Evolutionary Ecology of Diamondback Moth, *Plutella xylostella* (L.) and *Diadegma insulare* (Cresson) in North America: A Review

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Authors' contributions

This work was carried out in collaboration between all authors. Author SM managed the literature searches and wrote the first draft of the manuscript. Author LMD supervised and critically reviewed the manuscript and author JTO helped in editing and final revision of manuscript. All authors read and approved the final manuscript.

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ABSTRACT

The diamondback moth (DBM), *Plutella xylostella* (L.), is recognized as a widely distributed destructive insect pest of Brassicaceae. The frequency and severity of *P. xylostella* outbreaks has increased in recent years, due to climate changes, high production of host plants (vegetable and oilseed Brassica crops), genetic flexibility of the pest that enables it to develop resistance to almost all known insecticides and establish quickly and easily in new environment. All life stages of *P. xylostella* are attacked by natural enemies but *Diadegma insulare* (Cresson) is one of the principal, effective and efficient larval parasitoids in North America. In this review, we synthesize published information on the primary aspects of *P. xylostella* origin, dispersal, migration, biology, and host plants and mainly focus on evolutionary ecology of bitrophic and tritrophic interactions among *P. xylostella*, its host plants and natural enemies.

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1. INTRODUCTION

*Plutella xylostella* is not only the most destructive pest of brassicaceous crops throughout the world but is also among the most difficult to manage [1,2]. It was first introduced from Europe to North America (Illinois), in 1854. *Plutella xylostella* now occurs throughout North America, wherever its host plants are cultivated [3]. Its management result in a US$4-5 billion annual cost to the world economy [4]. A few review articles on *P. xylostella* host-plant interactions, management and ecology have been published but a focus on detailed evolutionary ecology of tritrophic interactions among *P. xylostella*, its host plants and its principle parasitoid are lacking. The main objective of this review paper is to address the gaps in the knowledge and understanding of *P. xylostella* and *D. insulare* evolutionary ecology and tritrophic interactions. It is believed that the information presented here will encourage researchers to work on important aspects of *P. xylostella* and its natural enemies and help designing appropriate management strategies involving complete and in depth awareness of tritrophic interactions in a particular agro-ecosystem.

2. DISTRIBUTION AND ORIGIN OF *P. xylostella*

*Plutella xylostella* is believed to be the most widely distributed species of Lepidoptera, occurring universally wherever *Brassicaceae* are grown [1]. Six economically important species of the Genus *Plutella* (Schrank) have been recorded worldwide but only *P. xylostella* is cosmopolitan in distribution [5]. It has been recorded throughout tropical and temperate zones, as far north as Iceland (60ºN) and as far south as New Zealand (45ºS) [6]. The geographical origin of *P. xylostella* is uncertain. Some have speculated its origin in Europe [7], the Mediterranean area [8] or China [9]. It is also assumed to have evolved in South Africa, based on the diversity of endemic Brassica plants and its indigenous diverse parasitoid fauna [5]. North American populations are most probably of European origin and were introduced about 150 years ago [7]. Recently, some climatic models have been developed to predict *P. xylostella* distribution and seasonal phenology in areas of its occasional occurrence. However, the abundance and distribution of the *P. xylostella* population in an area is regulated by climate, availability and quality of host plants and the presence of its natural enemies [10].

3. BIOLOGY

The biology of *P. xylostella* has been studied extensively in both laboratory and natural conditions in relation to ecological factors. However, its biological and developmental parameters vary due to differences in host plant species, temperature, and geographical population distribution [11]. The moth is multivoltine and can produce four to 20 generations per year in temperate and tropical regions, respectively [12,13]. In North America, it can produce three to five generations per year [14]. At constant temperature, development can occur from 8-32ºC and under fluctuating temperature from 4 to 38ºC [15]. *Plutella xylostella* development has been studied by Bahar et al. [16] at different constant (7,22,30ºC) and fluctuating temperatures (0-14,15-29ºC, and 23-37ºC). The development was very slow at lowest constant (7ºC) and fluctuating temperatures (0-14ºC) while fast development of *P. xylostella* was recorded at highest constant (30ºC) and fluctuating temperatures (23-30ºC).

*Plutella xylostella* has four life stages: egg, larva, pupa and adult. Oviposition mainly occurs at night in the first 24 to 48 hours of mating and then declines gradually. Egg laying reaches zero in 10 days after adult emergence [11]. Each female can lay more than 200 eggs either singly or in small clusters [17,18]. Oviposition is greatly influenced by host plant species. For instance, oviposition on brassicaceous host plant (*Brassica napus* L.) is reported to be higher than non-brassicaceous hosts (*Cleome hassleriana* Chod. and *Tropaeolum majus* L.) [19].

