



Mitigating the effects of insecticides on arthropod biological control at field and landscape scales



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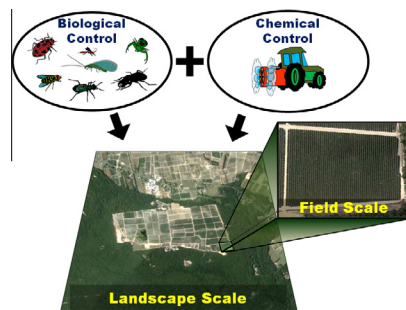
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HIGHLIGHTS

- Global changes in agriculture affect pesticide use and biological control.
- Insecticides can have lethal and sub-lethal effects on natural enemies.
- Disruption of biological control can be mitigated using a variety of methods.
- Impacts can be managed at the landscape scale to enhance area-wide IPM.

GRAPHICAL ABSTRACT



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ABSTRACT

Integrated pest management (IPM) programs emphasize the combination of tactics, such as chemical and biological control, to maintain pest populations below economic thresholds. Although combining tactics may provide better long-term sustainable pest suppression than one tactic alone, in many cases, insecticides and natural enemies are incompatible. Insecticides can disrupt natural enemies through lethal and sub-lethal means causing pest resurgence or secondary pest outbreaks. Legislative actions such as the Food Quality Protection Act (US) and the Directive on Sustainable Use of Pesticides (EU) have placed greater restrictions on insecticides used in agriculture, potentially enhancing biological control. Here we focus on the effects of insecticides on biological control, and potential mitigation measures that can operate at different scales. At the farm scale, natural enemies can be conserved through the use of selective insecticides, low doses, special formulations, creation of refugia, special application methods, and targeted applications (temporal or spatial). At the landscape scale, habitat quality and composition affect the magnitude of biological control services, and the degree of mitigation against the effects of pesticides on natural enemies. Current research is teasing apart the relative importance of local and landscape effects of pesticides on natural enemies and the ecosystem services they provide, and the further development of this area will ultimately inform the decisions of policy makers and land managers in terms of how to mitigate pesticide effects through habitat manipulation.

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1. Introduction

Over the past century, agriculture has experienced rapid intensification across much of the planet, particularly in the regions where food and fiber production are possible (Millennium Ecosystem Assessment, 2005). This intensification has increased

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net primary production from farmland for the human population, but this has had negative effects on biodiversity including birds (Donald et al., 2001), butterflies (Flick et al., 2012), bees (Kremen et al., 2002), and insect biological control agents (Thies and Tschantke, 1999). While this latter group of insects provide valuable pest regulation, this ecosystem service can be compromised in agricultural systems where their survival is reduced through exposure to pesticides. Sustainable agricultural systems must be based on balancing the needs for production with support of the biodiversity upon which agricultural systems depend (Bianchi et al., 2006; Crowder and Jabbour, 2014), and managing pesticide risks to beneficial insects is an essential aspect of this.

With the needs for biodiversity protection in agriculture to support ecosystem services and their contributions to crop production in mind, is it possible to integrate chemical and biological pest control? This was the original objective of the integrated control concept, the precursor to integrated pest management (IPM) (Stern et al., 1959; van den Bosch and Stern, 1962). Advances in synthetic organic chemistry prior to and during World War II resulted in the proliferation and use of many inexpensive and efficacious pesticides (National Research Council, 2000), often without full consideration of how they might impact the environment or non-target organisms. Increasing awareness of the risks of reliance on pesticides led to the development of alternative control strategies and a return to integrated methods of pest management (Perkins and Patterson, 1997). Most recent legislation such as the Food Quality Protection Act (FQPA 1996) and the Directive on Sustainable Use of Pesticides (EU 128/2009/EC) put greater restrictions on pesticide use and specifically products with broad-spectrum activity. This has provided additional impetus to adopt insecticide chemistries with a more benign environmental profile and to find approaches that can integrate chemical and biological control. In fact, the Directive calls for European Union member states to develop national action plans for sustainable pesticide use by 2014, and has essentially two goals: encourage adoption of IPM and decrease pesticide use (Hillocks, 2012). While this mandate is broad, in this review we focus on insecticides, rather than fungicides and herbicides, because of their greater impact on arthropod natural enemies. However, we recognize that side effects on natural enemies by these other classes are relevant to the potential delivery of biological control (Theiling and Croft, 1988; Yardim and Edwards, 1998).

Biological control constitutes an essential component of many pest management programs in multiple ecosystems (e.g. Hoy, 1994; Bale et al., 2008). Gentz et al. (2010) argued that in the context of an IPM program, selective chemical compounds used in tandem with biological control agents may provide more comprehensive management than either approach alone. It may not be broadly applicable in all agricultural situations, but with new technology such as geographic information systems (GIS) and genetically modified (GM) crops, and with further research into development of sustainable agriculture, the compatibility between chemical and biological control can be enhanced. If insecticides and biological control are to be compatible (or as close to compatible as possible), three key factors in insecticide use will need to be addressed: chemistry, timing, and location (Hassan and Van de Veire, 2004). Chemistry, the inherent toxic properties of the insecticide, relates to physiological selectivity which is based on differences in physiologies between a particular pest and its predators and parasitoids (Ripper et al., 1951). Application timing can be adjusted so insecticides do not interfere with natural enemy release or applications are made when natural enemies are in less susceptible life stages (Hassan and Van de Veire, 2004). Spatially-targeted pest management can reduce the amount of active ingredient used by applying insecticides only to areas where pest density is high or plant damage tolerance is near zero (National

Research Council, 2000). If a pest's spatial distribution is not uniform, insecticides may not need to be applied to the entire field to achieve effective control. Areas of low pest density that remain untreated can enhance biological control by providing a steady host source for natural enemies in addition to leaving a portion of the natural enemy population unexposed (Van Driesche and Heinz, 2004).

