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REVIEW ARTICLE

Landscape ecology and expanding range of biocontrol agent taxa enhance prospects for diamondback moth management. A review

Geoff M. Gurr[1,2,3,4] · Olivia L. Reynolds[2,4,5] · Anne C. Johnson[4] · Nicolas Desneux[6] · Myron P. Zalucki[7] · Michael J. Furlong[7] · Zhenyu Li[8] · Komivi S. Akutse[1,2,3,10] · Junhui Chen[1,2,3] · Xiwu Gao[9] · Minsheng You[1,2,3]

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Abstract

Diamondback moth (*Plutella xylostella*) is a globally significant pest of Brassicaceae crops that has attracted enormous research investment. It is typical of many agricultural pests, with insecticides remaining the most common method of control, despite frequent cases of resistance in pest populations and the potential for other management options such as natural enemies to provide suppression. Here we review scope to make better use of neglected natural enemy taxa and integrate recent work on landscape ecology to identify opportunities for more effective pest suppression. Our main findings are as follows: (1) relatively neglected taxa of natural enemies, especially predators and entomopathogens, are now attracting growing levels of research interest, although parasitoids remain most frequently used and researched; (2) knowledge of the spatio-temporal dynamics of populations at the landscape scale have advanced rapidly in the last decade; (3) ecological insights open new possibilities for exploiting spatial heterogeneity at scales larger than individual fields and even farms that influence pests and their natural enemies; (4) there is evidence for landscapes that selectively favor particular guilds and this knowledge could be developed to favor targeted natural enemies over pests in focal crops; and (5) landscape-scale effects can even over-ride field-scale management practices. The significance of these advances is that future management of diamondback moth and similar pests will benefit from a move away from reliance on the use of particular species of biological control agents, especially exotic parasitoids, and strategies that depend on use of broad-spectrum insecticides. Together with this move, we call for greater use of area-wide management that exploits the potential of landscapes to promote diverse assemblages of natural enemy species.

Keywords *Plutella xylostella* · Conservation biological control · Habitat management · Donor habitat · Landscape connectivity · Area-wide management · *Bacillus thuringiensis* · Entomopathogen · Predator · Parasitoid

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✉ Minsheng You
msyou@iae.fjau.edu.cn

[1] State Key Laboratory of Ecological Pest Control for Fujian and Taiwan Crops, Institute of Applied Ecology, Fujian Agriculture and Forestry University, Fuzhou 350002, China

[2] Joint International Research Laboratory of Ecological Pest Control, Ministry of Education, Fuzhou 350002, China

[3] Fujian-Taiwan Joint Innovation Centre for Ecological Control of Crop Pests, Fujian Agriculture and Forestry University, Fuzhou 350002, China

[4] Graham Centre (an alliance between NSW Department of Primary Industries and Charles Sturt University), Wagga Wagga, New South Wales 2650, Australia

[5] NSW Department of Primary Industries, Elizabeth Macarthur Agricultural Institute, Menangle, New South Wales 2568, Australia

[6] INRA (French National Institute for Agricultural Research), CNRS, UMR 1355-7254 Institute Sophia Agrobiotech, Université Côte d'Azur, 06903 Sophia-Antipolis, France

[7] School of Biological Sciences, The University of Queensland, St Lucia 4072, Australia

[8] Institute of Plant Protection, Guangdong Academy of Agricultural Sciences and Guangdong Provincial Key Laboratory of High Technology for Plant Protection, Guangzhou 510640, China

[9] Department of Entomology, China Agricultural University, Beijing 100193, China

[10] International Centre of Insect Physiology and Ecology, P.O. Box 30772-00100 Nairobi, Kenya

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1 Introduction

The diamondback moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), is the most destructive insect pest of *Brassica* spp. crops worldwide (Furlong et al. 2013; Li et al. 2016a) and is estimated to cost the world economy US$4–5 billion a year (Zalucki et al. 2012). Its pest status in brassica vegetable crops increased dramatically following the widespread adoption of broad-spectrum insecticides (Ankersmit 1953) and the absence of effective natural enemies across several areas of its range (Talekar and Shelton 1993). More recently, it has become a major pest of the oil-seed crop, canola (*Brassica napus* L.), the production area of which has increased markedly in industrialized countries over recent decades (Furlong et al. 2008a). The importance of the diamondback moth as a global pest of brassica crops is reflected in publication metrics, with Web of Science holding over 3800 papers on this pest. More than 125 new papers have been added each year over the last decade. Critical reviews of this large volume of literature are, therefore, important to synthesize emerging knowledge of diamondback moth and integrate this with advances in related fields. Landmark reviews of this pest were published by Talekar and Shelton (1993) and Furlong et al. (2013), with reviews on biological control agents (Sarfraz et al. 2007), conservation biological control (Liu et al. 2014), multitrophic interactions (Verkerk and Wright 1996), and the ecology and management in the USA (Philips et al. 2014) and China (Li et al. 2016a) following suit. Each of these reviews contained information on the biology and use of various natural enemies.

Among taxa that attack diamondback moth, parasitoids have historically attracted the most research. Toxins derived from the entomopathogenic bacterium *Bacillus thuringiensis* (*Bt*) have been widely used against this pest but here we will not consider *Bt* to be a biological control agent. Although formulated *Bt* products may contain bacterial spores as well as crystal toxins (Crickmore 2006), and the spores enhance toxicity (Burges et al. 1976), they are more properly considered as insecticides, albeit non-synthetic. Here we widen attention by considering other biological control agent taxa, such as predators and various entomopathogens, to assess whether these are becoming better represented in the literature and the extent that they could complement parasitoids in future diamondback moth management approaches.

