

Comparison of organic and conventional farms: challenging ecologists to make biodiversity functional

Deborah K Letourneau* and Sara G Bothwell

With the rise of organic farming in the United States and worldwide, ecologists are being presented with new opportunities to link basic and applied ecology through research on biodiversity and ecosystem services. We present evidence from our own research and a review of the literature to assess the evidence for enhanced insect pest control as a consequence of greater biodiversity on organic farms. Despite the frequency of claims in the literature that biodiversity is beneficial, we found that few studies have measured biodiversity effects on pest control and yield on organic farms compared to conventional farms. Relevant studies in agricultural or natural settings suggest that an increase in the diversity of insect predators and parasitoids can have positive or negative effects on prey consumption rates. We therefore call for a stronger scientific basis for evaluating pest suppression effects due to enhanced natural enemy diversity. We suggest several avenues of research to assess the relationship between biodiversity and effective biological control, to obtain the information needed to manage natural enemy diversity, and to estimate the value-added component of on-farm biodiversity in terms of pest control services.

Front Ecol Environ 2008; 6(8): 430–438, doi:10.1890/070081

Profitable organic farming enterprises are emerging around the world in response to burgeoning consumer demand and concerns about human and environmental health (Maeder *et al.* 2002; Kristiansen 2006). Previously restricted to health food stores and farmers' markets, organic food is now a mainstream commodity. In 2000, US consumers purchased more organic food in supermarkets than in any other venue (Dimitri and Greene 2002). The amount of land under organic management in many

European Union countries has risen dramatically in the past decade, and is expected to increase further due to market opportunities and various government mandates and incentives (Stoltz 2005; Ryden 2007). Organic agriculture is now considered a viable option in food security discussions (Badgley *et al.* 2006; Zanolli *et al.* 2007). Research support for these alternative farming operations is gaining ground through targeted federal funding and the establishment of certified organic experimental fields by academic institutions (Sooby 2001). Past studies comparing ecological processes on organic versus conventional farms have been limited by a lack of funding and appropriate test sites. However, new studies can take advantage of growth in organic production to strengthen the scientific basis for evaluating and implementing practices designed to foster ecosystem function, improve human health, and produce sustainable yields. To illustrate how ecologists can help to meet research needs at this critical time, we examine the connection between enhanced biodiversity on organic farms and a key ecosystem service – pest control. Ideally, biodiversity that is conserved on organic farms promotes beneficial biological processes that compensate for practices (such as application of synthetic insecticides) that are disallowed under organic certification requirements.

Conventional agriculture is managed using a wide range of cultural, biological, and chemical practices and tools (Letourneau and van Bruggen 2006). Organic agriculture, which also encompasses a wide range of practices, is subject to additional national and international regulations. Certification standards differ around the world, but all promote farm management with agronomic, biological,

In a nutshell:

- Fueled by consumer demand for healthier food and environments, the amounts of arable land, research funding, and research station test sites devoted to organic agriculture are increasing worldwide
- Organic farming's public appeal is partly due to its ability to foster biodiversity; beyond biodiversity conservation for its own sake, ecologists argue that increased biodiversity enhances ecosystem services, including pest control
- Although field studies show that organic farms tend to conserve more biodiversity than conventional farms, including natural enemies of insect pests, the effect of biodiversity on insect pest control on organic farms has not been tested fully
- Organic agriculture provides an opportunity for tests and applications of ecological theory
- We urge ecologists to clarify the links between biodiversity and ecosystem services, either by determining how to foster biodiversity for more effective pest control or by assessing the likelihood of enhanced ecosystem services through incremental or targeted increases in biodiversity

Department of Environmental Studies, University of California, Santa Cruz, CA *(dletour@ucsc.edu)

and mechanical methods, while restricting the use of synthetic pesticides, herbicides, and fertilizers, as well as certain forms of genetic modification (FAO 1999).

Organic farming systems are challenged by many of the same crop protection issues as conventional farming systems. Approaches to insect pest control in organic agriculture differ widely among growers, both at regional and global scales. Here, we distinguish between three general types of organic farming: (1) substitution-based operations that replace synthetic insecticides with organic certification-approved materials (eg mineral, bacterial, or botanical insecticides); (2) holistic systems, which incorporate a wide range of soil management and cropping practices aimed at preventing insect pest outbreaks; and (3) subsistence cropping, which relies on cultural pest control methods, in part because growers have no access to synthetic inputs (Figure 1). Organic agriculture in the holistic-systems category differs fundamentally from conventional agriculture, not only in the range of tactics used by growers, but in the conceptual approaches that frame crop management strategies (Altieri 1986; Letourneau and van Bruggen 2006). Prophylactic, as opposed to curative, pest control measures integrate farming practices that continuously act to disrupt pest colonization or slow population growth. This allows, for example, off-season cover or trap plantings, cropping schedule considerations for community-level resistance to pest outbreaks, and surrounding habitats and weeds as resources for promoting biodiversity of natural enemies of crop pests (Letourneau and van Bruggen 2006).

