Quantitative food webs of herbivore and related beneficial community in non-crop and crop habitats

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ABSTRACT

Quantitative food webs were constructed from the data collected, using visual observation technique, from May to July in 2005 and 2006 to describe separately the trophic relationships between the community of aphids and their natural enemies of predators and parasitoids in agricultural and semi-natural habitats in Gembloux, Belgium. In the web, a total of six aphid attacked by six parasitoid and 21 predator species were recorded in this study; 50 and 33 links between aphid and natural enemy species were respectively observed in 2005 and 2006. Aphid density varied seasonally and among years, and three species of aphid were particularly common in different habitats. The ratios of the number of aphid species to the number of species of either predators or parasitoids changed also seasonally. Most communities of insect herbivores are likely to be structured by apparent competition mediated by shared natural enemies more than to be structured by resource competition. The potential of two guilds of natural enemies to contribute in structuring aphid community through indirect interactions was assessed. The potential strengths of apparent competition between hosts mediated by parasitoids and predators were assessed using quantitative parasitoid/predator overlap diagrams. Symmetrical links were uncommon, and rare species were severely influenced by the presence of common aphids with which they shared parasitoids or predators or both. The study's results suggest that (i) stinging nettle aphids, acting as potential sources of apparent competition mediated by natural enemies, may be important in these highly connected communities and can control whole-community dynamics, and (ii) stinging nettle habitats, in providing an important alternative prey for natural enemies, are likely to play a key role in conservation biological control.

1. Introduction

Semi-natural habitat diversity may promote natural pest control in annual arable cropping systems (Gurr et al., 2003; Tscharntke et al., 2007). Non-crop habitats like forests, hedgerows, tree lines and field margins including herbaceous habitats, such as stinging nettle *Urtica dioica* L., are essential for the conservation of a diversity of natural enemies in agricultural landscapes that can play a role in suppressing pest populations in crops (Greig-Smith, 1948; Perrin, 1975; Marshall and Moonen, 2002; Duelli and Obrist, 2003; Frank and Reichhart, 2004; Gurr et al., 2005; Bianchi et al., 2006; Alhmedi et al., 2007, 2009). Non-crop habitats may provide plant-derived food resources, e.g. nectar or pollen, alternative prey, refuge from pesticides and other disturbances, shelter, a moderate microclimate and hibernation sites (Landis et al., 2000). By providing these resources, non-crop habitats can support natural enemy populations and help enhance their impact on pest population dynamics (Wilkinson and Landis, 2005).

Terrestrial ecosystems support a diversity of insect species that are directly and indirectly linked to each other within food webs that span multiple trophic levels. Insect herbivore communities may be structured by different ecological processes such as competition, predation and parasitism. These communities often consist of species that are restricted to feeding on non-overlapping sets of plant species and therefore cannot interact through interference or resource competition. Prey species that share natural enemies may show apparent competition, which is an indirect interaction defined as a reduction in the population density of one prey species when that of another prey species increases, with the interaction mediated by an increase in the natural enemy species (e.g., Holt, 1977; Holt and Lawton, 1994; Abrams and Matsuda, 1996; van Veen et al., 2006b). Apparent competition can be meaningful in structuring communities in which resource competition is not predominant (Abrams et al., 1996). Host–parasitoid communities should be especially prone to apparent competition because parasitoids have generation times similar to their hosts, show remark-

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able responses to changes in host abundance, and constantly regulate host populations below carrying capacity (Holt and Lawton, 1993). There is in fact little evidence from field studies to support this hypothesis (but see van Nouhuys and Hanski, 2000; Morris et al., 2001, 2004). There is also evidence for apparent competition mediated by parasitoids among leafhoppers (Settle and Wilson, 1990) and among rainforest leafminers (Morris et al., 2004). Short-term apparent competition between herbivorous insects mediated by predators has been demonstrated in field experiments (Karban et al., 1994; Müller and Godfray, 1997; Rott et al., 1998).

Boller (1992) has found that the provision of flowers and alternative prey has been very successful at keeping pests below their economic thresholds. The advantages of providing alternative hosts for the natural enemies of crop and forestry pests that presupposes indirect effects between herbivores have received much attention in the last few years (e.g. Landis et al., 2000; van Veen et al., 2006a). Recently, methods have been developed to allow the quantification of interactions at the community scale (Müller et al., 1999), thereby giving a more robust description of community structure, and providing insights into the dynamic processes that structure ecological communities (Morris et al., 2004). Food webs can be used for describing trophic interactions, and to examine the potential for indirect interactions, such as apparent competition (Cohen et al., 1990; Polis and Winemiller, 1996). Quantitative food webs consist of sets of binary links between 'trophic species' representing feeding interactions. Most early studies of food webs traced the presence or absence of trophic links between trophic species (e.g., Cohen et al., 1990; Rott and Godfray, 2000). On the other hand, some field research constructed food webs that included quantitative information on trophic interactions and provided information on the potential for apparent competition (Memmott et al., 1994; Müller et al., 1999; Rott and Godfray, 2000; Valladares et al., 2001; Lewis et al., 2002; van Veen et al., 2008; Hirao and Murakami, 2008). Communities of hosts and parasitoids provide good systems for studies using quantitative food webs, because the trophic links between hosts and parasitoids are relatively easy to establish and to quantify when compared with predators. A number of such parasitoid webs have now been described (e.g., Memmott et al., 1994; Müller et al., 1999; Rott and Godfray, 2000; Valladares et al., 2001; Lewis et al., 2002).

The aim of this study was to construct sets of quantitative food webs associating two guilds of natural enemies attacking communities of aphids in non-crop (stinging nettle) and crop (wheat and green pea) habitats, and to compare their properties in particular with regard to the potential for apparent competition. Based on these quantitative webs, we assessed (i) the extent to which the potential for apparent competition is likely to occur between aphid species feeding on the different host plant species, and (ii) the potential of stinging nettle aphids to be a source of natural enemies for potential biocontrol of neighboring pests. The impact of a natural enemy on a focal prey species can depend on the availability of alternative prey (Holt and Lawton, 1994). Then, we constructed parasitoid and predator overlap diagrams to estimate the potential for seasonal apparent competition.

