Interactions between conventional and organic farming for biocontrol services across the landscape

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Abstract. While the area of organic crop production increases at a global scale, the potential interactions between pest management in organic and conventionally managed systems have so far received little attention. Here, we evaluate the landscape-level co-dependence of insecticide-based and natural enemy-based pest management using a simulation model for parasitoid–host interactions in landscapes consisting of conventionally and organically managed fields. In our simulations conventional management consists of broad-spectrum or selective insecticide application, while organic management involves no insecticides. Simulations indicate that insecticide use can easily result in lose–lose scenarios whereby both organically and conventionally managed fields suffer from increased pest loads as compared to a scenario where no insecticides are used, but that under some conditions insecticide use can be compatible with biocontrol. Simulations also suggest that the pathway to achieve the insecticide reduction without triggering additional pest pressure is not straightforward, because increasing the proportion of organically managed fields or reducing the spray frequency in conventional fields can potentially give rise to dramatic increases in pest load. The disruptive effect of insecticide use, however, can be mitigated by spatially clustering organic fields and using selective insecticides, although the effectiveness of this mitigation depends on the behavioral traits of the biocontrol agents. Poorly dispersing parasitoids and parasitoids with high attack rates required a lower amount of organically managed fields for effective pest suppression. Our findings show that the transition from a landscape dominated by conventionally managed crops to organic management has potential pitfalls; intermediate levels of organic management may lead to higher pest burdens than either low or high adoption of organic management.

Key words: aphid; biological control; ecosystem service; insecticide; Leslie matrix; parasitoid; pest management; spatiotemporal dynamics.

Introduction

Synthetic insecticide applications are standard practice in conventional farming systems because they are simple to use, relatively cheap, and often effective in providing short-term reduction in pest densities. Yet, their effectiveness as a sustainable pest management strategy is being questioned (Lewis et al. 1997, Bommarco et al. 2011, Gross and Rosenheim 2011, Krauss et al. 2011), and undesirable side effects are increasingly recognized, such as negative impacts on human health and biodiversity, air and water pollution, and evolution of resistance in targeted pests (Pimentel et al. 1992). These side effects are causing growing consumer concerns, leading to increased demand for pesticide free crop production. For instance, in 2009 global organic food and drink sales expanded by roughly 5% to US$54.9 billion (Willer and Kilcher 2011). Furthermore, policies are being developed to reduce the use of harmful synthetic insecticides (e.g., European Union Council Directive 91/414/EEC of 15 July 1991) and promote the adoption of "integrated pest management" (IPM) (e.g., European Union Council Directive 2009/128/EC of 21 October 2009). As part of legislation to achieve the sustainable use of pesticides (effective 1 January 2014), EU member states will be required to take all necessary measures to promote low pesticide-input pest management and give priority to nonchemical methods.

One of the prime pest control mechanisms in IPM (i.e., combination of pest control techniques that discourage the development of pest populations and keep pesticides to levels that are economically justified) and organic farming is top-down control of pest populations by natural enemies. This ecologically based pest management can lead to higher natural enemy

diversity (Macfadyen et al. 2009a) and evenness (Crowder et al. 2010), and higher natural enemy abundances (Furlong et al. 2004, Koss et al. 2005) in comparison to conventionally managed crops. As a consequence, ecologically based pest management can potentially result in effective top-down pest control (Bommarco et al. 2011, Krauss et al. 2011), but also involves higher risk than conventional pest management (e.g., Koss et al. 2005, Macfadyen et al. 2009b).

Conventional pest management is potentially incompatible with biocontrol by natural enemies when practiced together (Furlong et al. 2004). Natural biocontrol requires agroecosystems that can support effective populations of natural enemies to keep pest densities relatively low. When pest outbreaks are rare, there is limited need for pesticide applications, and in turn little disruption of the natural enemy complex, which further reduces the need for pesticide applications. However, as natural enemies typically do not eliminate pest populations, a minimum level of pest infestation needs to be tolerated, and in many circumstances natural enemies actively need to be maintained. Insecticide applications can disrupt biocontrol and release pests from control by natural enemies, in particular when broad-spectrum insecticides are used that kill pests and natural enemies indiscriminately. In this case, insecticide treatments need to be repeated, with the risk of a cascade into intensive application of insecticides (i.e., the pesticide treadmill; Hansen 1986).

The growing consumer and governmental pressure to shift from insecticide-based to natural enemy-based pest management (Ekström and Ekbom 2011; EU directive 2009/128/EC) raises numerous scientific questions. For example, how do conventional pest management and biocontrol interact at the landscape level? Do organic farms act as a refuge for natural enemies and provide a pest suppression benefit to neighboring conventional farms via spillover effects? Conversely, do these same farms provide a refuge for pests resulting in increased immigration rates of pests to surrounding farms and landscape? Does broad-spectrum insecticide use by conventional farms reduce the biocontrol potential at organic farms? These questions highlight the need to understand how pest–natural enemy interactions are influenced by insecticide use at the landscape scale.

We developed a mechanistic spatially explicit simulation model of parasitoid–host interactions in landscapes consisting of conventionally (subject to broad-spectrum or selective insecticide application) and organically managed fields (no insecticides applied). While we acknowledge that conventional and organic management differs in many aspects, and that pest management in organic agriculture may involve the use of certified organic pesticides, we will here focus on the contrast between insecticide-based and natural enemy-based pest management. We focus specifically on parasitoids as biological control agents because in many cropping systems partial or complete control of

pests by parasitoids is possible (Hawkins et al. 1997). As fields under different management share the same pest and natural enemy pool in the landscape, and natural enemies and pest are mobile, insecticide applications in one field can influence natural enemy–pest interactions in other fields via reduced pest and/or natural enemy immigration from treated fields. Here, we explore how the impacts of insecticide on parasitoid–host interactions can vary depending on: (1) the dispersal capacity and attack rate of parasitoids, (2) the proportion and spatial distribution of conventionally and organically managed fields in the landscape, and (3) the selectivity of the insecticide (broad-spectrum vs. selective). We evaluate the outcomes of conventional vs. organic management in terms of host densities and fraction parasitism, and also crop yield reduction under two hypothetical, but plausible, relationships between host density and crop yields.

