



## Editorial

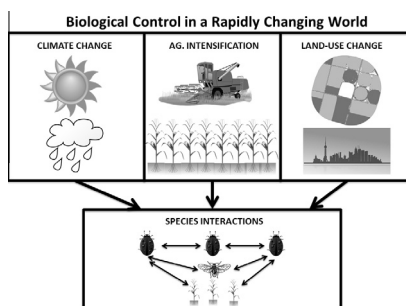
## Promoting biological control in a rapidly changing world



## HIGHLIGHTS

- We highlight advances made by articles in this special issue.
- Farm-scale and integrative studies are needed in agroecosystems.
- Climate change studies need to consider more than temperature.
- We need more studies on yields and economics to promote biological control.

## GRAPHICAL ABSTRACT



## ARTICLE INFO

## Article history:

Available online 30 April 2014

## Keywords:

Agricultural intensification  
Climate change  
Conservation  
Ecosystem functioning  
Habitat modification

## ABSTRACT

Sustainable agriculture must provide for growing human demands for crops while minimizing impacts on ecosystems. This is a daunting challenge as agroecosystems have trended towards monocultures with intensive synthetic inputs. Moreover, agricultural landscapes often lack natural habitats that are necessary to support biodiversity. Furthermore, problems associated with agricultural intensification and land-use change may be exacerbated by climate change, which increases the frequency of disturbances, modifies the suitability of habitats, and changes the way species interact. To meet this challenge, farmers must increasingly rely on integrated pest management strategies, including biological control. Biological control of arthropods, weeds, and diseases can promote the stability and diversity of agricultural communities and aid in reducing synthetic inputs. Promoting biological control may thus help farming systems adapt to a rapidly changing world. This special issue considers how multiple global change drivers such as agricultural intensification, land-use change, and climate change affect biological control. Here, we discuss these papers and highlight concepts that remain relatively unexplored in the context of global change and biological control. Future research addressing these issues will promote biological control and enhance agricultural sustainability in a rapidly changing world.

© 2014 Published by Elsevier Inc.

## 1. Introduction

Agriculture covers nearly 40% of Earth's terrestrial land (Ramankutty et al., 2008). Growth in agriculture has been spurred by rapid advances in crop breeding and technology over the past 50 years (Matson et al., 1997; Krebs et al., 1999; Benton et al., 2003). However, the expansion of agriculture has resulted in widespread loss and fragmentation of natural habitats, increased carbon emissions, and reduced biodiversity (e.g., Matson et al., 1997; Vitousek et al., 1997; Kleijn et al., 2006). A major challenge for agriculture is to continue to meet the demands of a growing human population while limiting these detrimental impacts. To meet this challenge, producers have increasingly adopted integrated pest

management (IPM) practices that limit chemical inputs through effective use of cultural, mechanical, and biological controls (Pedigo and Rice, 2008). Indeed, IPM has improved yields and economic returns for many farmers (Pedigo and Rice, 2008). For example, cotton growers in Arizona save over \$200 million per year by adopting IPM schemes that reduce insecticide use and increase yields (APMC, 2007).

Despite the abovementioned successes, biological control is threatened by rapid global change. Many predators and parasitoids rely on non-agricultural habitats for shelter, prey, alternate sources of nutrition (e.g., pollen and nectar), and overwintering sites (Landis et al., 2000; Bianchi et al., 2006; Rodriguez-Saona et al., 2012). Widespread conversion of non-agricultural habitats to

farmland can therefore reduce the fitness of biological control agents and diminish their ability to disperse into agricultural fields (Bianchi et al., 2006). However, such habitats occasionally act as sinks for natural enemy populations (Bianchi et al., 2006). Similarly, biological control agents are often highly susceptible to synthetic pesticides and fertilizers (Pedigo and Rice, 2008; Roubos et al., 2014). Reductions in the density of biological control agents due to pesticide use can lead to reduced biodiversity, secondary pest outbreaks, and losses of crop yields (Pedigo and Rice, 2008).

Climate change, species invasions, and declines in biodiversity may also limit the effectiveness of biological control. For example, changes in climate can disrupt overlap between natural enemies and pests in space and time (Davis et al., 1998; Evans et al., 2012); such phenological mismatching can limit biological control. Invasive species might similarly be detrimental for biological control if they reduce the density of biological control agents through competition or intraguild predation (Crowder and Snyder, 2010). Sih et al. (2010) provided compelling evidence that traits of certain invasive herbivores make them well adapted to become pests during periods of human-induced rapid-environmental change. However, invasive predators may also thrive during periods of rapid change (Sih et al., 2010) and this might improve biological control if these species are particularly voracious (Crowder and Snyder, 2010).

This special issue considers many of the factors that may influence biological control in a rapidly changing world, with a particular emphasis on species interactions. Here, we review conceptual advances made by papers in this special issue and highlight key areas that need to be addressed. Our objective here, and in the special issue as a whole, is to promote research that will help adapt biological control to the challenges presented to agriculture in the 21st century.

## 2. Concepts covered in this issue

The papers in this special issue cover a range of topics, but in general can be grouped into the effects of three global change drivers: (1) agricultural intensification; (2) land-use change; and (3)

climate change on agricultural communities and interactions between natural enemies, pests, and plants in agroecosystems (Fig. 1). Many of the papers cut across multiple areas (Fig. 1), and we highlight major concepts from each here.