■ Biodiversity and critical ecosystem services

Agricultural intensification, including conventional use of pesticides, has resulted in biodiversity losses worldwide (Stoate *et al.* 2001; Butler *et al.* 2007). Holistic organic agriculture, with its attention to ecosystem processes and a softer ecological footprint (*sensu* Butler *et al.* 2007), potentially restores biodiversity and associated ecosystem services. Organic practices might be expected to increase conservation biological control, defined as the maintenance of natural enemies of insect pests through reduced use of broad-spectrum pesticides and enhancement of natural enemies through habitat manipulation (Barbosa 1998). For many decades, the ecological literature has been replete with claims about a link between biodiversity and pest control. Pimentel (1961) related increases in the diversity of parasitoids and predators with reduced pest population outbreaks. Root (1973) predicted that herbivores would be suppressed to a greater extent in mixed vegetative stands with a higher species diversity of predators and parasitoids. Gliessman (1989) warned that, as biological diversity is reduced, trophic structures tend to become simplified and vacant niches appear, leading to increased risk of catastrophic pest outbreaks. A recent position paper cautioned that critical ecosystem services such as pollination and pest control for food production both support and depend on biodiversity (MA 2003).

The same linkages have been expressed for organic farming operations with higher biodiversity than conventional farms (Kasperczyk and Knickel 2006; Letourneau and van Bruggen 2006).

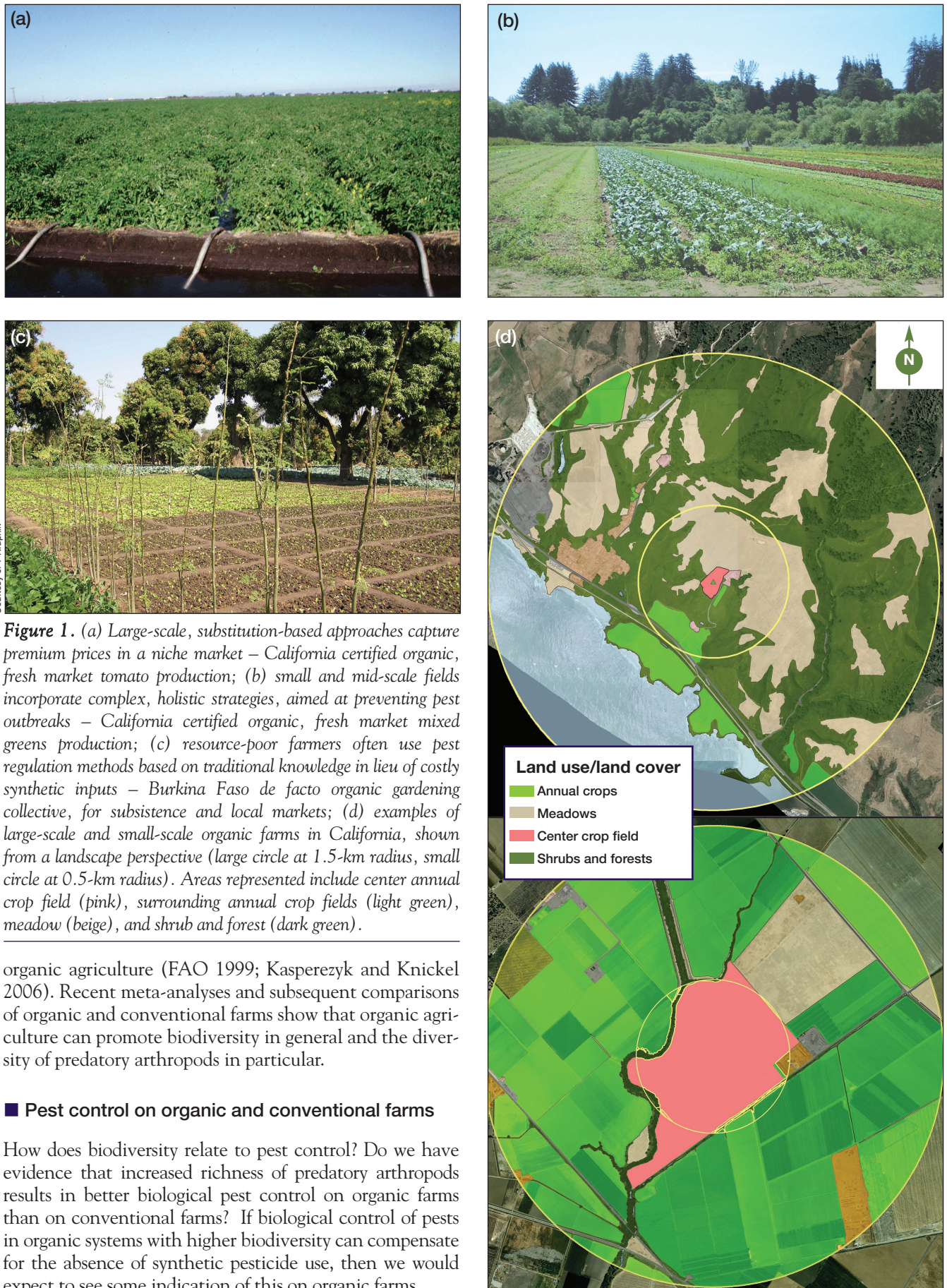
■ Biodiversity on organic versus conventional farms