Material and Methods

Landscape and biological system

The model simulates the spatiotemporal dynamics of hosts and parasitoids in landscapes consisting of equally sized conventionally and organically managed fields. In conventionally managed fields, pest (and parasitoid) populations are controlled by insecticide applications when pest populations exceed a threshold density, whereas in organically managed fields no pesticides are used. To give biologically plausible scenarios, we tailored the model to suit the parasitoid *Aphidius ervi* Haliday (Hymenoptera: Braconidae) and pea aphids *Acyrthosiphon pisum* (Harris) (Homoptera: Aphididae) feeding in pea or bean crops (see Plate 1). The model consists of a grid of 50×50 cells (fields) with wraparound boundaries, so that individuals moving off the grid on one edge are reintroduced on the opposite edge. The interactions within each field are determined by a stage-structured model for pest and parasitoid, and the cells are linked together by pest and parasitoid dispersal (see *Host and parasitoid dispersal*). We assume that pea aphids are the only hosts available to parasitoids, so there are no alternative hosts in either conventionally or organically managed fields. A similar model has been shown to accurately describe aphid–parasitoid interactions as observed in short-term field cage experiments (Snyder and Ives 2003).

Although the model was tailored for the pea aphid–*A. ervi* system, it has features that are common to many cases of biocontrol in agricultural systems. In particular, many pests are effectively specialists on a narrow range of crop species, and many natural enemies such as parasitoids are specific to a narrow range of pest species. While we recognize that generalist natural enemies are often important in biocontrol, and biocontrol of pea aphids in particular (Cardinale et al. 2003, Snyder and Ives 2003), specialist pests and natural enemies are likely to be particularly sensitive to insecticide applications if they do not have refuges on other plants that are not

treated. Therefore, the issues involving insecticide applications are particularly important for specialists. Finally, the model applies to pea aphids that have generation times of 2–3 weeks and can therefore rapidly build up their population size during the growing season. As a consequence, the model is not appropriate for univoltine pests. Nonetheless, many pest species share these features with pea aphids and therefore can be described qualitatively by the model.

Host–parasitoid dynamics

The model explicitly includes stage structure of the host population, dividing the population into five instars. Host dynamics were modeled using a Leslie matrix (Caswell 1989) in which density-independent survival of all host stages is given by the parameter s, and adult fecundity is F. We also included density-dependent mortality as decreases in survival for all host stages with increases in the total host density (including parasitized but still-living hosts). The combined density-dependent and density-independent survival is given by

$$S(t) = s\left(1 + kx(t)\right)^{-1} \tag{1}$$

where $x(t)$ is the total density of hosts at time t, s is the density-independent survival, and k is a parameter giving the strength of density dependence, whereby higher k values result in stronger density dependence. Density-dependent and density-independent mortality caused by generalist predators, parasites (other than parasitoids), and other sources are implicitly incorporated into host survival. Thus, in the absence of parasitoids the dynamics of hosts is given by

$$X(t+1) = \mathbf{L}\left(X(t)\right) \times X(t) \tag{2}$$

where $X(t)$ is the 5×1 vector of densities of the five stages of hosts at time t, and

$$\mathbf{L}\left(X(t)\right) = \begin{bmatrix} 0 & 0 & 0 & 0 & FS(t) \\ S(t) & 0 & 0 & 0 & 0 \\ 0 & S(t) & 0 & 0 & 0 \\ 0 & 0 & S(t) & 0 & 0 \\ 0 & 0 & 0 & S(t) & S(t) \end{bmatrix}.$$

This description assumes that the four immature host stages last the same length of time, which is approximately the case for pea aphids (Hutchinson and Hogg 1985). Thus, the time it takes for hosts to traverse a developmental stage sets the time scale of the model.

Parasitoids have host instar-specific attack rates, with relative attack rates on stage i given by α_i ($\Sigma\ \alpha_i = 1$). Although Ives et al. (1999) demonstrated that *A. ervi* shows a type II functional response, the functional response curve is close to linear over the range of densities typically exhibited by pea aphids in the field, so for simplicity we assumed that parasitoids have a type I functional response. Letting $y(t)$ denote the density of parasitoid adults, the proportion of hosts in instar i that are parasitized is given by

$$1 - e^{-ax_iy(t)} \tag{3}$$

where a is the overall attack rate (searching efficiency).

It takes parasitoid larvae five host-development time units to kill their hosts and initiate pupation; in the case of aphids, parasitoids pupate within the exoskeleton of the aphid, which forms a "mummy." Because parasitized first-instar aphids always reach adulthood before mummies are formed, we assumed that larval parasitoids go through all five host developmental stages, during which time they suffer density-dependent survival equal to that of unparasitized aphids (Rauwald and Ives 2001). The development of parasitoid pupae takes three time units during which survival is given by s_m. The final (eighth) stage is parasitoid adults that are assumed to have survivorship s_w. Thus, the parasitoid population at time t is given by the 8×1 vector $\mathbf{Y}(t)$, with the last element of $Y(t)$ being adults, $y(t)$. The overall dynamics of hosts and parasitoids are given by

$$X(t+1) = \mathbf{A}\left(X(t)\right) \times \mathbf{L}\left(X(t)\right) \times X(t) \tag{4}$$

$$Y(t+1) = \mathbf{S}_w \times Y(t) + \mathbf{J} \times \left[\mathbf{I} - \mathbf{A}\left(X(t)\right)\right]$$
$$\times \mathbf{L}\left(X(t)\right) \times X(t) \tag{5}$$

where the matrix $\mathbf{A}(X(t))$ gives the proportion of hosts escaping parasitism (see Eq. 6, below).

$$\mathbf{A}\left(X(t)\right) = \begin{bmatrix} \exp\left(-a\alpha_1 y(t)\right) & 0 & 0 & 0 & 0 \\ 0 & \exp\left(-a\alpha_2 y(t)\right) & 0 & 0 & 0 \\ 0 & 0 & \exp\left(-a\alpha_3 y(t)\right) & 0 & 0 \\ 0 & 0 & 0 & \exp\left(-a\alpha_4 y(t)\right) & 0 \\ 0 & 0 & 0 & 0 & \exp\left(-a\alpha_5 y(t)\right) \end{bmatrix}. \tag{6}$$

I is the 5×5 identify matrix, $\mathbf{S}_w$ is the 8×8 matrix giving parasitoid survival,

$$\mathbf{S}_w\big(X(t)\big) = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ S(t) & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S(t) & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S(t) & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S(t) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & s_m & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & s_m & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & s_m & s_w \end{bmatrix}$$

and $\mathbf{J}$ is an 8×5 matrix containing ones in the top row and zeros elsewhere that aggregates newly produced parasitoid larvae from hosts parasitized in different stages.

Host and parasitoid dispersal

The landscape on which hosts and parasitoids interact consists of a 50×50 grid of cells, with the interactions of hosts and parasitoids within cells given by the model Eqs. 1–5. Cells are divided into two categories to represent conventionally and organically managed fields. Conventionally managed fields are treated with insecticide when host densities exceed a critical threshold, while organically managed fields are not treated with insecticide.

