	0	0	0	0	0	1	0	2	3
Trochosa sp.	2	5	6	2	2	3	7	0	7	1	5	20
Trochosa ruricola (De Geer 1778)*	14	27	23	19	10	28	65	0	9	2	45	121
Trochosa terricola Thorell, 1856	2	7	3	6	1	0	14	0	1	1	3	19
Lycosidae sp.	43	47	16	10	12	5	51	8	14	1	59	133
Mimetidae												
Ero canionis Chamberlin & Ivie 1935	0	2	0	0	0	0	2	0	0	0	0	2
Mimetus eperoides Emerton 1882	0	0	1	0	0	0	0	0	0	0	1	1
Philodromidae												
Thanatus striatus C. L. Koch 1845	0	1	0	1	0	0	0	0	2	0	0	2
Tibellus maritimus (Menge 1875)	0	1	0	0	0	0	0	0	0	0	1	1
Tibellus oblongus (Walckenaer 1802)	0	1	0	2	0	0	0	0	0	0	3	3
Philodromidae sp.	4	0	2	1	2	1	7	0	2	1	0	10
Pisauridae												
Dolomedes triton (Walckenaer 1837)	1	0	0	0	0	0	0	0	0	1	0	1
Tetragnathidae												
Pachygnata autumnalis Marx 1884	0	1	0	0	0	0	0	0	0	0	1	1
Pachygnata xanthostoma C. L. Koch 1845	2	5	0	2	0	0	8	0	0	0	1	9
Theridiidae												
Crustulina sticta (O. P.-Cambridge 1861)	0	1	0	0	0	0	1	0	0	0	0	1
Robertus spinifer (Emerton 1909)	1	0	0	0	0	0	0	0	0	0	1	1
Theridiidae sp.	1	0	0	0	0	0	1	0	0	0	0	1
Thomisidae												
Ozyptila sp.	1	1	0	0	0	0	0	0	1	0	1	2
Ozyptila distans Dondale & Redner 1975	11	6	0	2	0	0	0	0	0	4	15	19
Ozyptila praticola (C. L. Koch 1837)	59	3	1	0	0	0	0	2	14	19	28	63
Xysticus sp.	1	0	0	0	0	0	0	0	1	0	0	1
Xysticus elegans Keyserling 1880	3	6	2	0	0	0	0	0	4	3	4	11
Xysticus ferox (Hentz 1847)	2	3	0	0	1	0	0	0	1	2	3	6
Thomisidae sp.	1	0	0	0	0	0	0	0	0	1	0	1
Unknown	1	1	0	0	0	0	1	0	0	0	1	2