REVIEW

Connecting scales: Achieving in-field pest control from areawide and landscape ecology studies

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Abstract Areawide management has a long history of achieving solutions that target pests, however, there has been little focus on the areawide management of arthropod natural enemies. Landscape ecology studies that show a positive relationship between natural enemy abundance and habitat diversity demonstrate landscape-dependent pest suppression, but have not yet clearly linked their findings to pest management or to the suite of pests associated with crops that require control. Instead the focus has often been on model systems of single pest species and their natural enemies. We suggest that management actions to capture pest control from natural enemies may be forth coming if: (i) the suite of response and predictor variables focus on pest complexes and specific management actions; (ii) the contribution of "the landscape" is identified by assessing the timing and numbers of natural enemies immigrating and emigrating to and from the target crop, as well as pests; and (iii) pest control thresholds aligned with crop development stages are the benchmark to measure impact of natural enemies on pests, in turn allowing for comparison between study regions, and generalizations. To achieve pest control we will need to incorporate what has been learned from an ecological understanding of model pest and natural enemy systems and integrate areawide landscape management with in-field pest management.

Key words ecosystem services; entomophagous arthropods; integrated pest management (IPM); natural enemies; pest control; predators and parasitoids

Introduction

Significant knowledge gaps exist for how to integrate areawide management of natural enemies (sensu entomophagous arthropods) of pests with in-field integrated pest management (IPM). Although there is a long history of pest control applied at an areawide basis, and a more recent interest and understanding of the role of noncrop habitat in agricultural landscapes supporting natural enemies (here after referred to as NEs), the consequences of these gaps is that approaches to link landscape ecological understanding with pest management are lacking. This paper sets out to address these knowledge gaps by proposing how we might better achieve management outcomes for in-field pest control from landscape ecology studies of NEs. To date studies have considered areawide pest control (Vreysen *et al.*, 2006), but there are few examples that focus on NEs. Others consider landscape structure and the relationship to biological control (Tscharntke *et al.*, 2005), but few have made the link to measures related to pest-control decision making. IPM programmes ostensibly encourage NEs at least indirectly by eliminating broad-spectrum insecticides to minimize disrupting them (Kogan, 1998), but studies rarely link to the landscape context. All of these areas of study have the

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objective of pest suppression in mind, and deal with the challenge of spatial scales, however to our knowledge no study has proposed an approach to connect the scales in order to move to pest management actions.

Research into arthropod pest management beyond the spatial scale of a field has a long history (Meyer & Simpson, 1996; Knipling, 1998; Klassen, 2005; Vreysen *et al.*, 2006). There are many practical examples, successful and unsuccessful, of pest control applied at an areawide basis (areawide management, AWM); essentially the control of the total pest population within a delimited area (Klassen, 2005; Hendrichs *et al.*, 2007). Successful AWM or control of pests is often highly coordinated, involves a regulatory framework, and integrates multiple pest control tactics (Hendrichs *et al.*, 2007). Examples of control actions for AWM include: coordinated timing of insecticide application (Smith, 1998; Lloyd *et al.*, 2010), release of sterile insects, for example, fruit fly (Hendrichs *et al.*, 1995) and tsetse fly (Vreysen *et al.*, 2013), coordinated growing of trap crops (Sequeira, 2001), coordinated orchard hygiene (Lloyd *et al.*, 2010), control of noncrop hosts, for example, weeds and grasses, near the crop and across the region (Mueller *et al.*, 1984; Abel *et al.*, 2007), cultivation to destroy a targeted life-stage, such as pupae to achieve wide-scale reduction in pest populations, for example, *Helicoverpa* spp. (Duffield, 2004; Lloyd *et al.*, 2008), and more recently wide-scale deployment of genetically modified insect resistant crops that has resulted in regional pest suppression (Carriere *et al.*, 2003; Hutchison *et al.*, 2010).

By far the majority of AWM examples target a specific pest, and far fewer consider the predators and parasitoids attacking pests (Malavasi *et al.*, 2007) even though theoretical and empirical work suggests that an areawide approach to managing NEs of pests can contribute significantly to pest suppression and in some cases pest control. Theoretical studies by Ives and Settle (1997) and Reeve (1990) consider the third trophic level and areawide suppression; both show that the combination of asynchronous planting of crops and highly mobile parasitoids resulted in areawide suppression of pests. Examples of areawide approaches indirectly managing for NEs include coordinated use of target-specific insecticides (e.g., less harmful on EAs; Hoque *et al.*, 2002), and coordinated spraying only when pests are above thresholds (Murray *et al*, 2005; Brier *et al.*, 2008).