We assumed that fraction m_h of adult hosts and m_p of adult parasitoids can disperse among fields. For adult hosts we assumed global dispersal in which individuals disperse to any cell in the grid with equal probability; this is consistent with the biology of aphids that, once aloft, can be carried great distances (Taylor 1986). For parasitoids, we assumed that dispersal is spatially restricted, whereby the probability of an individual dispersing a distance d follows a rotationally symmetric negative exponential function (a Laplace kernel). Note that even when the proportion of the adult parasitoid population that disperses is 1, a fraction of adults will nonetheless remain in the natal fields.

Parameterization

We selected baseline parameter values of $F = 8$, $s = 0.8$, $k = 100$, $s_m = 0.9$, and $s_w = 0.5$. Relative attack rates α_i were experimentally estimated for *A. ervi* as 0.12, 0.27, 0.39, 0.16, and 0.06 for the respective host stages (Ives et al. 1999). Under the assumption that a development stage takes 48 hours (as is approximately the case at 20°C for pea aphids; A. R. Ives, *unpublished data*), the host parameters F and s give an intrinsic rate of increase of $r = 0.18$, a net reproductive rate of $R_0 = 13.1$, and a generation time of 14.4 days. The value of $s_w = 0.5$ corresponds to a half-life for parasitoid adults of two days. For attack rate we used $a = 2 \times 10^4$ (~7 per minute) and $a = 3 \times 10^4$ (~10.5 per minute) for parasitoids showing a low and high response to hosts, respectively. We assumed that all adult hosts disperse ($m_h = 1$); although this is not the case for pea aphids (Ives et al. 1999), it is likely for numerous other pests.

We also considered the case in which only 10% of adult hosts dispersed, but this did not substantially alter the qualitative results (data not presented). For adult parasitoids, we assume that all adults disperse ($m_p = 1$), and for dispersal we used $d = 3$ for poorly dispersing and $d = 9$ for good dispersing parasitoids, resulting in mean dispersal distances of 1.52 and 7.74 field lengths per time unit (two days).

Simulated crop management

Simulated broad-spectrum insecticide applications inflict 70% mortality across all stages of hosts and parasitoids in conventionally managed fields, whereas selective insecticides result in 70% mortality in host populations, but no direct mortality in parasitoids (Neil et al. 1997, Abo El-Ghar and El-Sayed 1998). However, the selective insecticides also cause 70% mortality of larval parasitoid stages within still-living hosts. We assumed that adult parasitoids and mummies are not affected by selective insecticides, although many insecticides considered to be selective can still cause low to moderate levels of mortality to natural enemies and sublethal effects (e.g., Desneux et al. 2007, Joseph et al. 2011). As such, we assumed the least disruptive effect that a selective insecticide can have. To account for different insecticide application regimes in conventionally managed fields, we considered a low- and high-tolerance regime with a low- and high-host density threshold to trigger insecticide applications, respectively. These thresholds reflect situations in which the costs and benefits of insecticide application vary. A low threshold might apply in situations in which the chemical insecticide is relatively cheap and the crop has a relatively high market value, whereas the high threshold might apply for a low-value crop and/or expensive chemical insecticide. The low-threshold host density is half of the high-threshold host density and therefore leads to more frequent insecticide applications.

We considered landscapes that span a gradient of 0% to 100% organically managed fields with a step size of 5%, in which conventionally and organically managed fields are distributed randomly or clustered across the landscape. Clustered landscape designs were generated by assigning probabilities that cells are organically managed according to a two-dimensional sine wave with four peaks on the 50×50 grid. This approach resulted in distinct regions with relatively high densities of conventionally and organically managed fields (Appendix).

Crop yield reduction

The consequences of insecticide and parasitoid-mediated control on crop yield were explored by assuming simple aphid load–yield relationships. As aphid load–yield relationships are influenced by many factors and are pest-crop system-specific, we postulated two generic relationships. The first assumes that yield reduction is linearly related to aphid load (e.g., Ragsdale

et al. 2007) and the second assumes that yield reduction is linearly related to the squared aphid load, which might apply for systems with a more pronounced threshold aphid load (e.g., when aphids are associated with the transmission of plant viruses). Exploring these two contrasting pest load–yield relationships provides an indication of the potential range of crop-yield reduction outcomes.

Initial conditions and data handling

At the start of the simulations, hosts and parasitoids are jointly introduced in 250 randomly chosen fields in the landscape (i.e., 10% of the fields). In these fields host densities are 10 times higher than parasitoid densities. Simulations were conducted for 1000 time steps. To eliminate transient dynamics, we discarded the simulation results of the first 250 time steps (burn-in period) and only used the results of the following 750 time steps (recording period). We calculated host load (the cumulative host days across all fields in the landscape during the recording period) and mean parasitism rate (proportion of host load parasitized during the recording period). To aid in comparisons among scenarios, we rescaled relative host load so that the scenario giving rise to the highest host load was set to 1. In some scenarios with frequent broad-spectrum insecticide applications in landscapes consisting of only conventionally managed fields, host and parasitoid populations went extinct and the simulation was terminated; this only occurred when the number of time steps t_{end} was >850. In these cases the simulated host load was multiplied by a factor 1000/t_{end} to account for the reduced number of time steps. Simulations were replicated 10 times and averaged values are reported.

RESULTS

The results are presented in five sections. First, we explored spatiotemporal dynamics of hosts and parasitoids in the presence and absence of broad-spectrum insecticide applications. Second, we evaluated host suppression by parasitoids with different attack rates and dispersal ability in the presence of broad-spectrum insecticide. Third, we explored how the spatial distribution of conventionally and organically managed fields influenced parasitoid–host interactions by contrasting random and clustered spatial arrangements. Fourth, we investigated the effect of insecticide selectivity on parasitoid–host interactions by contrasting broad-spectrum with selective insecticides. Finally, we explored how scenarios of parasitoid- vs. insecticide-mediated aphid control translate to crop yield. In all scenarios, we investigated the impacts of insecticides as the proportion of organic fields in the landscape varied.

Spatiotemporal dynamics

In the absence of insecticide applications, when pest control is only obtained by top-down control of hosts, parasitoid–host interactions result in stable limit cycles with an average parasitism rate of 44% (range, 36–54%) and 21% (range, 3–81%) for parasitoids with a low ($a = 2 \times 10^4$) and high ($a = 3 \times 10^4$) attack rate, respectively (Fig. 1A, B). Populations build up quickly for parasitoids with high attack rates, which can cause strong boom–bust cycles leading to a lower average parasitism rate than parasitoids with a low attack rate. After initial transient dynamics, there is no spatial variation; fields are synchronized so that each field has similar host and parasitoid densities, which fluctuate through time (Fig. 1A, B). We refer to this situation as the stable state of biological control. With increasing insecticide applications, parasitoid–host interactions generate a range of dynamics, including complex dynamics (Fig. 1C, D) and boom-and-bust limit cycles caused by insecticides in conventionally managed fields that are decoupled from the dynamics in organically managed fields (Fig. 1E). With further increases in insecticide applications, parasitism is virtually absent (Fig. 1F). In the scenarios with insecticide applications, conventionally and organically managed fields have dissimilar parasitoid and host densities; in the case of complex dynamics (Fig. 1C, D) the spatial pattern of parasitoid and host densities is perpetually changing (Fig. 2), whereas for decoupled boom-and-bust cycles (Fig. 1E, F) there is no spatial variation in parasitoid and host densities.