2. Materials and methods

2.1. Study site

During the 2005 and 2006 growing seasons, the aphid–natural enemy community was studied in non-crop (stinging nettle) and cropping (wheat *Triticum aestivum* L. and green pea *Pisum sativum* L.) habitats located in the Gembloux Agro-Bio Tech experimental farm, Gembloux, Belgium. Crop fields were 3–5 ha in size, and surrounded on one side by damp woodland containing natural area of stinging nettle *U. dioica* L., and on the three sides by buildings,

fallows, grasslands and crop fields (wheat and rape). Established 100 m apart, two sampling areas (10×20 m each) of wheat and two others of green pea were respectively selected each year in wheat and green pea fields. Two stinging nettle patches of similar size, placed 100 m away from each another, were also delimited within the natural nettle area (≈ 1000 m^2) located on 3 ha of woodland. No insecticide treatment was applied to field crops. In total, six insecticide-free patches were sampled each year.

2.2. Quantitative food web construction

The quantitative food webs were constructed in two steps. First, the total numbers of herbivores and their natural enemies observed throughout the season. Second, food webs describe the densities of herbivore and related beneficial community corresponding the three monthly sampling periods. From early May to late July and on every sampling occasion, ten plants per patch of every plant species were randomly selected and sampled for aphids. The density of each aphid species on plant species was estimated by counting once a week the number of individuals per plant. Predator and parasitoid densities were estimated at the same as aphids by counting the number of predator individuals and parasitoid mummies associated with each plant. To assess the composition of the parasitoid communities, parasitoid mummies observed on plants were taken back to the laboratory on each sampling date for adult emergence and identification. The parasitoid mummies were reared individually in plastic capsules, and the adult insects were identified using the keys in Mackauer (1959); Starý (1966), Stary (1976) and Pungerl (1983). Aphids were often fully consumed by the parasitoid larvae and the species were practically indistinguishable. Therefore, it was assumed that parasitoid species sharing the same plant species had trophic interactions with aphid species in equal proportion to the abundance of each aphid species on the shared plant (Rott and Godfray, 2000; Hirao and Murakami, 2008).

A similar challenge was found with building a predator web, where the unit of measurement is of a predator individual on a host plant rather than the actual predation event itself. One predator can feed on individuals from different aphid species on the same host plant or on different host plants. Difficulties arise more particularly when there are more than one prey species present on the same plant at the same time. Therefore, we constructed predator webs based on the assumption that each predator feeds on the aphids sharing the same host plant in proportion to their abundance. More field and laboratory research on food specificity on aphidophagous predator guild is needed for describing more accurately the predator web. Prey unsuitability may be the reason why some introduced predators fail to establish (Hodek, 1993). According to Hodek and Honěk (1996), a food may unambiguously be considered suitable/essential for predators only when tested by experiments.

The aphids were identified using the keys of Blackman and Eastop (1984) and of Taylor (1981). For the predators we concentrated on specialist predators of aphids, specifically Coccinellidae (adults and larvae), Syrphidae (larvae), Chrysopidae (larvae) and Anthocoridae (adults and nymphs). These were identified using the standard identification manuals for each group. The abundance of each species was estimated as counts per plant.

2.3. Apparent competition and quantitative natural enemy overlap diagrams

A necessary condition for apparent competition between two hosts to occur is that the two species share natural enemies. We follow Bersier et al. (2002) and use a series of metrics based on Shannon (1948) information theory. Different host aphid species are linked using the quantitative measure d_{ij}, representing the

probability that a parasitoid or a predator attacking species *i* develop on species *j*. The quantitative index d_{ij} for each pair of aphid species is calculated as

$$d_{ij} = \sum_{k} \left[\frac{\alpha_{ik}}{\sum_{l} \alpha_{il}} \frac{\alpha_{ik}}{\sum_{m} \alpha_{mk}} \right],$$

where α_{ik} is the absolute density of the trophic link between host *i* and parasitoid *k* (and, hence, the summations in *k* and *l* are over all parasitoids and in *m* over all hosts). The extent to which aphid species were linked was conventionally represented using parasitoid overlap diagrams (Müller et al., 1999), where host species are represented by discs of varying diameters and arranged in a circle, numbered sequentially. The area of each host disc indicates the contribution of the aphid species as a source of its own parasitoids and predators. These diagrams consist of a set of vertices, each representing an aphid species. Two aphid species are connected by an edge when they share at least one parasitoid or one predator species. For example, if a pair of hosts, say *i* and *j*, share parasitoids, the two species' discs are linked by a bar. The width of the bar at *i* is a measure of the importance of species *j* as a source of parasitoids attacking species *i* (and similarly the width of the bar at *j* is a measure of the converse).

The measure of importance that we use, d_{ij}, is the probability (d_{ij}) that a parasitoid or predator attacking species *i* developed on species *j* (where *j* may be the same species: d_{ii}). In summary, in parasitoid or predator overlap diagrams, (a) the number and width of the connections between host discs reflect the frequency and strength of potential indirect effects; (b) asymmetrically connecting bars suggest that one species has a strong effect on another but not vice versa, and (c) the extent to which host discs are shaded black reflects their predicted dynamical independence from the rest of the community. All graphics and computing were performed in the Mathematica software for statistical computing.

3. Results

3.1. Quantitative food webs

The two summary quantitative food webs were constructed as a whole community structure using the aphid, parasitoid and predator abundances estimated from all samples (Fig. 1).

In drawing the webs we use the same conventions as in an earlier work (Müller et al., 1999). Hosts are arranged as a series of bars in a lower register with the width of each bar proportional to the aphid's cumulative abundance over the year. The total host density is given in the legend below, the units being cumulative aphids on plants per square meter (aphids were sampled once a week and their densities added together to get a cumulative total). Natural enemies are arranged as a series of bars in an upper register with again the width of each bar being proportional to species' cumulative abundance. The width of the natural enemy bars are magnified relative to those of the aphids by the factor given in the upper legend. Natural enemies and aphids are linked by triangular wedges, the relative widths of which at the natural enemy register represent the contribution of each aphid species to the diet or host range of the natural enemy. All species are numbered and their identities are provided in Table 1.