More recently, there has been interest in the relationship between landscape structure and biological pest control, which has been driven by the desire to conserve biodiversity and natural biological pest control (Thies & Tscharntke, 1999; Tscharntke *et al.*, 2005). Reviews and meta-analyses suggest the general trend is for greater abundance and richness of NEs in complex than simple agricultural landscapes (Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011; Veres *et al.*, 2013); far fewer studies (Chaplin-Kramer *et al.*, 2011) have considered landscape complexity and pests, which typically show no relationship; for example, similar number of no-effect results as do those that show an effect (Veres *et al.*, 2013). Many studies recognize that natural enemies and the pests that they attack are influenced by factors operating at multiple spatial scales (Thies & Tscharntke, 1999; Bommarco & Banks, 2003; Tscharntke *et al.*, 2005; Schellhorn & Andow, 2005; Schellhorn *et al.*, 2008a; O'Rourke *et al.*, 2011; Rusch *et al.*, 2011; Bommarco *et al.*, 2013), and for NEs, the importance of noncrop habitat as possible source populations (Landis *et al.*, 2000; Fahrig *et al.*, 2011; Bianchi *et al.*, 2013; Macfadyen *et al.*, 2015). The majority of studies provide data on spatial pattern and measure the abundance and species richness of NEs. However, some do demonstrate impact, showing reductions in pest density with complexity or biological control services increasing with landscape complexity (Gardiner *et al.*, 2009; Holland *et al.*, 2012; Chaplin-Kramer & Kremen, 2012).

How can areawide pest management integrate with field-scale pest management? IPM is primarily concerned with keeping pest populations below economic injury level (EIL) and achieving this aim by integrating chemical, cultural and biological pest control (Kogan, 1998). Pest suppression from NEs is encouraged indirectly by eliminating broad-spectrum insecticides to minimize disruption and encourage NE conservation. The majority of pest management decisions are made at the field scale independent of the context of the surrounding area. Arguably the current "best practice IPM" includes routine arthropod monitoring, the use of soft-chemistry which is less harmful on NEs, and monitoring of pests and NEs after a spray to determine efficacy (Kogan, 1998; Schellhorn *et al.*, 2009; Zalucki *et al.*, 2009, 2015). Minimizing harm to NEs is the first step in making sure they are present and active in a landscape, and this can be achieved by selecting insecticides that minimize lethal and sublethal effects (e.g., avoiding broad-spectrum formulations). Beyond inundative releases (e.g., Smith, 1996), the majority of examples of management of NEs include the provision of a noncrop habitat adjacent to a crop or as a ground cover that provides food, alternative prey and habitat free from disturbance (Bugg *et al.*, 2009; Walton & Isaacs, 2011; Marko *et al.*, 2013), planting and mowing ground cover in orchards (Lu *et al.*, 2008), and strip mowing of Lucerne (alfalfa) or ploughing a flowering refuge to encourage the movement of natural enemies into crop fields (Bishop *et al.*, 1991; Hossain *et al.*, 2001; Samu, 2003; Schellhorn *et al.*, 2008b). In

agricultural landscapes dominated by annual crops, the immigration of NEs to newly emerging crops is dependent on immigration locally from adjacent crops or habitats, and at landscape scales (Corbett & Rosenheim, 1996; Schellhorn *et al.*, 2014). However, in most instances NE arrival to crop fields is completely left to chance, and can be highly variable, which makes for tenuous link between the landscape context, NEs and pest control. The high variability and high uncertainty of the timing, number and frequency of NEs arriving and high variability and uncertainty of NEs suppressing pests means that many farmers are reluctant to consider NEs as a formal component of pest management.

Here we focus on the connection between the landscape surrounding crop fields and pest control in the crop field. First, we provide a review of approaches that consider recruitment of NEs. Second, we evaluate how these approaches link the landscape context and in-field pest control. Third, we identify knowledge gaps that limit pest management actions in the crop field. Finally, we suggest how we might better achieve in-field pest control from landscape ecology studies of arthropod natural enemies.

How is the landscape surrounding crop fields connected with pest control at the field scale?

The science of understanding the abundance and diversity of pests and NEs in agricultural fields has scaled up, and moved beyond the field to the landscape surrounding the field at scales of hundreds of meters to kilometers. Biodiversity conservation has been a primary driver with particular emphasis on the role of noncrop habitat, such as forest, roadside verges, hedgerow, and meadows (Tscharntke *et al.*, 2005; Bianchi *et al.*, 2006). What does the increased emphasis on landscape complexity and habitat diversity mean for IPM, and are we any closer to achieving impact or management effects such as greater pest control, reduced pesticide use, and reduced pest population fluctuation?

From measuring to managing: what's being measured?

Thies & Tscharntke (1999) demonstrated the need to consider biological control and invertebrate pest management beyond the scale of the crop field. This seminal paper showed that with increasing amount of noncrop habitat in the landscape surrounding oil seed rape crops, parasitism was higher and pod damage by pollen beetle was lower. The authors used a correlative approach of spatially indexed regression (SIR) to assess relationships between pest control response variables (e.g., pollen beetle

abundance, parasitism, pod damage) and predictor variables such as noncrop habitat at varying spatial scales (e.g., 0.5, 1.0, 1.5, 2.0 km) around the point of observation. The uptake by researchers of the SIR method has grown and the approach is now widely used. Since the seminal paper in 1999, more than 50 studies have been conducted to date that consider relationships between landscape metrics and arthropod abundance and diversity. Three reviews of these studies (Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011; Veres *et al.*, 2013) provide evidence of positive relationships between abundance of NEs in crops and the proportion of noncrop habitat in a defined area. However, studies showing an impact on pests of this pattern of NE abundance, and/or the likely mechanisms underlying these relationships are rarely identified. This situation is perhaps not surprising due to the challenge of linking a land use class variable to pest suppression, and due to the challenge of exploring mechanisms related to arthropod movement. These gaps in our understanding are impediments to improved pest management.