Parasitoid attack rate and dispersal ability

To investigate how parasitoid traits influence biocontrol, we considered parasitoids with either good or poor dispersal, and with either low or high attack rates in landscapes with randomly distributed organically and conventionally managed fields (Fig. 3). In all cases, a minimum proportion of organic fields was needed to sustain the parasitoid population, but this proportion was lowest when parasitoids are poor dispersers with high attack rates (Fig. 3C). Conversely, a high proportion of organic fields was needed when parasitoids are good dispersers with low attack rates (Fig. 3E). Spraying regime also had a marked effect on the proportion of organic fields required to establish biocontrol, with a higher proportion required with the low tolerance regime resulting in a high spray frequency. Parasitism can be very sensitive to the proportion of organic fields, such that a small increase in the proportion of organic fields can result in a sudden switch from insecticide-mediated control to biocontrol.

Broad-spectrum insecticide applications affect host populations directly by inflicting host mortality, but can indirectly release host populations from biocontrol as broad-spectrum insecticides also kill parasitoids. For parasitoids that have a low attack rate, broad-spectrum insecticide applications can give rise to a higher host load in both conventionally and organically managed fields (Fig. 3B, F). Increasing the proportion of organically managed fields in landscapes that are largely
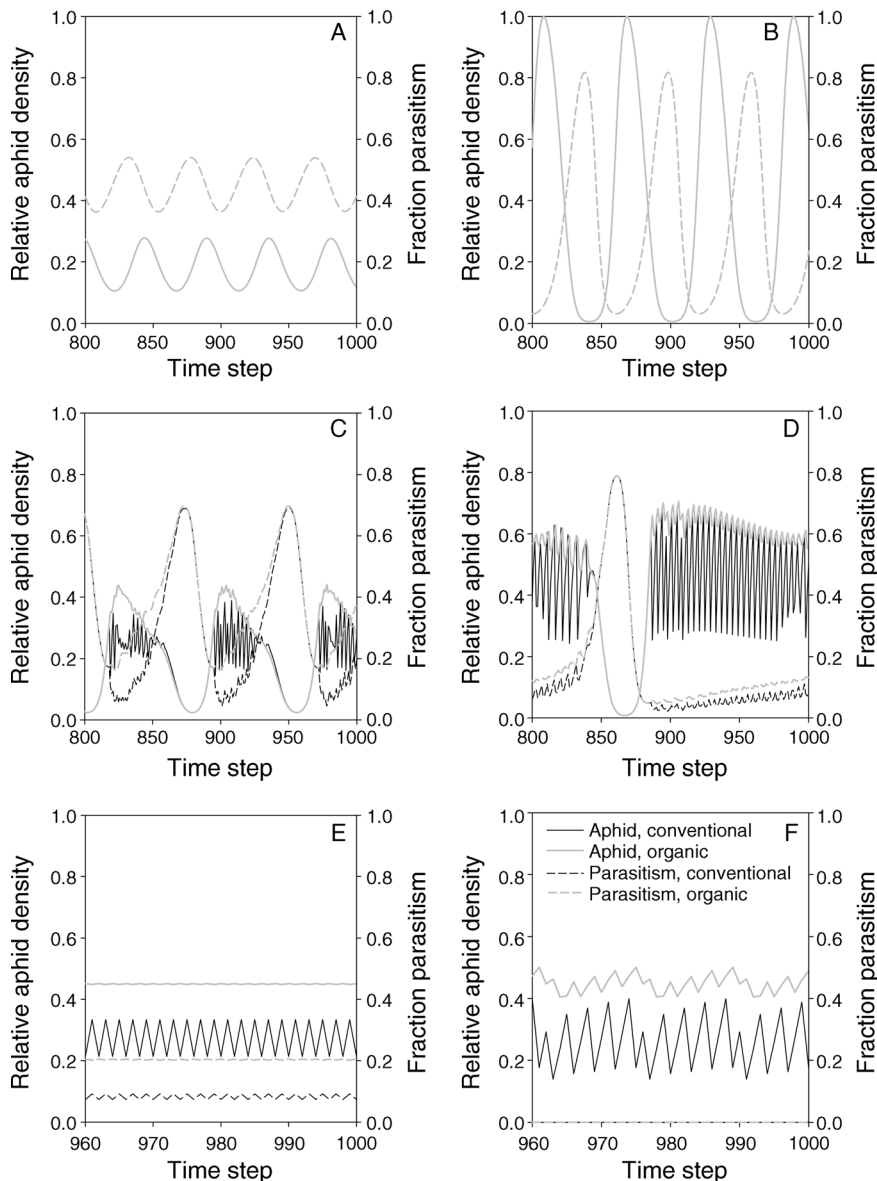
F. J. J. A. BIANCHI ET AL.

