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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 ($\approx$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