



Review

Predicting the effects of climate change on natural enemies of agricultural pests

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ABSTRACT

Climate change can have diverse effects on natural enemies of pest species. Here we review these effects and their likely impacts on pest control. The fitness of natural enemies can be altered in response to changes in herbivore quality and size induced by temperature and CO₂ effects on plants. The susceptibility of herbivores to predation and parasitism could be decreased through the production of additional plant foliage or altered timing of herbivore life cycles in response to plant phenological changes. The effectiveness of natural enemies in controlling pests will decrease if pest distributions shift into regions outside the distribution of their natural enemies, although a new community of enemies might then provide some level of control. As well as being affected by climate through host plants and associated herbivores, the abundance and activity of natural enemies will be altered through adaptive management strategies adopted by farmers to cope with climate change. These strategies may lead to a mismatch between pests and enemies in space and time, decreasing their effectiveness for biocontrol. Because of the diverse and often indirect effects of climate change on natural enemies, predictions will be difficult unless there is a good understanding of the way environmental effects impact on tritrophic interactions. In addition, evolutionary changes in both hosts and natural enemies might have unexpected consequences on levels of biocontrol exerted by enemies. We consider interactions between the pest light brown apple moth and its natural enemies to illustrate the type of data that needs to be collected to make useful predictions.

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1. Introduction

There has been a lot of discussion in the literature on the effects of climate change on plant productivity (see Fuhrer, 2003 for review). Experiments indicate that higher levels of CO₂ generally increase productivity of plants (Long et al., 2004). However this can be countered by effects mediated through high temperatures and reduced water availability. There is already evidence that these factors are having a negative impact on productivity of grains and other crops (Challinor et al., 2005; Anwar et al., 2007; Torriani et al., 2007) rather than a positive effect.

Apart from having direct effects on plant productivity, climate change can also influence productivity through indirect effects mediated by changes in pests and diseases. There is abundant evidence that climate change can influence the distribution of phytophagous insects and particularly Lepidoptera (Sequeira and Mackauer, 1994; Cannon, 1998; Parmesan et al., 1999; Batalden et al., 2007; Trnka et al., 2007). Climate change is also influencing the phenology of insects including arrival times of Lepidoptera (Parmesan, 2007) and emergence time of a range of insects (Dewar and Watt, 1992; Whittaker and Tribe, 1996). Many of the species

being affected are pest herbivores, leading to new pests appearing and others disappearing, and altered pressures from existing pest species (Gutierrez et al., 2008a; Jepsen et al., 2008). While the impact of herbivores on productivity will be influenced by a diverse range of factors including plant nutritional changes and changes in plant allocation to defensive compounds with increased CO₂ (Coviella et al., 2002), the effectiveness of natural enemies in controlling the herbivores will be a major influence. The prediction of an increase in the frequency and intensity of herbivore outbreaks through disruption of parasitoid-herbivore dynamics as climate becomes more variable is substantiated by meta-analysis (15 databases from previously published reports) (Stireman et al., 2005).

Over one-third of the total variance in caterpillar parasitism is explained by variability in precipitation (although this does not mean precipitation *per se*) despite a wide diversity of host and parasitoid species, and ecosystems at different latitudes being considered. This variance in parasitism is largely driven by hymenopteran parasitoids which are relatively host-specific (Hawkins, 1994) rather than tachinids which generally have large host ranges (Belshaw, 1994).

In this paper, we consider the diverse ways in which climate change will influence interactions between plants, natural enemies and herbivores and illustrate some of the challenges of making predictions with reference to a specific example. Some of these

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interactions have previously been reviewed by Hance et al. (2007) who focus on parasitoid responses to temperature extremes, and changes in synchrony between parasitoids and their hosts. In this review we take a broader approach that covers various ways climate change might influence natural enemies of herbivorous pests. This is followed by discussion of a specific example, the control of lightbrown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), a pest of orchard, vineyard and horticultural crops.

The rather diverse ways climate change might impact on natural enemies are outlined in Fig. 1. Plants growing under increased CO₂ and temperature extremes as well as decreased precipitation will provide different nutritional resources for invertebrate hosts, indirectly influencing the fitness of predators and parasitoids feeding on these hosts. There is also the potential for climate change to influence overlap between the appearance and abundance of natural enemies at times when crops are under pressure from herbivores. The ability of natural enemies to track their hosts will depend on their tolerance of environmental extremes relative to their herbivore hosts as well as their movement rates. Many effects of climate change on natural enemies will be mediated by new management practices as farmers grow crops under drier and warmer conditions, and in new areas. We discuss each of these factors in turn, and highlight the type of data that needs to be collected when making predictions about their likely impact on natural biocontrol. We also briefly address the extent to which these effects could be attenuated through evolutionary changes in host and enemy populations.