FIG. 1. Examples of population dynamics of aphids (solid lines) and parasitism rates (dashed lines) in conventionally managed fields (black) and organically managed fields (gray) generated for different parameter values and scenarios. (A) Stable state of biocontrol with low attack rate, poorly dispersing parasitoids, and proportion organically managed fields = 1; (B) stable state of biocontrol with high attack rate, poorly dispersing parasitoids, and proportion organically managed fields = 1; (C) complex, decoupled parasitoid–host dynamics in organically and conventionally managed fields with high attack rate, poorly dispersing parasitoids, proportion organically managed fields = 0.5, broad-spectrum insecticide, random spatial distribution of organically managed fields, and low-tolerance insecticide application regime; (D) complex, decoupled parasitoid–host dynamics in organically and conventionally managed fields with high attack rate, good dispersing parasitoids, proportion organically managed fields = 0.3, broad-spectrum insecticide, random spatial distribution of organically managed fields, and high-tolerance insecticide application regime; (E) decoupled boom-and-bust limit cycles in organically and conventionally managed fields with low attack rate, good dispersing parasitoids, proportion organically managed fields = 0.6, broad-spectrum insecticide, random spatial distribution of organically managed fields, and low-tolerance insecticide application regime; (F) decoupled boom-and-bust limit cycles in organically and conventionally managed fields with parasitism virtually absent and low attack rate, poorly dispersing parasitoids, proportion organically managed fields = 0.2, broad-spectrum insecticide, random spatial distribution of organically managed fields, and low-tolerance insecticide application regime. Relative aphid density is scaled according to the highest aphid density obtained in panel B.
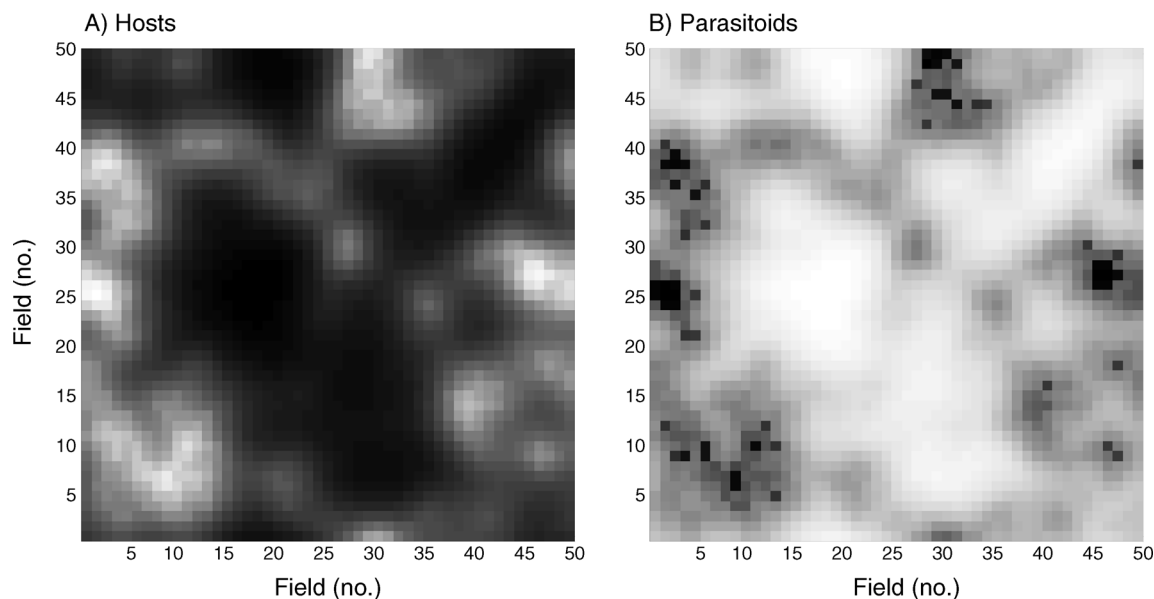
Fig. 2. Snapshot of the spatial pattern of (A) hosts and (B) parasitoids after 1000 time steps for the complex, decoupled parasitoid–host dynamics in organically and conventionally managed fields of Fig. 1C. Each cell represents a field with an organic or conventionally managed crop. Dark and light cells represent high and low population densities, respectively.

dominated by conventionally managed fields can initially lead to increased host loads in organically managed fields because parasitism is virtually absent (Fig. 3A, E). As the high host populations in organically managed fields also disperse to conventionally managed fields, host loads in conventionally managed fields can also increase despite insecticide applications (Fig. 3B, F). Because parasitoids with a high attack rate are less effective in reducing host populations, broad-spectrum insecticides can generate lower host loads in conventionally managed fields than could be achieved by biocontrol alone (Fig. 3D, H). Nonetheless, there may still be an advantage of having surrounding organic fields because the best control of hosts in conventional fields occurs when there is a high proportion of organic fields (Fig. 3D, H). Organically managed fields may also benefit from broad-spectrum insecticide applications in conventionally managed fields provided that the proportion of organic fields is sufficiently high that parasitoids are maintained in the landscape. This occurs because conventional management reduces the host load at the landscape scale and therefore limits host colonization in organically managed fields (Fig. 3D, H).

Spatial arrangement of fields

Clustering of organically and conventionally managed fields limits the disruptive effect of broad-spectrum insecticide applications in neighboring organically managed fields because the average distance between conventionally and organically managed fields increases. This effect manifests especially for poorly dispersing parasitoids, as most of these parasitoids remain in clusters of organically managed fields where parasitoid mortality is reduced (Fig. 4) and is less pronounced for good dispersing parasitoids (results not shown). As a consequence, the proportion of organic fields required to establish biocontrol for poorly dispersing parasitoids in landscapes with clustered conventionally and organically managed fields is lower than landscapes with randomly distributed fields (Fig. 4A, C vs. Fig. 3A, C), which is also reflected in reduced host load (Fig. 4B, D vs. Fig. 3B, D). Furthermore, for parasitoids with a high attack rate, maximum parasitism levels are higher in clustered fields than for randomly distributed fields (Fig. 4C vs. Fig. 3C).

Insecticide selectivity

Selective insecticides target just hosts and only kill parasitoids if they are in still-living hosts. Selective insecticide use results in a lower proportion of organic fields required for the establishment of parasitism as compared to broad-spectrum insecticides (Fig. 5A, C vs. Fig. 3A, C). For poorly dispersing parasitoids with a high attack rate, high-tolerance spraying regimes are compatible with biocontrol; host load is always below the stable state of biocontrol, even when no organic fields are present (Fig. 5D). However, selective insecticide use can still lead to unfavorable situations for poorly dispersing parasitoids with a low attack rate, in which case host load can exceed levels obtained by the stable state of biocontrol in the absence of insecticide use (Fig. 5B).