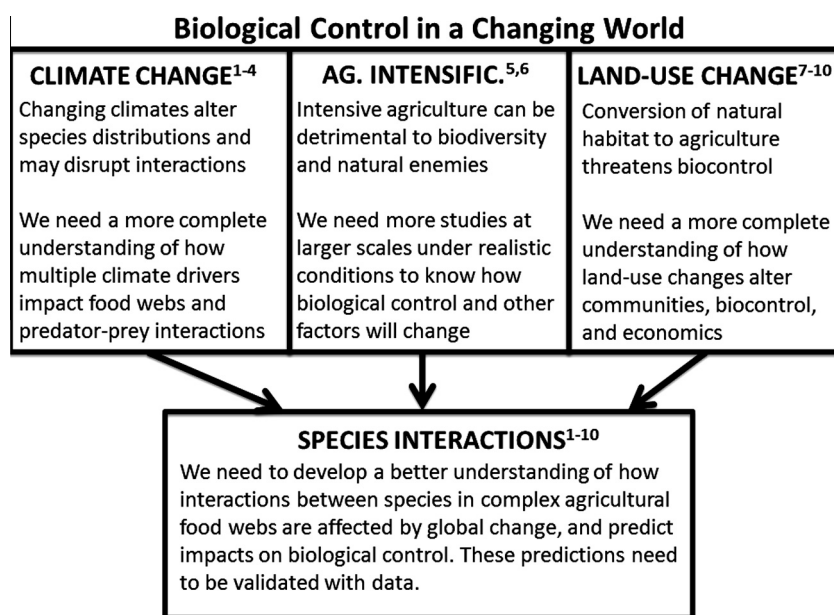
### 2.1. Agricultural intensification and biological control

Agricultural systems around the world have intensified by producing more crops per unit area, or per unit time, to meet the demands of a growing human population (Matson et al., 1997; Vitousek et al., 1997). This presents challenges for biological control. Frequent applications of broad-spectrum pesticides for insect and weed control can kill predator and parasitoid species and alter their development and behavior (Croft and Brown, 1975; Cloyd, 2012; Roubos et al., 2014). A myriad of strategies exist to adapt biological control in a chemically-intensive world, including site-specific applications, low doses of pesticides, genetically-modified crops, increasing pesticide selectivity, and refuges of non-sprayed areas. Incorporating these practices in IPM systems will improve biological control in modern intensive agricultural systems.

Agricultural intensification can also influence biological control by altering the structure of natural enemy communities (Crowder and Jabbour, 2014). Intensive systems often have reduced natural enemy diversity, which can weaken biological control (Griffin et al., 2013). For example, more sustainable agricultural practices such as organic, biodynamic, or integrated agriculture might help mitigate this by promoting more diverse and effective natural enemy communities (Crowder et al., 2010, 2012; Crowder and Jabbour, 2014). Other environmentally-friendly practices such as conservation tillage or no-till that promote abundant and diverse natural enemy communities will also likely improve biological control.

### 2.2. Land-use change and biological control

Global landscapes are being modified due to agriculture and changing concentrations of human populations in urban areas (Burkman and Gardiner, 2014; Chisholm et al., 2014; Roitberg



**Fig. 1.** Conceptual layout of the special issue, including the challenges facing biological control associated with each of three global change drivers: (1) climate change; (2) agricultural intensification; and (3) land-use change on biological control. Each of these drivers also affects species interactions. Including in each conceptual area are the papers in the special issue addressing those topics. 1. A'Bear et al.; 2. Schmitz and Barton; 3. Tylianakis and Binzer; 4. Welch and Harwood; 5. Crowder and Jabbour; 6. Roubos et al.; 7. Burkman and Gardiner; 8. Chisholm et al.; 9. Dreyer et al.; 10. Roitberg and Gillespie.

and Gillespie, 2014). Many studies have shown how the conversion of habitat to cultivated acreage can influence biological control. For example, agroecosystems surrounded by large acreages of natural habitat generally have more diverse and abundant natural enemy assemblages than those bordered by farmland (Chisholm et al., 2014). Moreover, Letourneau et al. (2011) showed crop damage decreased on farms embedded in complex landscapes. Urban landscapes are also of increasing importance for agriculture due to greater demand for locally-sourced food and changing populations of humans in urban areas (Burkman and Gardiner, 2014). In general, promoting more diverse vegetation and large natural habitat patches in urban centers might promote biodiversity of natural enemies and biological control (Burkman and Gardiner, 2014). Understanding how these dynamics affect biological control is a critical issue in need of further research due to the expansion of urban agriculture.

Global land-use change has also led to habitat fragmentation, which increases connections between vastly different landscapes, such as urban–rural boundaries. Dreyer and Gratton (2014) show that connectivity of patches in agroecosystems and other interfaces might influence biological control. For example, influxes of midges (Diptera: Nematocera) from water habitats into terrestrial settings can boost natural enemy populations by providing alternative prey that enhance population growth and ultimately increase pest control (Dreyer and Gratton, 2014). Thus, a better understanding of linkages between habitats, natural enemy and pest dispersal, and biological control will improve our ability to design landscapes to maximize biological control.

### 2.3. Climate change and biological control

Understanding how climate change might impact biological control is challenging because of the complex nature of interactions in agricultural food webs (Sutherst et al., 2007; Staudinger et al., 2013; Schmitz and Barton, 2014; Tyljanakis and Binzer, 2014; Welch and Harwood, 2014). Rising surface temperatures, for example, can directly affect biological control by causing variation in overlap between natural enemies and pests in space and time (Harrington et al., 1999; Bale et al., 2002; Both et al., 2009; Welch and Harwood, 2014). Evans et al. (2012) showed that the warming temperatures disrupted biological control of the cereal leaf beetle, *Oulema melanopus* L. (Coleoptera: Chrysomelidae), by the parasitoid wasp *Tetrastichus julis* Walker (Hymenoptera: Eulophidae). In this system, the beetles' development was more impacted by warming temperatures than the parasitoid, creating phenological misalignment between the parasitoid and prey. Changes in species ranges due to warming temperatures might also impact biological control (Davis et al., 1998). For example, if pests are able to expand their ranges more rapidly than their natural enemies, they might escape predation and reach outbreak levels in their new ranges.