2. Biological control in a changing world

Global trade is increasingly bringing insect pests into new regions of the world, causing disruption to well-established and stable IPM programs (Pimentel, 2007). In many cases these IPM programs have provided reduced levels of pesticide use and have supported transition away from broad-spectrum insecticides, either through market incentives such as better prices for organically-produced food and fiber, or in response to policies. These include the EU Directive on Sustainable Use of Pesticides and the FQPA that were mentioned above. While these widespread changes in the intensity of pesticide use have been expected to increase the levels of biological control, such progress is in jeopardy in many systems due to the arrival and establishment of invasive pests.

Rapid adaptation of IPM approaches to respond to the new challenges of invasive pests is essential for continued profitability of crops facing this type of challenge. For example, the tomato leaf-miner, *Tuta absoluta* (Meyrick), recently moved from South America to Europe and the Mediterranean Basin, and caused significant increase in the use of insecticides to prevent crop damage. Rapid screening of insecticides for their safety against the complex of natural enemies that can affect *T. absoluta* in this new geographic range allowed informed decisions to be made about which chemical tools should be used for its management (Desneux et al., 2010; Urbaneja et al., 2012). This was particularly critical in protected culture where many tomatoes are produced. A similar situation faced the cotton and vegetable farmers of Arizona when the whitefly, *Bemisia tabaci* (Gennadius) Biotype B, developed large populations causing millions of dollars of lost revenue (Ellsworth and Jones, 2001). The response to this pest is a classic example of how the original integrated control concept (Stern et al., 1959) remains relevant 50 years after its introduction. Through a series of coordinated research projects and statewide implementation partnerships, this invasive pest was brought under control by a combination of natural enemy conservation and well-timed use of selective growth regulator insecticides, with widespread use of thresholds for spray decision-making so that money was not wasted, and so that biological control agents could be conserved. For instance, when this species first invaded there was widespread use of broad-spectrum insecticides, which killed its natural enemies and promoted rapid evolution of resistance. It was not until farmers moved towards growth regulators that the problem improved (Naranjo and Ellsworth, 2009a,b).

High levels of insecticide use are common in response to a new invasive pest but with appropriate support for research and education programs, there can be longer-term transition to selective and more biologically based controls that can be integrated into ongoing IPM programs (Naranjo and Ellsworth, 2009a). When this happens, biological control has a chance for establishment and providing significant contributions to pest suppression. In some cases, the effectiveness of selective insecticides may not be sufficient to meet demanding pest management targets, making biological control very challenging. This is the current situation for the recent invasion of the fruit pest *Drosophila suzukii* Matsumura into North America and Northern Europe (Cini et al., 2012), though research is currently underway to develop conservation and classical biological control for this pest.

In addition to invasive species driving higher pesticide use, the earlier springs and warmer summers brought about by global climate change (IPCC, 2007), are expected to cause pest range expansion and additional generations that will increase the need for pest control (Cannon, 2004; Tobin et al., 2008). Increasing reproductive potential of crop pests may be counteracted by similar increases in natural enemies, although phenological mismatches can cause unexpected dynamics in the levels of biological control (Parmesan, 2006; Thompson et al., 2010; Welch and Harwood, 2014).

Projections into the future indicate a continued need for pest management and a high likelihood that pest populations will become more of a burden on agricultural production. This will be driven by climate change, pest range expansion, invasive species, regulatory restrictions, and mismatches with biological control agents. As the human population continues to grow and require increased agricultural production (Godfray et al., 2010), sustainable intensification is being considered for meeting the potentially competing demands of greater net productivity without damaging the biodiversity that provides important ecosystem services such as biological control (Tilman et al., 2011). This will be a major challenge for the coming decades, and finding ways to minimize pesticide effects on beneficial organisms such as natural enemies will need to be a component of such efforts (Crowder and Jabbour, 2014).

3. Impact of insecticides on natural enemies

The economic importance of beneficial insect protection from harm due to pesticides can be seen by the value of these insects to agriculture. The magnitude of natural pest control across the United States (US) has been valued at \$4.49 billion by Losey and Vaughan (2006), but there has been increasing interest in how the level of biological control is affected by the use of insecticides. This information is not available for most crop systems, but the value calculated for one example shows that this earlier estimate may be much too low. Quantification of the biocontrol services provided to the corn-soybean rotation crop system in just four Midwestern states found that farms adopting IPM practices had an estimated \$239 million benefit (Landis et al., 2008). This highlights the significant implications of conserving biological control function in agriculture.

3.1. Assessment of pesticide effects on natural enemies

The impacts of insecticides on natural enemies are typically measured with laboratory or field bioassays, and standard methods for testing non-target effects have been developed by the International Organization for Biological Control (Hassan, 1989). Insecticides disrupt natural pest control in several ways. Direct impacts related to contact toxicity are easily recognized. Indirect effects on natural enemies may occur when their food source is reduced by insecticides or through secondary poisoning from contaminated prey (Croft and Brown, 1975; Stark et al., 2007). Natural enemies and pest species tend to respond differently to a given insecticide, with natural enemies being more susceptible to conventional products (e.g., broad-spectrum organophosphate and carbamate insecticides). Additionally, the duration of negative effects on natural enemies can be greater than that for pests (Tang et al., 2010), further limiting their population growth. Differential susceptibility cannot be assumed in all cases, but it can explain the ecological disruption that has been observed in many pest management scenarios where insecticides toxic to natural enemies have been used (Pedigo, 2002). For the majority of reduced-risk insecticides, which are more selective, the inverse is true with natural enemies being typically less susceptible than pests. Susceptibility to an insecticide

can be a function of physiology or population structure (Stark et al., 2004), and it can vary greatly among natural enemy species.

