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Effects of an invasive plant on the performance of two parasitoids with different host exploitation strategies

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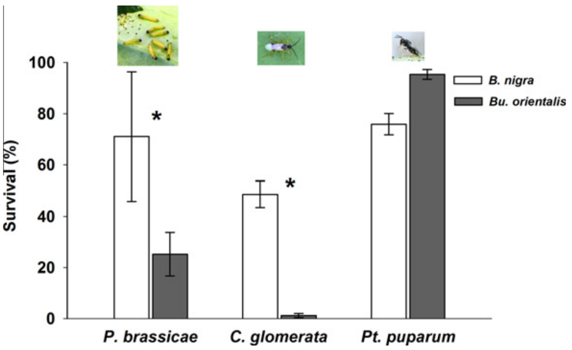
HIGHLIGHTS

- ▶ Study of multitrophic interactions on an invasive and a native plant.
- ▶ Emphasis on parasitoid host exploitation strategies.
- ▶ Specialist herbivore and larval parasitoid performed worse on the exotic plant.
- ▶ Pupal parasitoid performance was similar on hosts from both plant species.
- ▶ Effects of invasive plants depend on the species with which they interact.

GRAPHICAL ABSTRACT



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ABSTRACT

In their new range, exotic plants create the possibility for novel interactions to occur with native consumers. Whereas there is evidence that these novel interactions can be negative for native insects, alien plants that are closely related to native species may in fact act as important food sources for native insects during the growing season. Thus far, studies with invasive plants have mostly focused on plant–herbivore interactions. However, to better understand how top-down and bottom-up processes may affect the success of potential invaders we also need to consider the effects of invasive plants on higher trophic levels. We examine multitrophic interactions on an exotic invasive crucifer, *Bunias orientalis*, and a native crucifer, *Brassica nigra*. The performance of a specialist herbivore, *Pieris brassicae*, and two of its gregarious endoparasitoids, the koinobiont *Cotesia glomerata* and the idiobiont *Pteromalus puparum*, was investigated. Emphasis was laid on parasitoid host-resource use strategies and how these may be differently affected by the quality of the exotic food plant. *P. brassicae* larvae performed poorly on the exotic plant, with lower survival, longer development time and a lower pupal mass, than on the native plant. The exotic plant affected the performance of the two parasitoid species in different ways. *C. glomerata* survival was strongly co-ordinated with the survival of its larval host, showing also high mortality. Adult wasps that survived on *Bu. orientalis* had an extended development time and small body size. By contrast, *Pt. puparum* survival was similar on pupal hosts reared on both plant species. Our results show that constraints imposed by differing plant quality of native and exotic plants on trophic interactions can depend on resource use strategies of the species involved, suggesting that effects of exotic species should be elucidated on a case-by-case basis.

1. Introduction

The introduction of exotic organisms into non-native ecosystems is considered to be a major threat to biodiversity. Invasive organisms have the potential to disrupt trophic interactions, which

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may ultimately lead to the unraveling of food webs and the weakening of ecosystem services with huge economic costs (Pimentel et al., 2000). However, recent evidence suggests alien species can also become integral components of the ecosystems that they invade. A recent study by Pattemore and Wilcove (2011) argues that invasive organisms often take on important biological roles, such as pollinators or pest controllers, once held by the species they either displaced or that have become rare due to other anthropogenic causes (e.g. climate change, habitat destruction). This suggests that our approach to the effects of alien species should be elucidated on a case-by-case basis (Davis et al., 2011).

Plants, amongst the most important of invasive organisms, can exhibit disproportionate effects on food webs because they occur at the bottom of the food chain. To understand the effects of exotic plants on natural and managed ecosystems, it is important to understand the potential mechanisms that allow a very small percentage of exotic species to become invasive. Several hypotheses have been proposed to address the relationship between phenotype and invasion success. For example, exotic plants may possess pre-adapted traits, such as chemistry or structure that are novel in the new range, enabling them to repel or resist attack from native herbivores and pathogens (Keane and Crawley, 2002; Mitchell and Power, 2003; Cappuccino and Arnason, 2006). Ecological fitting, described by Janzen (1985), states that organisms are able to persist in novel environments if a suite of evolved traits they bring from their native habitat enables them to enjoy realized fitness in the new habitat. Therefore, in the short term, phenotypic characteristics of many associations that occur in nature are not necessarily the result of long co-evolution, but of recent novel interactions (Agosta and Klemens, 2008).