The second distinct gap that we explore is the prospect to use conservation biological control approaches that more effectively address the unmet need for control of diamondback moth using non-chemical, ecologically based approaches that enable sustainable management. Specifically, we explore the potential of habitat management approaches that promote natural enemy impact on pest densities (Gurr et al. 2017; Landis et al. 2000). These approaches tend to use diversification of the cropping system to provide resources such as source habitat, alternative prey, and plant foods to natural enemies. Resources for natural enemies are often lacking in brassica crop systems but can be provided by interventions that reintroduce aspects of diversity found in traditional agricultural systems (Fig. 1). Importantly, habitat management often operates at a spatial scale larger than individual fields and can extend to the landscape several kilometers from a focal field (Perović et al. 2010; Schmidt et al. 2005; Tscharntke et al. 2012). To date, landscape-scale research has been little considered in relation to biological control of diamondback moth, despite the strong dispersal capacity of the adults of this species (Furlong et al. 2013) and even their parasitoids (Dosdall et al. 2004) as well as the significance of this movement to insecticide resistance management in diamondback moth (Talekar and Shelton 1993; Sarfraz and Keddie 2005; Tabashnik et al. 1987). Accordingly, we assess the potential for exploiting advances in knowledge of spatial ecology to provide better biological control of this pest.

2 The global context

Arthropod pests continue to cause extensive crop loss and this drives the use of large amounts of synthetic insecticides (Bradshaw et al. 2016). Although biological control of pests has been actively pursued for over a century and the last decade has seen an acceleration of research efforts to better understand the biology and ecology of natural enemies, insecticides remain the mainstay of pest management in many crop systems (Adamson et al. 2014). Here we focus on diamondback moth as an example of a serious, globally distributed pest and consider how biological control and related cultural practices, especially at scales larger than individual fields, might be used more effectively. Diamondback moth is, however, not

Fig. 1 Contrasting brassica vegetable production systems. Top: monoculture with bare ground, no weeds or non-crop vegetation, and amid urban infrastructure (Fujian Province, China). Bottom: polyculture with weeds, adjacent non-crop perennial vegetation, and little bare ground (Galapagos Islands, Ecuador). These factors can strongly influence the diversity of natural enemies and overall strength of biological control. (Photos: GM Gurr)

dissimilar to many other serious, cosmopolitan pests of crops other than brassicas such as *Helicoverpa* spp. (Downes et al. 2017), *Bemisia* whiteflies (Perring 2001; Brown et al. 1995), and *Nilaparvata lugens* (Bentur and Viraktamath 2008), in which vagility and propensity for developing insecticide resistance demand improved management strategies. Accordingly, notwithstanding the obvious need for pest management systems to be tuned to the specific ecology of a given pest, the present review of diamondback moth has wider relevance, providing insights and potentially fruitful leads for other pest species.

3 Diamondback moth movement and implications for biological control

Although movement of diamondback moth is typically trivial when host plants are available (Mo et al. 2003), the adult has the capacity to migrate large distances and rapidly colonize suitable hosts (Chapman et al. 2002). Recent research in China has demonstrated that annual northerly migrations can result in the movement of insecticide-resistant populations over thousands of kilometers (Wei et al. 2013; Li et al. 2016a). In North America, meteorological data provides strong evidence that the diamondback moth populations invading Canadian canola crops in summer can originate from vegetable crops as far away as northern Mexico and that the > 3000-km journey can be made over a matter of days (Dosdall et al. 2004). Similarly, there is indirect evidence that the diamondback moth adults reaching vegetable production areas in Tasmania in late spring/early summer originate from canola crops on mainland Australia (Schellhorn et al. 2008). The scale, intensity, and timing of these migrations may contribute to population increases and pest status (Li et al. 2016b).

In addition to multiplication within host crops, diamondback moth can persist and build up on brassicaceous weeds and native plant species that might be located great distances away from a focal crop which is the eventual site of economic impact (Niu et al. 2014). The diamondback moth populations of non-crop host plants can extend over vast areas (Furlong et al. 2008b) and managing them is difficult, especially in native brassica habitats. However, local/regional weather conditions such as temperatures and precipitation are strong drivers of diamondback moth population growth (Li et al. 2016b) and targeted monitoring of potential source populations when conditions for diamondback moth population growth are likely to be favorable (Zalucki and Furlong 2011) could provide useful management information. The development of bioclimatic simulation models linked to wind trajectory models has been advocated as an aid to forecasting possible diamondback moth outbreaks in vegetable and canola crops (Furlong et al. 2008b; Zalucki and Furlong 2011). Such an approach could predict the movement of diamondback moth into crop growing regions where local landscape management can be configured to ensure that endemic natural enemies are conserved.

Diamondback moth is a typical r-selected species; its high vagility and relatively high intrinsic rates of increase enable it to cope with seasonal unavailability of host plants in a given area and move to locate fresh resources. Associated with this dispersal capacity is the ability to evade natural enemies, as diamondback moth can leave habitats where it is under heavy attack, with enemies typically, but not always (Dosdall et al. 2004), lacking comparable powers of dispersal. This can result in the herbivore multiplying rapidly in new areas of (relatively) enemy-scarce habitat, especially as it moves from uncultivated to cultivated brassica host plants (Fox and Eisenbach 1992). This theme will be revisited below because a major challenge in achieving more consistently effective biological control is to facilitate two groups of ecological phenomena. The first of these is to maximize the persistence of diverse natural enemy assemblages in regions where brassica production takes place (meaning the non-crop habitat patches as well as the brassica fields), thereby increasing the likelihood that they might colonize nearby brassica crops. The second is the facilitation of rapid population increases of natural enemies on arrival in brassica habitat so that the establishment and maintenance of biological control is not impeded by factors such as insecticide use or the lack of complementary resources such as nectar.

4 Biological control and historical trends among agent types

There is considerable evidence that in brassica agroecosystems, diamondback moth is a secondary or induced pest and that in the absence of broad-spectrum insecticides, natural enemies (Furlong et al. 2013) and crop management (Li et al. 2016b) can suppress populations so that they can be effectively managed by more tactical interventions with selective compounds (Furlong et al. 2008a; Furlong et al. 2004b; Zalucki et al. 2009). The research literature on natural enemies of diamondback moth has grown dramatically over the last quarter century, from four papers published during 1992 to more than 50 during 2016 (Fig. 2). There was a marked escalation of the annual numbers of papers in 2004, due, in part, to the publication of a series of biological control papers from the fourth international workshop on diamondback moth. Shelton (2004) noted the changed emphasis from the previous three workshops in that series with an increasing trend towards research into biological control and IPM. However, in the 2006 and 2011 workshops, this trend was reversed reflecting increased research into the management of resistance to the suite of insecticides that had been introduced in the previous decade. Such inconsistency characterizes diamondback moth research over the past 40 years (Furlong et al. 2013).