2. Plant phenology and physiology indirectly influencing enemy fitness

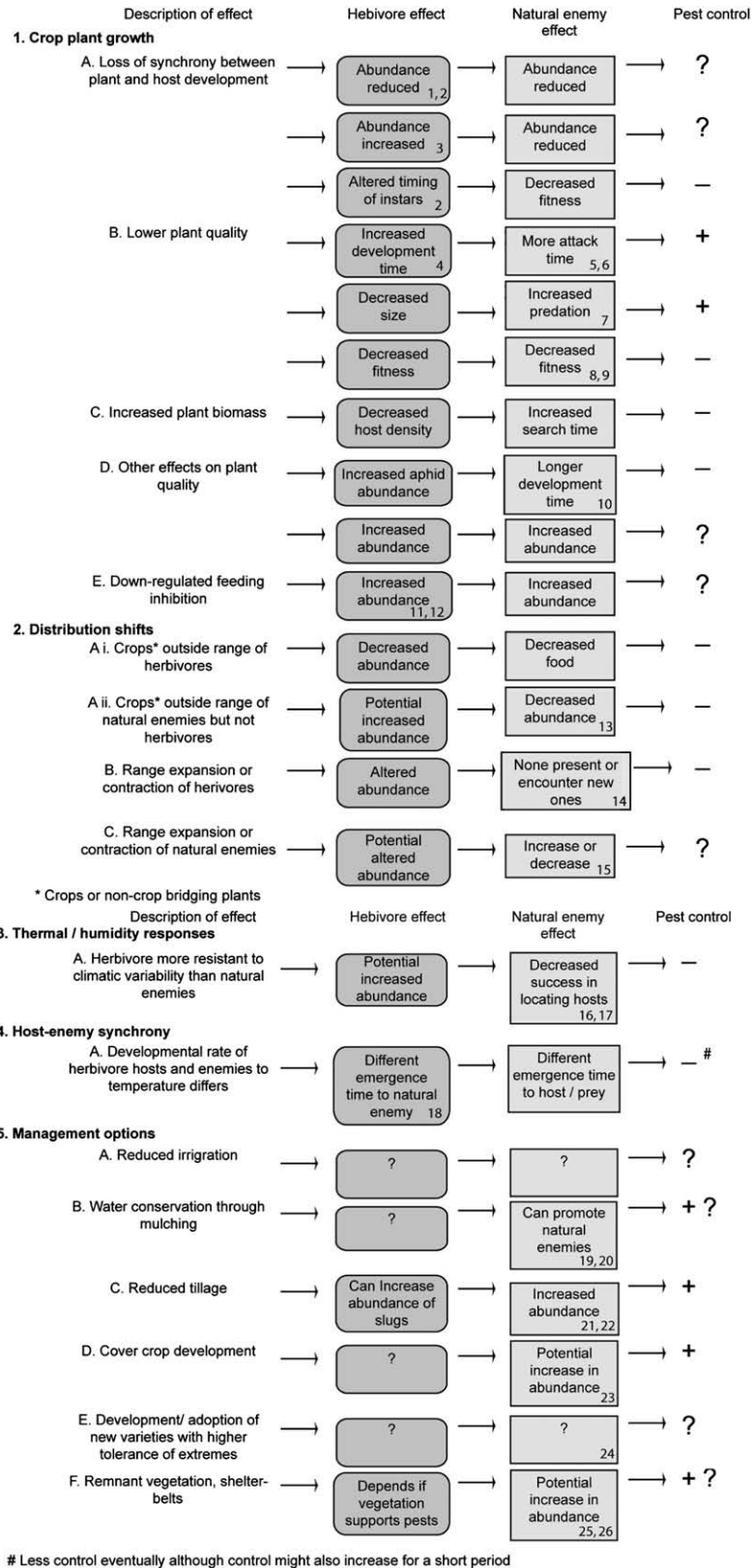
Increases in atmospheric CO₂, shifts (usually downward) in precipitation and particularly increases in temperature will alter plant phenology, influencing herbivore growth and abundance, and indirectly affecting the abundance of prey and hosts for natural enemies (1A in Fig. 1). A change in phenology including the timing of seed germination, dormancy breaking or bud burst could decrease synchronization between herbivores and their hosts. For forest insects, the performance of insect larval herbivores depends on the type of plant tissue available for consumption (Lindroth et al., 1993). The quality of foliage is higher closer to budburst, so hatching too long after budburst disadvantages herbivores (Dewar and Watt, 1992). Synchrony between bud burst and larval emergence is critical for survival; if the cues for each (say day length and temperature) differ then the association may be broken to the detriment of the herbivore. For example, even for a generalist herbivore such as gypsy moth, *Lymantria dispar* L. (Lepidoptera: Lymantriidae), the loss of a single host can be catastrophic. This moth develops on red and black oaks, *Quercus rubra* and *Quercus velutina*, and egg hatch before budburst leads to starvation, while egg hatch too long after budburst and reduced foliage quality leads to reduced fecundity (Ward and Masters, 2007). This change in food availability, due to stage of bud or shoot development when herbivore eggs hatch, also influences herbivore growth and survival in a range of forest defoliators including pine beauty moth, *Panolis flammea* (Denis & Schiffermüller) (Lepidoptera: Noctuidae), eastern spruce budworm *Choristoneura fumiferana* (Clemens) (Lepidoptera: Tortricidae), the green oak tortrix *Tortrix viridana* L. (Lepidoptera: Tortricidae) and winter moth *Operophtera brumata* L. (Lepidoptera: Geometridae) (Dewar and Watt, 1992). Although loss of synchrony will disadvantage herbivores in many instances, there are exceptions. Populations of a willow catkin eating psyllid, *Cacopsylla moscovita* (Andrianova) (Hemiptera: Psyllidae), may increase under higher temperatures (Hill and Hodkinson, 1996), as a rise in temperature increases rate of development of psyllids pro-

portionately more than catkins. Thus hosts and prey food available for natural enemies will generally decrease due to lack of synchrony, but may increase in some situations.

As well as being affected by synchronization with plant hosts, herbivore abundance and fitness may also be influenced by changes in plant tissues in response to CO₂ and perhaps precipitation (1B in Fig. 1). In general, elevated levels of CO₂ reduce the nutritional value of plants, including decreased nitrogen, leading to increased plant consumption rates in some guilds of pests (Bezemer et al., 1998). This might result in an increased level of plant damage because the pests have to consume more plant tissue to acquire similar levels of nutrition; however, responses are variable and few studies have shown significant shifts in the size of insect herbivore populations (Whittaker, 1999). An increased feeding rate is a common response in foliage feeders but is not as clear in sap suckers which, unlike miners and chewers, do not respond to a reduction in nitrogen predicted under CO₂ enrichment by compensatory feeding (Hamilton et al., 2004). There are inconsistent reports of the effects of increased CO₂ on sucking pests, and in some cases fecundity and abundance of this group can increase (Bezemer et al., 1998). Increased feeding rates do not always compensate for reduced quality of food (Cannon, 1998), and consumption of plants grown under conditions of higher CO₂ can decrease the performance of invertebrates feeding on them (Zvereva and Kozlov, 2006). There is a tendency not only for herbivores to consume more plant material, but also to grow more slowly (Lindroth et al., 1993), take longer to develop, show reduced fecundity and suffer heavier mortality (Watt et al., 1995).