Increasingly there are studies exploring the relationship between habitat complexity, NE abundance and diversity, and impact on pest populations. In an attempt to explore the value of the grasslands created as part of the agri-environment scheme across Europe, Holland *et al.* (2012) examined the impact of epigeal and aerial NEs on aphids in cereal-based systems. Excluding NEs resulted in significantly more aphids compared to when NEs had access to aphids with aerial enemies contributing the most. The levels of aphid control were positively related to the proportion of linear grass margins within several 100 meters of the fields. Chaplin-Kramer and Kremen (2012), using exclusion experiments were able to show aphid suppression as a function of local scale and landscape scale complexity, and that complexity at a local scale can substitute for complexity at the landscape scale. Rusch *et al.* (2013), also using exclusion experiments with aphids showed greater pest suppression with increased landscape complexity and lower variability in parasitism with longer and more diverse rotations. These studies combine experimental manipulation and landscape correlation to relate potential impact of NEs, and relate this to local versus landscape features, which can guide management practices and decisions.

From measuring to managing: patterns of abundance and links to pest suppression

One approach to close the gap between patterns of invertebrate abundance and better pest control is to reconsider both the dependent (response) and independent (predictor) variables measured in the

Table 1 Major invertebrate pests of grain crops across 4 countries. Their pest status is described as a: (A) persistent or priority pest, (B) persistent pest but rarely warrants control, (C) sporadic pest that requires control when outbreaks occur, and (D) secondary pest that rarely causes damage but can be exacerbated by management (e.g., insecticides or rotation).

Pest group		UK	USA	Australia	China
Aphididae	Aphids (multiple species)†	A	A	A	
	Sitobion avenae (Fabricius)				A
	Schizaphis graminum (Rondani)				A
	Rhopalosiphum padi (L.)†			B	A
Lepidoptera	*Helicoverpa armigera* (Hübner)			B	D
	Armyworms, cutworms and stalk boreres		C	C	
	Budworms (*Helicoverpa punctigera* [Wallengren])			C	
	Wireworms (*Agrotis* spp.)	D	D	D	
Coleoptera	*Anomala corpulenta* (Motschulsky) (Coleoptera: Scarabaeoidea)				B
	Cereal leaf beetle (*Oulema melanopa* [L.])	B	A		
	Pleonomus canaliculatus (Faldermann)				B
Hemiptera	Stink bugs (many species)		C		
	Rutherglen bug (*Nysius vinitor* [Bergroth])			C	
	Laodelphax striatellus (Fallén) (Homoptera, Delphacidae)†, ‡				D
Diptera	Hessian fly (*Mayetiola destructor* [Say])		A		
	Fruit fly (*Oscinella frit* [L.])	A/B			
	Leather jackets (Crane fly larvae)	A			
	Yellow cereal fly (*Opomyza florum* [F.])	B			
	Saddle gall midge (*Haplodiplosis marginate* [Roser])	A			
	Orange wheat blossom midge (*Sitodiplosis mosellana* [Gehin]), *Contarinia tritici* [Kirby])	C			C
	Wheat bulb fly (*Delia coarctata* [Fallën])	A			
	Wheat stem maggot (*Meromyza americana* [Fitch])		C		
	Sawfly (*Cephus cinctus* [Norton])		C		
	Sawfly (*Dolerus tritici* [Chu])				D
Arachnida	Mites‡		D	A	
	Wheat spider mite, (*Pentfaleus major* [Duges])				A
	Wheat spider, (*Petrobia latens* [Muller])				A
Orthoptera	*Gryllotalpa africana* (Beauv) (Gryllotalpidae)				B
	Gryllotalpa unispina (Saussure) (Gryllotalpidae)				B
	Plague locust (multiple species)		C	C	C
Collembolla	Lucerne flea (*Sminthurus viridis* [L.])			B	
Thripidae	Thrips		D		
Dermaptera	European earwig (*Forficula auricularia* [L.])			C	

Notes: Information has been collected from FAO (2002); websites hosting pest information www.syngenta-crop.co.uk; comprehensive identification manual and education resource called "I Spy" ISBN: 978–0–0646-53795–5 www.grdc.com.au/i-spy-manual; and a handbook on China Wheat Pests: Occurrence and Monitoring, China National Agro-Tech Extension and Service Center (2008).
†Vector of Barley yellow dwarf virus.
‡Vector of Wheat streak mosaic virus.