As Shelton (2004) predicted, following the rise in the number of crucifer monocultures, year-round production and the consequent control failures of diamondback moth, the need for “more sustainable and reliable strategies” would result in increasing efforts to understand the mechanisms of biological control and IPM strategies. As diamondback moth developed resistance to an increasing number of insecticides, various resistance management programs were proposed that included the judicious use of insecticides, area-wide rotation of insecticide groups with complimentary agronomic practices, and biological control (Sarfraz and Keddie 2005; Zhao et al. 2006; Talekar and Shelton 1993).

Partitioning research outputs according to the taxa and guilds of biological control agents reveal marked trends. Much effort has focused on parasitoids, several of which, particularly *Diadegma semiclausum* (Hellén) (Hymenoptera: Ichneumonidae), *Diadromus collaris* (Gravenhorst) (Hymenoptera: Ichneumonidae), and *Cotesia vestalis* (= *plutellae*) Haliday (Hymenoptera: Braconidae) have been widely introduced as classical biological agents (Sarfraz et al. 2007). Indeed, parasitoids have been the natural enemy guild that has consistently received the most research attention over the last 25 years. Searching Web of Science core collection for “parasitoid*” finds 357 papers on biological control of diamondback moth published since 1992 and at least a dozen each year over the last decade (Fig. 2). Predatory arthropods, in contrast, have received far less attention, a total of 118 papers over the same period. While the number of papers published each year on diamondback moth predators has increased to a greater extent than parasitoid-related papers, the annual number published remains low (Fig. 2). Predators can play an important role in controlling diamondback moth as shown in work in various countries including the USA (Muckenfuss et al. 1992), Australia (Furlong et al. 2004a), China (Liu et al. 2005), and North Korea (Furlong et al. 2008a), though their impact is contingent on avoiding pesticide-induced mortality of the agents. Recent work shows that diamondback moth predators, which principally attack early instars, and parasitoids which typically attack second instar and older larvae, can complement each other and that resource partitioning among these taxa can minimize intraguild predation (Furlong et al. 2014).

The relative neglect of predators in preference for parasitoids reflects the research on a small number of parasitoid species that have been introduced to multiple countries in classical biological control programs (Sarfraz et al. 2007). Although parasitoids can be promoted by local habitat management (Lu et al. 2014; Gillespie et al. 2016), there is potential for enhancement of predators by habitat management at the landscape scale (Gonçalves et al. 2017). This is because a diversity of habitat vegetation promotes continuity of availability of food, especially prey (Gurr et al. 2017). This, in turn, provides opportunities for a diversity of predator guilds to persist in a landscape that are ready to exhibit prey switching to diamondback moth when brassica crops are present in sufficient numbers as prey populations begin to increase. The theme of promoting natural enemies by habitat management is explored in detail in the following section. In contrast to the volume of papers on arthropod biological control agents, only 57 papers were published on entomopathogenic fungi and just 35 on entomopathogenic nematodes. Notably, however, the numbers of papers on these entomopathogens have increased rapidly in the last 20 years (Fig. 2).

5 Habitat management, ecological interactions, and the importance of scale

Despite the clear potential for natural enemies to impact diamondback moth populations and serve as the foundation for

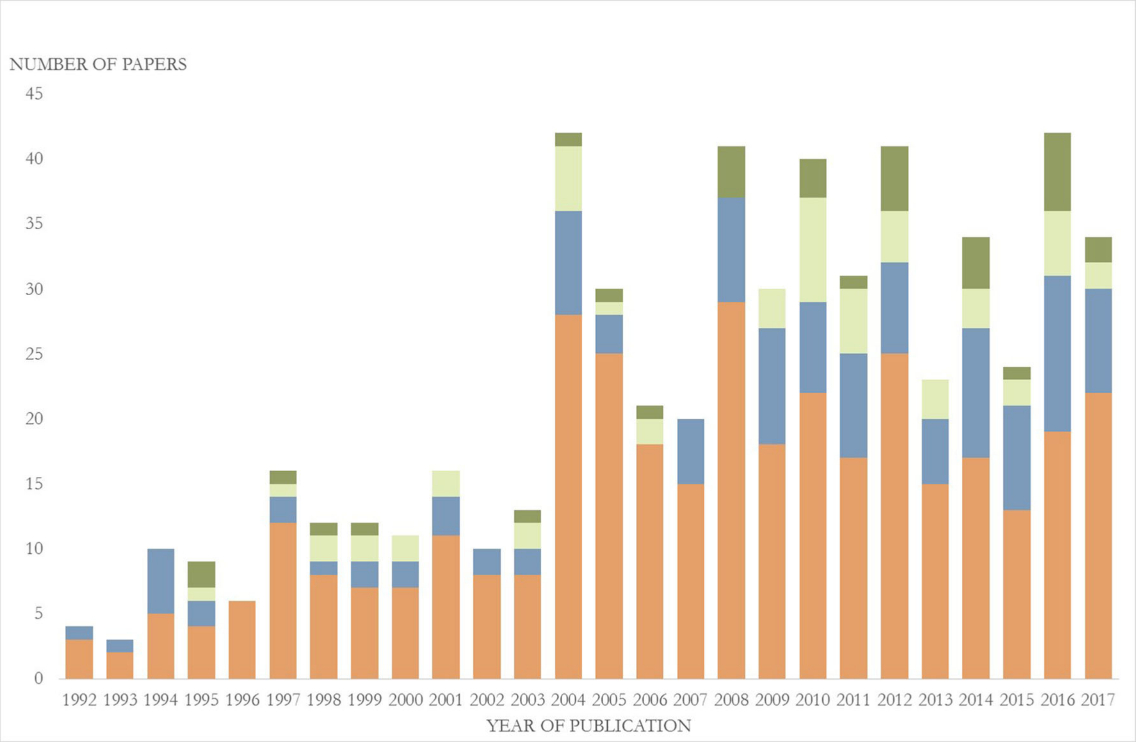

Fig. 2 Historical trend in the research effort for contrasting diamondback moth natural enemies: orange, parasitoids; blue, predators; light green, entomopathogenic fungi; dark green, entomopathogenic nematodes