Although several studies explore how overlap between species might vary under predicted climate change (Welch and Harwood, 2014), few have examined effects of climate change on species interactions (Gilman et al., 2010; Barton and Ives 2014; A'Bear et al., 2014; Schmitz and Barton, 2014; Tyljanakis and Binzer, 2014). Tyljanakis and Binzer (2014) note that while factors such as nitrogen deposition have predictable effects on plant–herbivore–predator interactions, responses of food webs to other climate change drivers are highly variable. A'Bear et al. (2014) also describe how changing precipitation, carbon and nitrogen deposition, and temperature influence populations of below-ground species. By influencing below-ground herbivores and predators, and potentially plant volatile profiles, climate change might also indirectly affect above-ground herbivores through complex below–aboveground interactions (A'Bear et al., 2014). More research on

food webs could improve our understanding of how agricultural communities will respond to climate change.

While research on food web interactions is rare, Schmitz and Barton (2014) review how variation in climatic drivers might influence interactions between particular species. For example, in an old-field system Barton and Schmitz (2009) showed that rising temperatures caused increased spatial overlap between two spider species, *Phidippus rimator* Peckham (Araneae: Salticidae) and *Pisaurina mira* Walckenaer (Araneae: Pisauridae), resulting in increased intraguild predation and a weakening of predation on the grasshopper *Melanoplus femurrubrum* De Geer (Orthoptera: Acrididae). Ultimately, to understand how climate change might influence biological control, we need to better understand how interactions between species such as these might vary across space and time (Welch and Harwood, 2014).

## 3. Research needs for biological control in intensive agricultural systems

### 3.1. Farm-scale studies

Many studies have examined broad effects of agricultural intensification on natural enemy communities. For example, pesticides have detrimental effects on predators and parasitoids (Roubos et al., 2014). However, all too often we have limited insight into the effectiveness of natural enemies in production farming systems. Molecular techniques such as gut-content analysis allow scientists to more precisely determine the types of prey fed upon (e.g., Harwood et al., 2007; Lundgren et al., 2009) or parasitized (e.g., Traugott et al., 2008; Macfadyen et al., 2009) by natural enemies. However, while these methods provide evidence of trophic linkages, they do not quantify biological control. Thus, we still often have limited insight into the true impact of biological control agents on farms. Even when statistically significant reductions in pest populations are recorded, it is usually unclear whether this translates to improved crop yields, as many factors affect crop growth.

More studies are needed that demonstrate causal relationships between natural enemies, pests, yields, and economic returns. This could require large-scale manipulations of natural enemies on farms. Several studies have done this, and shown that biological control can provide positive economic benefits for pests (reviewed by Ferron and Deguine, 2005). However, when large-scale manipulations are not feasible, statistical techniques such as path analysis, principal components analysis, or general linear models might be used to “tease-apart” factors operating in agroecosystems to isolate the effectiveness of biological control.

### 3.2. Examining specific crop management strategies

Several studies have shown that reduced-input farming systems promote abundance and diversity of natural enemy communities (Bengtsson et al., 2005; Hole et al., 2005; Crowder et al., 2010, 2012); in turn, experimental studies have shown these communities provide more effective biological control (Snyder et al., 2006; Crowder et al., 2010; Griffin et al., 2013; Northfield et al., 2010). However, we often have limited insight into which specific management strategies promote abundant, diverse, and highly-effective biological control communities.

Reduced-input farming systems often have diverse plant communities that may support alternative prey and provide shelter for natural enemies, allowing them to reach high densities and more effectively colonize crop plants (Crowder and Jabbour, 2014). Similarly, Gil et al. (2008) showed that the abundance of three microbial natural enemies, Actinomycetes, *Trichoderma* spp.

(Hypocreales: Hypocreaceae), and *Gliocladium* spp. (Hypocreales: Hypocreaceae), were higher in no-till compared with conventional till peanut farms. In turn, these species lowered the incidence of Fusarium root rot on peanut plants in no-till systems. Future studies should similarly attempt to characterize entire farming systems or use whole-farm (or large plot) manipulations to identify specific factors that promote abundant and effective natural enemy populations. Moreover, while much work has been done to compare specific farming systems (i.e., conventional vs. organic), fewer studies have examined how combinations of tactics from different farming systems (i.e., integrated farming) might influence biological control. Identifying the combination of tactics that promotes effective biological control in different contexts is essential for adapting biological control to changing agricultural systems.

### 3.3. Biological control and other ecosystem services

To be sustainable, agroecosystems must promote a myriad of natural ecosystem services such as biological control, pollination, and nutrient cycling. Yet, few studies have examined interactions between these factors. [Swope and Parker \(2012\)](#) investigated complex interactions between an invasive weed, the yellow-star thistle (*Centaurea solstitialis* L. (Asterales: Asteraceae)), the yellow star-thistle hairy weevil that acted as a bud herbivore and seed predator (*Eustenopus villosus* Boheman (Coleoptera: Curculionidae)), a fly seed predator (*Chaetorellia succinea* Costa (Diptera: Tephritidae)) and the honey bee *Apis mellifera* L. (Hymenoptera: Apidae), the primary weed pollinator. In this system, bud herbivory by *E. villosus* decreased the attractiveness of the weed to the more voracious predator, *C. succinea*, weakening overall biological control. However, honey bees were deterred from flowers due to oviposition by *C. succinea*, which decreased plant fitness and strengthened biological control. This study exemplifies how interactions between plants, herbivores, predators, and pollinators can influence biological control. More work is needed, however, to explore how multiple ecosystem service providers interact to influence biological control and other processes in agroecosystems.