Do organic farms support greater biodiversity than conventional farms? Biodiversity can be measured at different levels of organization (eg genetic diversity within species, species diversity within taxa and trophic levels, functional diversity in communities) and at different spatial scales (eg plots, habitats, ecosystems, landscapes, regions). Documented comparisons of organic and conventional farms have primarily measured species richness of one or several taxonomic groups by sampling in crop fields or other farm habitats. Although results vary among taxonomic groups, biodiversity is clearly enhanced on organic farms compared to conventional farms in most studies (Bengtsson *et al.* 2005; Hole *et al.* 2005; Kasperczyk and Knickel 2006).

Bengtsson *et al.* (2005) conducted a meta-analysis of biodiversity on organic versus conventional farms, using 42 comparative studies that provided adequate variance measures. Species richness was, on average, 30% higher on organic farms, with stronger effects likely in intensively managed landscapes. Positive effects of organic farming in the meta-analysis were measured for plants, all arthropods, carabid beetles, other predatory insects, and birds, but not for non-predatory arthropods or soil microorganisms. Hole *et al.* (2005) reviewed 76 studies that compared single or multiple taxonomic groups on organic and conventional farms. Summing comparisons for all taxa, they showed a positive effect of organic agriculture on species abundance and/or richness in 66 cases; 25 had neutral or mixed outcomes, and only eight showed a negative effect (Hole *et al.* 2005). Whereas a majority of the studies reviewed by these authors on plants, birds, and predatory and non-predatory arthropods showed an increase in abundance, richness, or both, on organic compared to conventional farms, the outcome for soil microorganisms was less predictable, and studies on mammals were scarce.

Papers published since Bengtsson *et al.* (2005) and Hole *et al.* (2005) continue to support a positive association between organic management and on-farm biodiversity for plants (Belfrage *et al.* 2005; Gabriel *et al.* 2006; Kleijn *et al.* 2006), predatory arthropods (Melnichuk *et al.* 2003; Purtauf *et al.* 2005; Schmidt *et al.* 2005; Kleijn *et al.* 2006), and non-predatory arthropods (Wickramasinghe *et al.* 2004; Kleijn *et al.* 2006). Bird diversity has been more strongly associated with crop or landscape diversity than with organic practices alone (Belfrage *et al.* 2005; Jones *et al.* 2005; Kleijn *et al.* 2006). Oehl *et al.* (2004) found a greater diversity of soil microorganisms on organic farms than on conventional farms.

Certification regulations and government mandates commonly mention biodiversity as a goal or standard for



Courtesy of T. Krupnik

Figure 1. (a) Large-scale, substitution-based approaches capture premium prices in a niche market – California certified organic, fresh market tomato production; (b) small and mid-scale fields incorporate complex, holistic strategies, aimed at preventing pest outbreaks – California certified organic, fresh market mixed greens production; (c) resource-poor farmers often use pest regulation methods based on traditional knowledge in lieu of costly synthetic inputs – Burkina Faso de facto organic gardening collective, for subsistence and local markets; (d) examples of large-scale and small-scale organic farms in California, shown from a landscape perspective (large circle at 1.5-km radius, small circle at 0.5-km radius). Areas represented include center annual crop field (pink), surrounding annual crop fields (light green), meadow (beige), and shrub and forest (dark green).

organic agriculture (FAO 1999; Kasperezyk and Knickel 2006). Recent meta-analyses and subsequent comparisons of organic and conventional farms show that organic agriculture can promote biodiversity in general and the diversity of predatory arthropods in particular.

■ Pest control on organic and conventional farms

How does biodiversity relate to pest control? Do we have evidence that increased richness of predatory arthropods results in better biological pest control on organic farms than on conventional farms? If biological control of pests in organic systems with higher biodiversity can compensate for the absence of synthetic pesticide use, then we would expect to see some indication of this on organic farms.

Aerial photos courtesy of the Association of Monterey Bay Area Governments

Field comparisons of arthropod natural enemy diversity (predators and parasitoids), pest abundance, and levels of pest damage between organic and conventional farms supported a biodiversity–pest control link. Commercial tomato growers use a wide range of management practices on farms classified either as organic or conventional. On ten organic and nine conventional farms in the Sacramento Valley, we sampled arthropods associated with the tomato crop, pest damage on tomato plants, and yield (for details of farming practices, design, and methods, see Drinkwater *et al.* [1995] and Letourneau and Goldstein [2001]). Despite a wide range of practices among organic and conventional farms, arthropod diversity was significantly greater for tomato plantings in organic than conventional fields. Pest injury levels, however, were similar in the two systems, despite a reduced level of pesticide use on organic farms.