The effects of insecticides on natural enemies have been studied in detail, with increasing understanding of the stage-specific and sub-lethal effects. To better understand these impacts for the blueberry systems in which we work, we performed a series of laboratory assays to evaluate the effect of insecticides on mortality of four generalist predators (Roubos et al., 2014). This study was complemented by a semi-field study in which *Hippodamia convergens* (Guérin-Ménéville) (Coleoptera: Coccinellidae) was exposed to insecticides on blueberry bushes after their residues had aged in the field for 0, 3, 7, or 14 days. For each residue age, shoots were cut (15 cm with 7–10 leaves) from treated plants and placed into 946 ml (32 oz) plastic deli cups. Ten *H. convergens* adults were added to each cup and acute effects (mortality and knock-down) were assessed at 24, 48, and 72 h. Insecticide treatment, residue age and the interactions were significant for the acute effects on *H. convergens*. The broad-spectrum insecticides phosmet and zeta-cypermethrin were consistently the most toxic, although mortality varied by residue age (Fig. 1). Acetamiprid and zeta-cypermethrin knocked down more beetles than they killed, with acetamiprid knocking down almost 85% when residues were fresh (Fig. 1). After 14 days in the field, residues of acetamiprid and phosmet, the two most toxic compounds initially, were not significantly different from the untreated control. This study shows the differential effect of insecticides of various chemical classes and highlights the need to explore potential side-effects of insecticides on natural enemies before integrating them into IPM programs.

The treatments described above were applied as foliar sprays, but the recent expansion of systemic insecticides as a significant component of the pest management toolbox has created additional routes for exposure to natural enemies, such as via various plant exudates. For example, Stapel et al. (2000) observed compromised foraging behavior by parasitoids after feeding on the nectaries of cotton plants treated with imidacloprid. Exposure via feeding from guttation and nectar may also be relevant for some crop systems, but this seems to have received much less attention than it has for bee exposure to pesticides (Thompson, 2010).

3.2. Population level effects

Secondary pest outbreaks occur when species previously of little or no economic concern become serious problems because their predators were eliminated by an insecticide application directed against a major pest (Van den Bosch et al., 1982). For instance, the European red mite, *Panonychus ulmi* (Koch), feeds on apple foliage, but populations are usually kept below damaging levels by the predatory mite *Amblyseius fallacis* (Garman) (Dover et al., 1979). Pyrethroids used against moth pests in apple are particularly devastating to *A. fallacis* (Hill and Foster, 1998; Stanyard et al., 1998), and without its predator, European red mite populations increase causing significant damage and requiring additional action to prevent severe feeding injury (Stanyard et al., 1998). Insecticides can also cause pest resurgence. Resurgence occurs when the pest population recovers faster than the natural enemy population following a disturbance, namely a pesticide application (Hardin et al., 1995). Consequently, the resulting pest density is higher than before the application. For example, when methomyl and methyl parathion were applied to control lepidopteran pests in soybean, pest densities were initially reduced, but within a few weeks their populations rebounded to levels twice as high as in untreated fields (Shepard et al., 1977), and treated fields also had significantly fewer predators. This phenomenon occurs because of the differential impact of insecticides on pests and natural enemies or differences in their respective life histories.

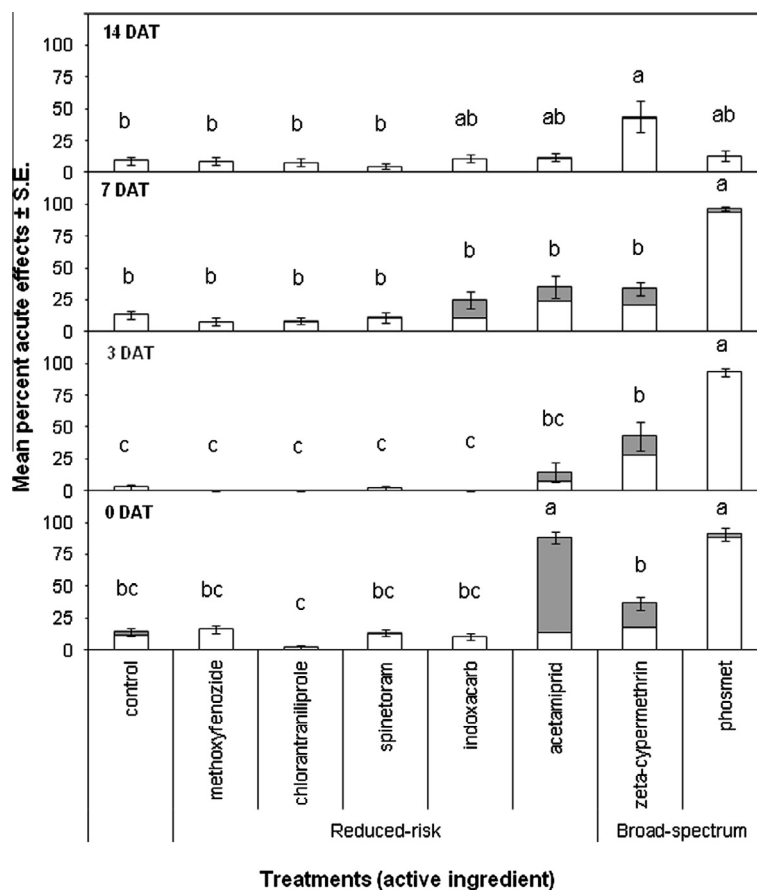


Fig. 1. Mean percent acute effect (mortality and knock-down) \pm S.E. of *Hippodamia convergens*, in semi-field experiments after 72 h exposure to insecticide residues aged 0, 3, 7, or 14 days after treatment (DAT). Dark portions of bars represent percent knock-down; light portions represent percent mortality. Bars with the same letter are not significantly different at $P < 0.05$ (Tukey's Honest Significant Difference test).

3.3. Sub-lethal effects

The majority of toxicity studies on the impact of insecticides on invertebrates have focused on acute mortality values such as the median lethal dose (LD_{50}) or concentration (LC_{50}) (Stark and Banks, 2003; Stark et al., 2007). Stark and collaborators (Stark et al., 1995; Stark and Banks, 2003) argued, however, that relying on mortality does not provide an accurate assessment of the potential impacts of insecticides. They make the case that demography and life table analysis should be included to elucidate long-term effects on natural enemy populations. Sub-lethal effects to natural enemy populations include reduced fecundity, longevity, and development rates, changes in sex ratios, morbidity, and altered behavior (Croft and Brown, 1975; Stark and Banks, 2003; Desneux et al., 2007; Cloyd, 2012). At the population level, changes in development rate can disrupt phenological synchrony between a natural enemy and its host or prey (Desneux et al., 2007). The impacts would be most severe if the predator or parasitoid had a longer generation time, more life stages, and a lower population growth rate than its prey or host (Stark et al., 2004). Differences in life history traits mean different species vary in the rate at which their populations recover following a disturbance such as an insecticide application (Stark et al., 2004, 2007), and thus it could take some time following the discontinuation of insecticide use for normal population dynamics to reestablish.