Eggs are oval and pale to strong yellow in color [11]. Egg hatching occurs in 4-8 days [14]. Larvae are pale yellow in color having a dark head in early instars, and are light to dark green colored in later instars. The larva has V-shaped anal legs. First-instar larvae are leaf miners, feeding in the spongy mesophyll tissue of leaves. Other larval instars feed on all tissues of leaves, buds, flowers, stems, and siliques [11,20]. The average development time from first to fourth instar is reported as 4.0, 3.6, 3.4, and 4.2 days respectively, under Canadian field conditions; pupation takes place over 7.8 to 9.8 days [14].
The adult moth is slender and greyish [21]. The mean longevity of females is significantly reduced relative to males [11]. Development and survival vary greatly depending on quality of food, quantity of adult feeding, difference in host plant cultivar and sources of carbohydrate [22,11].

4. DISPERAL AND MIGRATION

Migration may evolve as a mechanism that permits individuals to avoid probable failures in survival [23]. Insects may develop migratory characteristics when their habitat deteriorates [24]. *Plutella xylostella* possesses a high migratory ability to disperse over long distances in a very short time. This can explain why it gets easily established in novel environments and newly planted Brassica crops [7,25,26]. *Plutella xylostella* does not diapause; therefore long-distance immigration through aerial currents is a major process affecting population outbreaks [27,28]. *Plutella xylostella* migration and population seasonality is well documented [1]. Similar seasonal migrations have been reported in Japan’s south western islands [29], in the United Kingdom [7,30], New Zealand, South Africa, and southern parts of Chile and Argentina [1], and Australia [31]. In both eastern and western Canada, *P. xylostella* re-establishes each year from annual adult population immigrations from the southern U.S.A. and Mexico [32,27,33]. *Plutella xylostella* adults have the ability to travel about 1500 km. Therefore, its densities can vary considerably from year to year [32,27,34,33]. *Plutella xylostella* cannot survive severe winters. Dosdall [35] reported its survival under mild winter conditions in western Canada. However, successful overwintering in northern latitudes in large numbers is considered to be an unusual phenomenon [36]. Hence, it is assumed that migration is the most probable cause of population seasonality in *P. xylostella*. It is a regular ecological event that occurs at approximately the same time of the year and a characteristic of the vast majority of insect populations [28]. Campos et al. [37] noted that low nutritional quality and short temporal persistence of mature host plants, reduced body size, prolonged longevity and delayed sexual maturation of moths due to unfavorable environmental conditions. This will increase the chances of reaching new reproductive sites. Moths having such characteristics have greater fitness and are active migrants, when the resources are limited and habitat deteriorated.

5. EVOLUTIONARY ECOLOGY OF INTERACTIONS AMONG *P. xylostella* AND ITS HOST PLANTS

*Plutella xylostella* has a wide ecological host range. The genetic and phenotypic flexibility of *P. xylostella*, and its ability to modify traits of its life history according to environmental conditions during development enables the pest to survive throughout the year in areas where environmental conditions are favorable and host plants are easily available, in the absence of other ecological and evolutionary pressures [28,37]. The moth feeds almost exclusively on plants of the family Brassicaceae, particularly the genus *Brassica*, which are widely distributed geographically, and include 338 genera and 3709 species [38] (Table 1).

*Plutella xylostella* is commonly considered a specialist on *Brassicaceae*. However, evidence of its occasional occurrence on sugar snap peas (*Pisum sativum* L., Fabaceae) in Kenya [70], Taiwan and the Philippines [55,64], the chenopodiaceous vegetable *Salsola kali* L. (prickly saltwort, Russian thistle) in Russia [71], and okra in Ghana [72] have been recorded. Genetic analysis indicated an incomplete evolutionary host range expansion and ability to complete development on the novel host plant (snap peas) by *P. xylostella* strain [67,68,70]. It has also been documented by Dosdall et al. [34] that an introduction of a novel crop into an area can increase insect pest problems, including *P. xylostella* infestations.