On average, morphospecies richness of plant-feeding insects and parasitoids was significantly higher on the commercial organic than conventional tomato crop (Figure 2). Carnivorous insect (predators and parasitoids) morphospecies richness was 37 in organic samples, compared to 21 in conventional field samples. Farm samples, on average, contained 223 parasitoid wasps on organic tomatoes and 119 parasitoid wasps on conventional tomatoes. Predatory arthropods numbered 97 and 58, respectively, per average farm sample. In contrast, leaf and fruit damage, which varied a great deal among farms, was not significantly different between organic and conventional tomatoes (Drinkwater *et al.* 1995). In particular, levels of leaf damage by common pests on tomatoes, such as thrips, flea beetles, leafminers, and leaf chewers (mostly caterpillars), were similar overall, as were levels of fruit damage by sucking insects (stinkbugs, leafhoppers) and chewers (mostly caterpillars; Figure 3). Similar levels of tomato damage and yield (Drinkwater *et al.* 1995) on organic and conventional farms in this study are consistent with the notion that enhanced biodiversity can lead to (1) more effective biological control of insect pests on organic farms, (2) possible pest dilution effects (Dyer and Stireman 2003), and (3) compensation for the absence of synthetic pesticides.

■ Natural enemy diversity and biological control potential

In the tomato comparison, the measured increase in number and species richness of parasitoids and predators should provide better control of the number and variety of pests found in organic fields. However, this outcome assumes that increased natural enemy diversity leads to greater parasitism and predation rates on crop pests. An

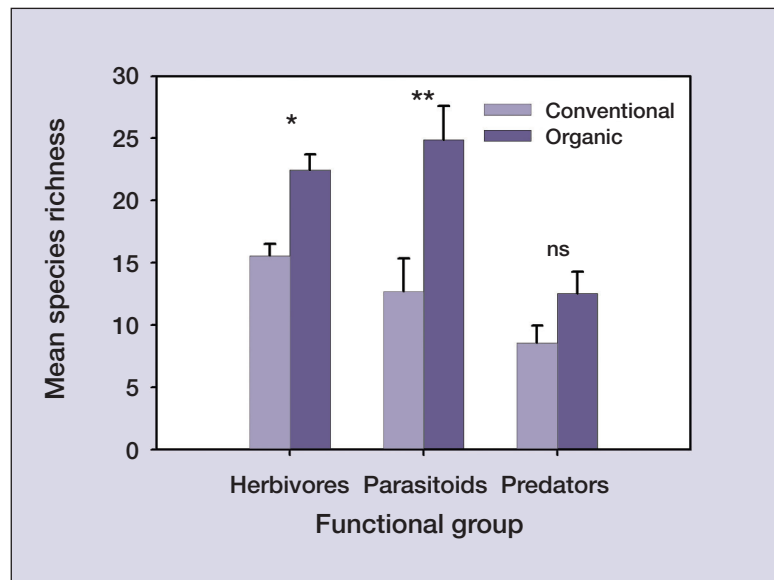


Figure 2. Species richness (determined as morphospecies counts of arthropods in vacuum samples) of herbivores (ANOVA, $F_{1,16} = 18.3$, $P = 0.0006$) and parasitoids (ANOVA, $F_{1,16} = 6.12$, $P = 0.0249$) was significantly greater on organic than conventional farms, whereas predator richness among management types was more similar (ANOVA, $F_{1,16} = 3.25$, $P = 0.0903$, each analysis using as the error term farm nested in type of management practice: organic or conventional). * = < 0.05 , ** = < 0.001 , ns = not significantly different.

increase in species richness would lead to more effective biological control if different natural enemies complement each other, by having either an additive or synergistic effect. This *species complementarity* model suggests that pest mortality due to the combined action of several natural enemy species is equal to (additive) or greater than (synergistic) the summed pest mortality caused by each natural enemy species on its own (Snyder *et al.* 2005; Stireman *et al.* 2005). Clearly, if each species of natural enemy were to prey on a different group of pests, or at different times in the season, or if natural enemies with different predatory behaviors interacted to facilitate prey capture, then niche differentiation among natural enemies would result in complementary mortality and enhanced biological control. Alternatively, the *lottery model* simply suggests that, as species richness increases, so does the probability of having a superior biological control agent present (Myers *et al.* 1989; Stireman *et al.* 2005).