The fitness of predators and parasitoids will decline as the quality of their herbivore hosts decreases (Wang et al., 2007). Host quality effects on predator fitness have been shown for several groups including spiders (Toft, 1995; Hvam and Toft, 2005), predatory bugs (Butler and O'Neil, 2007) and carabid beetles (Bilde and Toft, 1999). Rates of parasitoid larval growth and development, together with adult biomass, are often significantly influenced by host size, age, stage of development and diet (see Godfray, 1994 for review). Quality of hosts may affect parasitoid fitness, particularly in koinobiont parasitoids whose hosts continue to feed after parasitisation. Given that parasitoid fecundity is often positively correlated with size, host quality represents an important constraint on parasitoid fitness (Harvey et al., 1999) with some exceptions (Harvey et al., 2004; Hackermann et al., 2007).

A decrease in prey size will not necessarily always lead to a reduction in the success of natural enemies. The number of prey consumed by predators might be increased and lead to improved pest control (Chen et al., 2005; Coll and Hughes, 2008). While few evaluations have been undertaken, Coll and Hughes (2008) considered the interaction between an omnivorous pentatomid bug, *Oechalia schellenbergii* Guérin-Méneville (Hemiptera: Pentatomidae), and the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), when feeding on peas (*Pisum sativum* L.). In this case, pea plants had reduced nitrogen content when grown under higher levels of CO₂ and this in turn influenced the size of the cotton bollworm larvae. The predatory bugs were more effective under higher CO₂ levels because they appeared to be better at subduing the smaller bollworm larvae. Similarly, the coccinellid predator, *Leis axyridis* Pallas (Coleoptera: Coccinellidae), of an aphid herbivore, *Aphis gossypii* Glover (Hemiptera: Aphididae), consumed more prey under conditions of higher CO₂ (Chen et al., 2005). In another aphid pest, *Sitobion avenae* F. (Hemiptera: Aphididae), Chen et al. (2007) found a negligible impact of elevated CO₂ on its coccinellid predator, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), but increased abundance of the braconid parasitoid, *Aphidius picipes* (Nees) (Hymenoptera: Braconidae), resulting in increased aphid parasitism in elevated CO₂ compared to ambient CO₂. In this case, the biocontrol efficiency of the parasitoid against



Less control eventually although control might also increase for a short period

Fig. 1. Outline of potential effects of climate change on natural enemies of herbivorous pests, as assessed through interactions with pests and their crop plant hosts. The individual pathways outlined may result in more control of pest species or less control of pest species, however, the net effect will depend on the magnitude of change for all these pathways combined and could result in more pest outbreaks, less pest outbreaks or no change in outbreak frequency. The signs at the end of the pathways indicate that pest control may increase (+) or decrease (–) under a particular scenario, or that it is not possible to determine the direction of change at this stage (?). Numbers refer to the following citations (1) Ward and Masters (2007); (2) Hill and Hodkinson (1996); (3) Dewar and Watt (1992); (4) Lindroth et al. (1993); (5) Haggstrom (1995); (6) Sequeira and Mackauer (1994); (7) Coll and Hughes (2008); (8) Wang et al. (2007); (9) Godfray (1994); (10) Gao et al. (2008); (11) Zavala et al. (2008); (12) Hamilton et al. (2005); (13) Menendez et al. (2008); (14) Gutierrez et al. (2008b); (15) Cornell and Hawkins (1993); (16) Stireman et al. (2005); (17) Hance et al. (2007); (18) Whittaker and Tribe (1998); (19) Thomson and Hoffmann (2007); (20) Schmidt et al. (2004a); (21) Nash et al. (2008); (22) Sharley et al. (2008); (23) Gurr et al. (2004); (24) Calatayud et al. (2002); (25) Olson and Wäckers (2007) and Schmidt et al. (2004b).

aphid hosts may be enhanced in elevated CO₂. These results suggest that higher CO₂ could make generalist predators more effective in controlling pests. However the searching time needed by predators to locate prey could be increased (1C in Fig. 1) as a consequence of extra plant foliage due to increased growth.

Increases in herbivore development time due to changes in plant nutrition can make herbivore prey more susceptible to predation due to the longer window of opportunity available to predators. The development of the willow feeding leaf beetle, *Galerucella lineola* F. (Coleoptera: Chrysomelidae), varies on different hosts; where development is longer, predation by a range of taxa including heteropteran families Pentatomidae and Nabidae, and spiders is higher (Haggstrom and Larsson, 1995). Changes in host development can also influence parasitoid activity and fitness; an increase in development time makes hosts more susceptible to parasitism, particularly if it leads to parasitoids encountering instar stages of the host that are relatively more susceptible to parasitism (e.g., Sequeira and Mackauer, 1994).

There are other ways that plant responses to climate change can influence herbivores and their control through natural enemies (1D in Fig. 1). In cassava *Manihot esculenta* Crantz, parasitism of mealybugs is reduced under conditions of water stress associated with drought conditions (Calatayud et al., 2002). Apparently the immune response of mealybugs is improved when these insects are grown on water stressed plants, leading to an increased rate of encapsulation ranging from 30% to 50% in three different species of encyrtid mealybug parasitoids (Calatayud et al., 2002). Elevated CO₂ can increase the susceptibility of plants to herbivory through changing gene regulation (1E in Fig. 1). Herbivory of soybean under field conditions is affected by down-regulating gene expression for a protease specific deterrent to coleopteran herbivores (Hamilton et al., 2005; Zavala et al., 2008). Plant effects on beneficials might involve changes in the expression of volatile organic compounds and the secretion of extrafloral nectar that are induced by insect feeding, which are now well recognized as providing protection from herbivores (Heil, 2008). Increases in temperature under climate change could influence the production and release of volatile compounds.