4. Comparison of guilds

4.1. Web size, seasonality and natural enemy–aphid ratios

The main summary statistics for the different webs are shown in Table 2. In the two study years, a total of six aphid species

was recorded, five species each year. Aphid density varied among years ($F = 123.89$, $df = 1, 1438$, $p < 0.001$), but three aphid species were particularly common in the total; *Microlophium carnosum* on stinging nettle, *Acyrthsiphon pisum* on green pea and *Sitobion avenae* on wheat. Natural enemy densities varied, roughly in line (proportionally) with those of aphids, and were as a consequence higher in 2005 compared with 2006 ($F = 149.22$, $df = 1, 1438$, $p < 0.001$). Among 27 beneficial species, aphid species shared 16 predator species, belonged to the Coccinellidae (six species), Syrphidae (eight species), Chrysopidae (one species) and Anthocoridae (one species) families, and seven parasitoid species belonged to the family Braconidae. Two predator species of Miridae and two other of Anthocoridae were also observed but only on stinging nettles (Fig. 1).

The number of aphid and natural enemy species changed seasonally throughout the three months from May to July (Figs. 2 and 3). In the 2005 and 2006 seasonal webs, both aphids and their natural enemies appeared earlier in May on stinging nettle compared to field crops sampled in the present work. The host/natural enemy species ratio also changed seasonally, and was higher in May 2005 and 2006 (respectively 0.444 and 1.500) than in June and July of 2005 and 2006 (respectively, 0.250 each; 0.222 and 0.333).

4.2. Connectance and compartmentalization

Connectance is one measure of interaction pattern and defined as the fraction of all possible links that are realized in a web (or as the proportion of all possible links that is realized in a web), but may be defined also as the number of links divided by the product of host and natural enemy numbers (Müller et al., 1999; Lewis et al., 2002). It is calculated in this study as $(L-P)/[(H-1).P]$, where *L* is the number of links, *P* is the number of natural enemy species, and *H* is the number of hosts. This measure ranges from 0 to 1 and reaches the maximum (1) when every natural enemy fed on every host or prey. In the present work, the number of links in the food webs varied from 50 in the 2005 web to 33 in the 2006 web, while the connectance was similar (0.270 and 0.266, respectively). According to the variation recorded between years for the studied guilds, there were fewer trophic links in 2006, the year when the least number of parasitoid and predator species was recorded. Visual comparison of the food webs in Fig. 1 shows that connectance decreased from predator guilds to parasitoid guilds. Hence, predators showed the highest potential to mediate apparent competition.

The realized connectance of the food webs also changed seasonally throughout the three months from May to July (Figs. 2 and 3). It was higher in June (0.238), July (0.204) in 2005 and in 2006 May (0.500) compared to the other months (0 in May 2005, 0.042 and 0.139 in June and July 2006, respectively).

Connectance is the best measure of sharing, whereas compartmentalization reflects how the sharing is arranged. Compartmentalization is the degree to which a food web is divided into non-connected subwebs. The number of compartments in a food web is defined as the number of subwebs with non-connection to any other subweb. The present study web constitutes a single compartment; in other words, all hosts that are parasitized are connected to all other hosts at their respective site. As a similar, predator web is fully connected (number of compartments = 1).

4.3. Potential for apparent competition and quantitative natural enemy overlap diagrams

Quantitative parasitoid and predator overlap diagrams for the web data are shown in Figs. 4 and 5. The six species of hosts are represented as numbered discs arranged on a circle. The area of
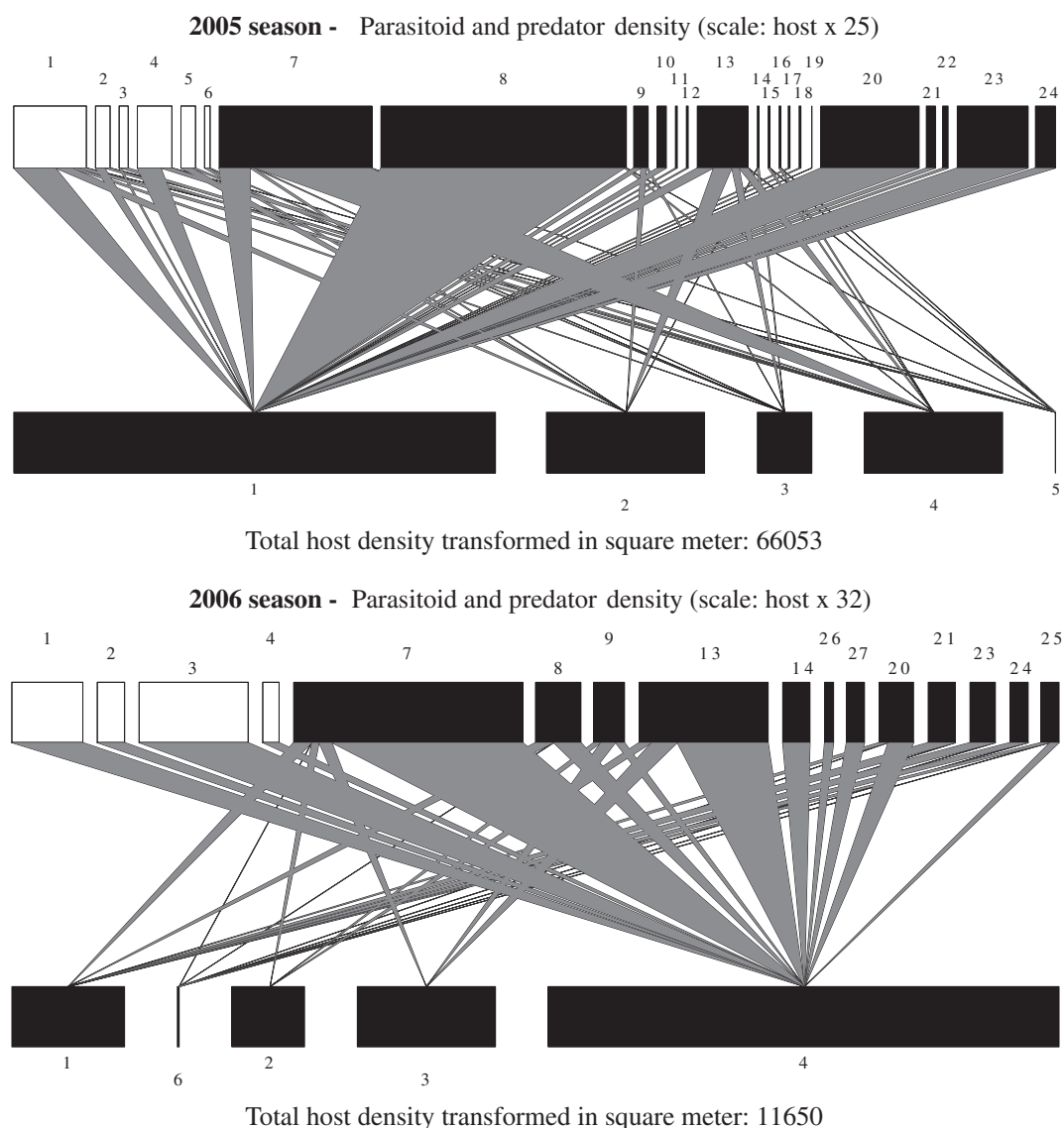
2005 season - Parasitoid and predator density (scale: host x 25)