integrated pest management (IPM), the level of adoption remains low (Furlong et al. 2013; Li et al. 2016a). A multiple-year regional study that quantified the effects of diamondback moth suppression by natural enemies in commercial brassica crops showed that the adoption of IPM based on the conservation of endemic natural enemies and the tactical application of selective insecticides could result in high crop yields with minimized insecticide inputs (Furlong et al. 2004b). Application of broad-spectrum insecticides caused significant disruption to the natural enemy complex; these effects persisted throughout the season and a single application of a pyrethroid or organophosphate insecticide inevitably necessitated further insecticide applications (Liu et al. 2005; Furlong et al. 2004b). Desneux et al. (2007) provide a comprehensive and broad review on acute and chronic toxicity of insecticides, as well as their sublethal effects. When broad-spectrum insecticides are used for diamondback moth management, high crop yields were possible but depended on frequent and significant application of synthetic insecticides (Furlong et al. 2004b). This is not only costly and harmful to the environment but also unsustainable, given the record of developing resistance to all insecticides deployed against this pest (Furlong et al. 2013; Li et al. 2016a; Verkerk and Wright 1997). By contrast, diamondback moth that migrated into brassica fields in North Korea were effectively managed by integrating endemic predators (Lycosidae and Carabidae) and parasitoids *C. vestalis*, *D. collaris*, and *Oomyzus sokolowskii* Kurdjumov (Eulophidae) with rational applications of *Bt* (Furlong et al. 2008a). That approach resulted in significantly improved yields compared with conventionally managed crops where frequent application of pyrethroid insecticide destroyed natural enemies, thereby promoting pest survival, resulting in extremely high densities of diamondback moth and other arthropod pests.

Local management at the farm scale can conserve endemic natural enemies, especially if *Bt* is used in place of more disruptive chemical insecticides. Accordingly, within the typically insecticide-intensive environments that brassica agroecosystems represent, elimination of chemical insecticides, especially broad-spectrum products, is a prerequisite to effective biological control. In order for biological control to operate to its maximum potential, two further aspects require attention. The first of these is the provision of key ecological resources that otherwise may limit the performance of individual natural enemies and their dynamics at population level. This approach to pest management is often referred to as conservation biological control (which generally includes avoidance of insecticide-induced natural enemy mortality) or, more narrowly, habitat management/manipulation (Landis et al. 2000; Gurr et al. 2017). A particularly well-researched category of the latter is nectar as food sources for adult parasitoids (Wäckers et al. 2006; Lu et al. 2014). The maintenance of landscape features such as effective refugia and habitat features that enhance connectivity (e.g., hedgerows) to serve as donor habitat and movement pathways for natural enemies (Perović et al. 2010; Schellhorn et al. 2008) can also be important. While a recent review has suggested that work on the significance of semi-natural habitats for biological control has tended to focus on the dynamics of the agents rather than the strength of the desired ecosystem service (Holland et al. 2017), there is a strong body of evidence that biological control in a focal crop can be heavily influenced by landscape-scale effects (Tscharntke et al. 2012). Australian studies have demonstrated, for example, that riparian vegetation, pastures composed of perennial native species, and remnant woodland close to farms can all serve as donor habitat for predators of diamondback moth. These natural enemies have been shown to move from such non-crop habitats to nearby brassica crops after spraying has reduced their numbers in the focal crop (Heimoana et al. 2017).

As is evident in the preceding section, the emphasis in habitat management of arthropod pests in general, as well as for diamondback moth in particular, is on the enhancement of impact by arthropod natural enemies through direct effects (i.e., predation and parasitism). The following two subsections aim to expand the scope of this theme by considering (i) the potential impacts of vegetation complexity on microbial natural enemies and the associated potential for habitat management by such agents and (ii) how indirect ecological interactions, i.e., those that operate via other species or are separate in time and space, may contribute to pest management.

5.1 Habitat management and entomopathogens

Entomopathogens are attracting increasing research interest for the suppression of diamondback moth (Fig. 2) as well as other key agricultural pests. Diamondback moth is attacked by a range of fungi, nematodes, bacteria, and viruses in the field. Research efforts, especially for fungi and nematodes, have focused on augmentation strategies to improve their impact (Stavely et al. 2004). The entomophthoralean fungi, *Zoophthora radicans* (Brefeld) Batko, *Erynia* spp. (Nowak. ex A. Batko) Remaud. & Hennebert., and *Pandora blunckii* (G. Lakon ex G. Zimm.) Humber can cause natural epizootics in diamondback moth populations, and methods have been developed for their dissemination (Furlong et al. 1995; Vandenberg et al. 1998; Vickers et al. 2004; Pell et al. 2001; Yeo et al. 2001). Diamondback moth is also susceptible to several species of Hyphomycetes including *Beauveria bassiana* (Bals.-Criv.) Vuill., *Isaria fumosorosea* (= *Paecilomyces fumosoroseus*) Wize, *I. sinclairii* (Berk.) Lloyd, *Metarhizium anisopliae* (Metchnikoff) Sorokin, *Nomuraea rileyi* (Farlow) Samson, and *Lecanicillium muscarium* R. Zare & W. Gams (Wilding 1986; Kirk et al. 2004; Cherry et al. 2004; Duarte et al. 2016) but these are less frequently associated with diamondback moth under natural conditions. Significant work has been done on the biology and utility of some of these fungi (Furlong and Pell 1997, 2001; Sarfraz et al. 2007). For example, *B. bassiana* formulated as Mycotrol® suppressed diamondback moth populations on seedlings grown in a nursery and on brassica crops in open fields in the USA (Vandenberg et al. 1998). *Beauveria bassiana* synergistically controlled three lepidopteran pests on brassicas when integrated with *Bt* (Vandenberg et al. 1999) and reduced the number of applications of *Bt*, so contributing to resistance management (Stavely et al. 2004).