However, negative interactions among different species of predators and parasitoids can have a negative effect on pest regulation (Finke and Denno 2004). As the number and species richness of natural enemies increases, so does the potential for intra-guild predation or behavioral interference, releasing pest populations from predation or parasitism pressure and possibly leading to outbreak dynamics (Rosenheim *et al.* 1999; Perez-Lachaud *et al.* 2004). Finally, an increase in natural enemy diversity could increase the chance of competitive interactions between superior and inferior control agents. If a less effective biological control agent out-competes, disrupts, or eventually

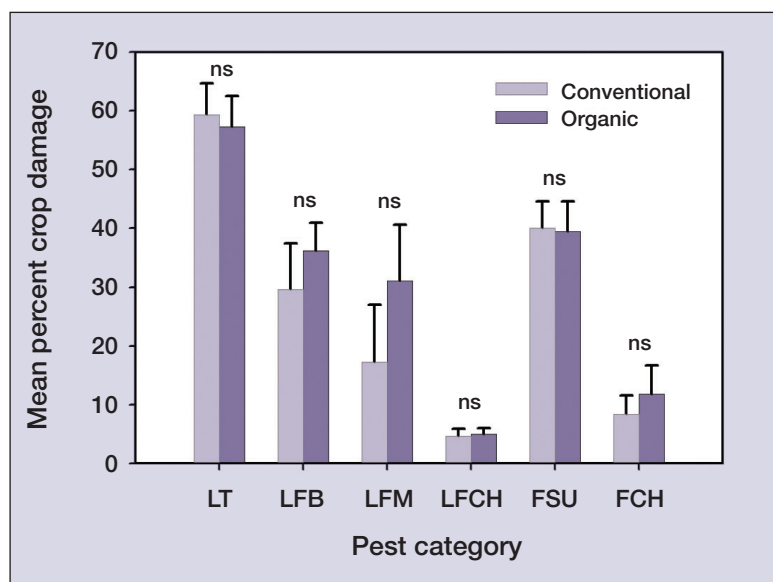


Figure 3. Neither damage to tomato foliage by thrips (LT), flea beetles (LFB), leafminers (LFM), or chewing insects (LFCH), nor fruit damage by sucking insects (FSU) and chewing insects (FCH), was significantly different on organic versus conventional tomato crops (ANOVAs, $F_{1,16}$ -values < 1.4, P -values > 0.2, with error term farm nested in type of management practice: organic or conventional). NS = not significantly different.

displaces a more effective species, pest mortality may again decrease with increased natural enemy diversity. These scenarios plague classical biological control efforts by forcing practitioners to decide between releasing a single (most effective) natural enemy species or else multiple species against a pest (Bellows and Hassel 1999). Enhanced biodiversity should lead to improved pest control when positive interactions or superior outcomes are more likely than negative interactions among natural enemy species.

■ Comparative studies of organic and conventional systems

It is certainly true that ecosystem services depend upon some level of functional biodiversity, and that services such as biological control of insect pests can be severely disrupted under extreme conditions of intensive farming with frequent, scheduled applications of broad-spectrum pesticides (Wilby and Thomas 2002). Organic agriculture practices clearly promote biodiversity, especially compared to intensively-managed conventional systems (Bengtsson *et al.* 2005). How often does that biodiversity pay off through augmented pest control services for organic growers compared to conventional growers? Despite the tendency for ecologists to generalize the connection between biodiversity and ecosystem services, and to leap from biodiversity to pest control, this connection requires a number of steps to be supported (Figure 4). However, we do not yet have documentation of all of these steps: that organic farming leads to greater biodiversity, that higher levels of biodiversity include more beneficial organisms, which then cause higher

mortality rates among pests, and that the ensuing increase in pest mortality results in lower or acceptable levels of pest damage for higher or equivalent yields compared to conventional farming methods. In fact, while numerous diversity comparisons on organic farms have been conducted worldwide over the past 20 years, across various cropping systems, only a few studies have examined the subsequent steps regarding pest impacts (Figure 5). Although enhanced biodiversity on organic farms compared to conventional farms may reliably lead to improved natural pest control services, entomologists working on biocontrol issues recognize that desirable outcomes can depend on having the “right biodiversity” for pest control, not increased biodiversity per se (Landis *et al.* 2000; Gurr *et al.* 2004).

■ Evidence from agricultural settings

How often does an increase in natural enemy diversity result in the “right biodiversity” for pest control? Is enhanced biodiversity more likely to result in positive interactions and

superior outcomes or in negative interactions among natural enemy species? Using a meta-analysis of studies in a wide range of ecosystems, Cardinale *et al.* (2006) found that a higher diversity of predators acting together resulted in a greater reduction of live prey compared to the average across the effects of single predators. However, within the constraints of their analysis, the effect of increased diversity was not significantly greater than the effect of the single most effective predator. Thus, their general outcome supported the lottery model, suggesting that greater biodiversity increases the likelihood of having the “best” predator in the mix (Denoth *et al.* 2002), and that other predators did not tend to disrupt the actions of that predator. This result is supported in some agricultural settings. For example, the presence and activity of a particular predatory species (earwigs, in this case) was more important than predator diversity per se in a vineyard study that monitored predation events using video cameras (Frank *et al.* 2007). However, synergistic effects of predators led to greater suppression of aphids in an alfalfa system (Cardinale *et al.* 2003), and increased ant diversity may enhance predation of borers in coffee ecosystems (Armbrecht and Gallego 2007). Functional diversity of predators in agricultural systems may be a key component of synergistic effects (Gove 2007), such that the “right biodiversity” for complementary effects on prey suppression requires natural enemies that differ sufficiently in their predatory behaviors. However, a priori determinations of functional groups may underestimate functional diversity, which might be fine-grained enough to be represented by species richness, even within closely related predators (eg Resetarits and Chalcraft 2007).