Crop yield

Relative yield was inversely related to aphid load (Fig. 6). For parasitoids with a low attack rate the highest
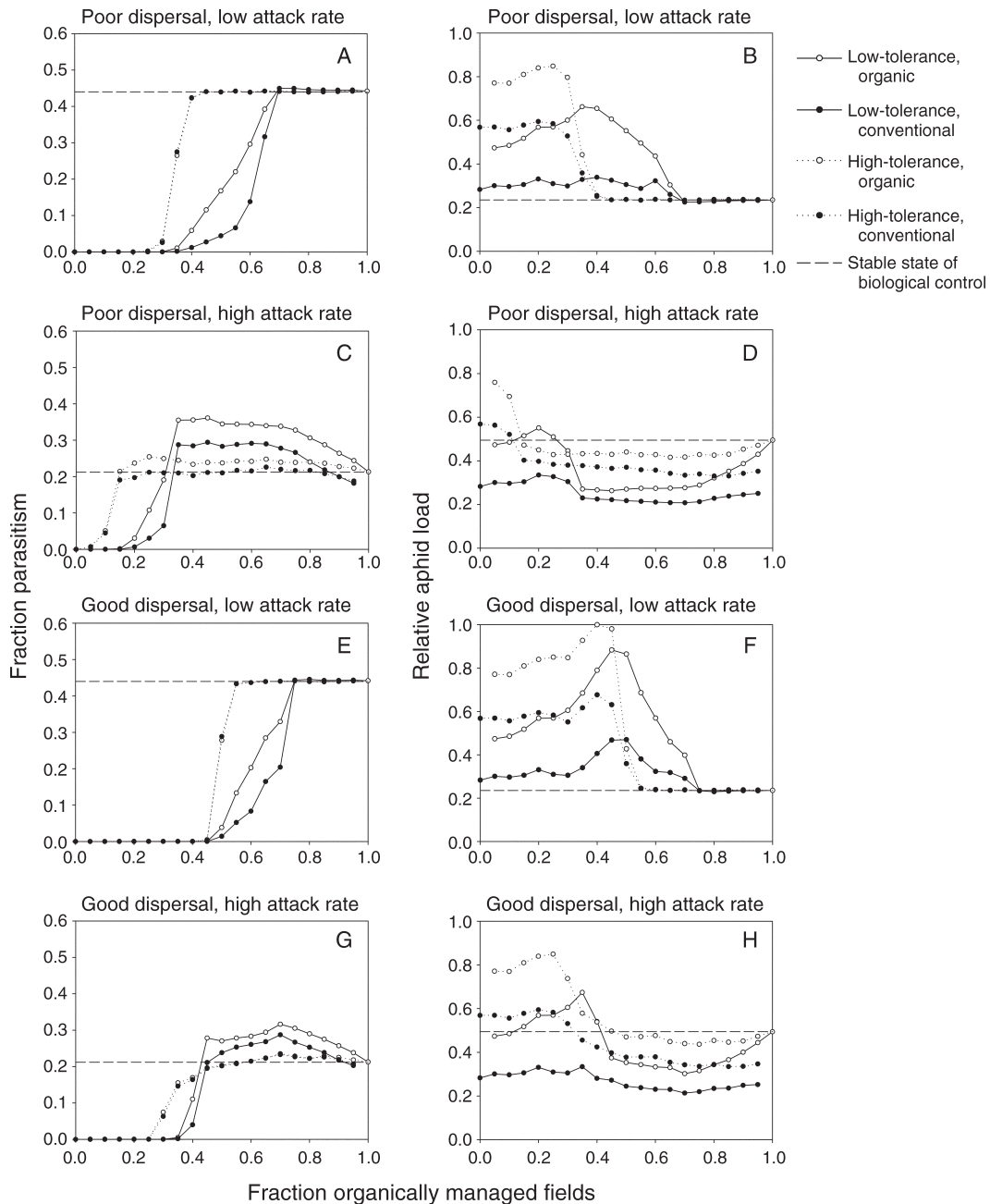
FIG. 3. (A, C, E, G) Fraction parasitism and (B, D, F, H) relative host load as a function of the proportion of organically managed fields for four parasitoid types (poor vs. good dispersal, and low vs. high attack rate) for low-tolerance (solid line) and high-tolerance broad-spectrum insecticide application regimes (dotted line) in conventionally managed fields. Organically and conventionally managed fields are randomly distributed and indicated with open and solid circles, respectively. The fraction parasitism and relative host load in the absence of insecticide applications (stable state of biological control) are indicated by the dashed lines.

relative yields were obtained for the stable state of biological control, and substantial yield loss was observed for high-tolerance insecticide application regimes in landscapes with <30% organically managed fields. This effect was more pronounced for the quadratic than for the linear relationship between aphid load and yield reduction because there is a larger penalty on the relative yield for high aphid densities (Fig. 6A, B). For parasitoids with a high attack rate, insecticide applications generally resulted in higher relative yields as compared to the stable state of biological control (Fig. 6C, D). In this case, low-tolerance insecticide application regimes were associated with the highest yield.
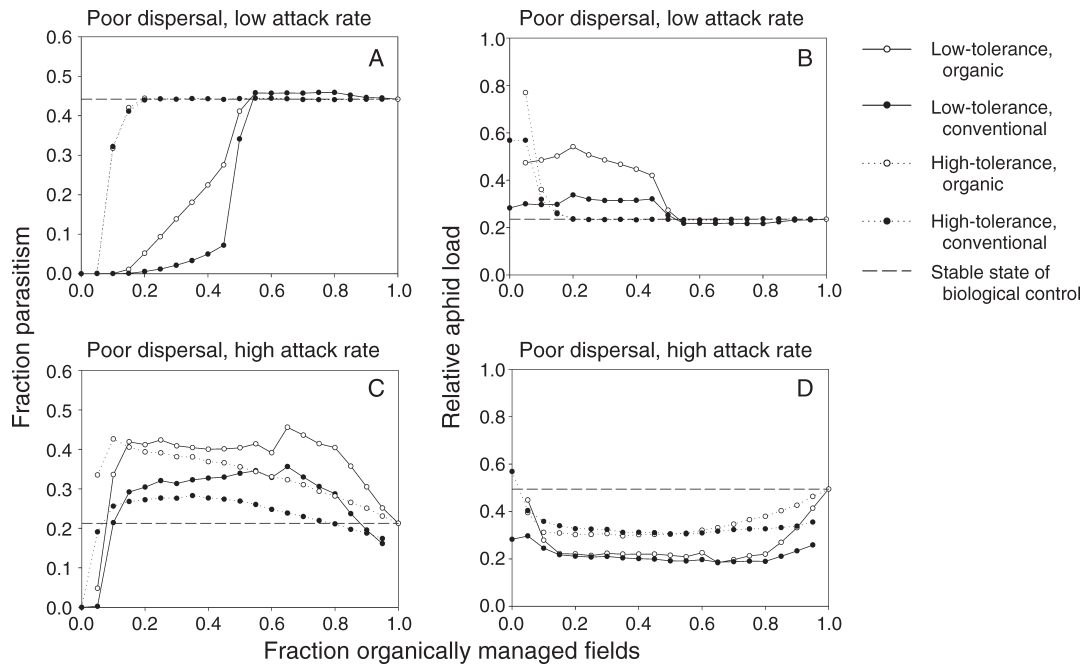
FIG. 4.   (A, C) Fraction parasitism and (B, D) relative host load as a function of the proportion of organically managed fields for parasitoids with poor dispersal and (A, B) low and (C, D) high attack rates. Organically and conventionally managed fields are spatially clustered. Solid and dotted lines indicate low- and high-tolerance broad-spectrum insecticide application regimes, and organically and conventionally managed fields are indicated with open and solid circles, respectively. The fraction parasitism and relative aphid load in the absence of insecticide applications (stable state of biological control) are indicated by the dashed lines.
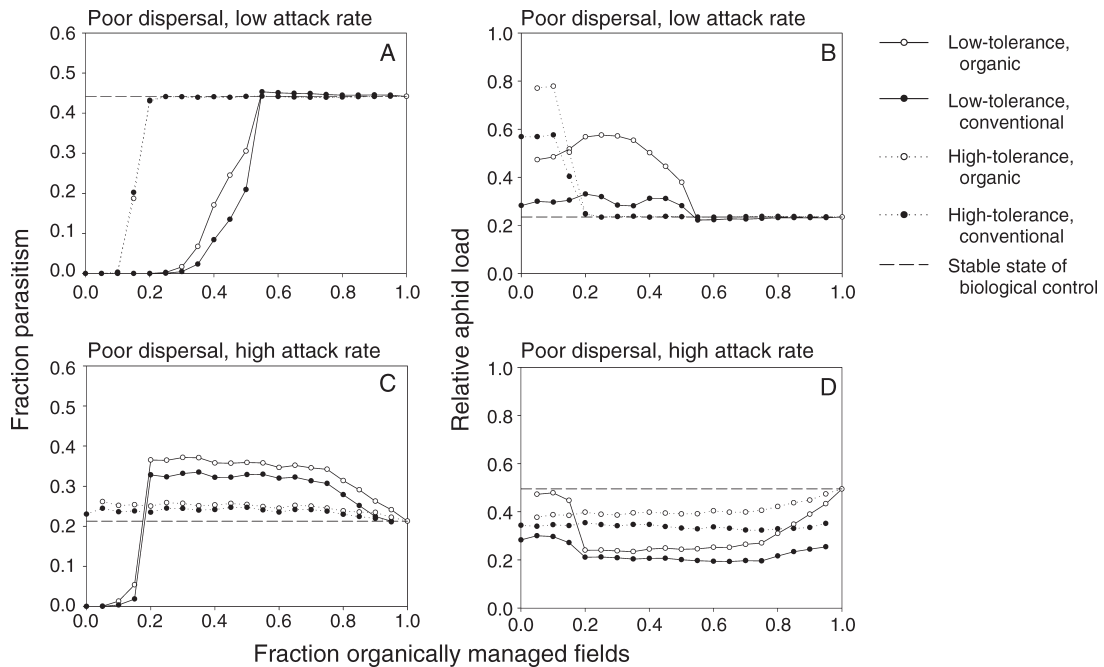