## 4. Research needs for biological control in changing landscapes

### 4.1. Habitat diversification, crop yields, and economics

While multiple studies have examined the relationship between habitat diversity and natural enemy communities, few have examined impacts on yields and economic returns in farming systems. Yet, because high yields and increased profitability should be the end-goal of any well-designed biological control program, studies that explore these factors are critical. In a seminal study, [Landis et al. \(2008\)](#) examined the economics of biological control in agricultural landscapes of the midwestern United States. In this study, the authors examined predation of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), by natural enemies at many field sites in Iowa, Michigan, Minnesota, and Wisconsin. These data were linked with an economic model to demonstrate that biological control services were valued at \$239 million annually. However, the authors showed that conversion of land to maize for biofuel production reduced the value of these services by 24%, or \$58 million annually.

[Werling et al. \(2014\)](#) conducted a similar study and showed that maize landscapes had higher biomass production than perennial grasslands. This was not surprising given that maize is a widely grown biofuel crop. However, perennial grasslands had greater methane consumption, pest suppression, pollination, and biodiversity. Although the authors did not examine economics, this study provided compelling evidence that such positive externali-

ties should be considered in studies of biological control across variable landscapes. These studies illustrate how biological control and other ecosystem services can be valued in landscapes of varying intensity and diversity. More studies of this type would improve our ability to design biological control strategies that maximize profitability and ecosystem functioning across variable landscapes.

### 4.2. Integrating models with data

As discussed by [Roitberg and Gillespie \(2014\)](#), studies that use models to explore biological control across variable landscapes remain rare. Yet, due to the difficulties involved with manipulating natural enemy communities in production farming systems, models can provide insight into factors affecting biological control across landscapes. For example, [Bianchi et al. \(2013\)](#) examined how natural enemies and insecticides affected pest control in simulated organic and conventional farming systems. They showed that disruptive effects of insecticide use across landscapes could be mitigated by clustering fields with no insecticide use (i.e., organic) or by using selective pesticides. They also showed that behavioral traits of simulated parasitoids might mediate biological control, with parasitoids having high-attack rates requiring less acreage under organic management to provide maximum control. Finally, a mixture of organic and conventional farms was expected to provide maximum biological control ([Bianchi et al., 2013](#)). Importantly, as farmers have many choices to make in terms of their management practices and spatial configuration of their crops, similar studies might improve the ability to design IPM programs in variable crop landscapes.

### 4.3. Resource pulses

Resource pulses are infrequent events of super-abundant resource availability ([Yang et al., 2010](#)), which have significant impacts on consumers ([Holt, 2008; Yang et al., 2010](#)). Like many other environmental perturbations, resource pulses, such as rapid pest outbreaks, are expected to increase in frequency due to global change. This could affect biological control through multiple processes. For example, [Korpimäki and Norrdahl \(1991\)](#) showed that short-eared owls, *Asio flammeus* Pontoppidan (Strigiformes: Strigidae), and long-eared owls, *Asio otus* L. (Strigiformes: Strigidae), had a remarkable ability to respond to pulses of their prey, two vole species (*Microtus agrestis* L. (Rodentia: Cricetidae) and *Microtus epiroticus* Miller (Rodentia: Cricetidae)). In a long-term study in Finland, vole pests fluctuated widely in density both within and across-growing seasons. The highly mobile owl predators were able to respond without time lags to fluctuations in the vole prey and increased their per-capita predation when voles were at peak densities, improving biological control. Similarly, [Gratton et al. \(2008\)](#) showed that resource pulses of midges (Diptera: Nematocera) from lakes boosted the density of linyphiid spiders (Araneae: Linyphiidae), lycosid spiders (Araneae: Lycosidae), and Opiliones, three important terrestrial predators. The increased density of these predators ultimately improved biological control near the lakes due to the resource pulses ([Dreyer and Gratton, 2014](#)). Additionally, within agroecosystems and surrounding habitats, pollen frequently provides an important pulse resource to natural enemies (e.g., [Lundgren et al., 2004; Peterson et al., 2010](#)) and these (and other) non-prey foods can provide valuable nutritional benefit to food-limited predators ([Lundgren, 2009](#)). Such a pulse resource thereby enhances survival of natural enemies and can increase subsequent biological control services provided by an enhanced population of predators. Despite these examples, empirical studies examining effects of resource pulses on biological control remain

sparse, and more studies are needed to characterize this important process in ecosystems.

#### 4.4. Genetically modified crops

Crops that are genetically modified to fight pests, such as those engineered to express insecticidal proteins from the bacteria *Bacillus thuringiensis* Berliner (Bacillales: Bacillaceae) (Bt crops), are increasingly grown throughout the world (James, 2012). Several studies have indicated that Bt crops typically do not have detrimental impacts on natural enemies (Romeis et al., 2006; Shelton et al., 2009). Moreover, because genetically-modified crops can reduce the use of broad-spectrum insecticides in crop systems, populations of natural enemies can be boosted (Romeis et al., 2006). Lu et al. (2012) showed that widespread use of Bt cotton in China for control of the cotton bollworm, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae), indirectly improved biological control of multiple aphid species (Hemiptera: Aphididae) by communities of lady beetles (Coleoptera: Coccinellidae), lacewings (Neuroptera: Chrysopidae) and spiders (Araneae). In this study, Bt cotton reduced the area-wide use of insecticides, resulting in an increase in natural enemy densities. These natural enemies moved out of cotton fields into neighboring cotton, peanut, maize, and soybean crops where they decreased aphid densities (Lu et al., 2012). This study shows how Bt crops might benefit biological control through a complex series of trophic changes. Similar studies on genetically-modified crops, and other pesticide-reducing tactics, could provide further insight into methods to improve area-wide biological control.