Altered behaviors resulting from insecticide exposure include impaired movement (knock-down effect, trembling, incoordination, excessive grooming) and problems navigating and orientating to prey (Longley and Jepson, 1996a,b; Desneux et al., 2004). Insec-

ticides have also been shown to have repellent effects that interfere with the feeding behavior of natural enemies (Singh et al., 2004; Desneux et al., 2007), and this may limit the degree of biological control. Few studies have assessed the importance of sub-lethal effects on natural enemies for pest population regulation, and there is increasing recognition that sub-lethal effects typically documented in laboratory bioassays can translate into effects on pest regulation under field conditions (e.g. Biondi et al., 2013).

When reviewing the literature on this topic, it is important to be aware that it is practically impossible to generalize about pesticide impacts across multiple natural enemy species because the effects can vary greatly depending on a number of factors including the type of natural enemy, life stage exposed, pesticide formulation, and sex (Stark et al., 2007; Cloyd, 2012). However, general themes can be summarized to guide pesticide selection for reduced impact on natural enemies in crop systems.

4. Methods to reduce natural enemy exposure to insecticides

IPM emphasizes the use of multiple tactics, i.e., biological and chemical controls, to maintain pest populations below an economic threshold (Stern et al., 1959; Smith et al., 1976). Under this concept, natural enemies and insecticides can be combined to reduce pest populations (Croft and Brown, 1975). In the following sections of this article we discuss ways in which biological and chemical control tactics can be integrated into pest management programs at field, farm, and landscape scales.

4.1. Farm-scale level

Farmers can employ various methods to reduce natural enemy exposure to insecticides within agricultural fields or entire farms, and thus conserve them and enhance biological control services. These methods are reviewed below.

4.1.1. Use of selective insecticides

Insecticide selectivity is defined as the capacity of a chemical control treatment to spare natural enemies while controlling the target pest (Bartlett, 1964). Farmers worldwide are increasing the use of GM crops, as well as selective reduced-risk insecticides (Devine and Furlong, 2007; Gentz et al., 2010), particularly in countries where some broad-spectrum insecticides have been banned or their use is restricted due to legislation (see Section 1). Reduced-risk insecticides have several advantages over broad-spectrum insecticides including shorter pre-harvest intervals due to their lower mammalian toxicity and greater compatibility with biological control because of their less harmful effects on natural enemies. Although desirable in IPM programs when compared with broad-spectrum insecticides, these more selective reduced-risk insecticides can sometimes be more expensive (Shearer et al., 2006; Agnello et al., 2009). In addition, reduced-risk insecticides exhibit a high degree of specificity not only to the target insect pest but also to a specific insect stage, requiring farmers to increase their monitoring efforts. Another challenge to the adoption of selective insecticides is in cases of cropping systems with multiple pests that cannot be suppressed by natural enemies—a situation that could lead to increases in the number of insecticide applications.

A few recent studies tested the effects of reduced-risk IPM programs, compared to conventional programs, on biological control in agro-ecosystems. In these studies, reduced-risk programs employed minimal (threshold-based) use of reduced-risk insecticides with and without behavioral and cultural control tactics, whereas conventional programs used broad-spectrum, organophosphorus and carbamate insecticides. Atanassov et al. (2003) found higher numbers of beneficial insects and greater rates of egg parasitism and predation in peach orchards under a reduced-risk program compared with those under a conventional program. O'Neal et al. (2005) reported eightfold higher activity of the predatory ground beetle *Harpalus erraticus* Say in reduced-risk managed compared with conventionally-managed highbush blueberry fields. Interestingly, in addition to a reduction in broad-spectrum insecticides, enhancement of *H. erraticus* activity required the presence of suitable habitats e.g. ground cover (O'Neal et al., 2005), which highlights the potential for interactions between natural enemy habitat and insecticide exposure (as further described in Section 4.1.8). In commercial vineyards, Jenkins and Isaacs (2007) found no differences between insecticide programs in parasitism of the grape berry moth, *Paralobesia viteana* Clemens, larvae or abundance of natural enemies between reduced-risk and conventional programs. The varying patterns of response to adoption of reduced-risk insecticides suggest system-specific benefits that may not be predictable without detailed investigation. Additionally, landscape context must be taken into account when designing and interpreting such studies since that can be an influential driver of pest-natural enemy dynamics.

4.1.2. Genetically-engineered crops to minimize pesticide exposure to natural enemies

Genetically modified crops are engineered to express genes from another organism, and for arthropod pest management, GM crops are modified to produce substances toxic to arthropods. The most well-known and widely grown GM crops for insect resistance are the Bt crops, those that express delta-endotoxins from

Bacillus thuringiensis Berliner. GM crops are widely grown in the US, China, and parts of South America, but are less acceptable in Europe and less accessible in developing countries (James, 2011). Because the insecticidal compound is produced within the plant the need for repeated insecticide applications, for instance, is reduced. Lu et al. (2012) studied the impact of Bt cotton adoption in China over a 20 year span and found that the frequency of insecticide sprays decreased following the introduction of Bt cotton. They also observed generalist predator (ladybirds, lacewings, and spiders) population levels increased after Bt cotton implementation, and this also had spillover effects where predator abundance increased in neighboring non-Bt crops (Lu et al., 2012).

GM crops, in spite of the controversy surrounding them (see Uzogara, 2000), have great potential to reduce reliance on insecticides delivered through foliar or soil applications. This does not mean, however, that GM crops automatically fit well within an IPM framework (Lundgren et al., 2009). GM crops themselves can have non-target effects on natural enemies. For example, predators and parasitoids could be exposed to a toxin through their prey or hosts which have fed on GM crops (Lundgren et al., 2009). In GM crops, toxins are expressed throughout the plant, not just in the parts of commercial interest. As a result, natural enemies could also be exposed to toxins through non-prey food sources such as pollen (Lundgren et al., 2009). Although GM crops are not completely benign to natural enemies, the benefits of reduced insecticide use associated with adoption of this technology may outweigh the risks, and there are increasing calls to incorporate this technology within sustainable intensification (*sensu* Garnett et al., 2013) to meet the challenge of global food security (Ronald, 2011).