Additionally, managing for coarse-grained functional diversity could promote intra-guild predation. Therefore, the degree to which natural enemy diversity enhances the efficacy of pest management services will probably vary from one agricultural system to another, depending upon pest–enemy interactions in the context of field size, crop composition and pattern, surrounding vegetation, and cultural management practices (Altieri and Nicholls 1999; Figure 1). Future research needs for understanding multi-trophic diversity effects were highlighted in Hooper *et al.* (2005), who also maintain that the right combination of functional attributes can be more important than diversity in determining ecosystem response.

Field experiments designed to test the roles of diversity and top trophic levels in ecosystem function are logistically difficult, costly, and require long-term commitments over large spatial scales.

Yet, without these studies, it is difficult to apply theory to predict with any certainty whether natural pest control, as an ecosystem service, will increase substantially with biodiversity increases of the magnitude and type found in organic versus conventional farming. A proactive approach to fostering the complementary or synergistic effects of pest control in organic agriculture may require biodiversity management, based on biological knowledge of interacting species and functional food webs (Gurr *et al.* 2004). Although few studies on ecological engineering approaches in organic agriculture exist, opportunities for such targeted management are likely to be greater on organic than on conventional farms, due to low pesticide usage and increased resource availability (alternate food sources and prey) for natural enemies (Zehnder *et al.* 2007). Studies in different types of organic agricultural systems and comparative studies with conventional agriculture that go beyond correlation to investigate mechanisms will allow us to answer questions and test theories relevant to ecosystem services for agriculture: Do improvements in ecosystem function level off with increasing biodiversity? Is herbivore regulation and plant protection through trophic cascades hampered in complex systems with high biodiversity? What are the relevant temporal and spatial scales to assess biodiversity enhancement and its effects on pest control?

■ Landscape versus management effects on biodiversity

A parallel, and inherently connected, body of literature shows that landscape diversity is positively associated with on-farm biodiversity. Recent reviews suggest that

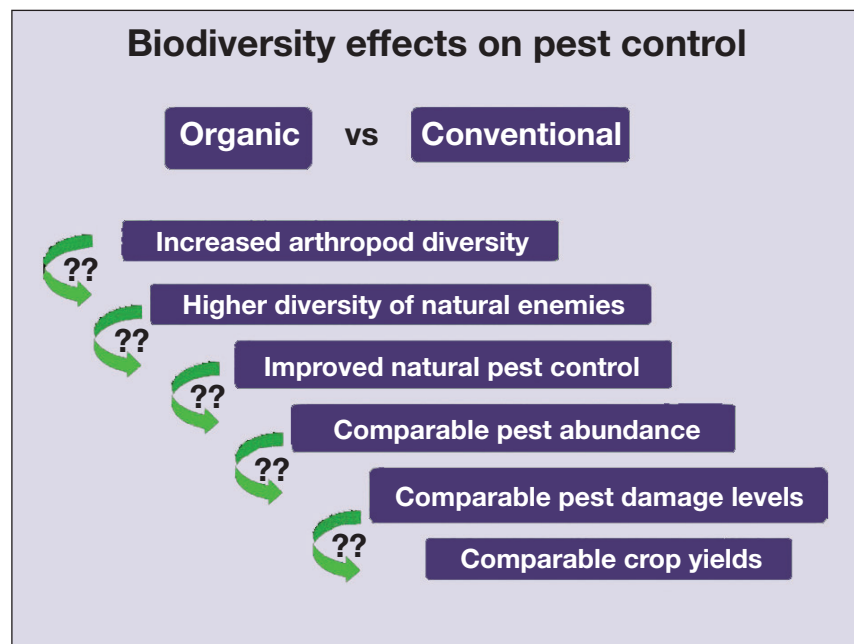


Figure 4. Step-by-step procedure required to link an increase in biodiversity with the effectiveness of pest control as an ecosystem service for organic and conventional growers.

non-crop habitats can serve as sources and stabilizers of natural enemies in crop fields (Bianchi *et al.* 2006), and that surrounding landscapes may be as or more important than within-field management practices for determining pest suppression potential in agricultural systems (Tscharrnke *et al.* 2005). Bianchi *et al.* (2006) point out research gaps, in the landscape context, between measuring diversity and predicting pest control services. Like comparisons of organic and conventional farm fields, comparisons of biodiversity and farm services in different landscapes often defy a mechanistic understanding, because many correlated factors that are difficult to test separately may be operating. For example, farms in complex landscapes are typically characterized by smaller field size than in simpler landscapes, and field size can also covary with management practices (Figure 1). However, Marino *et al.* (2006) began to tease apart landscape effects by investigating the quality of particular classes of non-crop vegetation in relation to alternative host availability for natural enemies of common agricultural pests.