Among the 24 identified entomopathogenic nematodes families, Steinernematidae and Heterorhabditidae in the order Rhabditida have been most widely researched as biological control agents. *Steinernema* sp. and *Heterorhabditis indicus* Poinar, Karunakar & David are reportedly effective against diamondback moth in Malaysia (Mason and Wright 1997) and studies in Pakistan (Ratnasinghe and Hague 1998) and Germany (Schroer and Ehlers 2005) report the effectiveness of *S. carpocapsae* (Weiser). Although ultra-low-volume applications of *Steinernema* sp. and *Heterorhabditis* sp. have been found effective in small-scale trials (Mason et al. 1999) , application over larger open fields is constrained by susceptibility of these agents to abiotic factors especially exposure to UV radiation and low humidity (Grzywacz et al. 2010), reflecting that they naturally occur in soil. The spray equipment for foliar application of entomopathogenic nematodes is only slightly modified from chemical spray equipment. The optimal equipment and formulation requirements for maximizing coverage, placement, and timing to improve efficiency of foliar application and reduce restraints of abiotic factors have not received great attention (Wright et al. 2005).

Diamondback moth is susceptible to two types of lepidopteran-specific viruses, Nucleopolyhedroviruses (NPV; *Alphabaculovirus* spp.) and Granuloviruses (GV; *Betabaculovirus* spp.) and strains of both are commercially available (Sun and Peng 2007; Yang et al. 2012). In experiments in Kenya, PlxyGV controlled diamondback moth populations on kale more effectively than the available chemical insecticides (Grzywacz et al. 2004).

Typically, entomopathogens have been applied by conventional application of a formulated product. To maximize the efficacy of these agents, environmental factors need to be considered and habitat management provides a mechanism whereby the requisite microclimates might be provided. Most arthropod species, including diamondback moth, experience their habitat at spatial scales beyond the scale of an individual field, with movement between crops and between crop and non-crop vegetation (Perović et al. 2010; Paredes et al. 2015; Tscharntke and Brandl 2004; Saqib et al. 2017). Accordingly, habitat manipulation may promote entomopathogen survival and impact in a given system by providing shade from UV and moderated humidity and temperature (Fernández-Bravo et al. 2016), either within the focal crop or in nearby areas from which infected insects may move to the crop. This offers scope to address adverse effects on entomopathogen distribution, persistence, and infection (Jaronski 2010). For example, for entomopathogenic fungi, temperature (Roberts and Campbell 1977), moisture (Inglis et al. 2001), and UV radiation (Klein 1978; Blumthaler et al. 1994; Inglis et al. 2001; Gao and Garcia-Pichel 2011; Braga et al. 2001) affect the rates of key infection processes (e.g., germination of conidia, hyphal growth) as well as the production of conidia from mycosed cadavers.

Realizing the potential of entomopathogens for the management of insect pests demands an understanding of how vegetation structure affects entomopathogen communities, flux of inocula into specific host or crops species, and how pathogens regulate insect pest populations in relation to habitat fragmentation (Pell et al. 2010). Work in this area is in its infancy compared with the larger research effort historically directed at habitat management for arthropod natural enemies (Gurr et al. 2017; Landis et al. 2000) but the limited available literature on entomopathogen-landscape interactions is encouraging. For instance, a reservoir of entomopathogenic fungi in aphids of non-crop habitats may result in higher infection rates of aphids in crops when insects spillover between these habitats (Ekesi et al. 2005). Entomopathogens can persist in the soil in the absence of hosts and this opens other potentially useful strategies. Fungi such as *B. bassiana* and *M. anisopliae* are commonly found in both cultivated and undisturbed soils, although their distribution appears to be linked to habitat (Bidochka et al. 2001; Keller et al. 2003; Meyling and Eilenberg 2006; Meyling et al. 2009), and their populations in soil are highly influenced by agricultural practices (Meyling and Eilenberg 2007; Jaronski 2010; Jaronski 2007; Hummel et al. 2002). Clearly, refuge areas where soil populations are free of adverse effects from tillage and agrochemicals may help landscape-scale persistence and density and allow recolonization of adjacent arable fields (Schneider et al. 2012). Permanent grassland, forest margins, and field margins as well as hedgerows have been suggested as refuges for entomopathogenic fungi (Meyling and Eilenberg 2007; Pell et al. 2010). The suitability of these habitats can be enhanced by specific seeding and mowing schemes (Marshall 2002; Fuxa 1998; Lacey et al. 2001; Meyling and Eilenberg 2007; Shah and Pell 2003). A specific illustration of this effect comes from Swiss work with some *Metarhizium* species that were found to be present at higher densities in low-input permanent grassland and improved field margins (Schneider et al. 2012). Similarly, in a comparative study entomopathogenic fungi occurrence in the soil of mid-field woodlots and cultivated fields in a conventional and organic system, soil from the woodlots was characterized by a richer species composition of entomopathogenic fungi (Tkaczuk et al. 2014; Tkaczuk et al. 2012).

A key consideration is how entomopathogens in the soil may reach diamondback moth on the crop plant. One potential mechanism is that many entomopathogenic fungi can grow endophytically within plants as well as being present in the soil. Both *B. bassiana* and *T. harzianum* can establish in cabbage host plants. *B. bassiana* growing endophytically in cabbage retarded growth and development of larvae and reduced oviposition by diamondback moth (Zhang 2014). Larvae feeding on *B. bassiana*-inoculated plants exhibited slower development and a lower body weight and this was reflected in adult female choice, laying significantly more eggs on control plants compared to the endophyte-infected plants. Similar effects were reported by Raps and Vidal (1998) when exposing diamondback moth to cabbage inoculated with an endophytic strain of *Sarocladium strictum* (W. Gams) Summerb. The disturbance levels of many brassica production systems are likely to reduce the continuity of endophyte-infested crop plants but areas of non-crop vegetation that include endophyte host plants could fill this temporal gap.