FIG. 5.   (A, C) Fraction parasitism and (B, D) relative host load as a function of the proportion of organically managed fields for poorly dispersing parasitoids with (A, B) low and (C, D) high attack rates for selective insecticides. Organically and conventionally managed fields are randomly distributed. Solid and dotted lines indicate low- and high-tolerance insecticide application regimes, and organically and conventionally managed fields are indicated with open and solid circles, respectively. The fraction parasitism and relative aphid load in the absence of insecticide applications (stable state of biological control) are indicated by the dashed lines.
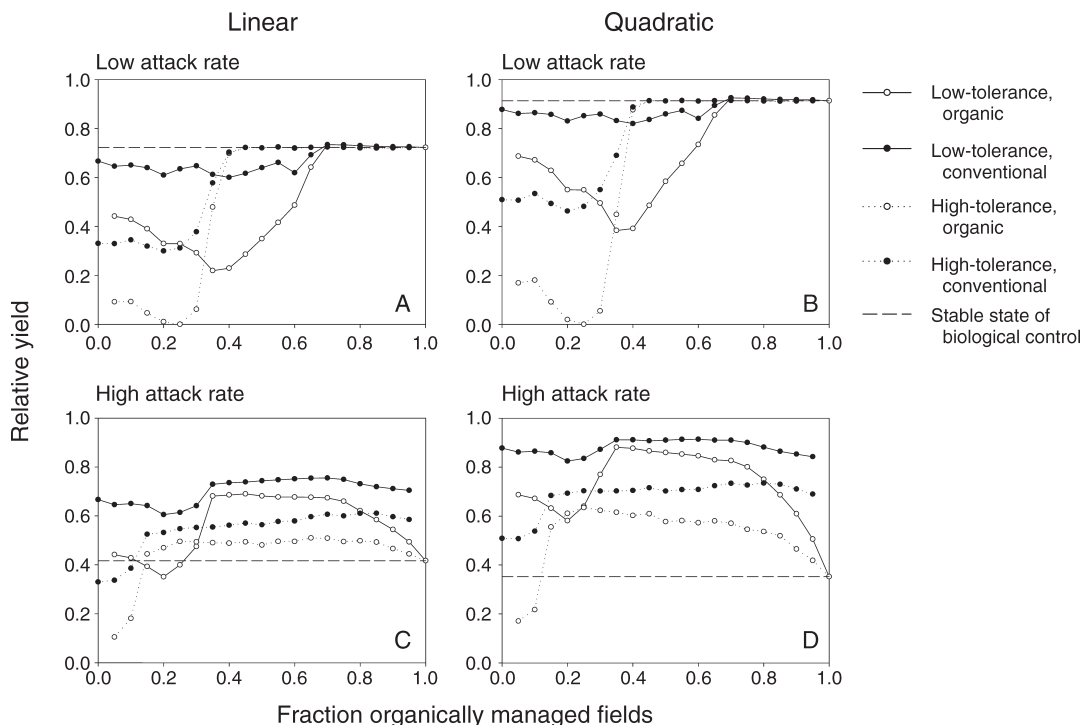
Fig. 6. (A, C) Relative yield for a linear relationship and (B, D) for a quadratic relationship between host load and yield loss as a function of the proportion of organically managed fields for poorly dispersing parasitoids with (A, B) low and (C, D) high attack rates. Organically and conventionally managed fields are randomly distributed. Solid and dotted lines indicate low- and high-tolerance broad-spectrum insecticide application regimes, and organically and conventionally managed fields are indicated with open and solid circles, respectively. The relative yield in the absence of insecticide applications (stable state of biological control) is indicated by the dashed line.

DISCUSSION

While the area of arable crop production under organic management is growing at a world-wide scale (5.5 million ha in 2009 with an annual increase of 13%; Willer and Kilcher 2011), the potential interactions between pest management in organic and conventionally managed systems have so far largely been ignored. Our simulations show that lose–lose scenarios can arise when there is a mix of organic and conventionally managed systems in the landscape (i.e., hump-shaped host load curves in Figs. 3–5); in these lose–lose scenarios, host loads are higher in both organically and conventionally managed fields than would be the case if only organic or only conventional management were used. This suggests that, even though widespread adoption of organic management might lead to high levels of biocontrol, the incremental decrease in insecticide use from a landscape dominated by organic management could trigger transient increases in crop losses due to pests. This underscores the need to consider pest management strategies at the landscape scale, which will often require concerted effort among the various actors including farmers and regulators (Schellhorn et al. 2008).