study systems. Studies exploring the link between pests, their NEs and land use classes often consider as the response variable individual species or groups of similar species often called functional groups (e.g., several species of aphids); for aphids see Elliott *et al.* (2002), Roschewitz *et al.* (2005), Thies *et al.* (2005, 2011), Rusch *et al.* (2013), Holland *et al.* (2012); for army worm and its braconid parasitoids see Marino and Landis (1996) and Menalled *et al.* (1999); for aphid and lepidopteran pest see Jonsson *et al.* (2012). This approach

lends itself to the "model system" idea; an aphid species or aphid complex associated with a host plant and the various predators and parasitoids that attack the aphids. This approach has increased our understanding of these invertebrate groups in agricultural landscape mosaics. Yet the information generated from a "model system" approach does not directly translate to levels of pest control needed to meet market standards. For example, crops rarely are attacked by a single pest or pest group. Therefore, farmers rarely make pest control decisions about a single pest. The three most common crop–pest natural enemy systems explored in studies considering the role of the landscape in pest suppression are: (i) Grains, with aphid pests, and their predators and parasitoids (as above), (ii) canola or rape, with beetles and parasitoids (Thies & Tscharntke, 1999; Thies *et al.*, 2003), and (iii) brassicas, with lepidopteran pests and their arthropod NEs (Bianchi *et al.*, 2005; Bianchi *et al.*, 2008; Chaplin-Kramer & Kremen, 2012; Jonsson *et al.*, 2012). The discipline has gleaned much insight from these studies, however, the crops from these studies have many primary and secondary pests, and these crops experience sporadic pest outbreaks, and controlling them is usually primarily based on insecticides (Table 1). As an example, cereal crops from around the world have pest complexes with varying degrees of pest status (FAO, 2002); a small subset is shown for the United Kingdom, the United States, China, and Australia (Table 1). Immigration of these pests to annual crops occurs at different times of the growing season, and may even be "sourced" from several different habitats (Macfadyen & Muller, 2013; Schellhorn *et al.*, 2014); similarly for the NEs that attack them. Therefore, the abundance and diversity of the pest complex associated with the crop is rarely considered, but see Letourneau and Goldstein (2001), and Bianchi *et al.* (2013). Another challenge lies with the independent variable. Land use classes and landscape features are used as predictors in spatially indexed regression models to explain variation in the response variables, usually a measure of control such as parasitisation rates (Table 2). The challenge of moving from a pattern showing a positive correlation of land use (such as the amount of noncrop habitat at 1.5 km) and NE abundance or attack to a management action, is that land use on a farm or in a region can rarely be changed in any substantial way in practice, especially intensely cropped landscapes; the exception being some examples of government subsidized agri-environment schemes. Furthermore, these pest complexes often have more than one host plant, they feed and reproduce on multiple crops, weeds and in some cases native plants (Norris & Kogan, 2000; Pease & Zalom, 2010; Schellhorn *et al.*, 2010), but we know relatively little about the diversity of plants used

by pests and NEs across their life-span (Bianchi *et al.*, 2013). Depending on the spatial and temporal availability of these various host plants, a management option to suppress these pest complexes at broad spatial scales may be achieved by: controlling the early spring weed host prior to a summer sown crop (Mueller *et al.*, 1984), controlling a late summer host prior to an autumn sown winter cereal host (Wiktelius, 1987), sowing time of cereals such as autumn versus spring planting (Leather *et al.*, 1989), the timing of an insecticide application in another crop or the frequency of application (den Belder *et al.*, 2002), the mowing or management of weed hosts or pasture at a particular time (Abel *et al.*, 2007; Yasuda *et al.*, 2011), or harvesting or cutting a crop (Jonsen & Fahrig, 1997; Holland & Fahrig, 2000). These types of management actions are likely to impact the NEs that feed on these pests. Including management actions as independent variables, as well as variables of land cover, can provide an indication of the strength of these interactions and prioritization for management action.

From measuring to managing: patterns of abundance–local versus landscape factors

Movement from surrounding habitats into crops has been suggested as a driver of the spatial patterns of abundance of pests and NEs, but few studies have quantified the timing, frequency, and intensity of immigration/emigration events into and out of crops (Bianchi *et al.*, 2009; Schellhorn *et al.*, 2014). The approach in the majority of studies, driven by the question of fragmentation and biodiversity, is to collect information on arthropod abundance at time points during crop development stages, aggregate the values into annual averages, or collect information later in the season during the crop reproductive phase (e.g., Thies *et al.*, 2005; Rand & Tscharntke, 2007; Thies *et al.*, 2011). Although these stages of crop development are critical and often need protecting from pests, the pests and NEs present may or may not be as a result of immigrants from surrounding landscapes, and instead may be due to local reproductive increase (see Schellhorn *et al.*, 2014). For example, depending on temperature and aphid host, parasitoids of aphids can complete their life-cycle in a timeframe of a dozen days to several weeks (e.g., Lajeunesse & Johnson, 1992). This translates into several parasitoid generations within a cropping season. By the time the crop has reached maturity parasitism rate is a combination of numerical increase from in-field reproduction and numerical increase from immigration. The reproductive increase of aphids can be driven by abiotic, bottom up as well as top down factors (Johnson, 2008; Dong *et al.*, 2013),

Table 2 Response and predictor variables used in a subset of studies that attempt to measure the functional link between pests and natural enemies as a response to the surrounding landscape at multiple spatial scales. Land use and land cover variables are frequently correlated (at some spatial scale) with response variables) in terms of reproduction or feeding/resting needs to be understood.