Total host density transformed in square meter: 66053

2006 season - Parasitoid and predator density (scale: host x 32)

Total host density transformed in square meter: 11650

Fig. 1. Summary quantitative aphid-natural enemy food webs constructed in 2005 and 2006. In the top, white bars represent parasitoid abundance and black bars represent predator abundance; in the bottom, black bars represent aphid abundance.

the disc represents the abundance of the different host species. Each host disc is a vertex, and two vertices are connected if the hosts they represent share parasitoids or predators. The extent to which a host disc is shaded black represents the fraction of parasitoids, for example, attacking that host that would have developed as parasitoids of that same species (d_{ii}) or of different species (d_{ij}). Consider an edge linking two host vertices, i and j, the width of the edge at species i and j represents d_{ij} and d_{ji}, respectively; that is, the importance of species j as a source of parasitoids attacking species i and vice versa.

The main patterns that emerge from the quantitative overlap diagrams for the food web (Figs. 4 and 5) are

1. There was a considerable potential for indirect effects between host species mediated by shared natural enemies. For most species, there were parasitoids and predators recorded as attacking them were likely to have developed on different host species (asymmetric connectance). Of the two hosts that are exceptions to this pattern and from Figs. 4 and 5 we can see that the most common species was number 1 and that the large majority of natural enemies attacking this species would probably also have developed on it ($d_{1,1}$ = 0.92 and 0.61 in the 2005 predator

and parasitoid webs, respectively; 0.67 in the 2006 predator web). In the 2006 web, parasitoids were only recorded attacking host number 4, thus all parasitoids in addition to a considerable quantity of predator species probably tended to have developed on the same host species ($d_{4,4}$ = 1 and 0.77, respectively). In the 2006 web, an absence of apparent competition mediated by shared parasitoids (specialist natural enemies) reflected the low densities of aphid populations, more particularly in non-crop area and wheat field. The sufficient presence of aphid predators recorded in 2006 may prevent the apparent competition mediated by parasitoids (in other words, the potential intra-guild interactions (e.g. intraguild predation) among aphidophagous guilds may influence the potential apparent competition).

2. In the 2005 web, the nettle aphid *M. carnosum* (number 1) was an important source of most natural enemy species attacking aphid populations in crop fields ($d_{2,1}$ = 0.29, $d_{3,1}$ = 0.29, $d_{4,1}$ = 0.21, $d_{5,1}$ = 0.21 in the predator web; $d_{2,1}$ = 0.30, $d_{3,1}$ = 0.30, $d_{4,1}$ = 0.53, $d_{5,1}$ = 0.64 in the parasitoid web) than vice versa ($d_{1,2}$ = 0.02, $d_{1,3}$ = 0.01, $d_{1,4}$ = 0.05, $d_{1,5}$ = 0.0003 in the predator web; $d_{1,2}$ = 0.12, $d_{1,3}$ = 0.04, $d_{1,4}$ = 0.22, $d_{1,5}$ = 0.001 in the parasitoid web). Despite the low density of *M. carnosum* recorded in 2006, which might account for the paucity that year

Table 1
Identity of species in the food webs.

Code	Aphid name – bottom bars	Code	Parasitoid name – top bars
1	*Microlophium carnosum* Buckton (1∗)	1	*Aphidius ervi* Halidae
2	*Sitobion avenae* F. (2)	2	*Aphidius urticae* Halidae
3	*Metopolophium dirhodum* Walker (2)	3	*Aphidius smithi* Sharma et Subba Rao
4	*Acyrthosiphon pisum* Harris (3)	4	*Aphidius picipes* Nees
5	*Macrosiphum euphorbiae* Thomas (3)	5	*Aphidius rhopalosiphi* De St. Perez
6	*Aphis urticata* Gmelin (1)	6	*Praon volucre* Haliday
			All Braconidae

	Predator name – top bars		
	Coccinellidae		Syrphidae (next)
7	*Coccinella septempunctata* L.	27	*Scaeva pyrastri* L.
8	*Harmonia axyridis* Pallas	18	*Eupeodes nitens* Zetterstedt
9	*Propylea 14-punctata* L.	19	*Eupeodes luniger* Meigen
10	*Adalia 2-punctata* L.		Anthocoridae
11	*Adalia 10-punctata* L.	20	*Orius minutes* L.
12	*Anatis ocellata* L.	21	*Anthocoris nemorum* L.
	Syrphidae	22	*Anthocoris nemoralis* F.
13	*Episyrphus balteatus* DeGeer		Miridae
14	*Melanostoma mellinum* L.	23	*Deraeocoris ruber* L.
15	*Eupeodes latilunulatus* Collin	24	*Heterotoma meriopterum* Scop
16	*Sphaerophoria scripta* L.		Chrysopidae
17	*Platycheirus scutatus* Meigen	25	*Chrysoperla carnea* Stephens
26	*Syrphus ribesii* L.		