Vegetation structure can also affect the field persistence and efficacy of entomopathogenic nematodes. To assess the effects of landscape types on the efficacy and population densities of entomopathogenic nematodes, Lawrence et al. (2006) conducted a series of investigations across four habitats (cultivated areas, grassy banks adjacent to cultivated areas, undisturbed shrub lands and forests) across the landscape of a vegetable production area in Ohio, USA. Entomopathogenic nematodes, *Heterorhabditis bacteriophora* Poinar and *Steinernema feltiae* (Filipjev), were detected only along grassy banks adjacent to the cultivated areas, an effect thought to be determined by soil moisture. More generally, a better understanding of nematode population dynamics in agricultural landscapes appears to be crucial for designing strategies to increase their occurrence, persistence, and effectiveness as biological control agents (Campbell et al. 1995; Campbell et al. 1998; Efron et al. 2001; Glazer et al. 1996; Lawrence et al. 2006).

5.2 Habitat management and indirect ecological interactions

As for other pests, much of the research on diamondback moth management has been conducted in the context of the local scale with the focus on an individual crop field or farm (Furlong et al. 2013). However, increased plant, microbe, and invertebrate diversity at farm and landscape scales promotes complex interactions among species, including indirect ones. Such interactions, although much less studied than more obvious direct interactions (Godfray 2011; Jervis and Kidd 1996; Wootton 1994), are actually major drivers in communities (Chailleux et al. 2014). By contrast to direct interactions, e.g., predation and parasitism, which are well characterized in many agroecosystems, indirect interactions have received much less attention, notably their possible impact on major ecosystem services in agroecosystems; this applies in the case of studies on interactions linked to the diamondback moth.

Unlike direct ones, indirect interactions occur between species that can be separated in time and/or space and they require (at minimum) one additional mediating species (Holt 1977; Wootton 1994). For example, herbivore species that do not directly interact can negatively affect each other through interactions with a shared host plant (Mouttet et al. 2011; Mouttet et al. 2013) and/or natural enemy(ies) (Chailleux et al. 2014). Such indirect interactions are not well studied for diamondback moth but are likely to be significant. For example, the aphid *B. brassicae* as well as whiteflies can modulate attractiveness of diamondback moth-infested plants for the parasitoid *D. semiclausum* through changes in the synomones emitted by infested plants (Zhang et al. 2013; Li et al. 2017), thus affecting the risk of parasitism of diamondback moth. Crop type can also affect levels of parasitism, for example, parasitism of diamondback moth by *D. semiclausum* was higher in *B. oleracea* var. c*apitata* crops than in *B. rapa* var. *Pekinensis*. (Verkerk and Wright 1997). In addition, plants pre-infested by *Pieris* spp. were less attractive to diamondback moth (Poelman et al. 2011). Diamondback moth also exhibited plant-mediated indirect interactions with *Acremonium alternatum* such that plants infested by this fungus prior to the arrival of the pest led to increased larval mortality and reduced growth rate (Raps and Vidal 1998). Plant volatiles from non-host species have also been investigated for their effects on diamondback moth sex pheromones with the aim of using plants for mating disruption (Wang et al. 2016; Philips et al. 2014).

Indirect effects likely take place in any community of three or more interacting species (Holt and Lawton 1994) and could have important impacts on crop yields (Wielgoss et al. 2012). They may represent a key mechanism in determining the strength of food web interactions in communities inhabiting agricultural landscapes (Barbosa et al. 1991), generating both short-term effects on species abundance and long-term effects on population dynamics (Wootton 1994; Abrams and Matsuda 1996; Tack et al. 2011). Thus, there are likely strong effects on biological control services provided by natural enemies inhabiting farmlands and neighboring habitats (Bompard et al. 2013; Chailleux et al. 2014), so these indirect effects need to be explicitly considered in future studies.

The nature and strength of the indirect interactions are strongly scale dependent (Koss et al. 2004; Tack et al. 2011; Chailleux et al. 2014). For example, predator aggregation to a single prey species in field studies proved consistent with indirect negative interactions between pests while cage experiments (smaller scale) had predicted positive indirect effects (Östman and Ives 2003). Heterogeneity at the landscape level promotes indirect interactions, for example, predator-mediated interactions among prey or other pests, alternative prey, non-pests, and natural enemies (Chailleux et al. 2014). This includes those organisms that are temporally and/or spatially distinct and that do not show overlap in the resources they used (Tack et al. 2011). Pests such as diamondback moth that specialize on a given crop taxon could still promote biological control services against other pests inhabiting other crops, as well as against other prey in neighboring non-cropped areas. If the diamondback moth leads to a build-up of generalist natural enemy populations including entomopathogens though some, such as Entomophthorales are relatively host specific, it follows that pest suppression could result from generalist enemies promoted by interventions in non-brassica crops or even in non-crop areas.

Spillover of biological control services from one habitat type to another can be considered as indirect interactions at the landscape level among pests that are present in various crops. Natural enemy populations can build up on a range of insect hosts in particular crops and then affect other pests in neighboring crops. This can occur through passive movement, by seasonal effects such as plant senescence, and by human intervention including harvesting events that trigger enemy dispersal and use of food sprays to attract enemies into a desired area (Wade et al. 2008). Such spillover likely involves more generalist natural enemies than those such as parasitoids that specialize on a single or few prey species (Meyling and Hajek 2010). In contrast to specialized natural enemies, a major benefit of polyphagy in generalist natural enemies is that they are loosely tied to any one particular resource and thereby buffered against spatio-temporal fluctuations in availability of that food type. This may be especially important in biological control of diamondback moth given its vagility. When seasonally absent in one location, predators may persist until the next season of brassica production by relying on various different prey and other foods. Switching diets allows such predators to persist locally, unlike specialists that are driven to local extinction. A caveat to this, however, is that the effects of polyphagous consumers, including spiders and other types of predators that are known to attack diamondback moth, may be reduced in complex food webs because their consumptive power is diluted across many weak trophic links (Halaj and Wise 2001; Denno and Finke 2006). This could limit their impact on the focal pest species though it has been suggested that not all predators are as polyphagous as generally assumed (Furlong and Zalucki 2010).