Although insecticide applications can give rise to lose–lose scenarios, win–win scenarios are also possible, occurring frequently for our simulated cases for a

parasitoid with a high attack rate (e.g., Fig. 3D, H). In these cases, greatest host suppression occurs in both organic and conventionally managed fields when there is a moderate to high proportion (but <100%) of the landscape under organic management. These win–win scenarios generally occur when there are complex temporal (Fig. 1C, D) and spatial (Fig. 2) dynamics. This will make the role of a parasitoid in suppressing pests hard to assess without extensive temporal and spatial data, because the impact of the parasitoid in a given field over a single growing season might be highly variable. Thus, win–win scenarios might be the product of biocontrol agents that seem to have only sporadic, though intense, impacts on pests, and consequently predicting win–win scenarios will likely be challenging.

We evaluated the outcome of the various scenarios in terms of fraction parasitism and host load. While we selected these variables because they are directly linked to the population dynamics and interactions of hosts and parasitoids, crop yield would be a more informative metric from the perspective of pest management decision making. Yet, the relationship between host load and yield can be complex. For instance, the impact of aphids on crops can depend on crop type, aphid species, and the timing of infestation (Migui and Lamb 2006, Rhainds et al. 2012). Our exploration of two generic host load–yield

PLATE 6.   The parasitoid wasp *Aphidius ervi* Haliday attacking pea aphids *Acyrthosiphon pisum* (Harris). Photo credit: A. R. Ives.

relationships indicated that the type of relationship (linear vs. quadratic) mattered for the quantitative outcome of yield reduction, but less so for the qualitative outcome of the different scenarios (Fig. 6). It should also be noted that yield does not translate linearly to profit. For instance, organic produce is generally subject to a price premium, and insecticide applications involve costs of insecticides, fuel, and labor, which reduce net profit. Therefore, in scenarios in which the yield of an organically grown crop is lower than a conventionally grown crop, the organic crop may still be more profitable.

We only considered landscapes comprising conventionally and organically managed fields to focus on the trade-off between chemical control and natural biocontrol. While the proportion of land under organic management is typically <5%, many agricultural landscapes comprise also grazing land and seminatural habitats that are devoid of insecticide applications and that can support pests and/or biocontrol agents by providing food, hosts, and/or refuge (Dyer and Landis 1997, Bianchi et al. 2006). This implies that, in real agricultural systems, the case of 100% of the land exposed to one or more insecticide treatments will be rare. In turn, seminatural habitats that support alternative hosts may have a similar function as organically managed fields in our simulations and may as such help

to bridge the gap to reach the required proportion of noninsecticide-treated land to obtain effective biocontrol.

Simulations indicate that the proportion of non-insecticide-treated habitat in the landscape is a key variable for managing biocontrol services. This finding aligns well with observations that the widespread use of transgenic *Bacillus thuringiensis* (Bt) cotton results in reduced pesticide applications and increased densities of generalist predators (lady beetles, lacewings, and spiders), which in turn suppress aphid populations in transgenic and neighboring conventional crops (Lu et al. 2012). Meehan et al. (2011) studied the relationship between landscape simplification and insecticide use in the midwestern United States, and they found that crop pest abundance increased with the proportion of harvested cropland treated with insecticides. Geiger et al. (2010) showed in a European-wide study that the intensity of insecticide use was positively correlated with median survival time of aphids in cereal fields, indicating that insecticide had a disruptive effect on biocontrol. In addition, Jonsson et al. (2012) found a negative association between pesticide application at the landscape scale and parasitism rate of aphids and diamondback moth (*Plutella xylostella*). These patterns match the trajectory predicted by our model of declining host load with increasing proportion of the landscape under

organic (noninsecticide-treated) management (Figs. 3–5). The study by Lu et al. (2012) suggests that the underlying mechanisms in our model (insecticide-mediated disturbances disrupting biocontrol, releasing pests from top-down control, and triggering further insecticide treatments) also occur in the real world. While the findings of Jonsson et al. (2012), Meehan et al. (2011), and Geiger et al. (2010) are based on correlations and therefore do not necessarily reflect causal relationships, our study provides additional support for the generality of these patterns by uncovering the possible underlying mechanisms.

Besides the proportion of noninsecticide-treated habitat in the landscape, the attained level of biocontrol was influenced by parasitoid traits. In general, less refuge was required to obtain effective levels of biocontrol for parasitoids with high attack rates. Thus, biocontrol by natural enemies with a limited potential for numerical response, such as parasitoids with low attack rates, is easily disrupted by broad-spectrum pesticides. This suggestion is supported by observations of Settle et al. (1996) and van den Berg et al. (1998) that showed that systems with rapidly recovering pest populations and slowly recovering natural enemies are vulnerable to secondary pest outbreaks. The importance of a rapid numerical response of specialist natural enemies for providing effective biocontrol of pea aphids has been demonstrated by Rauwald and Ives (2001) who showed that the parasitoid *A. ervi* can successfully control pea aphids after harvest of alfalfa fields because *A. ervi* can persist in their host over the harvesting event.

We also found that less refuge was required to obtain effective levels of biocontrol when parasitoids have poor, rather than good, dispersal abilities. This seemingly counterintuitive result occurs because poorly dispersing parasitoids are less likely to leave organic fields where they have relatively high host abundances and do not suffer from insecticides. The consequent build-up of parasitoids in organic fields can then serve as sources of biocontrol agents into conventional fields; the low dispersal rates of parasitoids are more than made up for by their higher population densities. Furthermore, a lower proportion of organically managed fields was required to establish biocontrol when selective insecticides are used as compared to broad-spectrum insecticides. As the host load does not differ greatly between broad-spectrum (Fig. 3B, D) and selective insecticides (Fig. 5B, D), this suggests that the main effect of insecticides in disrupting biocontrol is removing hosts that would otherwise be available for parasitism or killing still-living parasitized hosts, rather than directly killing parasitoid adults.

In conclusion, our simulations show that conventional and organic farming can lead to either lose–lose or win–win scenarios for pest suppression at the landscape scale. On the one hand, the use of synthetic insecticides at conventional farms can disrupt parasitoid-mediated biocontrol at organic farms. On the other hand, the large-scale suppression of pest populations by synthetic insecticides can in some cases lessen the pest colonization rates at organic farms. The possibility of lose–lose scenarios represents a particular challenge to current policy changes to increase biological and cultural pest control; if this is done on an incremental basis, there is the possibility that we will see increased pest loads until a substantial proportion of the growers in the agricultural landscape adopt low pesticide and integrated pest management.

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SUPPLEMENTAL MATERIAL

Appendix

Example of a random and a clustered landscape design for conventionally and organically managed fields (*Ecological Archives* A023-079-A1).