Crop, area, study	Study system	Natural enemy species studied	Response variables	Spatial scales	Land use/land cover variable	Other predictor variables	Number and types of crops in the landscapes
Alfalfa, CA[1]	Alfalfa weevil *Hypera postica* and all alfalfa-specialist weevils	None	A (*H. postica* & alfalfa weevil specialist), NS (alfalfa weevil and number of families all insects), A (total number of insects collected)	1 km of the field perimeter and adjoining field	Length of woody border within 1 km of the field perimeter and surrounding field	% cover of alfalfa, time since field was converted to alfalfa, harvesting, field age	Unspecified
Alfalfa, CA[2]	A range of herbivores: Curculionidae (Coleoptera), weevils, and Cicadellidae (Auchenorrhyncha) leafhoppers	None	A, NS (herbivores: specialists and generalists)	1 km radius from edge of alfalfa field	Proportion of 9 habitat types, Shannon-Wiener diversity index used to measure landscape patch type diversity; isolation measured as the edge-to-edge distances of the sampled alfalfa field to all other alfalfa fields in each landscape	Sample field size, age & number of times cut during the study; within-field vegetation diversity and proportion of legumes for some analyses	Corn, cereal grain, hay, alfalfa, soybean and pasture
Almond, USA[3]	Navel Orangeworm (NOW) *Amyelois transitella*	Parasitic wasps, Predatory spiders	A & D (NOW), A (parasitoids), A and D (other insect pests and arachnid pests), A (predators on "mummy" nuts), D (vertebrate pests)	1 km radius	% of natural habita.	Proportion of vertebrate nut damage, number of understory plant species, understory ground cover with vegetation, local management (conventional versus organic), study region and distance of sample point from orchard margin in meters	Unspecified

(to be continued)

Table 2 Continued.

Crop, area, study	Study system	Natural enemy species studied	Response variables	Spatial scales	Land use/land cover variable	Other predictor variables	Number and types of crops in the landscapes
Brassica (Broccoli), USA[4]	Cabbage aphid *Brevicoryne brassicae*	Mostly syrphid flies, parasitic wasp coccinellids, lacewings aphid midge spiders, mixed predators	S (aphids- in closed and open cages exposed to natural enemies)	1 km radius around farm and within-farm	% of natural or seminatural habitat; "local Complexity" of habitat on-farm (field size, crop diversity & noncrop floral resources)	Temperature and season as well as presence of mustard and natural enemy density in surrounding fields	Unspecified
Brassica (Brussels sprouts), EU[5]	Cabbage moth *Mamestra brassicae* eggs	Parasitic wasp; Staphylinidae and Carabidae	S (lepidopteran eggs)	0.3, 1, 2, and 10 km diameter around each field	Twenty variables. At each spatial scale: amount of habitat type; length of (several different) linear features; number of solitary trees	None	Four agricultural crops, unspecified horticulture and orchards
Brassica (Brussels sprouts), EU[6]	Diamondback moth *Plutella xylostella*	Parasitoid *Diadegma* spp.	S (II & III instar larvae after 2 d)	0.3, 1, 2, and 10 km diameter around each field	Twenty variables. At each spatial scale: amount of habitat type; length of (several different) linear features; number of solitary trees	None	Four agricultural crops, unspecified horticulture and orchards
Cabbage, EU[7]	Lepidoptera: *Pieris rapae* & *P. brassicae* & the cabbage looper *T. ni*	No focal species, 3 main guilds of natural enemies: aerial; epigeal; and birds	S (exclusion treatment cages: pest density, herbivory and biomass)	300 m radius around fields	Percentage of seminatural habitat	Level of natural enemy exclusion, crop and management type of the nearest surrounding field	Unspecified
Cotton, Aus[8]	Thysanoptera (thrips), and cicadellidae, *Frankliniella schultzei, F. fusca, Thrips tabaci* and *T. imaginis* & others	Predatory beetle, spiders, parasitic wasps	A (arthropod density)	120, 750, 1500, and 3000 m around each sampling quadrat within fields	Proportions and connectivity (cost-distance) of noncrop land use surrounding crop field	None	Unspecified

(to be continued)

Table 2 Continued.