However, although some exotic plants might be released from the natural enemies from their native range, interactions between these plants with competitors and natural enemies in the new range are still very likely to occur (Gerber et al., 2008; Verhoeven et al., 2009). Consequently, rather than escaping from their consumers, exotic plants might simply interact with new insect assemblages in their new range (Müller-Schärer and Steinger, 2004; Liu and Stiling, 2006). Invasive plants can have negative effects on native insects, with implications for their conservation. For example, the garlic mustard, *Alliaria petiolata*, which is native to Eurasia, has become a dominant weed in much of eastern North America. It has displaced native food plants of several native white butterflies, *Pieris oleracea* and *Pieris virginiensis*, that in turn readily lay their eggs on *A. petiolata* but whose larvae die early during their development (Keeler and Chew, 2008). In contrast, in some cases exotic plants can be beneficial to native consumers (Graves and Shapiro, 2003; Pattemore and Wilcove, 2011; Harvey and Fortuna, 2012). For instance, in North America exotic plants (e.g. *Plantago lanceolata*, *Taraxacum officinale*, as well as several Brassicas) now constitute important food sources for the larval stages of many native butterflies species, including *P. oleracea* (Graves and Shapiro, 2003). This shows that exotic plants have the potential to become an integral part of the native flora and to fit in naturally with many native fauna (Davis et al., 2011; Pattemore and Wilcove, 2011).

Furthermore, although many studies have demonstrated either positive or negative effects of novel interactions on the behavior and development of naïve herbivores (Wolfe et al., 2004; Keeler and Chew, 2008; Harvey et al., 2010a; Oduor et al., 2011), multitrophic interactions, i.e. between exotic plants, herbivores and their natural enemies, have been little studied (Cronin and Haynes, 2004; Stenberg, 2012). Because of this, important information on ecophysiological aspects of these interactions is lacking (Harvey et al., 2010b; Harvey and Fortuna, 2012). Carnivorous insects have long been recognized to play a significant role in affecting the structure and function of terrestrial communities (Price et al., 1980). Parasitoids generally rely on a limited amount of resources that are obtained from a single host. Because of this, their ontogeny is strongly correlated with host quality, defined as variation in the host size or nutritional value, which consequently affects parasitoid fitness (Price, 1973; Godfray, 1994; Harvey, 2005). Many studies have shown that differences in plant quality can affect parasitoid development via its effect on their host (Campbell and Duffey, 1979; Harvey, 2005; Bukovinszky et al., 2008). However, parasitoid performance is not always affected by lower quality host resources (Gols et al., 2008), showing that the effects of plants on trophic interactions is generally highly association-specific (Harvey, 2005). Amongst parasitoids species, host resources are exploited in two different ways. Idiobiont parasitoids are species that develop in non-growing hosts, such as eggs, paralyzed larvae or pupae. In contrast, koinobiont parasitoids attack hosts that continue to grow after parasitism (Askew and Shaw, 1986). Mackauer and Sequeira (1993) proposed three models, one for idiobionts, and two for koinobionts, to predict the effects of host quality on parasitoid development. The idiobiont model predicts that offspring development is dependent on the quality and amount of resources available at the time of oviposition, because idiobionts exploit host resources that are effectively static (Mackauer and Sequeira, 1993). Consequently, host size can generally be taken as an index of host quality and large hosts are usually assumed to be of higher quality because they contain more resources for parasitoid development (Godfray, 1994). Alternatively, the koinobiont models predict that host quality is dependent on the rate of host growth after parasitism and on the final size of the host, because host resources exploited by koinobionts are dynamic. Although the models have been empirically tested at the level of two (host–parasitoid) trophic level interactions (e.g. see review by Harvey, 2005) they have rarely been tested when incorporating the food plant as an additional constraint on host (and in turn parasitoid) development.

The Turkish rocket, *Bunias orientalis* L. (Capparales: Brassicaceae), is a perennial wild crucifer native to SE-Europe and SW-Asia (Tutin et al., 1993). Over the past 30 years it has become a highly invasive species in many parts of northern and central Europe establishing on roadsides, edges of arable land and more recently, in meadows, orchards and vineyards (Steinlein et al., 1996). At the same time, the plant remains less common (although increasing) in other parts of Western Europe, including The Netherlands (Harvey et al., 2010a). *Bu. orientalis* is a good example of a ruderal invader, which behaves opportunistically and is well adapted to anthropogenic disturbance regimes such as mowing and soil perturbation (Steinlein et al., 1996).

In the current study we examine the development and survival of the specialist herbivore, *Pieris brassicae*, and two of its gregarious primary parasitoids, the koinobiont larval parasitoid *Cotesia glomerata* L. (Hymenoptera: Braconidae) and the idiobiont pupal parasitoid *Pteromalus puparum* L. (Hymenoptera: Pteromalidae), on the exotic invasive crucifer, *Bu. orientalis*, and on the native crucifer, *Brassica nigra* L. (Capparales: Brassicaceae). *B. nigra* is an annual crucifer abundant in The Netherlands and serves as a main food plant for the larvae of pierid butterflies, including *P. brassicae* (Feltwell, 1982; Gols et al., 2008; Harvey et al., 2010a). This study aimed to reveal (a) how local insect assemblages respond both developmentally and behaviorally to the novel plant, and (b) how natural enemies of important herbivores may prove to be an impediment in the control of the invasive plant. We tested two hypotheses: (1) the native plant is of higher quality for the herbivore development than the invasive plant; (2) the koinobiont parasitoid will suffer larger costs in fitness than the idiobiont, because host quality is less predictable for the former parasitoid at the time of oviposition.