*Plutella xylostella* is often studied in its relationship with its host plant’s specific chemistry. The plants of the family *Brassicaceae* are characterized by the presence of sulphur-containing secondary metabolites known as glucosinolates that play a key role in plant defense against herbivores [73]. Some glucosinolate hydrolysis products like isothiocyanates are highly toxic to insect herbivores, but those insects specialized in feeding on plants with these secondary compounds have a mechanism to overcome this toxicity [74,75]. Very little is known about the mechanisms evolved by herbivores to overcome these defensive plant compounds [73]. There is some evidence of temporal association between the diversification of the host plants and insect herbivores [75]. However, the origin of an evolutionary novel defense mechanism and diversification of *Brassicales* (90-85 mya) were most probably followed by co-evolution of insect
herbivores and their host plants [76,77]. In Brassicaceae, the glucosinolates co-occur with myrosinases and are together known as “mustard oil bomb” [78]. These two compounds are compartmentalized in plants but come together upon plant tissue damage and release toxic isothiocyanates. The larvae of P. xylostella have evolved a defensive mechanism to detoxify glucosinolate (mustard oil bomb) and its toxic hydrolysis products by an enzyme glucosinolate sulfatase present in their gut. The enzyme actively prevents the formation of toxic hydrolysis products by converting glucosinolates to desulfo glucosinolates rather than more toxic nitrile and isothiocyanates. This mechanism enables P. xylostella herbivory on wide range of Brassica plants [54,74].

Plutella xylostella adults rely on morphological and chemical cues (glucosinolates like sinigrin, sinalbin and glucocheirolin) for host plant location, recognition, oviposition, stimulation and feeding initiation [79,80,74]. The performance of P. xylostella varies on cultivars of the same plant species with different glucosinolate contents and profiles; for example, high performance of larvae has occurred in plant species with intermediate glucosinolate content [81] or with low myrosinase content [82]. Similarly, higher densities of P. xylostella larvae are reported to be associated with plant cultivars having higher glucosinolate contents [83]. High concentrations of allyl isothiocyanates are reported to be toxic for larvae and adults [82]. In fact, glucosinolates are not the only plant compounds that stimulate oviposition and feeding activity; other aspects of host plant nutritional quality, such as host plant volatiles, morphology and chemistry or a combination of these also play an important role [48,75].

Some plant compounds like saponins, present on the leaf surface of some Barbara spp., act as deterrents for larval development but attractants for oviposition. The presence of these compounds supports their ecological role in host recognition and stimulation of oviposition for the diamondback moth [84]. Plutella xylostella adults can also respond differently to different host plant volatiles emitted as a result of insect damage. Females rely on these volatile cues to recognize acceptable hosts for its progeny survival, fitness and to reduce competition for food [85]. Reddy & Guerrero [86] reported three cabbage green leaf volatiles that are highly attractive to P. xylostella females.

Brassicaceae host plant species and cultivars vary considerably in their level of susceptibility for P. xylostella. Sarfraz et al. [40] proposed that Sinapis alba L. and Brassica rapa L. are highly preferred for oviposition. The developmental time, longevity, body weight, and other parameters are greatly affected by host plant species; e.g., larval and pupal developmental times of females are faster on Brassica juncea (L.) Czern. and S. alba than on several other Brassicaceae.

Accumulating evidence indicates that host plant morphological characteristics like leaf color, size, and their position on the plant, epicuticular waxes, trichome density, chemosensory stimulation and abiotic factors affect P. xylostella oviposition, development and herbivory [79,80]. For instance, P. xylostella females prefer glossy cultivars (i.e., low surface wax) over waxy cultivars (normal wax bloom) for oviposition; though larval survival is reduced on glossy cultivars [48]. Some studies reported oviposition preference of P. xylostella on lower leaf surfaces of host plants [11,87,88], while some reported a higher oviposition preference on the upper surfaces of crucifer leaves [14,1]. Similarly, number of eggs laid and trichome density were positively correlated [17,89]. A recent study showed a positive correlation between P. xylostella oviposition choice and larval survival on undamaged host plants [90]. Variations in the host plant nutritional quality can affect the pest directly. Usually sulphur-deficient plants are less attractive but plants grown under a high fertilizer regime are more attractive for P. xylostella oviposition [91,92].

