Temporal dynamics of parasitoid assemblages parasitizing the codling moth

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HIGHLIGHTS

- The parasitoid community of the codling moth was analyzed in apple orchards.
- The same tree parasitoids attacked codling moth larvae all along the season.
- Parasitism rates differed between sites and between young and mature larvae.
- Parasitism rates in mature larvae increased with times.
- The proportion of hyper-parasitoid increased with times.

GRAPHICAL ABSTRACT
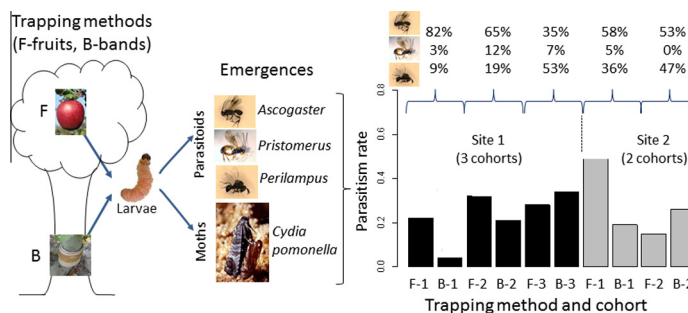
ABSTRACT

Population dynamics of parasitoid–host interaction is primary important knowledge to develop an efficient biological control strategy of insect pests. We analyzed the seasonal dynamic of the parasitoid community of the codling moth in two sites in South-Eastern France, which differed by the number of codling moth annual generations. Parasitism was estimated by sampling both young larvae collected within apple fruits and mature larvae in band traps wrapped around the trunk of the apple trees. Parasitism rates differed between sites and between young and mature larvae. Parasitism rate were higher in young larvae (29% in average) than in the mature ones (21% in average) and globally increased along the season among cohorts of mature codling moth larvae (from 4% to 34%). The three most abundant species in the parasitoid community – *Ascogaster quadridentata*, *Pristomerus vulnerator* and *Perilampus tristis* – were observed at both sites, in each codling moth cohort and in both young and mature larvae. Among all the parasitoids, the proportion of *Perilampus* – an hyper-parasitoid attacking both *Ascogaster* and *Pristomerus* primary parasitoids – increased among the codling moth cohorts (from 9% to 53%) whereas the proportion of *Ascogaster* decreased (from 82% to 35%). This shed light on the importance to characterize the dynamic of the whole trophic network (including hyperparasitism) to design biological control strategies.

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1. Introduction

To ensure the success of biological control programs it is important to understand the ecology of beneficial parasitoids, notably how parasitoids interact with biotic and abiotic parts in the agroecosystems as these interaction factors have huge impact on the population dynamic of their hosts (*e.g.* Godfray, 1994; Pearce et al., 2006; Quicke, 1997; Van Driessche and Bellows, 1996).

First, understanding the synchrony between parasitoids and their hosts is important for successful introduction, propagation and release of biological control agents (Messenger and van den Bosch, 1971). The level of phenological asynchrony between a

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parasitoid and its host affects the population dynamics, abundance and distribution of both species (Stenseth and Mysterud, 2002; Voigt et al., 2003). For a stable host–parasitoid interaction it is required that not all hosts within a population are parasitized (Van Nouhuys and Lei, 2004). Phenological asynchrony can create a temporal refuge for hosts when the risk of parasitism is low allowing stabilizing the interactions. The synchrony between the phenology of the parasitoids and their hosts may be modified by both climatic changes (Hance et al., 2007; Henri et al., 2012; Voigt et al., 2003) and selective pressures in the host–parasitoid interaction (Forde et al., 2004; Sait et al., 1997). High synchronization of the phenology of the parasitoid on that of its host increases the parasitism pressure, which may drive to local extinction of both host and parasitoid populations. In case the host does not go extinct, the small size of parasitoid populations in the following generation may provoke a parasitoid population crash or local extinction followed by an outbreak of the host (Hance et al., 2007). Contrarily, phenological asynchrony may expose an insufficient number of hosts to parasitoids causing the decline of parasitoid population to extinction and host demographic outbreak (Godfray et al., 1994). As insect phenologies mainly depend on temperature, with specific levels of accumulated degree days required for reaching each developmental stage (Hodgson et al., 2011; Nylin and Gotthard, 1998), we hypothesize that both seasonal and geographical variations in temperature may largely impact the synchrony of the parasitoids with their host and consequently the level of their interaction.

Second, parasitism rates may depend on the composition of the parasitoid community. Parasitism rates can be promoted by a higher parasitoid diversity if species have additive or synergistic interactions. Alternatively, negative interactions between parasitoids (*e.g.* hyperparasitism), may reduce the control of insect pests (Rosenheim, 1998). Parasitoids that attack their hosts at an early stage of their development have access to a more abundant host resource than those attacking their host later (Chesson, 1991; Price, 1972), which may also result in exploitative competition between parasitoids (Harvey et al., 2013; Hawkins, 2000; Schoener, 1983; Teder et al., 2013). Specialist parasitoids of a given host are known to contribute more to mortality of this host than generalist parasitoids (Elzinga et al., 2007; Godfray et al., 1995; Stefanescu et al., 2012). Because parasitoids occupy a relatively high position in food chains and because of their sometimes high level of specialization they are directly sensitive to variation in the population dynamics of their host and indirectly to those of other parasitoids with which they compete (Hance et al., 2007; Stireman et al., 2005; Van Baaren et al., 2010; Walther, 2010). We hypothesize that seasonal variation in parasitism rates largely depend on variation in the composition of the parasitoid community and the level of specificity of the parasitoids to their hosts.