### 5. Research needs for biological control in changing climates

#### 5.1. Moving beyond studies of temperature and instantaneous change

Most studies examining effects of climate change on biological control have focused on instantaneous changes in temperature. Yet, climate change does not result in large, instantaneous variation; rather, subtle changes accumulate over many years. Experimental studies with fluctuating temperatures better mimic natural variability while those mimicking extreme events such as heat shocks may better anticipate climate change impacts. Studies that incorporate this variability are appearing (e.g., Harmon et al., 2009; Butler and Trumble, 2010; Bahar et al., 2012; Knapp and Nedved, 2013; Sentis et al., 2013) but they are scarce. Similarly, climate change research needs to expand into new areas such as variation in precipitation, wind, CO<sub>2</sub>, and combinations of these factors. For example, Barton and Ives (2014) showed that drought reduced quality of alfalfa plants, which lowered pea aphid, *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae) densities. This indirectly weakened biological control of spotted aphids, *Therioaphis maculata* Buckton (Hemiptera: Aphididae), because ladybeetle predators experienced reduced fitness when pea aphid densities were low. Such complex interactions are likely to be the norm, rather than the exception, in climate change research. In turn, more studies examining multiple climatic drivers that move beyond simple manipulations of temperature are required (see, for example, Hoover and Newman, 2004; Dyer et al., 2013).

#### 5.2. Climatic effects on food-webs

Several studies have shown how interactions in food webs might affect biological control. For example, Chase (1996) showed that reduced temperature and radiation increased biological control of a grasshopper, *Melanoplus sanguinipes* F. (Orthoptera: Acrididae), by a wolf spider, *Pardosa* spp. (Araneae: Lycosidae). This

effect occurred because grasshoppers fed less in reduced temperature environments, allowing spiders to exert stronger top-down control. In contrast, Barton and Schmitz showed how biological control of grasshoppers (*M. femurrubrum* De Geer (Orthoptera: Acrididae)) by two generalist spiders (*Phidippus rimator* Chamberlin & Ivie (Araneae: Salticidae) and *Pisaurina mira* Walckenaer (Araneae: Pisauridae)) might be weakened by climate change (Barton and Schmitz, 2009; Schmitz and Barton, 2014). In this system, increased temperatures resulted in greater spatial overlap between spiders and strong intraguild predation, releasing grasshoppers from predation and weakening biological control. Despite this literature, few studies have examined how interactions within food webs might influence biological control during periods of climate change (de Sassi and Tylianakis, 2012; Tylianakis and Binzer, 2014). Yet, such interactions might significantly impact biological control. For example, Gilman et al. (2010) suggested that specialists are more likely to be influenced by climate change than generalists because they are less capable of adapting to shifts in prey communities. If true, biological control might be more resilient to climate change in food webs comprised of many generalists. However, as discussed by Tylianakis and Binzer (2014), research on predator-prey food webs is lacking. Research on food-web interactions in changing climates could improve our understanding of biological control in future climates.

#### 5.3. Incorporating host-plant effects

Most research on climate change and biological control has focused only on predator and prey trophic levels. This ignores important interactions with crop plants that may significantly alter the effectiveness of biological control (Gutierrez et al., 2008; A'Bear et al., 2014). For example, Dyer et al. (2013) showed that increases in CO<sub>2</sub> or temperature decreased nutritional quality of alfalfa host plants. On nutritionally-deficient plants, beet-armyworm, *Spodoptera exigua* Hubner (Lepidoptera: Noctuidae), caterpillars had reduced development time. In turn, larvae of the parasitoid wasp *Cotesia marginiventris* Cresson (Hymenoptera: Braconidae) were unable to complete development and parasitoids went locally extinct, weakening biological control. Similarly, studies have shown that the production of herbivore induced plant volatiles are sensitive to ambient temperatures (Gouinguene and Turlings, 2002; Yuan et al., 2009). Alterations in volatiles, which are used by natural enemies to locate plants, could alter biological control. Nonetheless, relatively few studies have examined how changes in host plant physiology and chemical signaling might indirectly influence interactions between natural enemies and pests. Understanding these interactions would therefore improve our understanding of how climate change might mediate the effectiveness of biological control.

#### 5.4. Evolutionary factors

Evolution mediates the effects of climate change on species interactions (Hoffmann and Sgro, 2011; McEvoy et al., 2012; Szucs et al., 2012; Norberg et al., 2012; Northfield and Ives, 2013). Harmon et al. (2009) showed how evolution in pea aphids affected biological control by two lady beetles, *Coccinella septempunctata* L. (Coleoptera: Coccinellidae) and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae). In this study, the authors showed that episodic heat shocks and predation led to extinction of pea aphid populations when aphids could not evolve. However, when aphids were able to evolve, selection led to an increase in frequency of aphids harboring symbionts that provided protection from high temperatures. In turn, aphids with protective symbionts had rapid population growth rates despite persistent heat shocks, weakening biological control. Similarly, Barton (2011) showed that

local-adaptation in spiders affected their ability to provide control of grasshoppers. In a reciprocal transplant experiment, spiders from a warm location (New Jersey, USA) provided similar biological control across a temperature gradient. However, spiders from a cool-location (Vermont, USA) were more effective at providing biological control in a warm environment, suggesting they were limited by cold temperatures in their native range. These results are relevant to classical biological control, as one might match populations for climatic similarity in imported and native ranges to maximize biological control. Further studies exploring impacts of evolution on biological control are needed to improve the effectiveness of biological control in a rapidly changing world.

## 6. Conclusions

The articles in this special issue highlight key research areas linking biological control to a rapidly changing world. Drivers of global change such as agricultural intensification, climate change, and land-use change threaten the biodiversity and stability of natural enemy communities and biological control. While we have made progress in studying the impacts of these and other global change drivers on biological control, more research is needed. We propose that more integrative approaches and farm-scale studies will improve our understanding of the factors influencing biological control in real production landscapes.