Host plants.
Stinging nettle host (*Urtica dioica*).
Wheat host (*Triticum aestivum*).
Green pea host (*Pisum sativum*).

of pathogenic fungi intensely occurring in nettle aphid colonies in 2005, it was an important source for most predators attacking the second nettle aphid A. urticata ($d_{6,1} = 0.67$).

3. Green pea aphid *A. pisum* (number 4) was the second most important species as a source of natural enemies attacking the other aphid species in the study site, particularly in 2006 ($d_{5,4} = 0.72$ in the 2005 predator web; $d_{1,4} = 0.30$, $d_{2,4} = 0.64$, $d_{3,4} = 0.64$, $d_{6,4} = 0.30$ in the 2006 predator web).

4. The greatest potential for apparent competition, at least as indicated by high values for d_{ij}, occurs when a rare species shares parasitoids or predators with a common or moderately abundant species. In the 2005 natural enemy web, species four was likely to be affected severely by the presence of species five, which was the source for a high proportion of its natural enemies ($d_{5,4} = 0.65$). In the 2006 natural enemy web, species six was likely to be suffered severely by the presence of species one, which was also the source for a high proportion of its natural enemies ($d_{6,1} = 0.67$). In all of these cases, the potential apparent competition is asymmetric. In part, this is due to a rare species cannot numerically be a major source of natural enemies attacking a common species.

5. The overlap graphs identify a species pair that is strongly, and relatively symmetrically connected; species two and three ($d_{2,3} = 0.15$ and 0.23; $d_{3,2} = 0.42$ and 0.12, in the 2005 and 2006 webs, respectively).

6. In the 2005 seasonal overlap diagrams for May (Figs. 4 and 5), all predators and parasitoids attacking aphid species on stinging nettle tended to have developed on the same host species ($d_{1,1} = 1$), which likely acted as the major source of natural enemies attacking other host species later in the season. According to the overlap diagrams for June, aphid species 1 was probably the predominant source of natural enemies attacking other host species ($d_{4,1} = 0.46$ and $d_{5,1} = 0.45$ in the predator web; $d_{2,1} = 0.56$, $d_{3,1} = 0.56$, $d_{4,1} = 0.73$ and $d_{5,1} = 0.72$ in the parasitoid web); wheat aphids number 2 and 3 shown rather of a symmetric apparent competition ($d_{2,3} = 0.31$ and $d_{3,2} = 0.69$ in the predator web; $d_{2,3} = 0.13$ and $d_{3,2} = 0.29$ in the parasitoid web); green pea aphids number 4 and 5 showed a strong asymmetric apparent competition, where the species 4 was probably an important source of natural enemies attacking species 5 ($d_{5,4} = 0.55$ and 0.26 in the predator and parasitoid webs, respectively). For the subsequent month (July), the large majority of predators attacking the common species 1, 2 and 4 would probably also have developed each on the same species ($d1,1 = 0.97$, $d_{2,2} = 0.57$ and $d_{4,4} = 0.88$). Wheat aphid species number 2 was probably an important source of predators attacking the second wheat aphid species number 3 ($d_{3,2} = 0.57$).

7. In the 2006 seasonal predator overlap diagrams for May (Figs. 4 and 5), species 6 was likely to be affected severely by the presence of species 1, which was the source for a high proportion of its predators ($d_{6,1} = 0.90$). In the overlap diagram for June, all predator species of nettle aphid species 1 tended to have developed on the same species ($d_{1,1} = 1$); similarly was found for this species in July. Aphid species 4 was probably an important source of predators attacking aphid species 3 ($d_{3,4} = 0.80$). While symmetric apparent competition was relatively found between the two wheat aphid species 2 and 3 in the overlap diagram of July ($d_{2,3} = 0.27$; $d_{3,2} = 0.41$), asymmetric apparent competition was found between aphid species 4 and both aphid species 2 and 3 ($d_{2,4} = 0.32$ and $d_{3,4} = 0.32$).

5. Discussion

We constructed and described a summary quantitative food web of a community structure including six aphid, six parasitoid and 21 predator species. Parasitoid and predator diversity and density were higher on stinging nettle than on field crops, particularly in the 2005 web. The predator web contains more links than the parasitoid web, and predator food web connectance tends to be higher than for the parasitoid guild. These findings are consistent with those reported by van Veen et al. (2008) for the aphid–natural enemy community studied in a damp field in UK. The present web study constituted a single compartment; this meaning that the beneficial webs were fully connected; and represent mainly generalist natural enemy species to aphid species.