Studies to date therefore suggest that the effects of climate change on natural enemies that are mediated by CO₂, temperature and moisture effects on plants can be complex. The effectiveness of natural enemies can be decreased because enemies have to feed on a lesser quality host, and in situations where hosts are more difficult to locate. However the effectiveness of natural enemies might also be increased because small prey items are easier to handle for predators, and because hosts are available for a longer time period for parasitism. The combined effects of temperature, CO₂ and nutrition levels might not be easily predicted because of interactions between these effects. This has been emphasized recently in models of the interaction between plants, aphid herbivores, and their parasitoids and predators (Hoover and Newman, 2004). For instance, Gao et al. (2008) found that the aphid *A. gossypii* may become a more serious pest under elevated CO₂ concentrations because of increased survivorship of the aphid, and the extended development time of its main predator, the coccinellid *Propylaea japonica* (Thunberg) (Coleoptera: Coccinellidae).

3. Distribution shifts in plants, hosts and natural enemies

The effectiveness of natural enemies in pest control may be reduced by changes in the distribution of crops, hosts and the enemies themselves (2A–C in Fig. 1). Crop ranges are predicted to move as climate change occurs, and herbivores may track these changes. The outcome will depend partly on the ability of natural enemies to concurrently expand their range or for new natural enemy populations to control the pest in its expanded range. Plants

may move outside the range of their herbivorous pests, but herbivores with high movement rates should be able to track climatic changes. Mobile species such as diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), bollworm and European corn borer, *Ostrinia nubilalis* (Hübner) (Lepidoptera: Pyralidae), should track climatically favourable locations as the crop becomes available (Trnka et al., 2007). However less mobile species such as coccids, eriophyoid mites or mealybugs may have difficulty tracking crop hosts at least initially as crops are grown in new areas (unless the herbivores are spread on plant material).

Cold-limited species may be able to increase their geographic range in the future. In the eastern forests of the United States, several beetles including the southern pine beetle *Dendroctonus frontalis* Zimmermann and mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae) are predicted to expand their range northwards (Williams and Liebhold, 2002; Tran et al., 2007). Warming will allow the cold intolerant pink bollworm, *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae), to expand its range on cotton into formerly inhospitable areas affected by heavy frosts, and damage rates will increase throughout its current range (Gutierrez et al., 2008b). The survival of palm thrips, *Thrips palmi* Karny (Thysanoptera: Thripidae), is currently limited in the United Kingdom due to lack of cold tolerance, and so this species may spread in the future (McDonald et al., 2000). Fruit flies like *Bactrocera tryoni* (Froggatt) (Diptera: Tephritidae) are expected to spread into colder areas (Sutherst et al., 2007). The reduced occurrence of low temperature or chill events may decrease mortality as in the case of pipevine swallowtail, *Battus philenor* L. (Lepidoptera: Papilionidae) (Fordyce and Shapiro, 2003). Range expansion will not be universal in response to climate change; there is considerable research on range contraction on the part of vertebrates (Carroll, 2007; Mitrovski et al., 2008). The distribution and importance of pest species requiring colder and/or wetter conditions may contract, as in the case of armyworms and tsetse flies (Hoffmann et al., 2008; Terblanche et al., 2008).

There have been marked changes in the distribution of many species in the northern hemisphere in response to unusually hot summers (Cannon, 1998). The northern boundaries of 65% of butterflies have shown northward movement (Parmesan et al., 1999). The magnitudes of these range shifts (35–240 km along a single boundary) are on the order of 5–50 times the colonization distances achieved by comparable butterflies in single colonization events. Range extension is predicted from models and predicted temperature changes in many species (e.g., Whittaker and Tribe, 1998; Olfert and Weiss, 2006) including pests (Williams and Liebhold, 2000; Jepsen et al., 2008).

These expansions of herbivores may lead to escape from natural enemies (2C in Fig. 1). The range of the brown argus butterfly, *Aricia agestis* Denis & Schiffermüller (Lepidoptera: Lycaenidae), has expanded northwards in Britain over the last 30 years in association with global warming and it suffers lower mortality from parasitoids in newly colonized areas compared to long-established populations (Menendez et al., 2008). Herbivores may also escape natural enemies as they move into new crops. For instance, the braconid parasitoid of European corn borer, *Macrocentrus gifuensis* Ashmead (Hymenoptera: Braconidae), killed 53% of larvae overwintering on mugwort *Artemisia vulgaris* L. but none overwintering on maize (Thomas et al., 2003). Diamondback moth can travel large distances to new cruciferous crop plantings; due to the low numbers of effective natural enemies and especially parasitoids, the moth is better able than its natural enemy complex to become established and increase population density (Talekar and Shelton, 1993).

Predictions about likely changes in natural enemies following host spread have often utilised information from invasive herbivores. Evidence from comparisons of parasitoid complexes on her-

bivore species in new (invasive) locations to those in native regions (Cornell and Hawkins, 1993) suggests that third-trophic-level insects are less able to disperse or colonise than second-trophic-level insects. An invading alien herbivore is likely to have fewer parasitoid species because it will generally lack native specialist parasitoids, and more generalist species may not search the herbivore niche occupied by the novel invader (Cornell and Hawkins, 1993). For invasive leaf miner species, the most important parasitoids may be specialists that spread with the host rather than generalist species (Godfray et al., 1995). In the herbivore moth, *Hadena bicruris* Hufnagel (Lepidoptera: Noctuidae), the solitary specialist ichneumonid parasitoid, *Eurylabus tristis* Gravenhorst (Hymenoptera: Ichneumonidae), produces a parasitism rate higher than a gregarious generalist species (Elzinga et al., 2007). Some specialist enemies can move large distances. For instance, *Cotesia flavipes* Cameron (Hymenoptera: Braconidae) has been introduced into several African countries from its native Asia, for the control of the stem borer *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae) in maize and sorghum but it has never been released in Ethiopia. It is now found >2000 km from the nearest known release sites in Kenya and Somalia, a movement rate of 200 km/year (Assefa et al., 2008). However, the movement rate of other beneficial species can be severely constrained. Beneficial species like predatory mites have low movement rates, limiting control of pests (Collier and Van Steenwyk, 2004), and parasitoids also show reduced movement relative to their prey (Anton et al., 2007).