## Acknowledgments

This project was supported by a USDA AFRI Grant (WNW-2010-05123) to DWC and University of Kentucky Agricultural Experiment Station State Projects KY008055 and KY008063 to J.D.H. The information reported in this paper (No. 14-08-023) is part of a project of the University of Kentucky Agricultural Experiment Station and is published with the approval of the Director.

## References

- A'Bear, A., Johnson, S., Jones, H., 2014. Putting the 'upstairs-downstairs' into ecosystem service: what can aboveground-belowground ecology tell us? *Biol. Control* 75, 97–107.
- Arizona Pest Management Center (APMC), 2007. IPM: Protecting Arizona's Environment, Human Health and Economic Vitality. University of Arizona Cooperative Extension, Tuscon, AZ, USA.
- Bahar, M.H., Soroka, J.J., Dossdall, L.M., 2012. Constant versus fluctuating temperatures in the interactions between *Plutella xylostella* (Lepidoptera: Plutellidae) and its larval parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Environ. Entomol.* 41, 1653–1661.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E., Harrington, R., Hartley, S.E., Jones, T.H., Lindroth, R.L., Press, M.C., Symrioudis, I., Watt, A.D., Whittaker, J.B., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biol.* 8, 1–16.
- Barton, B., 2011. Local adaptation to temperature conserves top-down control in a grassland food web. *Proc. R. Soc. Lond. B* 278, 3102–3107.
- Barton, B.T., Ives, A.R., 2014. Species interactions and a chain of indirect effects driven by reduced precipitation. *Ecology* 95, 486–494.
- Barton, B., Schmitz, O.J., 2009. Experimental warming transforms multiple predator effects in a grassland food web. *Ecol. Lett.* 12, 1317–1325.
- Bengtsson, J., Ahnstrom, J., Weibull, A.-C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J. Appl. Ecol.* 42, 261–269.
- Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* 4, 182–188.
- Bianchi, F.J.J.A., Booij, C.J.H., Tscharntke, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity, and natural pest control. *Proc. R. Soc. B* 273, 1715–1727.
- Bianchi, F.J.J.A., Ives, A.R., Schellhorn, N.A., 2013. Interactions between conventional and organic farming for biocontrol services across the landscape. *Ecol. Appl.* 23, 1531–1543.
- Both, C., van Asch, M., Bijlsma, R.G., van den Burg, A.B., Visser, M.E., 2009. Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J. Anim. Ecol.* 78, 73–83.
- Burkman, C.E., Gardiner, M.M., 2014. Urban greenspace design and landscape context influence natural enemy community composition and function. *Biol. Control* 75, 58–67.
- Butler, C.D., Trumble, J.T., 2010. Predicting population dynamics of the parasitoid *Cotesia marginiventris* (Hymenoptera: Braconidae) resulting from novel interactions of temperature and selenium. *Biocontrol Sci. Technol.* 20, 391–406.
- Chase, J., 1996. Abiotic controls of trophic cascades in a simple grassland food chain. *Oikos* 77, 495–506.
- Chisholm, P.J., Gardiner, M.M., Moon, E.G., Crowder, D.W., 2014. Tools and techniques for investigating impacts of habitat complexity on biological control. *Biol. Control* 75, 48–57.
- Cloyd, R.A., 2012. Indirect effects of pesticides on natural enemies. In: Soundararajan, R.P. (Ed.), *Pesticides—Advances in Chemical and Botanical Pesticides*. InTech, Rijeka, Croatia, pp. 127–150.
- Croft, B.A., Brown, A.W.A., 1975. Responses of arthropod natural enemies to insecticides. *Annu. Rev. Entomol.* 20, 285–335.
- Crowder, D.W., Jabbour, R., 2014. Relationships between biodiversity and biological control in agroecosystems: current status and future challenges. *Biol. Control* 75, 8–17.
- Crowder, D.W., Northfield, T.D., Gomulkiewicz, R., Snyder, W.E., 2012. Conserving and promoting evenness: organic farming and fire-based wildland management as case studies. *Ecology* 93, 2001–2007.
- Crowder, D.W., Northfield, T.D., Strand, M.R., Snyder, W.E., 2010. Organic agriculture promotes evenness and natural pest control. *Nature* 466, 109–112.
- Crowder, D.W., Snyder, W.E., 2010. Eating their way to the top? Mechanisms underlying the success of invasive insect generalist predators. *Biol. Invasions* 12, 2857–2876.