Regarding the apparent competition between hosts via a shared parasitoid or predator, inferences about dynamic interactions from quantitative webs provide necessary evidence to confirm the
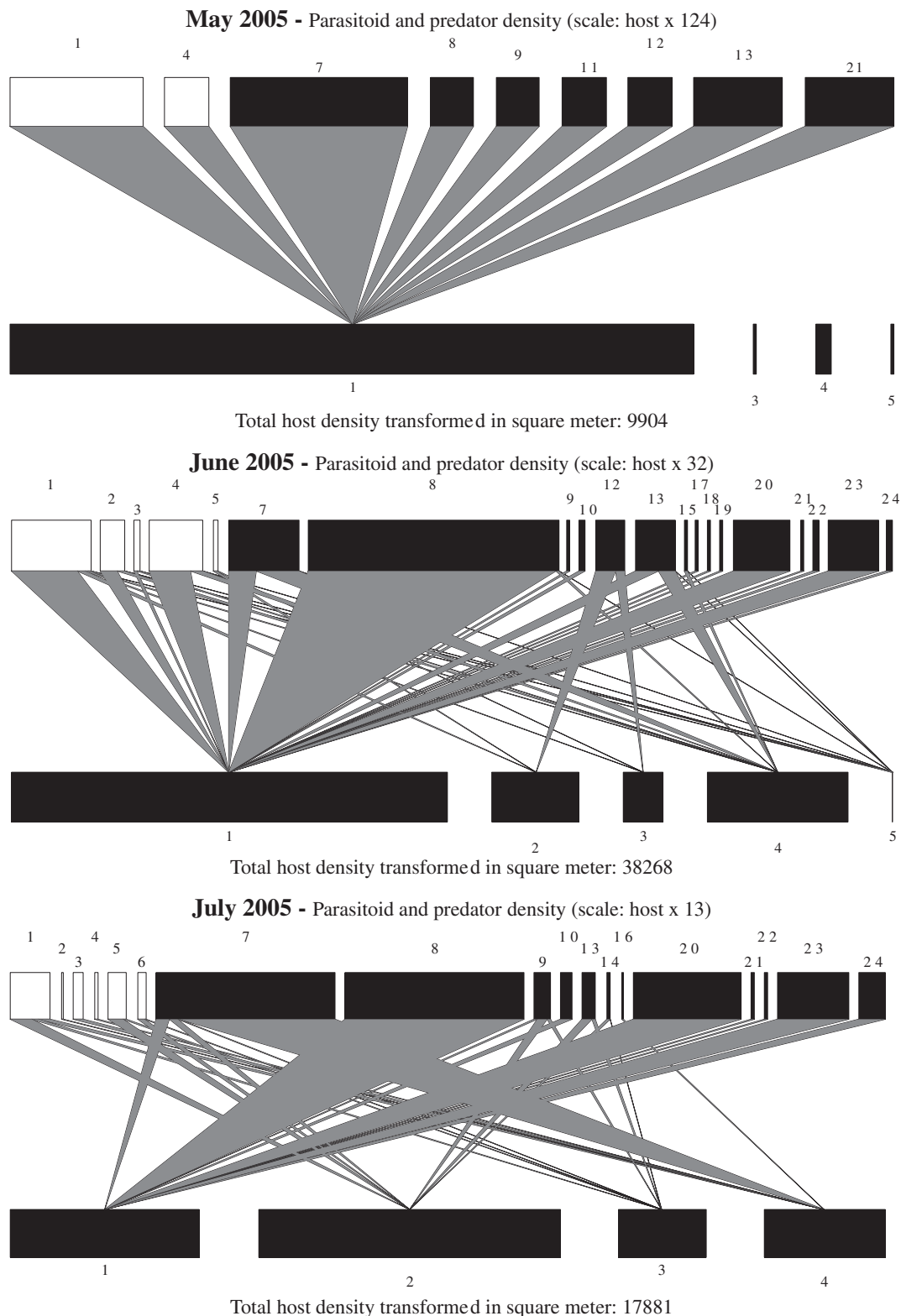
Table 2
Summary of food web statistics for the summary and seasonal webs.

	2005				2006			
	Summary	May	June	July	Summary	May	June	July
No. host species	5	4	5	4	5	3	3	4
No. natural enemy species	24	9	20	18	16	2	12	12
Host : natural enemy ratio	0.21	0.44	0.25	0.22	0.31	1.5	0.25	0.33
No. links	50	9	39	29	33	4	13	17
Realized connectance	0.27	0	0.24	0.20	0.27	0.50	0.04	0.13
No. compartments	1	1	1	1	1	1	1	1

May 2005 - Parasitoid and predator density (scale: host x 124)

Total host density transformed in square meter: 9904

June 2005 - Parasitoid and predator density (scale: host x 32)

Total host density transformed in square meter: 38268

July 2005 - Parasitoid and predator density (scale: host x 13)

Total host density transformed in square meter: 17881

Fig. 2. Seasonal quantitative aphid-natural enemy food webs constructed in 2005. In the top, white bars represent parasitoid abundance and black bars represent predator abundance; in the bottom, black bars represent aphid abundance.

occurrence of apparent competition. Thus, the main motivation behind this study was to compare the potential for apparent competition mediated by the two guilds of aphid natural enemies. The majority of aphids present in our community cannot compete directly because they feed on different host plants. If our commu-

nity is structured by biotic interactions then they must be mediated by processes other than resource and interference competition. A likely route is that aphid species on different host plants interact through shared natural enemies. The analysis of the webs clearly shows that predators have the highest potential
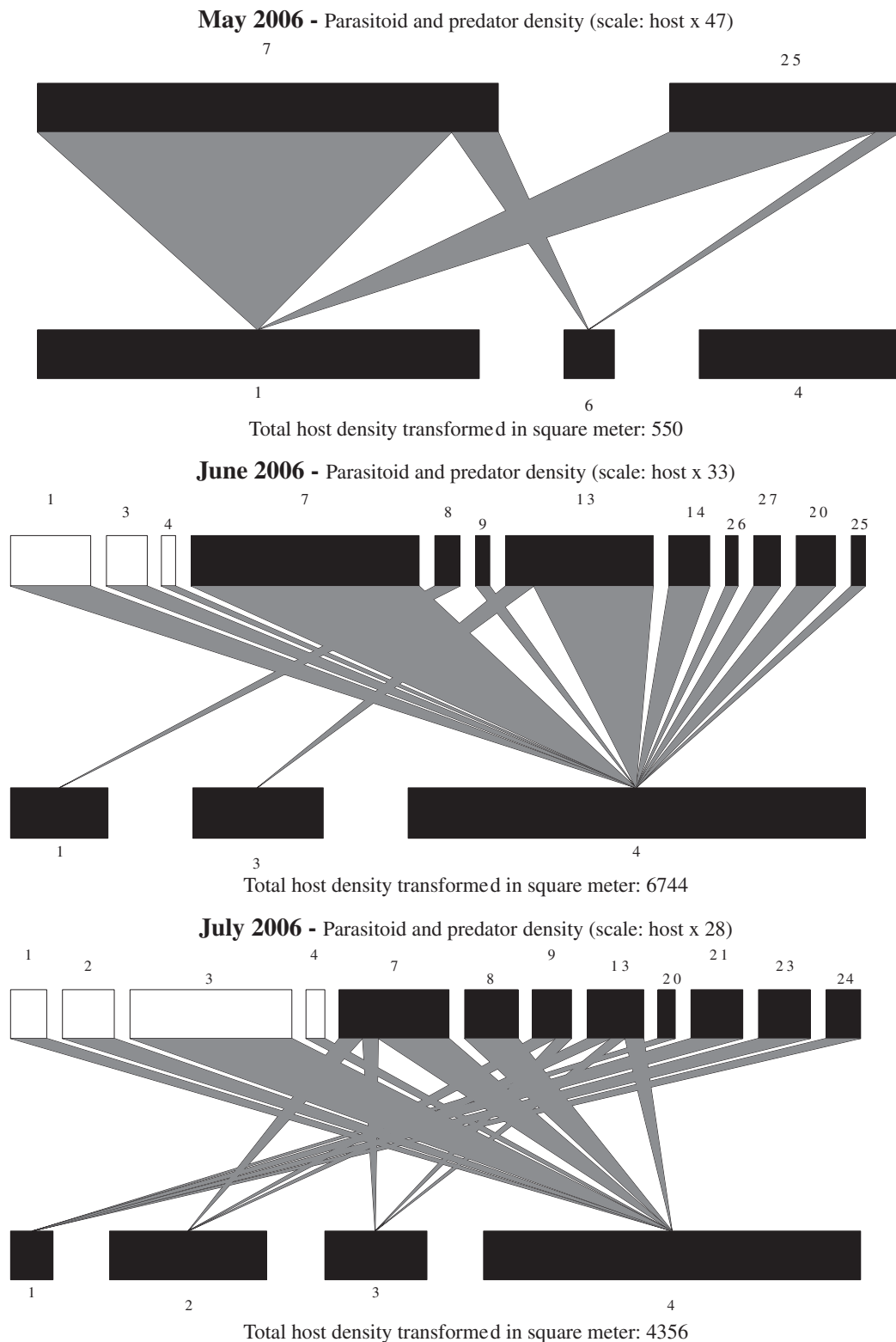
May 2006 - Parasitoid and predator density (scale: host x 47)