Crop, area, study	Study system	Natural enemy species studied	Response variables	Spatial scales	Land use/land cover variable	Other predictor variables	Number and types of crops in the landscapes
Leeks, EU[9]	Onion thrips, *T. tabaci*	None	A (adult and nymph thrips)	Landuse at 2 spatial scales, 1 and 5 km around centroid of study fields	Total area of woodlots, natural and agricultural areas	Pesticide application	Agricultural crops (maize, potatoes, sugarbeet), and other horticultural crops, pastures and other natural areas
Olive, EU[10]	Olive fruit fly *Bactrocera oleae*	Parasitic wasps	A (pest, parasitoids found on fruit samples)	0.5, 0.75, 1, 1.5, and 2 km diameter around the centroid of each olive grove	Percentage of landscape occupied by woodland at each scale and the "splitting index" (fragmentation) of woodland	None	"Arable land" as a single class. Vineyards and olive groves
Soybean, USA[11]	Soybean aphid, *Aphis glycines* and coccinellids	Coccinellids	A (soybean aphids, and coccinellids on yellow sticky cards)	0.5, 1.0, 1.5, and 2 km radius around field centroid	Proportion of seminatural habitat and Simpson's Diversity Index measuring landscape heterogeneity	None	Corn, soy, wheat, and forage crops
Spring sown cereal (barley or wheat), EU[12]	Aphids (many species)	Multiple species of parasitoids, and specialist and generalist predators	A (aphids, parasitoids, and predators); exclusion experiments for aerial and epigeal natural enemies	1 km radius around the field	The landscape complexity around each field was characterized by the proportion of annually tilled arable land (PAL)	Margin distance, crop characteristics (cereal height, cereal growth stage, cereal cover and weed cover) & meteorological variables	Unspecified
Tomatoes, USA[13]	Multiple pest species; pest damage	Multiple NEs	A & NS (many pest of tomatoes and natural enemy species)	1 km and 5 km radius around each field	Agriculture practice (conventional *vs.* organic) and % landscape feature, e.g., natural land	Farm type (organic *vs.* conventional), fallow management, transplant date	Unspecified

(to be continued)

Table 2 Continued.

Crop, area, study	Study system	Natural enemy species studied	Response variables	Spatial scales	Land use/land cover variable	Other predictor variables	Number and types of crops in the landscapes
Winter wheat, EU[14]	Cereal aphid *Sitobion avenae*	Two predator guilds (epigeal and aerial)	S (aphids) Impact of predators on aphids	250, 500, and 750 m radius of centroid of each transect.	Proportion and area of uncropped land (grass strips/hedgerow/trees); Shannon indices of uncropped land diversity and crop diversity	Presence/absence of epigeal and aerial predators, year	Cereal, broadleaf crop, pasture
Winter wheat, EU[15]	Cereal aphids *S. avenae, Metopolophium dirhodum & Rhopalosiphum padi*	Parasitic wasps	A (aphids, parasitoids) Parasitism rate	1, 1.5, 2, 2.5, and 3 km radius around each study site	Landscape "complexity" = percentage of arable land	Farming system (organic vs. conventional), year, host plant density & aphid host density	Unspecified
Winter wheat, EU[16]	Cereal aphids *S. avenae, M. dirhodum & R. padi*	Five genera of parasitoids	A (aphids, parasitized aphids [mummies])	0.5, 1, 2, 3, 4, 5, and 6 km diameter around each study field	Landscape "complexity" = percentage of arable land	Year, host plant density, & aphid host density	Cereals, sugar beets, oilseed rape and corn
Winter Wheat, EU[17]	Cereal aphids *S. avenae, M. dirhodum & R. padi*	Parasitic wasp, Aphidiidae	A & NS (aphids and parasitoids)	500 m radius around field	Landscape complexity = percentage of arable land.	None	Unspecified

Notes: Response variables, () = insect type; A () = abundance, NS () = number of species, D () = damage estimate, S () = sentinels for predation or parasitism.
[1]Holland and Fahrig (2000); [2]Jonsen and Fahrig (1997); [3]Eilers and Klein (2009); [4]Chaplin-Kramer (2011); [5]Bianchi *et al.* (2005); [6]Bianchi *et al.* (2008); [7]Martin *et al.* (2013); [8]Perovic *et al.* (2010); [9]den Belder *et al.* (2002); [10]Boccaccio and Petacchi (2009); [11]Woltz *et al.* (2012); [12]Caballero-Lopez *et al.* (2012); [13]Letourneau and Goldstein (2001); [14]Hollandr *et al.* (2012); [15]Roschewitz *et al.* (2005); [16]Thies *et al.* (2005); [17]Vollhardt *et al.* (2008).

therefore the contribution of the landscape may be difficult or impossible to detect if life-stages are sampled many days past the arrival of the first immigrants. In addition, cumulative measures, such as aggregating annual averages are likely to cloud the effect of landscape composition on pests and NEs (Chaplin-Kramer *et al.*, 2013; Schellhorn *et al.*, 2014). As an example, the landscape may only contribute immigrants early in the season and not again. The study by Topping & Sunderland (1998) showed that population increase of a lycosid spider was primarily driven by in-field reproductive increase (similarly shown by Pearce *et al.*, 2005), and that immigration occurred early and was thereafter infrequent. This has important implications when we consider disturbance from insecticides and harvest. Ultimately identifying key mechanisms will facilitate links to management actions to consider and actions to avoid that lead to an increase in NE arrival (when), numbers (how many), and types (what kind) into target crops or pest delay in arrival, lower numbers and fewer types into target crops (Schellhorn *et al.*, 2014).

Capturing pest control from habitats surrounding crop fields

There is an important distinction between pest suppression and pest control (see breakout box 1)

> **Break out box 1**. Pest suppression and pest control. Are they the same thing? Pest suppression is evidence of reduction in pest numbers as it relates to an experimental control, whereas pest control is the density of pest not causing crop economic injury or loss.