4.1.3. Lower dosage of insecticides

Biological control can be combined with chemical control if insecticides are used at dosages that reduce their negative impacts on natural enemies while still providing sufficient control of the target pest. Reducing insecticide doses can also have the advantage of retarding resistance in pests and promoting resistance in natural enemies (Tabashnik and Croft, 1982). To achieve this, knowledge of the lowest dose of an insecticide needed to both maintain the pest(s) population below an economic threshold while preserving natural enemy populations is needed. As Johnson and Tabashnik (1999) pointed out, reducing the insecticide dosage to conserve natural enemies will not be feasible if the target pest(s) does not have effective natural enemies and if it has an extremely low economic threshold. For example, Hoyt (1969) and Collyer (1976) found that reduced dosages of the organophosphate insecticide, azinphosmethyl, increased survival of the predatory mites, *Typhlodromus occidentalis* Nesbitt and *T. pyri* Scheuten, while still providing good control against the codling moth, *Cydia pomonella* L., and the European red mite, *P. ulmi*, respectively. Acheampong and Stark (2004) found, under laboratory conditions, a 90% reduction in the level of infestation by the cabbage aphid, *Brevicoryne brassicae* L., when low dosages of the selective aphicide pymetrozine were combined with the seven-spotted lady beetle, *Coccinella septempunctata* L., and an 84% reduction of aphids when the aphicide was combined with the aphid parasitoid, *Diaeretiella rapae* M'Intosh. Recently, Dammer and Adamek (2012), using a sensor-controlled field sprayer to control the amount of insecticide applied to winter wheat fields, found that aphids were killed rapidly under high-dose insecticide applications but when low dosages were used, fields were colonized by lady beetles and eventually aphids and lady beetles disappeared from fields after three weeks. In contrast, Hull et al. (1985) found that reducing the dosage of the synthetic pyrethroid, fenvalerate, does not prevent outbreaks of European red mite due to the elimination of the mite predator, *Stethorus punctum* LeConte, at both high and low dosages.

4.1.4. Timing of insecticide applications

Natural enemy interaction with pests has an inherent periodicity, within the annual cycles of planting, growth and harvest as well as within diel and seasonal phases (Welch and Harwood, 2014). The negative impact of insecticides on natural enemies can be avoided or minimized by timing insecticide applications when natural enemies are either absent or present at the most insecticide-resistant life stage (Bartlett, 1964; Ruberson et al., 1998). For holometabolous natural enemies, for example, these applications could be done at the prepupal and pupal stages because these are the more tolerant life stages to insecticides (Hull and Beers, 1985). Most insecticide applications are based, however, on the pest phenology and do not necessarily take into account the phenology of natural enemies. To avoid disruption of biological control by insecticides, knowledge on the seasonal activity of key natural enemies and when biological control is most effective is needed. Regular sampling of the susceptible stages of a pest at sites that are natural or minimally-managed followed by rearing of the insects can reveal the parasitoid community present in a region and their phenology relative to the pest. For predators, sentinel prey or video observations can be employed to gain similar insights (Grieshop et al., 2012). Although this information is often not available, there is increasing interest in finding ways to minimize negative effects of insecticides on natural enemies through more selective timing of applications (e.g. Horton et al., 2012; Woods et al., 2012). In cases of augmentative biological control, releases of natural enemies should be done after completion of insecticide applications and when insecticide residues have declined to levels that maximize natural enemy survival (Ruberson et al., 1998; Tang et al., 2010).

Timing insecticide applications to conserve natural enemies is likely to be more critical when using broad-spectrum insecticides that are more detrimental to these organisms than reduced-risk insecticides, and thus may become less of an issue as farmers move towards increased use of the latter class of insecticides. Hull and Beers (1985) and Johnson and Tabashnik (1999) provide classic examples that demonstrate the importance of timing of pesticide sprays to conserve natural enemies. Davis and Hoyt (1979) suggested using the carbamate insecticide carbofuran against the alfalfa weevil, *Hypera postica* Gyllenhal, in early spring when the weevil's parasitoid, *Bathyplectes curculionis* Thompson, is still at the pupal stage. Similarly, Weires et al. (1982) recommended applying the carbamate oxamyl against the spotted tentiform leaf-miner, *Phyllonorycter blancardella* Fabr., prior to the emergence of its parasitoid *Apanteles ornigis* Weed. Hull and Beers (1985) also recommended use of organophosphorous insecticides instead of synthetic pyrethroids at times when the predator *S. punctum* colonizes apple trees because this class is less harmful to the predator.

In cranberries in New Jersey and blueberries in Michigan, we recommend farmers avoid the use of broad-spectrum insecticides or, if needed, use reduced-risk insecticides such as methoxyfenozide or chlorantraniliprole early in the season for the control of lepidopteran pests when predator abundance and egg predation rates are at the highest levels (C. Rodriguez-Saona and R. Isaacs, unpublished data).

4.1.5. Special insecticide formulations

The negative impact of insecticides on biological control can be reduced if they are applied in ways that minimize natural enemy exposure. For example, Van Timmeren et al. (2012) found that soil applications of systemic neonicotinoid insecticides (imidacloprid, clothianidin, thiamethoxam and dinotefuran) in vineyards provide high levels of control against the potato leafhopper, *Empoasca fabae* Harris, Japanese beetle, *Popillia japonica* Newman, and grape berry moth, *Paralobesia viteana*, and argued that this approach can reduce foliar pesticide applications and protect natural enemies.

Populations of natural enemies may also be spared when using baits and seed treatments because they often contain lower insecticide dosages and have reduced contact toxicity on non-targets (Hull and Beers, 1985; Johnson and Tabashnik, 1999). Baits have been used extensively to control ants such as the red imported fire ant, *Solenopsis invicta* Buren, in agro-ecosystems (Lofgren, 1985). Studies have shown, however, adverse effects of neonicotinoid seed treatments on generalist predators (e.g. Seagraves and Lundgren, 2012) and parasitoids can pick up insecticide from feeding on guttation drops (Stapel et al., 2000).