The intersection of these two lines of inquiry raises the question: which factor has more influence on in-field natural enemy diversity and pest control – management or landscape? Few studies effectively weigh the contributions of management and landscape to in-field diversity and pest control by including both organic and conventional farms and a range of landscape conditions. Schmidt *et al.* (2005) showed, in such an integrative design, that landscape factors were stronger predictors of spider diversity than were crop management practices. However, the majority of studies designed to address the role of management in influencing biodiversity or some measure of pest control have used paired study fields. The fields were

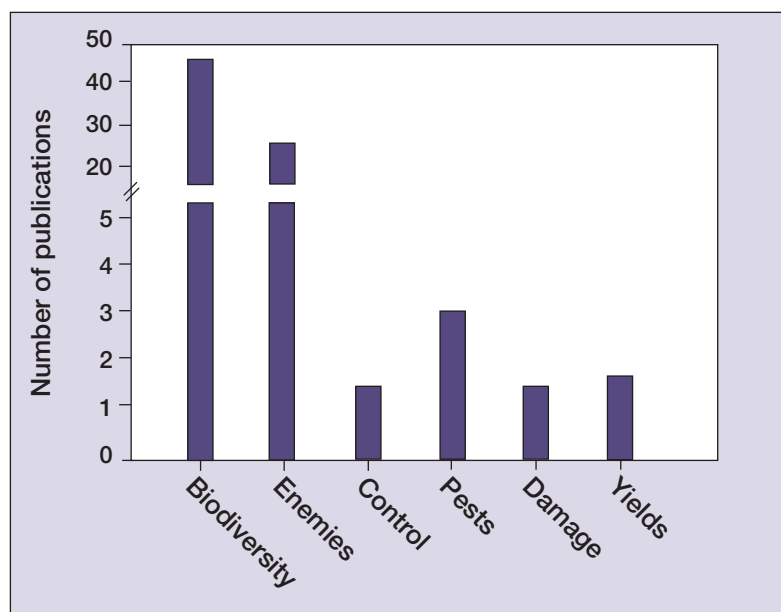


Figure 5. Rapid decline in the number of publications, reviewed by Hole et al. (2005) and included in Appendix 1 of Bengtsson et al. (2005), comparing biodiversity and natural enemy diversity on organic and conventional farms for each of the following steps linking biodiversity with insect pest impact: biodiversity, diversity of natural enemies of insect pests, pest mortality through biological control, pest levels, damage levels to crop, and crop yield.

selected to isolate the effects of management and landscapes (among other factors) as much as possible. In the same way, the majority of studies designed to address the question of landscape influence have attempted to isolate extra-farm differences rather than on-farm differences. Large-scale studies with replicated pairs of organic and conventional fields across a range of landscape contexts are likely to be limited by the availability of conventional farms at the complex end of the landscape continuum and, to a lesser degree, by the availability of organic farms at the simple end of the continuum. Nonetheless, determining their relative contributions will be important for success in both pest control and biodiversity conservation goals.

■ Managing biodiversity for pest control services on organic farms

At least three types of ecological research programs will allow us to evaluate the potential for biodiversity on organic farms to improve pest control in those agroecosystems: (1) on-farm comparisons, (2) mesocosm experiments, and (3) performance risk assessments. Together, these research approaches should advance both ecological theory and practical management recommendations for growers.

First, on-farm systems comparisons can test the general hypothesis that pest control increases with increased biodiversity. These field tests require mechanistic components to trace aspects of biodiversity through pest impact to measures of marketable yield (Figure 5). Although limited to measuring correlations among a range of variables,

tests for association between the biodiversity of natural enemies and pest control levels are not trivial, because they represent outcomes derived from real farming operations. This first step will be more informative if multivariate analyses and path analyses are used to assess what proportion of pest control advantage is explained by natural enemy diversity or particular components of the natural enemy assemblages. Correlation analyses can identify what conditions and systems are associated with increased biodiversity of natural enemies, whether pests in those systems do or do not show increased biological control, and what aspects of the community (eg non-crop vegetation diversity, predatory insect composition, cropping patterns) best explain differences in pest abundances, attack rate by natural enemies, and crop-damage levels.

The next step in this approach includes efforts to measure predation and parasitism rates of pests (by monitoring natural occurrences or by using sentinel pest experiments), assess which enemies are causing pest mortality, and create quantitative food webs (eg Tylianakis et al. 2007). These more detailed

data can be used to determine the differences in how pests and natural enemies interact in organic versus conventional agriculture. Whereas biodiversity conservation has intrinsic value, actual measures of productivity gains or pesticide savings through biodiversity conservation would provide a powerful incentive for growers to adopt new practices and consider alternative land-use priorities.