In contrast, specialist natural enemies such as the diamondback moth parasitoids mentioned above may disperse over longer distances (Dodsall et al. 2004) since they are less able to sustain themselves using resources present in non-brassica crops or close neighboring habitats than generalist natural enemies (Symondson et al. 2002). Using temporary plant infrastructures in non-cropped areas, for example, banker plants (Parolin et al. 2012) in hedgerows or wild plants showing characteristics enhancing natural enemy establishment and/or population build up, could help sustain natural enemies when target pest species are scarce or seasonal conditions are unsuitable for the persistence of specialist natural enemies (Huang et al. 2011).

6 Area-wide management: a platform for more effective biological control of diamondback moth

Moving from a crop or farm-scale paradigm for diamondback moth management to a larger, coordinated approach that can exploit landscape-scale effects to promote biological control is made easier by preexistence of the area-wide management (AWM) concept and its acceptance by farmers and authorities (Zalucki et al. 2009; Downes et al. 2017). AWM has a long history of use in a range of geographical areas against a variety of crop pests. In the case of diamondback moth, AWM has been suggested as important, particularly from the perspective of insecticide resistance management, cultural control and enhancement of biological control (Talekar and Shelton 1993). This is especially relevant here due to the migratory capacity of adult diamondback moth that can lead to the establishment of resistant populations, even in areas where there has been limited local selection for insecticide resistance (Zhao et al. 2006; Feng et al. 2011; Gao et al. 2016).

Globally, AWM is increasingly used for highly mobile pests, operating over a geographically defined area and characterized by being preventive (rather than reactive), as well as spatio-temporally coordinated (Hendrichs et al. 2007). The central premise of AWM is that all individuals of a pest population are managed, both in space and in time, in crops and in non-crop hosts, and year-round rather than only during the production season (Hendrichs et al. 2007). AWM does employ conservation biological control, especially against highly mobile species (Klassen 2005) and provides important guidance to natural enemy-focused efforts in terms of both scientific principles and the practical, management dimension. The more traditional field-by-field management approach is focused on remedial intervention triggered when a pest population reaches a certain threshold. Such localized control is suboptimal, particularly when exercising biological control through promotion of diverse taxa and guilds of natural enemies and when pests are mobile and making use of various host plants, as is the case for diamondback moth. The need to adopt a landscape-scale approach to promote natural enemies through habitat management is driven by (i) generalist species are often favored by continuity of availability of a range of prey species and plant-based foods; (ii) specialist species often exhibit life history omnivory, for example, adult stages of many parasitoids require access to nectar; (iii) food and shelter are required during periods when crops are either absent or are yet to be infested with pests; and (iv) while natural enemies have markedly differing dispersal ranges, they are often larger than the dimensions of a single crop and may be in the order of several kilometers (Tscharntke et al. 2012; Perović et al. 2010). Accordingly, the land uses immediately around crops and further afield become critical in providing appropriate resources to, and serving as donor habitat for, natural enemies.

Exploiting spatial barriers (even if semi-permeable) to the immigration of pests, especially mated females, into an area is key to AWM. Accordingly, geographically or topographically isolated locations or settings such as greenhouse complexes are good candidates (Casey et al. 2007). While some brassica crops are grown in greenhouses, they are in the minority so the vagility of diamondback moth adults means that barriers are of relatively low importance. Importantly, however, the reverse philosophy applies to the dynamics of natural enemies. For these beneficial species, barriers to immigration need to be minimized so that crops are rapidly colonized by large numbers of individuals from a range of guilds. Accordingly, a key challenge is to engineer landscapes that selectively promote population size and spatio-temporal flux of enemies while having the opposite effects on their prey. Achieving this is clearly challenging but work by Perović et al. (2010) suggests that perennial woody vegetation can promote landscape-scale connectivity for enemy immigration into cotton crops with no benefit to at least some herbivores (Macfadyen et al. 2015). More recent work in European managed grasslands showed that landscape simplification—a syndrome common in many agricultural areas (Fig. 1)—tends to favor arthropods with generalized feeding traits, larger body sizes, and longer seasonal activity periods (Gamez-Virues et al. 2015); all traits that could be predicted to allow persistence in habitats with larger patch sizes and carrying capacity. In contrast, landscape heterogeneity—as often evident in more traditional agricultural systems (Fig. 1)—tends to favor arthropods with more specialized feeding traits, smaller body sizes, and shorter activity periods. Importantly, this effect persists irrespective of high levels of management intensity within fields sited in such landscapes showing, essentially, that the landscape scale is more important than generally recognized, overriding differences at the more local scale (Gamez-Virues et al. 2015). Though that work took place in grasslands, it has direct implications for biological control of pests including diamondback moth. Landscape-scale strategies that are able to support a more diverse community of natural enemies would provide better pest suppression as a result of enemies partitioning the prey resource, thereby reducing intra-guild predation and competition. It also affords the system increased resilience to environmental disturbances, such as droughts or storms resulting from climate change (Yachi and Loreau 1999; Mori et al. 2013). Although the aforementioned work of European managed grasslands focused on arthropods, other results from the same large-scale study suggest that land use simplification has effects on multiple guilds and trophic levels and extend to below-ground taxa (Gossner et al. 2016; Perović et al. 2018).