4.1.6. Site-specific applications

Knowledge of the distribution of the target pest(s) and their natural enemies is a powerful tool to reduce insecticide use and protect natural enemies from exposure. Farmers can use this information to target applications only in fields or parts of the field with high pest pressure, i.e., above an economic threshold, and where natural enemies are less frequent, a concept commonly referred to as site-specific or precision pest management (Weisz et al., 1995; Hughes, 1996; Fleischer et al., 1999). Geospatial technologies such as remote sensing and GIS are being used increasingly by researchers, extension specialists, and farmers for making pest management recommendations and decisions. Several studies have combined intensive field sampling with geospatial analyses to understand the distribution of pests and their natural enemies. In general, these indicate that generalist predators are not distributed randomly within agricultural fields but aggregate in areas of high pest population density (Pearce and Zalucki, 2006). For example, Winder et al. (2001) conducted a field-scale study on the spatio-temporal dynamics of two aphid species (*Metopolophium dirhodum* Walker and *Sitobion avenae* F.) and a generalist predator, the carabid *Pterostichus melanarius* Illiger, and found a strong response by the beetle population to aphid patches. Similarly, Warner et al. (2003) found a significant spatial correlation between predatory carabid beetles and the larvae of the chrysomelid beetle, *Psylliodes chrysocephala* L., a pest of oilseed rape.

To our knowledge, however, no studies have investigated the impact of site-specific pest management on conservation biological control in agro-ecosystems. Because the spatial distribution of pest populations are often positively correlated with that of their natural enemies (as discussed in this section), farmers face the challenge of using crop protection measures aimed at areas of high pest infestation (precision agriculture) that at the same time conserve biological control agents. This approach is currently being tested within Michigan grape vineyards where spatial distribution of grape berry moth at vineyard borders, coupled with the availability of highly selective insecticides for control of this pest, provides an opportunity for growers to reduce their insecticide costs without compromising fruit quality and increasing the contributions of biological control (R. Isaacs, unpublished data).

If pests and natural enemies aggregate in specific areas within plants, pesticide applications can be directed to these parts rather than the entire plant. For example, Hoyt (1969) showed that applications of the carbamate carbaryl to upper and peripheral areas of apple trees conserve the predatory mite *T. occidentalis*, which inhabits the inner areas of trees; this approach reduces resurgence of tetranychid mites. Similarly, increases in survival of the predatory *Orius* spp. – that attack *Heliothis* spp. eggs and larvae – were observed at the top of cotton plants when the organophosphate azinphosmethyl was applied only to bottom parts of plants to control the pink bollworm, *Pectinophora gossypiella* Saunders (Watson, 1975; Davis and Hoyt, 1979). Parasitoids of *Liriomyza* leafminers on watermelon, found mainly in the lower leaves, can be conserved when applications of oxamyl to control *Thrips palmi* Karny are directed to the vine tips (Lynch and Johnson, 1987).

4.1.7. Special application methods

If insecticides are applied to areas where both pests and natural enemies are present, the negative impacts of insecticides can be reduced if they are only applied to parts of plants or fields. As a result, natural enemies are not totally eliminated from these fields because they can survive in the untreated parts of plants or fields, and then move into the treated parts after insecticide break-down.

Alternate-row middle spraying is a technique for reducing pesticide usage and increasing protection of natural enemies (Fig. 2A). Pesticides are concentrated to one side of plants and at reduced levels on the other side, compared to every-row middle spraying where both sides of the plant are sprayed. This method has been successfully implemented in apple orchards in Pennsylvania since the 1960s (Lewis and Hickey, 1964; Hull et al., 1983). A requirement for the alternate-row middle spraying to work is that the low rates applied to the offside are as effective in controlling the pest as the side receiving the full rate. This method allows for increased survival of natural enemies in the side of plants receiving the low rates. For instance, survival of the predator *S. punctum* was greater when apple trees were sprayed with the alternate-row middle spray technology than the every-row middle spraying method (Hull and Beers, 1985), thus reducing secondary outbreaks of the European red mite.

Other methods such as border sprays (Fig. 2B) can also reduce insecticide use, delay onset of insect resistance, and minimize non-target impacts. Border-row sprays can be used if pests are distributed along the field perimeters. This concept has been tested for plum curculio, *Conotrachelus nenuphar* Herbst, in apple orchards (Chouinard et al., 1992; Leskey et al., 2008), for blueberry maggot, *Rhagoletis mendax* Curran, in blueberries (Collins and Drummond, 2004), and for grape berry moth in vineyards (R. Isaacs, unpublished data). However, whether border-row sprays increase biological control of these or other pests remains unclear.

4.1.8. Creation of refugia

Farmers can create natural enemy supporting habitats (i.e., refugia) within farms, and ideally outside of insecticide-treated areas, to support natural enemy populations. By incorporating these areas into their land, farmers may be able to rely more on biological control and less on chemical control. These areas may also increase the re-colonization of natural enemies into crop fields after application of insecticides toxic to non-target species (Walton and Isaacs, 2011). The size of the refuge and the intensity of the

insecticide program are both expected to influence the magnitude of the natural enemy population and their function. We predict an inverse relationship between pesticide intensity and the size of habitat refugia on the abundance of natural enemies such that natural enemy abundance should increase with increasing size of refugia and decrease as pesticide inputs increase (Fig. 3). For example, Halaj et al. (2000) found that modular habitat refugia constructed of chicken wire loosely filled with bedding straw increased predator abundance and reduced insect damage in soybean fields. Beetle banks are strips typically planted with perennial grasses within a crop field to enhance populations and provide over-wintering habitat for beneficial organisms such as predatory beetles and spiders (Thomas et al., 1991; Thomas, 2001), and these can reduce the negative impacts of insecticide applications on natural enemy populations (Lee et al., 2001).