(Chaplin-Kramer *et al.*, 2013; Schellhorn *et al.*, 2014). Studies evaluating the relationship between landscape complexity and the abundance and diversity of NEs and pests primarily imply the potential for pest suppression, see reviews by Bianchi *et al.* (2006), Chaplin-Kramer *et al.* (2011), Veres *et al.* (2013), with more recent studies evaluating impact in terms of pest mortality (e.g., 3 examples listed above, also see Macfadyen *et al.*, 2015). Yet these measures are still decoupled from pest control; the pest level necessary to avoid economic injury to the crop (Chaplin-Kramer *et al.*, 2013; Schellhorn *et al.*, 2014). The density of pests and the relationship to EILs (a measure of destructive status indexed by pest numbers) and economic thresholds (ET–an operational rule such as a population density at which control should occur) has been developed for many primary pests of the major

agricultural crops (e.g., MacRae, 1998; Oakley, 2003; Brier *et al.*, 2008; Flowers & Mass, 2010; Pedigo, 2013). Measures of pest control can be understood and standardized across regions by bench marking against ET in practice. These measures may be used as response variables in statistical analyses where an amount of the variation in pest threshold is explained by land use class variables or management actions. The response variables that may be considered are those directly related to arthropod population processes and pest control decision making, and include: (i) whether pest populations stay lower (below threshold) for longer, (ii) the number of times pest populations go above threshold, and (iii) the amount of time pest populations stay above threshold. Mechanisms can be identified to explain each of these measures and includes: (i) pests immigrating in low numbers, infrequently, and/or late in the season, (ii) pests experiencing poor reproductive performance (bottom-up factors), (iii) NEs immigrating in high numbers, often and early in the season, and (iv) NEs eating pests and reproducing (classic functional and numerical responses). With the exception of bottom up effects, which are primarily driven by host plant resistance, habitats in the surrounding landscape contribute pests and NEs to emerging annual crops via the process of immigration at some spatial scale. This process is highly variable, and although immigration of NEs to crops may be sufficient to achieve pest control, the spatial and temporal variability is large (Bommarco & Banks, 2003; Schellhorn *et al.*, 2014); certainly too variable to be relied on for pest management. What is needed are rules of thumb and thresholds to know when NE populations are insufficient to achieve pest control, and therefore other control options need to be accessed, for example, inundative release. This is analogous to other resources required by the crop such as water, and fertilizer, and the need to identify supply–demand mismatches.

Using the ET approach as the measure of impact can address the request by several researchers that the gap needs to be filled between natural pest control, crop damage, and crop yield (Cullen *et al.*, 2008; Jonsson *et al.*, 2008; Bommarco *et al.*, 2013). The results from studies that have evaluated yield in relation to natural pest control are quite variable (Macfadyen *et al.*, 2014). In part this may be due to the nonlinear relationship between yield, insect density, and insect damage. Yield can be strongly influenced by numerous factors, for example, the rotation from the previous year (Meisner & Rosenheim, 2014), time of planting, field-to-field and within-field variability in soil nutrition and type. In addition, the agricultural landscapes and agronomic practices surrounding the target crop can greatly impact on the abundance of predators and in turn their impact on pests. Monteiro *et al.* (2013)

showed that predation on coddling moth eggs was lower in orchards surrounded by large areas of conventional orchards, and in orchards with more toxic crop protection practices. The ET approach is a direct measure that demonstrates the effect size of pest control as a function of population processes connected with adjacent habitats and surrounding landscape; an approach that avoids the problem of high variability in yield, but still provide evidence of impact. In addition, simple calculations can show the pest control savings from local interventions such as planting of strips of semi-natural habitat and/or the landscape context. For example, if pest populations stay below threshold for longer, therefore fewer sprays are required, then simple calculations can show the savings in labor, chemicals, fuel, and machine operation (see break out box 2).

Break out box 2. How to strengthen the link between the surrounding landscape and in-field pest control:

(1) estimate NE and pest arrival and departure (time, numbers, and type);
(2) bench mark against pest ET;
(3) include multiple pest species more aligned with the realities of agricultural crops, and a mix between pests that are persistent and those that are sporadic.

How can we achieve management outcomes for in-field pest control from landscape ecology studies of arthropod NEs? Embedded in standard guidelines to farmers practicing IPM (see break out box 3) is the objective to

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Break out box 3. Standard guidelines provided to farmers for practicing IPM include:

(1) reduce or eliminate the use of broad-spectrum insecticide;
(2) use soft-chemistry that targets the pest and minimizes disruption to their NE;
(3) consider a coordinated approach to pest control by working with neighbors to use less disruptive insecticides; and
(4) identify areas that might harbor pests for coordinated control.