- Davis, A., Jenkinson, L., Lawton, J., Shorrocks, B., Wood, S., 1998. Making mistakes when predicting shifts in species range in response to global warming. *Nature* 391, 783–786.
- de Sassi, C., Tylianakis, J.M., 2012. Climate change disproportionately increases herbivore over plant or parasitoid biomass. *PLoS One* 7, e40557.
- Dreyer, J., Gratton, C., 2014. Habitat linkages in conservation biological control: lessons from the land–water interface. *Biol. Control* 75, 68–76.
- Dyer, L., Richards, L., Short, S., Dodso, C., 2013. Effects of CO<sub>2</sub> and temperature on tritrophic interactions. *PLoS One* 8, e62528.
- Evans, E.W., Carlile, N.R., Innes, M.B., Pitigala, N., 2012. Warm springs reduce parasitism of the cereal leaf beetle through phenological mismatch. *J. Appl. Entomol.* 137, 321–400.
- Ferron, P., Deguine, J.-P., 2005. Crop protection, biological control, habitat management and integrated farming. A review. *Agron. Sustain. Dev.* 25, 17–24.
- Gil, S.V., Pedelini, R., Oddino, C., Zuza, M., Marinelli, A., March, G.J., 2008. The role of potential biocontrol agents in the management of peanut root rot in Argentina. *J. Plant Pathol.* 90, 35–41.
- Gilman, S., Urban, M., Tewksbury, J., Gilchrist, G., Holt, R., 2010. A framework for community interactions under climate change. *Trends Ecol. Evol.* 25, 325–331.
- Gouinguene, S.P., Turlings, T.J., 2002. The effects of abiotic factors on induced volatile emissions in corn plants. *Plant Physiol.* 129, 1296–1307.
- Gratton, C., Donaldson, J., Zanden, M.J.V., 2008. Ecosystem linkages between lakes and the surrounding terrestrial landscape in northeast Iceland. *Ecosystems* 11, 764–774.
- Griffin, J.N., Byrnes, J.E., Cardinale, B.J., 2013. Predator richness and prey suppression: meta-analysis reveals importance of scale and phylogenetic diversity. *Ecology* 94, 2180–2218.
- Gutierrez, A.P., Ponti, L., d'Oultremont, T., Ellis, C.K., 2008. Climate change effects on poikilotherm tritrophic interactions. *Clim. Change* 87, S167–S192.
- Harmon, J., Moran, N., Ives, A., 2009. Species response to environmental change: impacts of food web interactions and evolution. *Science* 323, 1347–1350.
- Harrington, R., Woiwod, I., Sparks, T., 1999. Climate change and trophic interactions. *Trends Ecol. Evol.* 14, 146–150.
- Harwood, J.D., Desneux, N., Yoo, H.J.S., Rowley, D.L., Greenstone, M.H., Obyrick, J.J., O'Neil, R.J., 2007. Tracking the role of alternative prey in soybean aphid predation by *Orius insidiosus*: a molecular approach. *Mol. Ecol.* 16, 4390–4400.
- Hoffmann, A., Sgro, C., 2011. Climate change and evolutionary adaptation. *Nature* 470, 479–485.
- Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, P.V., Evans, A.D., 2005. Does organic farming benefit biodiversity? *Biol. Conserv.* 122, 113–130.
- Holt, R.D., 2008. Theoretical perspectives on resource pulses. *Ecology* 89, 671–681.
- Hoover, J.K., Newman, J.A., 2004. Tritrophic interactions in the context of climate change: a model of grasses, cereal aphids and their parasitoids. *Global Change Biol.* 10, 1197–1208.
- James, C., 2012. Global status of commercialized biotech/GM crops: 2012. International Service for the Acquisition of Agri-Biotech Applications Brief No. 44, Ithaca, NY, USA.
- Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Juhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol. Lett.* 9, 243–254.
- Knapp, M., Nedved, O., 2013. Gender and timing during ontogeny matter: effects of a temporary high temperature on survival, body size and colouration in *Harmonia axyridis*. *PLoS One* 8, e74984.
- Korpimäki, E., Norrdahl, K., 1991. Numerical and functional responses of kestrels, short-eared owls, and long-eared owls to vole densities. *Ecology* 72, 814–826.
- Krebs, J.R., Wilson, J.D., Bradbury, R.B., Siriwardena, G.M., 1999. The second silent spring? *Nature* 400, 611–612.
- Landis, D.A., Gardiner, M.M., van der Werf, W., Swinton, S.M., 2008. Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proc. Natl. Acad. Sci. U.S.A.* 105, 20552–20557.