Farmers can also select crop varieties that provide refugia and promote natural enemies. For example leaf domatia, which are minute invaginations often filled with hairs along the veins on the underside of leaves, provide safe refuge for small beneficial organisms such as predatory mites (Karban et al., 1995; Norton et al., 2000). Indeed, English-Loeb et al. (2005) found significant genotypic variation in the size of domatia in grapes, which had implications for the level of biological control of pest mites on the vines, as well as the levels of powdery mildew that some predatory mite species consume for nutrition.

Natural enemies utilize volatile organic compounds emitted from the plant and their host during foraging (Price et al., 1980). Predators and parasitoids of agricultural pests are often attracted to lures containing plant volatiles under field conditions, one such compound being methyl salicylate (Rodriguez-Saona et al., 2011); however, whether these compounds can be used to lure natural enemies away from fields prior to insecticide applications remains unknown (Rodriguez-Saona et al., 2012).

4.2. Landscape-scale mitigation of pesticide risk to natural enemies

IPM programs are typically deployed at the field or farm level, yet there is considerable linkage among adjacent farms and other land use types in terms of the exchange of pest and beneficial insects (Ekbohm et al., 2000; Rand et al., 2006; Diekötter et al., 2008; Chisholm et al. 2014). The development of GIS technology over the past decade has made possible the integration of biological and pest management information in a spatial context,

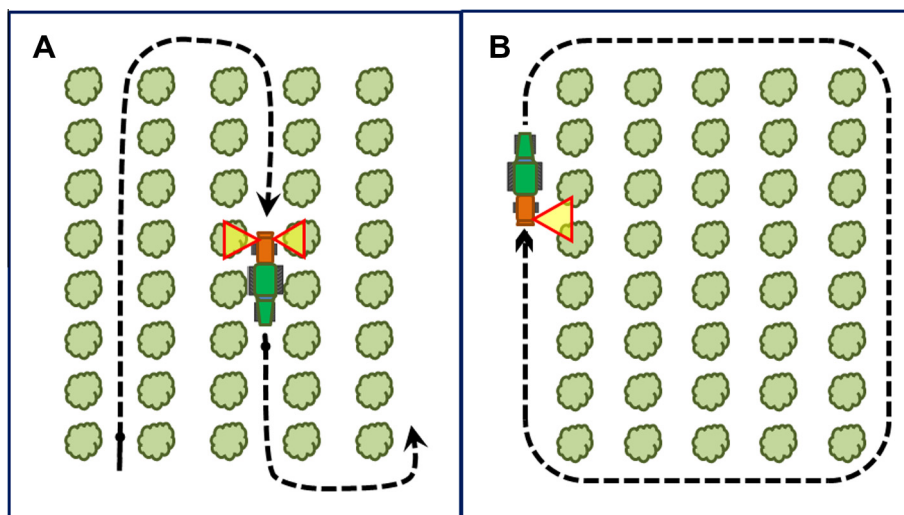


Fig. 2. Two application methods that minimize the adverse impacts of pesticides on natural enemies are by: (A) alternate-row middle sprays (after Hull and Beers, 1985); (B) border-row sprays.

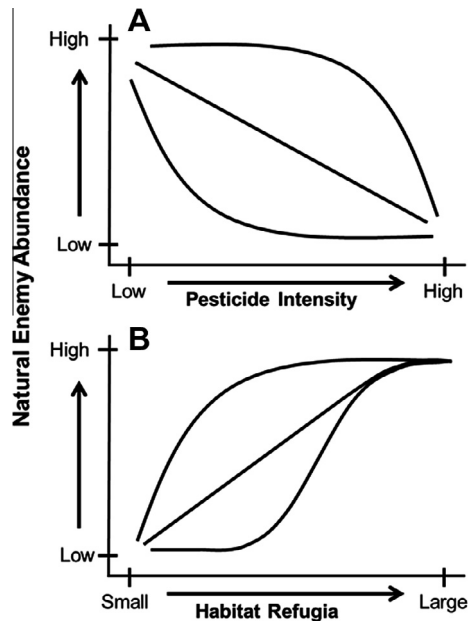


Fig. 3. Differential effects of pesticide intensity (A) and habitat refugia (B) on the abundance of natural enemies in agricultural fields. Different lines/curves indicate different scenarios. For example, insecticides might have stronger negative effects at low/high dosages on some natural enemies than others. Also, the abundance of different natural enemies is expected to respond differently to amount of refugia and at some point reach a plateau where increasing the amount of refugia does not increase the abundance of natural enemies.

allowing greater insights into how knowledge of the distribution of insects across the landscape can be used to enhance IPM (Carrière et al., 2006; Dminić et al., 2010).

Natural enemies are mobile and can disperse across agricultural landscapes, exploiting habitat features for shelter and food, and to locate insect prey. The distribution of these resources can have significant impacts on natural enemies (Hunter and Price, 1992; Elliott et al., 2002), with greater abundance and higher levels of biological control found in landscapes with greater proportion of natural habitat (Thies and Tschamtkke, 1999). The addition of targeted resources such as refuges (see Section 4.1.8) is expected to have varying benefit for biological control in nearby crops, dependent on the landscape context into which the resources are added (Tschamtkke et al., 2007). We expect that the positive interaction between adding habitat to enhance natural enemies and the surrounding landscapes is expected to have a similar but opposite form when considered for pesticides affecting natural enemies and the ecosystem services they deliver across landscapes (Fig. 4). Thus, in simple landscapes with low background populations of natural enemies, the negative effects of insecticides would have relatively little effect on the level of biological control because it is already low. In highly diversified landscapes with high levels of natural enemy activity, the negative effects of insecticides may be more transitory because there is already a high background level of natural enemies, and they can re-colonize the treated area once the pesticide residue has declined. Relative to the highly diverse landscapes, natural enemies in intermediate landscapes are expected to be at greater relative risk from the side effects of insecticide applications, because they will have lower background natural enemy abundance and also weaker contributions from landscape reservoirs. This is similar to the ideas put forth by Tschamtkke et al. (2005) for enhancement of biodiversity through agri-environment schemes, except in the context of negative effects of pesticides on natural enemies.