The preferences and performance of P. xylostella vary significantly among brassicaceous wild and cultivated species. Sinapis alba is a most preferred host followed by B. rapa, B. juncea, and Brassica napus L. among the cultivated species [36], while Sinapis arvensis L. followed by Erysimum cheiriroides L. and Capsella bursa-pastoris (L.) are preferred wild brassicaceous hosts [59]. One of the main reasons for variation in development and fecundity of P. xylostella on different plant species or different cultivars of the same species is due to the differences in plant quality, reflected either in insect nutrient requirements or phagostimulation of P. xylostella [93].
Table 1. Host plants of *Plutella xylostella*

<table>
<thead>
<tr>
<th>Cultivar/Species</th>
<th>Common name</th>
<th>Plant type</th>
<th>Ref. No</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Brassica carinata</em> L.</td>
<td>Ethiopian mustard</td>
<td>Vegetable, Oilseed</td>
<td>[39,40,41]</td>
</tr>
<tr>
<td><em>Brassica juncea</em> L.</td>
<td>Indian mustard, brown mustard</td>
<td>Vegetable</td>
<td>[42,43,40,44]</td>
</tr>
<tr>
<td><em>Brassica napus</em> L.</td>
<td>Canola, Canadian turnip, rutabaga</td>
<td>Vegetable, Oilseed</td>
<td>[45,42,40,41,46,47]</td>
</tr>
<tr>
<td><em>Brassica nigra</em> L.</td>
<td>Black mustard</td>
<td>Vegetable, Oilseed</td>
<td>[45]</td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L. var. acephala</td>
<td>Collard, flowering kale</td>
<td>Vegetable, Spice</td>
<td>[45]</td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L. var. alboglabra</td>
<td>Kale</td>
<td>Vegetable</td>
<td>[1]</td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L. var. botrytis</td>
<td>Cauliflower</td>
<td>Vegetable</td>
<td>[45,50,46]</td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L. var. sabauda</td>
<td>Savoy cabbage</td>
<td>Vegetable</td>
<td>[51]</td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L. var. capitata</td>
<td>Cabbage</td>
<td>Vegetable</td>
<td>[52,45,46,47]</td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L. var. gemmifera</td>
<td>Brussels sprouts</td>
<td>Vegetable</td>
<td>[1]</td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L. var. gongylodes</td>
<td>Kohlrabi</td>
<td>Vegetable</td>
<td>[50,46]</td>
</tr>
<tr>
<td><em>Brassica oleracea</em> L. var. italica</td>
<td>Broccoli</td>
<td>Vegetable</td>
<td>[45,50]</td>
</tr>
<tr>
<td><em>Brassica rapa</em> L. var. pakchoi</td>
<td>Pak choi</td>
<td>Vegetable</td>
<td>[1]</td>
</tr>
<tr>
<td><em>Brassica rapa</em> L. var. pekinensis</td>
<td>Chinese cabbage</td>
<td>Vegetable</td>
<td>[17,53,47]</td>
</tr>
<tr>
<td><em>Arabidopsis thaliana</em> (L.) Heynh</td>
<td>Thalecress, mouse-ear cress</td>
<td>[54]</td>
<td></td>
</tr>
<tr>
<td><em>Barbarea vulgaris</em> (L.) R. Br.</td>
<td>Yellow rocket, rocketcress</td>
<td>[45,55,48]</td>
<td></td>
</tr>
<tr>
<td><em>Berteroa incana</em> (L.) DC.</td>
<td>Hoary alyssum</td>
<td>[45]</td>
<td></td>
</tr>
<tr>
<td><em>Capsella bursa-pastoris</em> L.</td>
<td>Shepherd’s purse, mother’s-heart</td>
<td>[45,56]</td>
<td></td>
</tr>
<tr>
<td><em>Cardamine flexuosa</em> With.</td>
<td>Flexuous bittercress</td>
<td>[57]</td>
<td></td>
</tr>
<tr>
<td><em>Descurainia sophia</em> L.</td>
<td>Flixweed</td>
<td>[1]</td>
<td></td>
</tr>
<tr>
<td><em>Erysimum cheiranthoides</em> L.</td>
<td>Wormseed mustard, treacle mustard</td>
<td>[58,45,56,59]</td>
<td></td>
</tr>
<tr>
<td><em>Erucastum arabicum</em> (Fisch. &amp; Mey.)</td>
<td>-</td>
<td>[60]</td>
<td></td>
</tr>
<tr>
<td><em>Lepidium campestre</em> (L.) R. Br.</td>
<td>Field pepperweed</td>
<td>[45]</td>
<td></td>
</tr>
<tr>
<td><em>Lepidium virginicum</em> L.</td>
<td>Virginia pepperweed, peppergrass</td>
<td>[61]</td>
<td></td>
</tr>
<tr>
<td><em>Raphanus raphanistrum</em> L.</td>
<td>Wild radish, wild rape, wild turnip</td>
<td>[45,49]</td>
<td></td>
</tr>
<tr>
<td><em>Rorippa indica</em> (L.) Hiern</td>
<td>Indian marshcress</td>
<td>[57,61]</td>
<td></td>
</tr>
<tr>
<td><em>Rorippa islandica</em> (Oeder)</td>
<td>Marsh yellowcress</td>
<td>[57]</td>
<td></td>
</tr>
<tr>
<td>Barba’s</td>
<td>-</td>
<td>[49]</td>
<td></td>
</tr>
<tr>
<td><em>Rorippa micrantha</em> (Roth.)</td>
<td>-</td>
<td>[49]</td>
<td></td>
</tr>
<tr>
<td>Cultivar/Species</td>
<td>Common name</td>
<td>Plant type</td>
<td>Ref. No</td>
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</tr>
<tr>
<td>Jonsell</td>
<td></td>
<td></td>
<td>[49]</td>
</tr>
<tr>
<td><em>Rorippa nudiuscula</em></td>
<td>(E.Mey. ex Sond.) Thell.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sinapis arvensis</em></td>
<td>L. (Brassica kaber (DC) Wheeler)</td>
<td>Wild mustard, crunch weed</td>
<td>[45,59,56]</td>
</tr>
<tr>
<td><em>Sisymbrium altissimum</em> L.</td>
<td></td>
<td>Tumbling mustard, tall hedge mustard</td>
<td>[1]</td>
</tr>
<tr>
<td><em>Thlaspi arvense</em> L.</td>
<td></td>
<td>Stinkweed, pennycress, French weed</td>
<td>[45]</td>
</tr>
<tr>
<td><strong>Non-cruiferous</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Tropaeolum majus</em> L.</td>
<td>Nasturtium, Indian cress</td>
<td>Flowering ornamental plant</td>
<td>[58]</td>
</tr>
<tr>
<td>Cleome species</td>
<td>Spider plant</td>
<td>Flowering plant</td>
<td>[62]</td>
</tr>
<tr>
<td><em>Pisum sativum</em> L.</td>
<td>Peas</td>
<td>Pulse</td>
<td>[63,64,65,66,67,68]</td>
</tr>
<tr>
<td><em>Hibiscus esculentus</em> L.</td>
<td>Okra, Lady fingers</td>
<td>Vegetable</td>
<td>[69]</td>
</tr>
</tbody>
</table>