In many cases, natural enemies present in an environment will provide poor control of novel invasive herbivores. Native parasitoids have little impact on populations of the European corn borer in North America, even 100 years after its invasion. Imported parasitoids from the native range continue to be more effective bio-control agents (Capinara, 2008). However, in other cases, resident natural enemies may provide effective control of a pest herbivore some time after an invasion. In *Liriomyza huidobrensis* (Blanchard) leaf miners (Diptera: Agromyzidae) invading Indonesia, high levels of damage were initially observed and associated with low levels of parasitism but after several years the impact of the local parasitoids increased and provided effective control of this species (Rauf et al., 2000; Hidrayani et al., 2005). The success of local natural enemies in controlling invasive pests may depend on the presence of related species of plants and herbivores in an area.

To summarize, studies undertaken so far suggest that crop plants might sometimes escape herbivores but it is more likely that herbivores will escape natural enemies. However there is only limited information on whether herbivores will escape natural enemies to the same extent found in invasive species. Movements of invasive species often involve large distances across continents or regions, whereas with range expansion under climate change distribution shifts will often be incremental. When this occurs, natural enemies might be able to track their hosts as long as movement rates are adequate. Where herbivores move into new areas, a resident community of natural enemies might also provide some control of the herbivore.

4. Thermal and desiccation responses

The extent to which herbivores can track crops, and natural enemies can track changes in herbivore hosts, will depend on their relative resistance to thermal extremes (3A in Fig. 1) as well as movement. Parasitoids can often develop across a broad thermal range (Wanderley et al., 2007; Pandey and Tripathi, 2008) although few studies have been completed on responses to short term thermal extremes (Hance et al., 2007). Within a life cycle stage, resistance to extremes in parasitoids can be increased by acclimation following exposure to non-lethal conditions (Scott et al., 1997; Thomson et al., 2001). Resistance can also be increased if parasitoids

enter diapause that usually is associated with a high level of resistance to thermal extremes and desiccation (Hance et al., 2007). Conversely, invasion might be prevented if conditions prevent the induction of diapause, which is one reason that the invasive generalist coccinellid predator *H. axyridis* may not have become established in the Azores (Soares et al., 2008).

Apart from surviving thermal extremes, natural enemies will also need to counter climate change by mating and then locating hosts effectively across a wider range of thermal and humidity conditions. Host location of the egg parasitoid, *Trichogramma carverae* Oatman and Pinto (Hymenoptera: Trichogrammatidae), falls off sharply at temperatures above 35 °C (Thomson et al., 2001), while fecundity reductions of 50% are commonly reported in *Trichogramma* at temperatures of 30 °C (e.g., *T. carverae* (Scott et al., 1997), *Trichogramma pretiosum* Riley and *Trichogrammatoidea bactrae* Nagaraja (Naranjo, 1993). Even small changes in thermal conditions might therefore influence the effectiveness of parasitoids in controlling pest species.

It is not clear how the thermal requirements of parasitoids or predators match those of their pest herbivore hosts. However at least in the case of parasitoids, they may deal more poorly with variable conditions than herbivore hosts. As mentioned earlier, control of pests exerted by natural enemies seems to depend on precipitation and decrease in dry conditions (Stireman et al., 2005). Field studies have also correlated climate data with egg parasitism of European corn borer by *Trichogramma* from 1993 to 1996; extremely dry and hot weather experienced in May 1993 in Slovakia meant that no eggs were successfully parasitized by *Trichogramma* (Cagan et al., 1998). In tachinid flies, field data for the period 1985–1987 also suggests a range of parasitism between 1% and 51% reflecting local climatic conditions (Grenier et al., 1990).

Thus while natural enemies have some potential to deal with changes in climatic variability through acclimation and diapause, and by having some innate resistance of thermal extremes, climatic variability may influence their effectiveness in controlling pests. Field data suggest that parasitoids are more sensitive to climatic variability than their hosts, possibly related to the greater intrinsic rate of population increase shown by herbivores following mortality of both groups.

5. Host–enemy synchrony

Temperature has a large effect on herbivore phenology (Bale et al., 2002), and temperature changes may alter the synchrony between herbivores and their natural enemies (4A in Fig. 1). The speed of development of herbivores will generally increase under climate change unless it is influenced by poorer nutrition. For instance the spittle bug, *Neophilaenus lineatus* L. (Hemiptera: Cercopidae), is expected to complete development 2–3 weeks earlier response to a 2 °C rise based on current data (Whittaker and Tribe, 1998). Higher temperatures may also allow an increase in the number of generations per year in multivoltine species due to more rapid development or altered timing of egg hatch. Longer growing seasons due to milder conditions may allow more generations of aphids (McVean et al., 1999) and the European corn borer (Trnka et al., 2007). Diapause in insects is typically associated with an interaction between day length and temperature (Denlinger, 2002) and altered patterns of diapause could influence generation number. In the grape berry moth, *Paralobesia viteana* (Clemens) (Lepidoptera: Tortricidae), voltinism is predicted by the number of degree days that accumulate before the post-summer photoperiod when oviposited eggs develop into diapausing larvae instead of adults. This will lead to increased numbers of generations under warming at some times of the year (Tobin et al., 2008).

The effects of these changes on the natural enemies of herbivore hosts can be unclear, particularly over the longer term (Godfray,

1994; Hance et al., 2007). If parasitoids emerge earlier than hosts because their development shows a sharper response to temperature, a very large population of parasitoids might cause a marked decrease in herbivore hosts, and this could even lead to eventual extinction of the parasitoid population. There may be few or no available hosts in the vulnerable stage and, depending on the extent of the mismatch, many parasitoids could die before hosts become available. However a late arrival of parasitoids might prevent much control and again lead to local extinction. A disconnect between host and parasitoid can also arise because of increased climate variability. Poor synchrony between a parasitoid and its host has been documented in a number of cases. For instance, hibernating parasitoids of leaf miners emerge at a time when no hosts are available, and this results in a low level of parasitism of the first generation of horse chestnut leafminers, *Cameraria ohridella* Deschka & Dimic (Lepidoptera: Gracillariidae), in the field (Grabenweger et al., 2007). Hance et al. (2007) also point out that changes in synchronization are particularly important when herbivores have evolved altered emergence patterns in response to parasitoids. In this case, any effects of climate change and weather variability on emergence patterns of the hosts or parasitoids that alter synchrony may be disastrous for the hosts.