Total host density transformed in square meter: 550

June 2006 - Parasitoid and predator density (scale: host x 33)

Total host density transformed in square meter: 6744

July 2006 - Parasitoid and predator density (scale: host x 28)

Total host density transformed in square meter: 4356

Fig. 3. Seasonal quantitative aphid-natural enemy food webs constructed in 2006. In the top, white bars represent parasitoid abundance and black bars represent predator abundance; in the bottom, black bars represent aphid abundance.

for mediating apparent competition that can theoretically occur in space (Holt, 1996), and spatial perspectives have been considered in recent years (e.g., Bonsall and Hassell, 2000; Holt and Barfield, 2003). A relatively significant fraction of the most common natural enemies attacking a particular host species in the study's commu-

nity is likely to have themselves developed on the same host species.

Over the two study years, the number of aphid species remained relatively constant despite the significant difference in overall aphid density. Field data are often difficult to interpret as
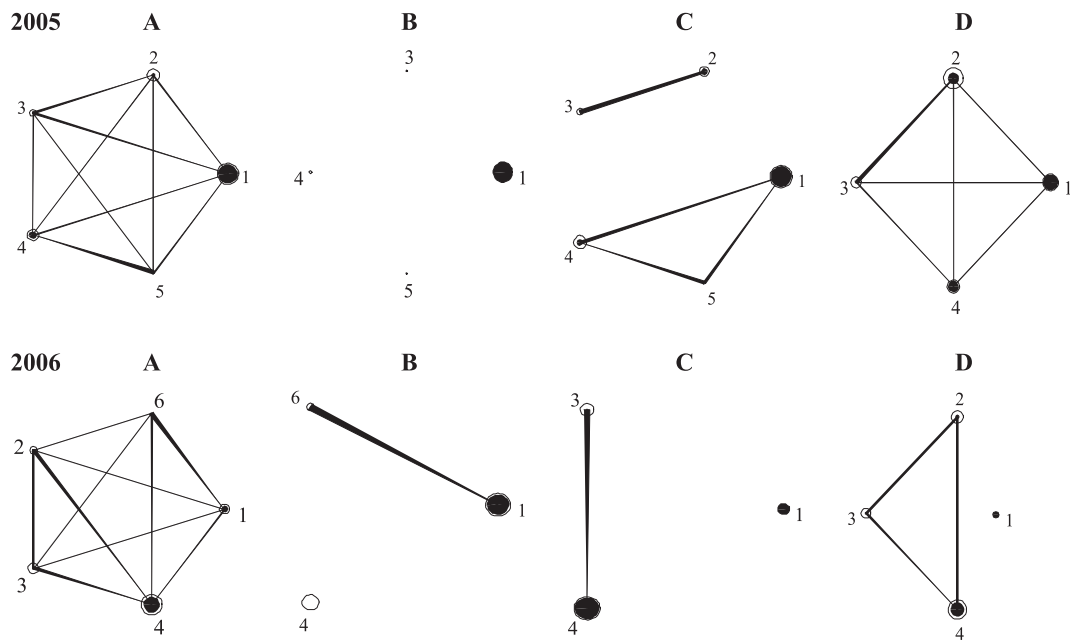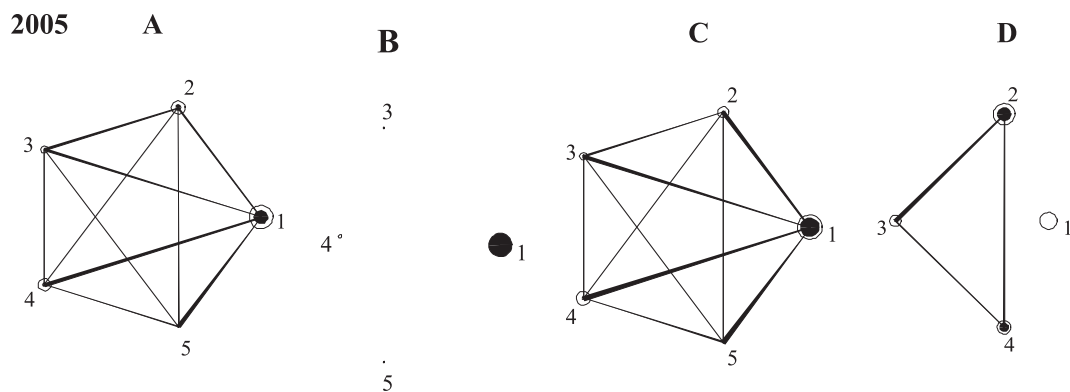
Fig. 4. Summary and seasonal quantitative overlap diagram constructed for the predator web. Each aphid species is represented by a numbered disk, the volume representing the aphid species' abundance. A: summary; B: May; C: June; D: July. A measure of predator overlap, d_{ij}, is defined in the Methods. The extent a species' disk is colored black represents d_{ii}; if two species, i and j are connected, then the width of the link at i represents d_{ij} and at j represents d_{ji}.