6. NATURAL ENEMIES OF *P. xylostella*

All stages of *P. xylostella* are attacked by various parasitoids and predators (Table 2).

Delvare [114] reported over 135 parasitoid species worldwide. Among these, the most common ones include six species of egg parasitoids, 38 larval, and 13 pupal parasitoids [115]. Egg parasitoids (genera *Trichogramma* and *Trichogrammatidae* (Hymenoptera: *Trichogrammatidae*) contribute little to natural control generally because of their nonhost-specific nature [116]. In addition, to utilize them in biological control initiatives requires frequent inundated releases [1]. Larval parasitoids are predominant and have maximum control potential. The most effective *P. xylostella* larval parasitoids belong to hymenopteran genera *Microplitis* (Braconidae), *Cotesia* (Braconidae), and *Diadegma* (Ichneumonidae) [115,1]. A few preupal and pupal parasitoids of the genus *Diadromus* (Ichneumonidae) also provide significant control [7,1,117,104,2]. Occasionally some species of *Pteromalus* (Hymenoptera: *Pteromalidae*) species parasitize *P. xylostella* pupae [100].

On a worldwide scale, large numbers of *P. xylostella* parasitoid species have been reported but some of them were misidentified [118,95]. Thompson [119] catalogued 48 species of parasitoids associated with *P. xylostella*, while Goodwin [120] reported over 90 such parasitoid species. Similarly, Mustata [121] listed 25 parasitoid species from Moldavia (Romania). Ten species of *Diadegma* that attack *P. xylostella* are recognized by Fitton & Walker [122]. Moreover, seven *Diadegma* species are revised by Azidah et al. [95]. Kirk et al. [104] reported 27 parasitoid species mainly of the hymenopteran genera *Diadegma*, *Cotesia* and *Oomyzus* on 115 populations of *P. xylostella* collected in 32 countries. The majority of these parasitoid species are known to come from Europe where *P. xylostella* is believed by some to have originated.