While the benefits of landscape diversity for supporting beneficial insects and greater regulation of pest populations are increas-

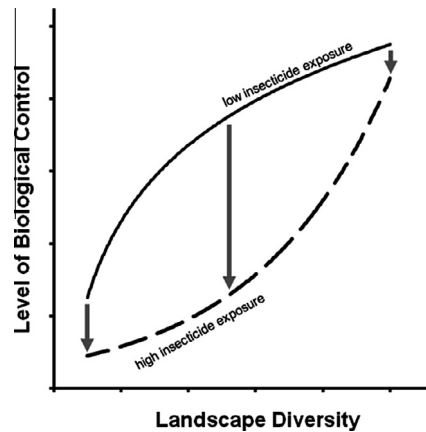


Fig. 4. Graphical representation of how insecticide exposure can have greater negative impact on the level of biological control in landscapes with intermediate levels of complexity, compared to low or high complexity landscapes. After Tschamtkke et al., 2005.

ingly well documented (Bianchi et al., 2006; Gardiner et al., 2009), there is much less information on how pesticides, local habitat quality, and landscape composition interact to influence the levels of pest biological control. A recent analysis by Geiger et al. (2010) aimed to disentangle some of the factors of intensification in European agriculture, finding that insecticide and fungicide use had consistent negative effects on biodiversity, and that agri-environment schemes and organic farming supported plant, insect, but not bird, components of biodiversity. Roitberg and Gillespie (2014) describe a mechanistic approach for understanding how natural enemies respond to habitat quality, which may provide a basis for experimental approaches to better understand the patterns of natural enemy response to local and landscape-scale habitat quality.

Local disturbance of natural enemy populations from application of insecticides to individual fields can lead to transiently higher pest pressure at that location, as described above (Sections 3.1 and 3.2). While this may then cause economic levels of damage to crops and also require additional insecticide applications, the surrounding landscape is expected to supply natural enemies to further suppress pest populations. However, in regions with highly simplified landscapes where individual landowners decide to treat with insecticide, there can be little rebound of natural enemies after spraying. This may result in widespread insecticide use, as documented recently by Meehan et al. (2012). Using data from the Midwestern US in 2007, they found that the proportion of cropland treated with insecticide increased with the proportion and field size of the crops and it decreased as the proportion of semi-natural habitat increased. Pest abundance (aphid pests of annual crops) also increased with the proportion of crop land treated with insecticide. The authors were able to conduct spatial mapping of the economic effect of this higher pest abundance, from yield loss and the higher insecticide use, to estimate that landscape simplification across the seven state area was associated with application of insecticides to 1.4 million hectares and higher costs of farming in that region totaling \$34103 million. While this study provides a correlative link between landscape simplification, higher pest density, and insecticide use there remains a need for greater mechanistic understanding of the spatial ecology of natural enemies to understand how prey distribution, landscape composition, and insecticides interact to affect insect populations and delivery of biological control ecosystem services to crop fields. A recent multi-year analysis of similar datasets has revealed significant inter-year variability in these patterns (Larsen, 2013), highlighting the need for a temporal component to fully understand how pesticide use will be affected by landscape-level changes.

4.2.1. Area-wide reduction of insecticide use

The greatest potential for landscape scale reduction of insecticide use lies between the extreme spatial scales of individual fields and regional landscapes. Under area-wide management programs, adjacent fields and even neighboring farms can be managed in a coordinated way to achieve the benefit of implementing pest management at this larger scale (Pimentel, 2007). This coordination can greatly aid in the efficacy of IPM tactics, such as coordinated planting dates to avoid certain pests, or deployment of mating disruption to reduce pest fecundity. Various area-wide programs have been developed specifically with the goal of insecticide reduction and many of these have succeeded through increased reliance on biological control. In some cases the increased contribution of biological control has enhanced the overall efficacy of the more targeted and coordinated management inputs, providing an effective alternative to insecticide dominated pest management. An example of successful area-wide pest control program implementation can be seen in how the apple industry has responded to a key insect pest. The codling moth area-wide suppression program was established in 1995 (Calkins and Faust, 2003), employing mating disruption for codling moth coupled with intensive orchard monitoring and transition to alternative insecticides to reduce dependence on organophosphate insecticides. By 2000, there were 21,800 hectares (54,000 acres) of orchards under mating disruption, with an 80% reduction in the use of broad-spectrum insecticides. Similar results were reported by Weddle et al. (2009) for the California pear industry, that had transitioned over 50 years from up to 14 insecticide applications per season to recently using only 3–5 insecticide applications, many of which are approved for organic production. This change was due in part to the emphasis on area-wide programs instigated through the codling moth program mentioned above. Based on these successes, further development of this area-wide effort has continued in the Pacific states of the western US, with greater emphasis on understanding natural enemy phenology and how insecticides affect the different life stages of insect natural enemies (Jones et al., 2009). This information can be used to develop area-wide pest management programs that balance the needs for pest control with conservation biological control based on informed decision-making related to pests and natural enemies. The successes in this region have also prompted deployment of similar programs in eastern US tree fruit recently, with pheromone-based management of codling moth achieving reduced cost per hectare, if growers can pass beyond the technological and social barriers to adoption (McGhee et al., 2011).

5. Conclusion

Natural enemies are particularly sensitive to insecticides, and the residues of sprays applied to control pest insects can remain toxic for many days, reducing their ability to deliver biocontrol ecosystem services, or for inundative releases to achieve control. These negative effects on natural enemies can occur at the plant, field, or landscape scales. As the spatial scale of insecticide application increases, the potential for re-colonization by natural enemies declines, raising the probability of a pest outbreak, although this effect is also expected to be modulated by the composition of the surrounding landscape. Similarly, the benefits of transition to reduced insecticide use, or to insecticides with lower impacts on natural enemies, are greater when this happens at larger spatial scales, and may also be affected by landscape context. Until now, the focus of research on this topic has largely been on enhancing natural enemy abundance both at small and large geographic scales, and on measuring the response of natural enemies. An important focus for future research will be to better understand how landscape-scale changes in pesticide use interact with landscape context to

affect pest and natural enemy populations, and more importantly how these changes affect the levels of pest biological control and crop yield.

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