Third, parasitoids are engaged in an obligate association with their hosts. Their fate is tied to that of their hosts, possibly under varying environmental conditions. Parasitoids perceive and respond to the physiological status of their host (Tauber et al., 1983). Many parasitoid larvae detect the fluctuations in endocrine titers in their host enabling them to assess their host's developmental stage (Brown and Friedlander, 1995). Some parasitoids regulate the induction and the termination of their diapause according to the physiology of their host (Fisher, 1971). Furthermore, many parasitoids are known to also induce behavioral and physiological changes in their host. These changes are thought to increase the parasitoid survival by decreasing the risk of predation (Adamo et al., 1997; Brodeur and Vet, 1994; Brodeur and McNeil, 1989; Godfray, 1994; Grosman et al., 2008) or winter mortality (Quan et al., 2013; Wharton, 1999). For example, the braconid *Glyptapanteles* sp. induce their host *Thyrinteina leucocerae* (Lepidoptera: Geometridae) to fight predators. After the parasitoids

egress from their caterpillar host to pupate, the host stops feeding and moving, but knocks off predators with violent head-swings to protect the parasitoid cocoons until the emergence of the adult wasps and dies before reaching adulthood (Grosman et al., 2008). This example shows how important the changes in the physiology and the behavior of the parasitized insects are in comparison with their uninfected congeners. Our hypothesis was thus that parasitized larvae may have modified dispersal ability and/or behavior, which may affect their trapping according to the sampling methodology (*e.g.* Josso et al., 2011). We also postulated that estimations of the parasitism would depend on the age of the sampled host since each species in the parasitoid community is likely to attack different instars of their host. Consequently, we assumed that estimations of parasitism rates may highly depend on the trapping methodologies.

Here, we studied the temporal dynamics of the parasitism in the codling moth (*Cydia pomonella* L., Lepidoptera, Tortricidae), which is the major insect pest in apple orchards (Barnes, 1991; Franck et al., 2007). High pest density can induce the total loss of an orchard production (about 50% of the phytoprotection costs are for controlling the codling moth). Damages are caused by young larvae, which attack the apple fruits. At the end of their development, the mature larvae leave the fruits and migrate downwards following the tree trunk, seeking for a shelter. Depending on temperature and photoperiod conditions, the mature larvae pupate to produce adults or diapause into a cocoon. The life cycle of the codling moth varies from one to four annual generations according to geographical (latitude and altitude) and seasonal variations of the temperatures (Shel'Deshova, 1967) and according to the host-plants (Barnes, 1991).

In a recent study (Maalouly et al., 2013), we observed that three parasitoid species mainly parasitize the overwintering codling moth larvae in commercial apple orchards from southeastern France: *Ascogaster quadridentata* (Braconidae), *Pristomerus vulnerator* (Ichneumonidae) and *Perilampus tristis* (Perilampidae), which was in agreement with previous observation of codling moth parasitism in Europe (Athanassov et al., 1997; Diaconu et al., 2000; Mills, 2005; Miñarro and Dapena, 2004; Rosenberg, 1934). However, no study has reported observation on the composition of the parasitoid community parasitizing non-diapausing codling moth larvae within season so far.

The braconid *A. quadridentata* is an ovo-larval endoparasitoid specialized on tortricid moths (Athanassov et al., 1997). The female is ready for oviposition soon after emergence. Parasitized codling moth larvae are only one-third of the size of non-parasitized larvae at the maximum of their development. The *A. quadridentata* larva emerges from the mature codling moth larva and entirely consumes the body contents of its host (Clausen, 1940). The ichneumonid *P. vulnerator* is a solitary endoparasitoid. The female deposits one egg in the young host larva after it entered the fruit. The parasitoid larva remains in latent state until the codling moth larva leaves the fruit and builds shelter to pupate (Coutin, 1974). The mature parasitoid larva leaves the host's body and weaves a hard elongated cocoon where development continues up to the adult stage (Diaconu et al., 2000). The ichneumonid *P. vulnerator* is known as a generalist parasitoid developing on several host species among the Lepidoptera (Diaconu et al., 2000; Rosenberg, 1934). The chalcidoid *P. tristis* was noted as a hyperparasitoid on the tortricids *via* its primary hosts, mainly Braconidae (Bogenschütz, 1991; Bouček, 1977). The chalcidoid female does not oviposit directly in its host or within the caterpillar host of the primary parasitoid. It might lay its eggs near the caterpillars but nothing is clearly known about how the *P. tristis* planidium reaches its caterpillar host (Smith, 1912). Clausen (1940) described the development of *P. tristis* in *Rhyacionia buoliana*. The *P. tristis* planidium penetrates the young diapausing caterpillar and spends