In different geographical areas of the world, various parasitoid species are responsible for suppressing *P. xylostella* populations. For instance, *Diadegma* spp. and *Diadromus* spp. predominate in Europe [7], New Zealand [123] and South Africa [124]. *Diadegma semicaudum* (Helle’n), *Diadegma rapi* (Cameron) and *Diadromus collaris* (Grav.) are collectively responsible for 93% parasitism in Victoria, Australia [120]. *Diadegma semicaudum* has been reported to keep the *P. xylostella* population below economic threshold levels in certain areas of Europe, Africa, Asia [1], Malaysia, Taiwan, Philippines, Indonesia, Thailand, Zambia, New Zealand and Australia [125,96]. The most abundant parasitoids in east Africa are *Diadegma mollipla* (Holmgren) and *Oomyzus sokolowskii* (Kurdjumov) [126]. In Ethiopia, *Diadegma* spp. and *Cotesia plutellae* (Kurdj.) are key parasitoid species [39]. *Cotesia plutellae* and *O. sokolowskii* are considered the most promising biological control agents in China [113]. In the relatively hotter lowlands of many Asia-Pacific regions, *C. plutellae* is the dominant and most effective larval parasitoid of *P. xylostella* [1]. In the Eastern Cape (South Africa), four species viz., *D. mollipla*, *C. plutellae*, *D. collaris* and *O. sokolowskii*, are recorded as main parasitoids of *P. xylostella* [127]. Similarly, seven species are observed in Brasilia but only...
two species, *D. leonitiniae* (Brethe’s) and *Apanteles piceotrichosus* (Blanchard) are dominant [128]. In general, few parasitoid species are responsible for a high level of parasitism in an area. Lim [125] noted that the ability to function as biological control agents varies between species, and usually depends on their direct relationships with their host, environment and interspecific interactions.

### Table 2. Example of some common natural enemies of *Plutella xylostella*

<table>
<thead>
<tr>
<th>Natural Enemies</th>
<th>Host stage attacked</th>
<th>Ref. No</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>A-Parasitoid</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trichogrammatoidea bactrae</em> (Nagaraja)</td>
<td>Egg</td>
<td>[94]</td>
</tr>
<tr>
<td><em>Trichogramma pretiosum</em> (Riley)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Trichogrammatidae</em> spp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Diadegma insulare</em> (Cresson)</td>
<td>Larva</td>
<td>[95]</td>
</tr>
<tr>
<td><em>D. fenestrale</em> (Holmgren)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. molipla</em> (Holmgren)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. varuna</em> Gupta</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. leonitiniae</em> (Bréthes)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. rapi</em> (Cameron)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>D. semiclausum</em> (Hellén)</td>
<td>Larva</td>
<td>[96]</td>
</tr>
<tr>
<td><em>Apanteles ippeus</em> (Nixon)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cotesia plutellae</em> (Kurdjumov)</td>
<td>Larva</td>
<td>[97]</td>
</tr>
<tr>
<td><em>Microplitis plutellae</em> Muesbeck</td>
<td>Larva</td>
<td>[25]</td>
</tr>
<tr>
<td><em>Oomyzus sokolowskii</em> (Kurdjumov)</td>
<td>Larva-Pupa</td>
<td>[98]</td>
</tr>
<tr>
<td><em>Tatrasichus ayyari</em> (Rohwen)</td>
<td>Pupa</td>
<td>[99]</td>
</tr>
<tr>
<td><em>Brachymeria phya</em> (Walker)</td>
<td>Pupa</td>
<td>[96]</td>
</tr>
<tr>
<td><em>Diadromus collaris</em> (Gravenhorst)</td>
<td>Pre-pupa, Pupa</td>
<td></td>
</tr>
<tr>
<td><em>D. subtilicornis</em> (Gravenhorst)</td>
<td>Pre-pupa, Pupa</td>
<td>[25]</td>
</tr>
<tr>
<td><em>Pteromalus</em> spp.</td>
<td>Pupa</td>
<td>[100]</td>
</tr>
<tr>
<td><strong>B-Pathogen</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bacillus thuringiensis</em> Berliner</td>
<td>Larva</td>
<td>[101]</td>
</tr>
<tr>
<td><em>Zoophthora radicans</em> Batko,</td>
<td>Larva</td>
<td>[102]</td>
</tr>
<tr>
<td><em>Beauveria bassiana</em> (Balsamo) Vuillemin,</td>
<td>Larva-Pupa</td>
<td>[103, 104]</td>
</tr>
<tr>
<td><em>Metarhizium anisopliae</em> (Metsch.) Sorokin</td>
<td>Pupa</td>
<td></td>
</tr>
<tr>
<td><em>Paecilomyces farinosus</em> (Holm ex Gray)</td>
<td>Larva-Pupa</td>
<td></td>
</tr>
<tr>
<td><em>Nomuraea rileyi</em> (Farlow) Sampson</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Fusarium</em> spp.</td>
<td></td>
<td></td>
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<tr>
<td><em>Pandora</em> spp.</td>
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<td></td>
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<tr>
<td><em>Erynia</em> spp.</td>
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<td></td>
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<tr>
<td><em>Conidiobolus</em> spp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Scopulariopsis</em> spp.</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Granuloviruses</em> (GVs)</td>
<td>Larva</td>
<td>[105,106]</td>
</tr>
<tr>
<td><em>Nucleopolyhedrovirus</em> NPVs</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cytopivirus</em> CPVs</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Steinernema carpocapsae</em> (Weiser)</td>
<td>Larva</td>
<td>[107]</td>
</tr>
<tr>
<td><em>Heterorhabditis</em> sp.</td>
<td></td>
<td>[108]</td>
</tr>
<tr>
<td><em>Nosema bombycis</em> (Negali)</td>
<td></td>
<td>[109]</td>
</tr>
<tr>
<td><em>Vairimorpha</em> sp.</td>
<td></td>
<td>[110]</td>
</tr>
<tr>
<td><strong>C-Predator</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lycosids</em></td>
<td>Mostly Larva</td>
<td>[111,112]</td>
</tr>
<tr>
<td><em>Linyphids</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Syrphids</em></td>
<td>Egg, Larva</td>
<td>[112]</td>
</tr>
<tr>
<td><em>Staphylinids</em></td>
<td></td>
<td></td>
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<tr>
<td><em>Reduviids</em></td>
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<td></td>
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<tr>
<td><em>Nabids</em></td>
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<td></td>
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<tr>
<td><em>Carabids</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Coccinella</em> spp.</td>
<td>Egg-Larva</td>
<td>[113]</td>
</tr>
</tbody>
</table>
Among parasitoids that attack *P. xylostella*, only a few solitary larval parasitoid species in the Ichneumonid genus *Diadegma*, solitary pupal parasitoids in the genus *Diadromus*, solitary larval parasitoids in the braconid genera *Microplitis* and *Cotesia*, and the gregarious larval-pupal parasitoid in the eulophid genus *Oomyzus* are considered to be predominant [2].