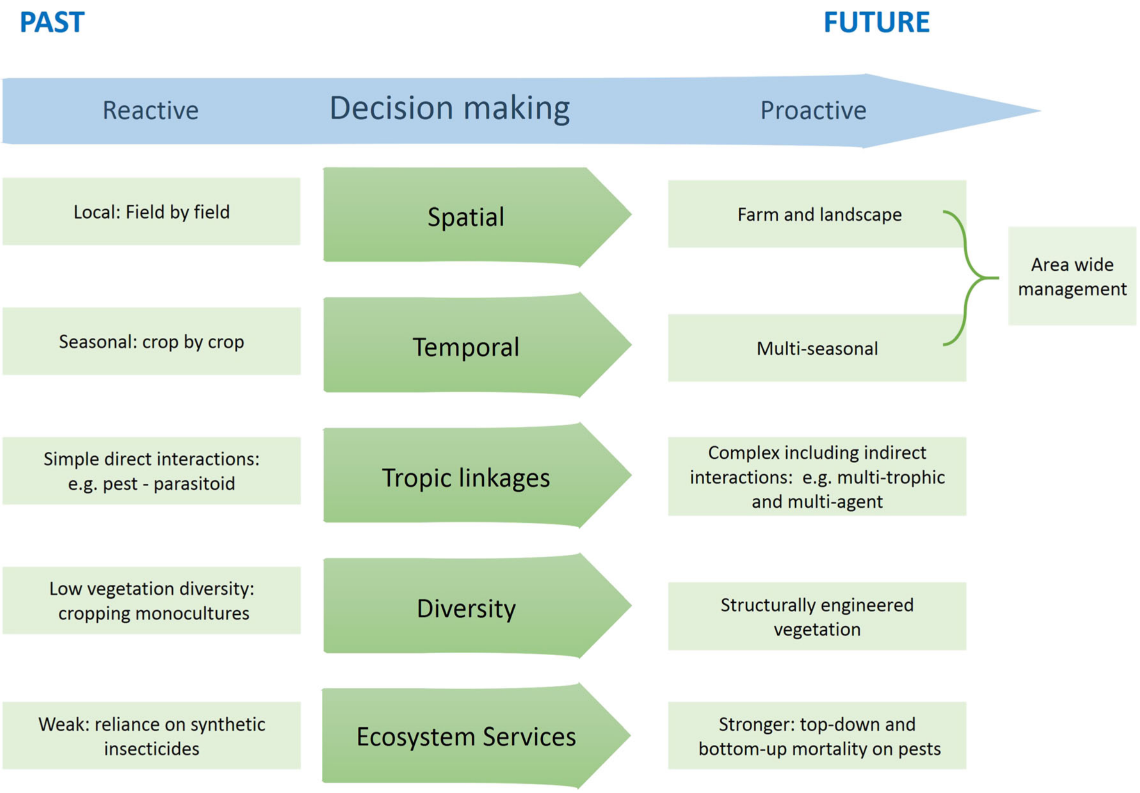

Fig. 3 Status of pest management for diamondback moth

Accordingly, non-arthropod natural enemies of pests such as nematode and microbial entomopathogens may be adversely impacted by landscape simplification, but amenable to promotion by diversification strategies (Meyling and Eilenberg 2007; Pell et al. 2010) such as those mentioned in Section 5.1.

Although landscape-scale effects can over-ride local management, there remains an important complementary role for local interventions. For example, a brassica crop in a diverse landscape may enjoy higher levels of natural enemies if certain practices are employed. These include the use of nectar plants to nourish parasitoids, an impactful approach which reduced the need for spraying, increased grain yield and enhanced profits in Asian rice (Gurr et al. 2016). A complementary approach is the application of semiochemicals to attract natural enemy movement into crops from nearby donor habitat, an approach shown to have potential in Australian studies that included broccoli crops (Simpson et al. 2011a; Simpson et al. 2011b). Species of arthropod natural enemies respond differentially to different semiochemicals, so there is potential to use these in a selective manner to drive natural enemy distribution, not only spatially and temporally but also in a species-specific manner. Food sprays and banker plants can also be used to support natural enemies at the more local scale provided that the wider landscape has the capacity to function effectively as donor habitat (Huang et al. 2011; Wade et al. 2008). The integrated use of pest control approaches such as those described above is important for implementing any conceptual plan for biological control-based AWM, a challenge that landscape ecologists will need to embrace.

7 Conclusion and prospects

Despite diamondback moth being the subject of intense research efforts over multiple decades, it remains a major cause of crop loss and driver of production costs. Changing this will require changes to the pest management approaches used by growers and the nature of the research efforts undertaken to provide the evidence base (Fig. 3). Historically, most biological control studies have focused on specific potential agents, chiefly parasitoids. There has, however, been a growth in the absolute numbers and relative research effort regarding predators and entomopathogens of diamondback moth. A move towards using multiple agents and conservation biological control is necessary. Associated with this, the efficacy of biological control is dependent on avoiding insecticide-induced mortality of agents. While this can be done by switching from broad-spectrum to more selective active ingredients (or microbial insecticides such as *Bt*), forms of habitat management that provide refuges in the landscape from which surviving natural enemies can re-colonize a sprayed crop offer potential (Heimoana et al. 2017).

Diamondback moth is highly vagile, and seasonal migrations allow exploitation of new brassica crops and subsequent rapid reproduction in enemy free space. As a consequence, landscape-scale programs are important so that diverse assemblages of natural enemies including entomopathogens can (i) persist in a given area during periods of pest absence and (ii) readily move into croplands and reproduce quickly to check pest build-up. Though farm- and local-scale interventions such as avoiding broad-spectrum insecticides, using nectar plant borders, semiochemical-mediated attraction, and banker plants have potential, they are contingent on the existence of sufficient donor habitat in the wider landscape from which natural enemies can move into the crop. Further, landscapes with high levels of vegetation diversity support a wider range of natural enemy taxa and guilds. This is advantageous in providing assemblages of natural enemies that can partition the prey resource (attacking all life stages for example) and able to cope with environmental change (higher temperatures and extreme weather events for example). Area-wide management is used successfully against various pests and offers the potential to be adapted as a delivery paradigm to improve biological control of diamondback moth. Components of this could include wider use of agroenvironment programs that are broadened in spatial extent to the landscape scale to motivate farmers and other stakeholders to adopt schemes beyond their individual farm (Gabriel et al. 2010). Similarly, certification programs for land stewardship that aim to maintain biodiversity and ecosystem services could be adapted to focus on the delivery of ecosystem services such as biological control to provide ecological intensification of agricultural systems (Geertsema et al. 2016). Essentially, these steps will move pest management from a reactive to preventative strategy. Finally, participatory approaches including the development and implementation of regional conservation programs should involve farmers so that multiple outcomes, including landscape-wide conservation of ecosystem service providers, are achieved (Westphal et al. 2015). While we believe these prospects apply strongly to diamondback moth, they have wider relevance to similarly r-selected pests, such as *Helicoverpa* spp. (Downes et al. 2017) and many Hemiptera pests, for which improved management is required.

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