Fig. 5. Summary and seasonal quantitative overlap diagram constructed for the parasitoid web. Each aphid species is represented by a numbered disk, the volume representing the aphid species' abundance. A: summary; B: May; C: June; D: July. A measure of parasitoid overlap, d_{ij}, is defined in the Methods. The extent a species' disk is colored black represents d_{ii}; if two species, i and j are connected, then the width of the link at i represents d_{ij} and at j represents d_{ji}.

they depend on a lot of uncontrollable factors regulating insect populations, such as weather (Campbell et al., 1974; Logan et al., 1976; Schowalter, 2000). Meteorological observations provided by a permanent official station adjacent to the experimental site (located at Walloon Agronomic Research Center in Gembloux) indicate that mean temperatures and rainfalls were higher in 2006 than in 2005 (22.2 °C and 2.7 mm/day, 20.8 °C and 1.4 mm/day, respectively). In the 2005 web, predators and parasitoids were more abundant in the different habitats than in 2006, this was not only associated with climate changes but also with a decline in the aphid population (Alhmedi et al., 2009). The major difference between the two years was that the most abundant aphid species in the 2005 web differ form that in the 2006 web, on which it was probably the main factor influencing the natural enemy distribution. A large potential for the occurrence of apparent competition, which is likely to be caused by a predominant aphid species on rare species. Although Askew and Shaw (1974) argued that plant species had a major effect on parasitoid fauna, the present study shows that the presence of a marginal plant species like

stinging nettle supporting a large population of a natural enemy may strongly affect the other aphid species particularly the rare ones; i.e., asymmetric apparent competition (Müller et al., 1999; Lewis et al., 2002), in which aphid species, particularly *M. carnosum*, on stinging nettle were likely the predominant source of parasitoids and predators attacking other host species. The earlier intense apparition of *M. carnosum* particularly in 2005 may support this hypothesis as an important source of natural enemies.

Predators and parasitoids could have selected to stay in the non-crop habitat where the aphid preys were present in sufficient amounts and did not migrate to crop fields. Rand et al. (2006) reported that as long as resources in the border are more abundant, the population of predators and parasitoids will stay within the borders of the field and do not migrate to field. The passage of natural enemies from the stinging nettle (or the border in general term) to the field might depend on factors such as the prevalence of alternative food (nectar, pollen) and preys but also the oviposition and prey preference (e.g., Sadeghi and Gilbert, 1999; Alhmedi et al., 2008). Parasitism and predation aggregate generally around

individual plants of species preferred by the predominant host or prey. The spatial aggregation of parasitism from predominant patches to other patches has been suggested in host–parasitoid systems (Brodmann et al., 1997; Maron and Harrison, 1997).

The overlap diagrams reveal a few cases of pairs of equally abundant hosts species that share parasitoids and predators relatively symmetrically, but a much more frequent pattern is for a common host to be a major source of natural enemies attacking a rare species. There are many possible reasons why the second species may be rare, but one possibility is the presence of a common host supporting a large population of a shared parasitoid. The asymmetric apparent competition observed in the parasitoid and predator overlap diagrams suggests that the effect of aphid and natural enemy dynamics, which would underpin the observed structure of the quantitative food webs. If two hosts share a common parasitoid or predator, but occur on spatially isolated plants that rarely grow in close proximity, the opportunities for apparent competition between these herbivores may be substantially diminished (Morris et al., 2005) highly for parasitoids compared with predators, this later contest is explicated by the difference in population dynamics between the two guilds. In our system, asymmetric apparent competition occurred highly between aphid species of the same host plant species but also it occurred between aphid species of different host plant species, which this may be underpinned by the observed structure of the quantitative food webs. If asymmetric apparent competition between aphid species occurs via a shared parasitoid or predator, it is expected that adult parasitoids or predators would disperse from plant species on which the predominant aphid species feeds to other plant species. We conclude that indirect interactions such as apparent competition that might structure aphid communities are most likely to be mediated by predators (Müller and Godfray, 1997; Rott et al., 1998; van Veen et al., 2008).

Food webs contain information only about the trophic interactions in a community while populations may interact by other means, which can affect community structure. For example, plants responding to herbivore attack by releasing volatile chemicals that attract parasitoids and predators (Turlings et al., 1990; Guerrieri et al., 1999; Zhu et al., 1999; Tinzaara et al., 2005). Interactions among the guilds of natural enemies may also play a role.

In conclusion, more experimental works in field and laboratory are needed to test the effect of nettle aphids on crop aphids via shared natural enemies taking into account intraguild interactions among these beneficials. Moreover, a permanent installation of the stinging nettle strip and the influence of this management on crop aphid population should be studied over longer periods on the crops implicated in the whole rotation. Stinging nettle habitats seem to be important refuge for natural enemies and may play an essential role in conservation biological control. Quantitative food webs and natural enemy overlap diagrams offer promise for future studies. Consideration of the biological and ecological needs of natural enemies is critical for the success of any biological control effort. It is one of the easiest ways for producers to initiate biological control on their farms and should be a major consideration in any importation or augmentation program. Apparent competition, mediated by a shared natural enemy, plays a key role in conservation biological control. Appropriate agroecosystems management may favour this type of indirect interaction. Because quantitative food webs have been constructed using standardized methods based on Müller et al. (1999) in a variety of communities and climates (e.g., Rott and Godfray, 2000; Valladares et al., 2001; Lewis et al., 2002), comparing these food webs would offer an opportunity to study geographic variation in the potential for apparent competition and macroecological patterns in food web structure.

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