6.1 Evolutionary Ecology of *Diadegma insulare*: A Key Larval Parasitoid of *P. xylostella*

The genus *Diadegma* Froster (Hymenoptera: Ichneumonidae: Campopleginae) represents a large group of koinobiont endoparasitoids of Lepidoptera with 201 species known to occur worldwide [129]. Several *Diadegma* species, such as *D. fenestrale* (Holmgren), *D. insulare* (Cresson), *D. leontiniae*, *D. molipla*, *D. rapi*, and *D. semiclausum*, are reported to attack *P. xylostella* [95,130]. There is a wide geographical variation in predominance of *Diadegma* species, with the majority (131 species) having a Palearctic and a few (33 species) having a Nearctic distribution [1].

*Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae: Campopleginae) is native to the Neotropics [95], and is a key parasitoid of *P. xylostella* in North America [131,132,133]. *Diadegma insulare* is also one of three major hymenopterans parasitoids of *P. xylostella* in Canada; the other two include a larval parasitoid *Microplitis plutellae* (Mues.), and a prepupal and pupal parasitoid, *Diadromus subtilicornis* (Grav.) [12,25,27]. The *D. insulare* origin in western Canada is unknown, but it likely migrates northward in spring along with its hosts rather than overwintering [134].

*Diadegma insulare*, a solitary endoparasitoid, feeds within the *P. xylostella* larva [12]. The number of generations per year corresponds to the number of generations of its host as one host larva supports only one parasitoid larva [135]. It can parasitize all four larval instars of *P. xylostella* [136]. The specific larval instars parasitized by *D. insulare* can affect the sex ratio of offspring. More males than females are produced when second instars are parasitized, but when third and fourth instars are parasitized the progeny comprise a greater proportion of females than males [137,138]. The parasitoid emerges as a mature larva from the pre-pupa of its host, and spins its own cocoon within that of the host where it can easily be distinguished [139,136]. On average, adult *D. insulare* live for 26 days and lay 814 eggs per female at 23°C [140]. Adults require a continuous nectar source for survival and longevity and as a result they prefer habitats with abundant food sources [141]; such habitats appear to enhance *D. insulare* fecundity and longevity [142]. For instance, sites with flowering plants like alyssum, Lobularia maritima (L.) Desv. (Brassicaceae) [143], or with borders of flowering buckwheat, Fagopyrum esculentum Moench (Polygonaceae) in cabbage fields enhance *D. insulare* populations [142]. The number of *P. xylostella* larvae parasitized by a single *D. insulare* female may vary from zero to 150, depending upon the food source [144]. Unlike its host, *D. insulare* developmental biology has not been studied extensively. However, in a recent study longer development time was recorded at constant and lower temperatures. High pupal mortality of *D. insulare* was also observed at higher temperature, and this may explain the greater effectiveness of this parasitoid in cooler regions [16].