To predict whether the effects of climate change will alter synchrony and levels of biocontrol, models are required that consider the effects of temperature changes as well as CO₂ on plants, herbivores and their natural enemies. One such model was constructed by Hoover and Newman (2004) on the general interaction between grasses, cereal aphids and their parasitoids. In this system, changes in CO₂ and higher temperatures affected plant growth but only temperatures altered developmental rate of the aphid hosts and their parasitoids. This resulted in a limited impact of combinations of CO₂ and temperature on the aphid population, and also a limited impact of parasitoids on the aphid population. A further challenge will be to construct similar models that encompass the large range of parasitoids and predators normally influencing populations of a pest species across a season. While a few specialist parasitoids can exert most control over a pest species (e.g., control of red scale *Aonidiella aurantii* (Maskell) (Hemiptera: Diaspididae) by the aphelinid parasitoid *Aphytis melinus* De Bach (Hymenoptera: Aphelinidae) (Murdoch et al., 2006)), a combination of parasitoids and predators with a variety of strategies are normally required to provide effective control of agricultural pests (Cardinale et al., 2006; Straub and Snyder, 2008). Generalist predators like spiders and lacewings are often important in agricultural systems (Frampton et al., 2000; Brown and Schmitt, 2001; Daane, 2001) and typically a high diversity of natural enemies is required to provide a high level of control (Tscharrntke et al., 2007). This complexity needs to be considered when considering the effectiveness of natural enemies in controlling field pest populations.

6. Management mediated changes

Farm enterprises are already starting to be managed differently to cope with increased temperatures, reduced water availability and increased climatic variability. New adaptive management strategies have potential impacts on natural enemies. Rainfall has become less predictable in many regions and irrigation water is less freely available. This means that less water is often being applied to crops and in a more targeted manner. The impact of this shift in practice is not well known (5A in Fig. 1). There are negative impacts of drought on abundance of predators including spiders and beetles, while ground dwellers like Carabidae can differ between irrigated and control treatments (Frampton et al., 2000; Morecroft et al., 2002). On the other hand, parasitism of leafminers can increase under drought conditions (Bjorkman et al., 1997; Staley et al., 2006) and densities of predators (anthocorids, spiders,

and coccinellids) may be higher in drought-stressed corn when compared to fully irrigated corn (Godfrey et al., 1991). This may reflect an increased vulnerability of herbivores to predation and parasitism when development time is extended due to poor plant growth as mentioned earlier.

Changes in agricultural practices have led to the widespread adoption of no-tillage or low tillage plantings and the use of mulches for water retention in a wide variety of crops. Mulches can increase predator and parasitoid populations within a field (5B in Fig. 1). For example, the abundance of carabids, parasitoid Hymenoptera and spiders, predatory and parasitic Diptera and predatory Hemiptera increased in a vineyard following applications of straw and compost as mulches to reduce water loss (Thomson and Hoffmann, 2007). Aphid pests are suppressed in mulched cereal fields due to improved parasitoid and predator biocontrol (Schmidt et al., 2004a). Spider abundance is increased by greater habitat complexity resulting from the addition of mulch to a cropping system (Rypstra et al., 1999), while reduced tillage encourages natural enemies including beetles (Nash et al., 2008; Sharley et al., 2008) (5C in Fig. 1). Concerns around water consumption as well as soil compaction are also changing patterns of intercropping. For example, there has been greater interest in the use of intercropped native grasses in vineyards rather than pasture grasses or flowering crops that compete for water with vines (5D in Fig. 1). Flowering (usually alien) ground cover plants can have positive effects on predator and parasitoid abundance with resultant benefits on pest control (for review see Gurr et al., 2004) and shifts to other species may decrease this benefit of intercropping.

As crops are being grown under increasingly variable conditions, varieties with higher tolerances to environmental stresses such as reduced water availability and increased salinity are being adopted. Recent progress has been made in the isolation and functional analyses of genes controlling yield and tolerance to abiotic stresses (Takeda and Matsuoka, 2008). However there is as yet very limited information about possible effects of these new varieties on natural enemies or even herbivores (5E in Fig. 1). Drought tolerant cassava, *M. esculenta* Crantz, is more susceptible to mealybug infestation; moreover mealybugs feeding on this type of cassava show lower rates of parasitism, suggesting a decreased level of pest control (Calatayud et al., 2002).

Environmental changes are leading to interest in maintaining remnant vegetation and revegetating areas on farms for a variety of reasons including salinity reduction and carbon capture. There are potential benefits of vegetated areas for pest control because these areas can support a high abundance and diversity of predators and parasitoids (Gurr et al., 2003; Schmidt et al., 2004b; Olson and Wäckers, 2007) (5F in Fig. 1). A diverse range of natural enemies can buffer against spatiotemporal disturbances. Under variable climatic conditions, maintenance of a diverse enemy assemblage may become particularly important. Complex landscapes characterized by highly connected crop to non-crop mosaics such as those introduced by revegetation of agricultural landscapes may be best for long-term conservation biological control and sustainable crop production (Tscharrntke et al., 2007). Implementation of revegetation programs in response to environmental concerns, including increased CO₂, may therefore have positive impacts on pest control. Provision of habitat for natural enemies may also be important following the occurrence of extreme weather events such as major storms, predicted as a consequence of climate change.

7. Evolutionary potential

Predictions about changes in herbivores and natural enemies under climate change normally assume that developmental responses, thermal thresholds and other forms of environmental

adjustment are static and cannot evolve. When correlative approaches are used to predict changes in the distributions of organisms, the assumption is that climatic limits are fixed. Thermal thresholds might be plastic as a consequence of acclimation and diapause/quiescence, but there is no allowance for the possibility that thresholds might evolve because of selection imposed by climate change.