- Landis, D.A., Wratten, S.D., Gurr, G.M., 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45, 175–201.
- Letourneau, D.K., Armbrrecht, I., Rivera, B.S., Lerma, J.M., Carmona, E.J., Daza, M.C., Escobar, S., Galindo, V., Gutierrez, C., Lopez, S.D., Mejia, J.L., Rangel, A.M.A., Rangel, J.H., Rivera, L., Saavedra, C.A., Torres, A.M., Trujillo, A.R., 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecol. Appl.* 21, 9–21.
- Lu, Y., Wu, K., Jiang, Y., Guo, Y., Desneux, N., 2012. Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. *Nature* 487, 362–365.
- Lundgren, J.G., 2009. Relationships of Natural Enemies and Non-Prey Foods. Springer, Dordrecht, Netherlands.
- Lundgren, J.G., Nichols, S., Prischmann, D.A., Ellsbury, M.M., 2009. Seasonal and diel activity patterns of generalist predators associated with *Diabrotica virgifera* immatures (Coleoptera: Chrysomelidae). *Biocontrol Sci. Technol.* 19, 327–333.
- Lundgren, J.G., Razzak, A.A., Weidenmann, R.N., 2004. Quantification of consumption of corn pollen by the predator *Coleomegilla maculata* (Coleoptera: Coccinellidae) during anthesis in an Illinois cornfield. *Agric. For. Entomol.* 7, 958–963.
- Macfadyen, S., Gibson, R., Polaszek, A., Morris, R.J., Craze, P.G., Planque, R., Symondson, W.O.C., Memmott, J., 2009. Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecol. Lett.* 12, 229–238.
- Matson, P.A., Parton, W.J., Power, A.G., Swift, M.J., 1997. Agricultural intensification and ecosystem properties. *Science* 277, 504–509.
- McEvoy, P.B., Higgs, K.M., Coombs, E.M., Karacetin, E., Starcevic, L.A., 2012. Evolving while invading: rapid adaptive evolution in juvenile development time for a biological control organism colonizing a high-elevation environment. *Evol. Appl.* 5, 524–536.
- Norberg, J., Urban, M., Vellend, M., Klausmeier, C., Loeuille, N., 2012. Eco-evolutionary responses of biodiversity to climate change. *Nat. Clim. Change* 2, 747–751.
- Northfield, T., Ives, A., 2013. Coevolution and the effects of climate change on interacting species. *PLoS Biol.* 11, e1001685.
- Northfield, T.D., Snyder, G.B., Ives, A.R., Snyder, W.E., 2010. Niche saturation reveals resource partitioning among consumers. *Ecol. Lett.* 13, 338–348.
- Pedigo, L.P., Rice, M., 2008. *Entomology and Pest Management*, sixth ed. Prentice Hall, Upper Saddle River, NJ, USA.
- Peterson, J.A., Romero, S., Harwood, J.D., 2010. Pollen interception by linyphiid spiders in a corn agroecosystem: implications for dietary diversification and risk assessment. *Arthropod Plant Interact.* 4, 207–217.
- Ramunkutty, N., Evan, A.T., Monfreda, C., Foley, J.A., 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochem. Cycles* 22, GB1003.
- Rodriguez-Saona, C., Blaauw, B.R., Isaacs, R., 2012. Manipulation of natural enemies in agroecosystems: habitat and semiochemicals for sustainable insect pest control. In: Soloneski, S. (Ed.), *Integrated Pest Management and Pest Control – Current and Future Tactics*. InTech, Rijeka, Croatia, pp. 89–126.
- Roitberg, B.D., Gillespie, D.R., 2014. Natural enemies on the landscape – an integrated theory. *Biol. Control* 75, 39–47.
- Romeis, J., Meissle, M., Bigler, F., 2006. Transgenic crops expressing *Bacillus thuringiensis* toxins and biological control. *Nat. Biotechnol.* 24, 63–71.
- Roubos, C.R., Rodriguez-Saona, C., Isaacs, R., 2014. Scale-dependent impacts of insecticides on arthropod biological control. *Biol. Control* 75, 28–38.
- Schmitz, O., Barton, B., 2014. Climate change effects on behavioral and physiological ecology of predator–prey interactions: implications for conservation biological control. *Biol. Control* 75, 87–96.
- Sentis, A., Hemptinne, J.L., Brodeur, J., 2013. Effects of simulated heat waves on an experimental plant–herbivore–predator food chain. *Global Change Biol.* 19, 833–842.
- Shelton, A.M., Naranjo, S.E., Romeis, J., Hellmich, R.L., Wolt, J.D., Federici, B.A., Albajes, R., Bigler, F., Burgess, E.P.J., Dively, G.P., Gatehouse, A.M.R., Malone, L.A., Roush, R., Sears, M., Sehnal, F., 2009. Setting the record straight: a rebuttal to an erroneous analysis on transgenic insecticidal crops and natural enemies. *Transgenic Res.* 18, 317–322.
- Sih, A., Stamps, J., Yang, L.H., McElreath, R., Ramenofsky, M., 2010. Grand challenges: behavior as a key component of integrative biology in a human-altered world. *Integr. Comp. Biol.* 50, 934–944.
- Snyder, W.E., Snyder, G.B., Finke, D.L., Straub, C.S., 2006. Predator biodiversity strengthens herbivore suppression. *Ecol. Lett.* 9, 789–796.
- Staudinger, M.D., Carter, S.L., Cross, M.S., Dubois, N.S., Duffy, J.E., Enquist, C., Griffis, R., Hellmann, J.J., Lawler, J.J., O’Leary, J.O., Morrison, S.A., Sneddon, L., Stein, B.A., Thompson, L.M., Turner, W., 2013. Biodiversity in a changing climate: a synthesis of current and project trends in the US. *Front. Ecol. Environ.* 11, 465–473.
- Sutherst, R.W., Maywald, G.F., Bourne, A.S., 2007. Including species interactions in risk assessments for global change. *Global Change Biol.* 13, 1–17.
- Swope, S.M., Parker, I.M., 2012. Complex interactions among biocontrol agents, pollinators, and an invasive weed: a structural equation modeling approach. *Ecol. Appl.* 22, 2122–2134.
- Szucs, M., Schaffner, U., Price, W.J., Schwarzlaender, M., 2012. Post-introduction evolution in the biological control agent *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae). *Evol. Appl.* 5, 858–868.
- Traugott, M., Schallhart, N., Kaufmann, R., Juen, A., 2008. The feeding ecology of elaterid larvae in central European arable land: new perspectives based on naturally occurring stable isotopes. *Soil Biol. Biochem.* 40, 342–349.
- Tylianakis, J.M., Binzer, A., 2014. Effects of global environmental changes on parasitoid–host food webs and biological control. *Biol. Control* 75, 77–86.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth’s ecosystems. *Science* 277, 494–499.
- Yuan, J.S., Himanen, S., Holopainen, J.K., Chen, F., Stewart, C.N.J., 2009. Smelling climate change: plant volatile organic compounds in changing environments. *Trends Ecol. Evol.* 24, 323–331.
- Welch, K.D., Harwood, J.D., 2014. Temporal dynamics of natural enemy–pest interactions in a changing environment. *Biol. Control* 75, 18–27.
- Werling, B.P., Dickson, T.L., Isaacs, R., Gaines, H., Gratton, C., Gross, K.L., Liere, H., Malmstrom, C.M., Meehan, T.D., Ruan, L., Robertson, B.A., Robertson, G.P., Schmidt, T.M., Schrottenboer, A.C., Teal, T.K., Wilson, J.K., Landis, D.A., 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proc. Natl. Acad. Sci. U.S.A.* (in press), <http://dx.doi.org/10.1073/pnas.1309492111>.
- Yang, L.H., Edwards, K.F., Byrnes, J.E., Bastow, J.L., Wright, A.N., Spence, K.O., 2010. A meta-analysis of resource pulse–consumer interactions. *Ecol. Monogr.* 80, 125–151.

David W. Crowder

Department of Entomology, Washington State University,

PO Box 646382, Pullman,

WA 99164, USA

E-mail address: [dcrowder@wsu.edu](mailto:dcrowder@wsu.edu)

James D. Harwood

Department of Entomology, University of Kentucky,

Lexington, KY 40545-0091, USA