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conserve NEs that can provide pest control services, and that pest control and NE conservation has to be considered beyond the scale of the field, and often beyond the farm (Table 2). However, more experimental evidence is needed to demonstrate the strength of these guidelines, if fully implemented. Protecting the ecosystem service of pest control is an areawide concept, and increasingly studies are demonstrating the on-farm intervention strategies can have greatest benefit in agricultural landscapes of moderate complexity (e.g., Haenke *et al.*, 2009). This work now needs to integrate varying levels of disturbance (especially disturbance causing direct mortality to NEs) in order to show the effective scale of disruption and in turn lead to strategies for intervention. For example, can the adjacent flower strip, forest or patch of native remnant vegetation provide a refuge for predators and parasitoids when insecticide is sprayed in the adjacent field? Are these flower strips sources for recolonization after a spray? These questions are about protecting the control agents and creating resilience in the system. Answering these questions with experiments would be valuable. Comparative information is needed on pest and NE movement (immigration and emigration at the field) out of and into field's sprayed and unsprayed with insecticide. This information could be gathered using bidirectional interception traps tracking insect movement over time with one of the treatments being before and after spraying. In addition, in-field estimates tracking ET over time would provide evidence of impact of NEs on pests as a function of the landscape and disturbance. The expectation would be that pests would recover quickly, growing above the damage threshold quickly, and staying there in pesticide-treated fields without an adjacent source habitat of predators and parasitoids or in a heterogeneous landscape. To answer the question as to whether insecticide use in an adjacent paddock impacts beyond the sprayed field, sentinel plants could be used; sentinels to show colonization of pests, and sentinel hosts or prey on sentinel plants to show attack by predators or parasitoids. Placing them at different distances from the disturbance in replicated fields that are imbedded in landscapes of varying degree of heterogeneity would prove useful. These approaches and questions are aligned to studies comparing organic versus conventional farming practice (Macfadyen *et al.*, 2009; Winqvist *et al.*, 2011), but with the added interest of focusing on the pest and the area of influence of the disturbance from insecticide.

Although the above mentioned empirical studies can provide insight to link between the field and landscape scale, such studies are costly, and still depend on correlation to some extent. Therefore, a triad of laboratory, field experiments and modeling provides a powerful approach to link species traits (pests and NEs), landscape features, and pest suppression (Schellhorn *et al.*, 2014). In particular, using simulation models overcomes some of the logistical constraints of empirical approaches when

dealing with individual behavior, population processes, and real landscape, which are highly variable. Although there are now many examples of spatially explicit predator–prey simulation models, they have continued to be highly abstract and theoretical (e.g., Cuddington & Yodzis, 2002; Baggio *et al.*, 2010), largely based on the analytical equations of Lotka (1920) and Volterra (1926) or governed by optimal foraging theory (e.g., Kindlmann & Dixon, 1993). Many such models usually conceptually reference vertebrate interactions and are rarely integrated with field data or empirical studies (but see for example Bianchi & Wäckers, 2008; Bianchi *et al.*, 2009). Treatment of space is typically unrealistic, ignoring boundary effects (as models are usually constrained to simulate on a grid) and this greatly simplifies movement behavior, ignoring the interaction between movement capacity and habitat properties (Cronin & Reeve, 2005), commonly simplifying movement capacity to uniform probabilities of traversing the matrix between suitable patches (metapopulations) (e.g., Baggio *et al.*, 2010). In order to explore elements of landscape complexity such models have tended to use artificial "neutral" landscapes, which represent measurable characteristics, in particular fragmentation, of real landscapes (e.g., Bianchi & van der Werf, 2003; Visser *et al.*, 2009). Such theoretical landscape studies have generated interesting hypotheses and insights, such as expected proportions of habitat to maximize pest control. However, these usually highly simplified, binary and static representations of real agricultural landscapes ignore important within-patch level processes, despite indications from models developed over 30 years ago on the importance of spatial heterogeneity in determining biological control of insect pests, due to differential exploitation of patches by pests (Beddington *et al.*, 1978). A more mechanistic approach that is integrated with empirical field research and real landscape data (e.g., includes crop growth stage or noncrop habitat composition), has the advantages of providing more complex insights from the scaling-up of findings from empirical studies, and facilitates the incorporation of the effects of heterogeneity in landscapes and arthropod interactions that may be better tied to realistic management actions (Potting *et al.*, 2005; Bianchi *et al.*, 2007; Parry *et al.*, 2012).

To conclude, ecological studies are advancing our understanding on how to protect and promote the ecosystem service of biological pest control; the importance of the landscape context and local interventions. Connecting these findings with measures of pest control and pest management decision-making has many benefits including, measures of impact that are standard across crops and regions, a knowledge pathway from mechanisms to impact, and on-the-ground action. Habitat interventions may soften the agricultural landscape matrix and in turn minimize species loss. However, to bridge the gap between ecological studies aimed at protecting and promoting biological pest control, ecologist have to consider the realities of food and fiber production, and pest managers have to believe that ecologist have knowledge to offer that will result in best-practice pest management.

Disclosure

All authors confirm "no conflict of interest" relevant to the subject of this manuscript.

Author contributions

NA Schellhorn and MP Zalucki developed the concept, and contributed to content and writing, HR Parry and S Macfadyen contributed content and writing, Y Wang contributed content.

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