Yet there is growing evidence for evolutionary shifts in insects exposed to climate change. This includes shifts in genetic markers and phenotypic traits in widespread *Drosophila* and mosquitoes (Bradshaw and Hozapfel, 2001; Hoffmann and Daborn, 2007). Few studies have addressed evolutionary shifts in natural enemies. However such responses might be expected for several traits including thermal responses, timing of reproduction and emergence and other traits (Fig. 1). Rates of evolutionary change in populations under climate change will depend on levels of heritable variation, genetic interactions among traits, and population processes (Lynch and Lande, 1993). Most quantitative traits are thought to exhibit high levels of genetic variance and evolutionary potential (Roff, 1997) although this conclusion may not always be justified (Kellerman et al., 2006).

Levels of heritable variation for traits likely to be involved in adapting to climate change have been investigated in several herbivores. Examples include recent work on variation in the timing of egg hatch in winter moths to counter an increasing mismatch between the herbivore and its host (van Asche et al., 2007) and variation in thermal responses of the pest beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae) (Lyytinen et al., 2008). In contrast, there is only limited data on the evolutionary potential of natural enemies. Enemies like egg parasitoids of the genus *Trichogramma* that are mass reared for biocontrol typically exhibit rapid adaptation to artificial rearing conditions (Kolliker-Ott et al., 2003), highlighting the potential for rapid evolutionary changes. There is evidence for genetic variation in populations of parasitoids to thermal extremes (Shufron et al., 2004) (A in Fig. 1) and evidence for rapid shifts in host adaptation when parasitoids are confined to new hosts (Rolf and Kraaijeveld, 2001; Pannebakker et al., 2008) (B in Fig. 1). Predatory mites can be selected for different diapause characteristics that influence their phenology with respect to prey (van Houten et al., 1995) (C in Fig. 1). Many parasitoids are univoltine, with generation time synchronized to the number of generations of the host through temperature responses. If herbivores alter voltinism under climate change, parasitoids or predators will need to evolve or respond by plastic changes to synchronize their development with their host (D in Fig. 1). We are unaware of any evolutionary studies in natural enemies that consider synchronization, although there is genetic variation in generation time at a particular temperature in parasitoids (Samara et al., 2008). There is also the potential for natural enemies to respond to the altered timing of prey availability through plastic changes, as has been seen in vertebrates such as birds (Seavy et al., 2008), although we are unaware of data on these types of responses in insect natural enemies (E in Fig. 1). Whether specialist parasitoids and predators show much evolutionary potential remains to be seen. Future studies should consider levels of genetic variation in natural enemies and their hosts, and assess the ability of enemies to track hosts through evolutionary changes, focusing on cases where herbivore pests are already altering their distribution and phenology in response to climate change.

8. Light brown apple moth, *E. postvittana*, as an Australian case study

Light brown apple moth, *E. postvittana* (Walker) (Lepidoptera: Tortricidae), is a lepidopteran leaf rolling pest that is indigenous to Australia and attacks many horticultural crops including stone

fruit, citrus fruit and grapevines (Geier and Briese, 1981). Within Australia, climate-based models suggest that *E. postvittana* will be displaced from the warmer parts of its current range in the future (Fig. 2; Sutherst, 2000). This herbivore feeds on a variety of host plants and is also found in New Zealand, New Caledonia, the British Isles, Hawaii and recently California in the United States of America (Varela et al., 2008). It has attained pest status in south-eastern Australia where damage to citrus fruit through larval feeding threatens exports, and costs Australian growers \$21 million per year (Sutherst, 2000; Anonymous, 2001). Crops such as oranges and grapes (grown in warmer areas) will benefit while cooler regions with apples, grapes and pears may see increased moth damage (Sutherst, 2000; Anonymous, 2001). These scenarios do not take into account interactions between *E. postvittana* and its natural enemies. Crucial to understanding how outbreaks of this species will impact crop productivity in the future is assessing how additional mortality agents such as predators and parasitoids will respond to climate change. In Australia (as with other Southern Hemisphere land masses), overall we expect to see a decrease in the amount of land suitable for producing high quality grapes (Jones, 2005). Regions that are currently producing high quality grapes but are at the margins of their climatic limits are most a risk from future climate change scenarios. New crop varieties grown in existing areas, and regions which become suitable for new crop types are also of concern because we have a limited understanding of what impact *E. postvittana* will have and whether suitable



Fig. 2. The predicted change in the sensitivity of areas of south-eastern Australia to light brown apple moth *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) with a 2 °C rise in temperature. The ecoclimatic index (EI) is a measure of the suitability of an area for persistence of a species based on environmental variables such as temperature, rainfall and climatic stress indices and is calculated using the CLIMEX program. Areas that show an increase in EI (dark grey) may experience more pressure from *E. postvittana* whereas areas with a decrease in EI (light grey) may experience less pressure under future climate change scenarios. This figure is based on modelling from Sutherst (2000) see figure 7, page 22.

natural enemies will be present. We have attempted to use the existing literature (mostly Australian studies) to speculate on the likely impact of climate change scenarios on the parasitoid community and highlight knowledge gaps that limit our ability to make accurate predictions.

The life-history parameters of *E. postvittana* have been studied across the south-east coast of Australia (Danthanararyana, 1983), and both climate and food impact population fluctuations. Population growth is best at temperatures 20–25 °C (max 30.7 °C, min 7.1 °C) (Danthanararyana et al., 1995). Populations of *E. postvittana* in warmer climates develop more slowly at immature stages, producing small moths but with a stronger capacity for flight in comparison to those from cooler climates (Gu and Danthanararyana, 2000). Only patchy reports exist on the distribution, parasitism rate and species composition of the 25 species of parasitoids known to attack *E. postvittana* in Australia (see Table 1 in Paull and Austin, 2006). It appears that the parasitoid complex differs between regions within Australia (Danthanararyana, 1983). Seventeen parasitoid species have been reared from *E. postvittana* in the Coonawarra region of South Australia, and 13 from south-central Victoria, with only 50% of these species in common to both regions (Paull and Austin, 2006). *E. postvittana* is attacked by approximately 4 pupal parasitoid species, 13 larval parasitoid species and 4 egg parasitoid species across Australia (Glenn et al., 1997; Paull and Austin, 2006).