Resource variation and their spatiotemporal distribution has a significant impact on the physiology of herbivore pests, which in turn mediates pest-parasitoid interactions, as well as the effectiveness, survival, development, size, longevity, and fecundity of parasitoids [145,146,147]. The density and distribution of a parasitoid’s population is correlated with the density and distribution of its herbivore’s host plant. For instance, field populations of *D. insulare* are often clustered, with distributions that correlate with their herbivore host populations and host plants having high sulphur content [148,19,36].

Parasitoid life history traits are influenced by the choice made by its herbivore host via mediated host plant quality [149,150]. The nutritional quality of plants consumed by the herbivore host of *D. insulare* affects the sex ratio of the parasitoid; more female parasitoids emerged from *P. xylostella* larvae on well-fertilized plants [137]. Similarly, the performance of *D. insulare* is improved when *P. xylostella* larvae are reared on highly fertilized plants [92,36]. Survival, parasitism, and development time of *D. insulare* varied considerably among the plant genotypes utilized by its *P. xylostella* host [41]. Percentage parasitism of *D. insulare* is higher and development time shorter on cultivated crucifers than on wild species [45]. Sarfraz et al. [41] reported that *S. alba* supports high *P. xylostella* parasitism levels and parasitoid survival, and
relatively rapid parasitoid development as compared to *B. napus* L. cv. Q2.

The role of plants in the ecology and biology of parasitoids is clearly evident in their effect of parasitoid host selection. Plant-associated visual cues are important in the process of host location by parasitoids [151]. Similarly, plants respond to herbivore damage by emitting complex mixtures of volatile compounds that attract natural enemies. Many field experiments suggested that parasitoids respond directly to both herbivores and their host plant volatile cues [152,153]. In these studies, *D. insulare* was assumed to be attracted to plant tissue damaged by *P. xylostella* larvae [133].

When the herbivore host of a parasitoid feeds on a narrow range of plants, with similarities in secondary chemistry, better discrimination for the parasitoid is possible. However, the choice to recognize a broad range of plants in many families as harbouring potential host larvae may reduce the ability of parasitoids to recognize and respond to qualitative differences among plants [152].

Different efficiencies of parasitoids are often correlated with the level of specificity of both host and parasitoids [150]. Host-specialist parasitoids are supposed to have greater efficiencies in searching hosts and have specialized adaptations to overcome host defense than generalist species that display relatively plastic foraging behaviours [154]. For instance, the host searching and parasitizing strategies employed by the specialist *D. semiclasum* are better adapted than those strategies employed by generalist parasitoids [154]. Moreover, *D. insulare* is an efficient host searcher and shows very flexible behavior by sitting motionless near the silken thread, waiting for the suspended *P. xylostella* larva to climb up and then attacking it again. Sometimes, it may follow down the suspended larva by its silken thread and attempt quickly to parasitize it [2].

Many studies indicate that parasitoids often experience high levels of mortality. Therefore, selection of hosts should favor developmental strategies that maximize progeny survival. It is also proposed that rapid development time at the cost of size may be preferred in parasitoids whose hosts confront high risks of predation [155,156]. This indirectly suggests that parasitoids have evolved under selection pressures exerted by risks of predation [157].

The mortality risks appear to be high for koinobionts (that cause the host temporary or nonlethal paralysis), through hyperparasitism and multiparasitism [158,159,160] as they are competitively inferior to idiobionts (cause permanent paralysis or death) [161,162]. Nonetheless, *D. insulare* has a significant ability to avoid multiparasitism and super parasitism [140].

7. CONCLUSION

In conclusion, understanding the evolutionary ecology of a pest, its host plants, and its parasitoid and their tritrophic interactions is very complex and variable. It requires detailed studies of pest and parasitoid behaviors, their life histories, factors affecting their development, and pest-parasitoid interactions in various agro ecosystems. For any effective management strategy whether it involves habitat management, biological control or integration of different control measures, up to date knowledge of pest and parasitoid behavior, population dynamics and also cautious evolutionary interpretation of tritrophic relationship in a particular agro ecosystem is crucial.

COMPETING INTERESTS

Authors have declared that no competing interests exist.

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