Successful control of *E. postvittana* by parasitoids requires a degree of temporal synchronization between the stage of the host that is susceptible to parasitism and active parasitoid adults. The most crucial time for host–parasitoid synchronization is at the end of the winter months when insects are exiting diapause (Hassell, 1993). If the cues used by the host and the parasitoid to exit diapause are different, this may result in phenological disruptions (Hassell, 1993). Some parasitoid species, under certain conditions, do not enter diapause, but rather slow normal development and then resume development when favourable environmental conditions return (Rundle and Hoffmann, 2003). Studies on the egg parasitoid, *Trichogramma funiculatum* Carver (Hymenoptera: Trichogrammatidae), have shown that this species does not appear to go into diapause in south-eastern Australia but instead goes into a period of slow development with increased adult longevity (Rundle and Hoffmann, 2003). This would suggest that egg parasitoids in general should be more effective mortality agents because (at least in south-eastern Australia) they may be better able to track *E. postvittana* host populations in the future. However *E. postvittana* overwinters as a larva on herbaceous plants, buds of trees, and other plant material. Egg parasitoids will need to exist on alternative hosts during the winter and may take some time to build up and reach useful levels of parasitism in the summer (Danthanararyana, 1980). Field studies have shown that egg parasitism on sentinel egg cards left exposed in field sites can be completely absent some years. Paull and Austin (2006) collected several *E. postvittana* egg masses from field sites in the Coonawarra region in South Australia and yet did not find any *Trichogramma* egg parasitism. In 2007–2008 only 31 of 3000 sentinel egg cards placed throughout south-eastern Australia were parasitized despite the presence of *Trichogramma* as detected by yellow sticky traps (L. Thomson unpub. data) in contrast to parasitism rates seen earlier (Glenn et al., 1997). The reasons behind the temporally patchy effect of this group of egg parasitoids are as yet unknown, however some research suggests that this may be partially due to lack of synchronization of the life cycles of parasitoid and host (Danthanararyana, 1980). Other contributing factors may include climate variability and extreme weather events (Stireman et al., 2005), changing canopy architecture in crops (Chen and Welter, 2007), proximity of crops to alternate host species in other habitats, and the presence or absence of a regional source population (Bell et al., 2006).

A number of parasitoids that attack *E. postvittana* show widespread distributions, are capable of high rates of dispersal and will opportunistically attack alternate host species. These species may contribute to *E. postvittana* mortality in the future even under extreme climate change scenarios. Of the pupal parasitoids, *Xanthopimpla rhopaloceros* Kreiger (Hymenoptera: Ichneumonidae) has been the most studied. It is widespread in Australia (Paull and Austin, 2006) and was introduced into New Zealand to control *E. postvittana* from 1967 to 1973. It is well established in areas with climatic conditions similar to those in Australia, however not all areas with a suitable climate are occupied (Munro, 1998). The rate of dispersal for *X. rhopaloceros* has been calculated at 13–24 km per year (Munro, 1998). Of the other pupal parasitoids, *Brachymeria phya* (Walker) (Hymenoptera: Chalcididae) has been recorded parasitizing pest diamondback moths at low levels (Furlong and Zalucki, 2007), suggesting that this species may be able to utilise a range alternate hosts. The larval parasitoid, *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae), is another widespread species that attacks a variety of leafroller species in vineyards and responds well to habitat manipulation via the provision of floral resources. Irvin et al. (2006) found that parasitism of *E. postvittana* was significantly higher with Alyssum and buckwheat under vine, and *D. tasmanica* abundance was more than two-fold higher in the Alyssum treatment. However there are potential problems with provision of such an understory in terms of water availability and temperature (Bone et al., in press). *D. tasmanica* has high dispersal rates and has been recorded influencing parasitism rates of *E. postvittana* up to 300 m away from a regional source population (Bell et al., 2006). There is also a number of parasitoids species that have more limited distributions and yet could be useful mortality agents on a regional basis. A lack of information on these species limits our ability to determine how they will impact *E. postvittana* mortality in the future.

In summary, a number of management strategies can be employed now as insurance against the affects of climate change on *E. postvittana* outbreaks through the loss of natural enemies. Firstly, habitats that support alternate host species (in particular those species that are suitable hosts for egg parasitoids) need to be available in close proximity to crops, to improve spatial synchrony between *E. postvittana* and its parasitoids. Secondly, a greater understanding of changes in species during the winter months is needed, particularly with regard to the presence and proximity of alternate host species, to provide strategies for encouraging temporal synchrony. Finally, ensuring that non-crop resources such as floral resources are available at the local and regional scale should encourage greater parasitoid diversity, and improve adult longevity and fecundity.

9. Concluding remarks

The effects of climate change on pest control will be complex, particularly when crops are moved to new areas and herbivores/disease vectors escape natural enemies at least temporarily. Once enough is known about the effects of climate change on the different interacting components of tri-trophic networks and ultimately crop yield, useful predictions for future planning might become possible about climate change effects (Gutierrez et al., 2008a). When predicting direct effects of climate change, phenotypic and genotypic flexibility of herbivores and parasitoids and interactions between species need to be considered (Ives, 1995; Harrington et al., 1999; Araújo and Luoto, 2007). Many current attempts to predict likely new distributions are based on climate change scenarios use present day distributions combined with current environmental variables. A more useful predictive framework lies in the development of models based on knowledge of their phenological processes, especially of insects and their host plants.

Movement rates and management changes on farms and in the surrounding landscape will complicate predictions but might be incorporated into more complex models. Longitudinal surveys will be required to test predictions and fine tune predictive models. These should be established for key pests and beneficial complexes in local agroecosystems. Controlled environmental experiments can inform likely effects of raised temperature and/or CO₂ for insects and plants. However long-term monitoring of the demographics of herbivores and their associated parasitoids in response to climate, as well as more geographically detailed models of local climate change, will be necessary to predict the responses of ecological communities (Stireman et al., 2005).

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