Second, manipulative experiments that examine species interactions in multi-species mixes of natural enemies and model potential prey suppression outcomes will clarify the components of high- and low-quality biodiversity for pest control in different cropping systems (Casula et al. 2006). Manipulative experiments can provide some of the knowledge of limiting resources, species interactions, and insect movement that is required for community engineering (Snyder et al. 2005) or targeted species enhancement. Encouraging particular mixes of natural enemies in a diverse assemblage will minimize negative interactions that disrupt pest control. Factorial experiments with field cages, for instance, have been used to examine numerical and behavioral predatory insect interactions and their roles in pest suppression within the context of trophic cascades theory and biodiversity–pest control outcomes (Costamagna et al. 2007). A synthetic treatment of previous research can supplement or guide the development of new experiments. For example, the biological control literature, though often limited to one pest–one enemy interactions, includes critical natural history information on alternative hosts and other resources for predators and parasitoids. The broad literature on intercropping and vegetation diversification for promoting natural biological

control of crop pests should be mined for examples of successful natural enemy combinations (Landis *et al.* 2000; Zehnder *et al.* 2007). To evaluate the effects of biodiversity on pest control services on a case-by-case basis, the on-farm studies described above could be coupled with mesocosm experiments to test for complementary or agonistic interactions among species represented on organic and conventional farms.

A third approach is to present growers with some level of performance risk assessment that would estimate ecosystem service returns for investments in biodiversity conservation (*sensu* Koellner and Schmitz 2006). This approach is fundamentally different from predicting how the level of pest control will change, on average, with the level of biodiversity. It emphasizes variability measures to estimate the risk of obtaining lower than expected returns on investment in biodiversity. The wider literature may contain enough mean effects and variability measures from studies on pest control and biodiversity, pest control and damage, and damage and yield to generate a probability function for risk–return characteristics of different management options. To more accurately determine portfolio values, Koellner and Schmitz (2006) call for experimental designs that quantify a function and its variance rather than measuring effects (regression rather than ANOVA), and that span the range of species combinations resulting from biological diversification efforts. Such a diversity portfolio risk assessment could replace the blanket prescription that biodiversity results in better pest control, and aid in management decisions regarding on-farm investments in biodiversity conservation.

As organic farming increases in prominence and research efforts to support sustainable agriculture expand, critical scientific analyses of the relationship between biodiversity and pest control services of these agroecosystems are needed. Studies at different scales, from laboratory to landscape, will be helpful in directing biodiversity conservation efforts, determining the path to on-farm value-added biodiversity, and gaining ecosystem services for farmers from both natural and managed ecosystems.

■ Acknowledgements

Support from USDA-NRI grant #2005-0288, USDA-LISA grant #88-COOP-1-3525, UCSC Faculty Research grants, Department of Environmental Studies, and STEPS Institute grants made this paper possible. We thank local growers for their participation, students for field and laboratory assistance, B Fulfroost for GIS assistance, C Shennan and P Barbosa for helpful discussions, and J Hagen, J Jedlicka, T Krupnik, and C Moreno for improvement of previous drafts.

■ References

- Altieri MA. 1986. The ecology of insect pest control in organic farming systems: toward a general theory. In: Vogtmann H, Boehncke E, and Fricke I (Eds). Importance of biological agriculture in a world of diminishing resources. Witzchenhausen, Germany: Verlagsgruppe Weiland.
- Altieri MA and Nicholls CI. 1999. Biodiversity, ecosystem function, and insect pest management in agricultural systems. In: Collins WW and Qualset CO (Eds). Biodiversity in agroecosystems. Boca Raton, FL: CRC Press.
- Ambrecht I and Gallego MC. 2007. Testing ant predation on the coffee berry borer in shaded and sun coffee plantations in Colombia. *Entomol Exp Appl* **124**: 261–67.
- Badgley D, Moghtader J, Quintero E, *et al.* 2006. Organic agriculture and the global food supply. *Renew Agr Food Syst* **22**: 86–108.
- Barbosa P. 1998. Conservation biological control. New York, NY: Academic Press.
- Belfrage K, Bjorklund J, and Salomonsson L. 2005. The effects of farm size and organic farming on diversity of birds, pollinators, and plants in a Swedish landscape. *Ambio* **34**: 582–88.
- Bellows TS and Hassel MP. 1999. Theories and mechanisms of natural population regulation. In: Bellows T and Fisher TW (Eds). Handbook of biological control. San Diego, CA: Academic Press.
- Bengtsson J, Ahnstrom J, and Weibull A. 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *J Appl Ecol* **42**: 261–69.
- Bianchi FJJA, Booij CJH, and Tscharntke T. 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity, and natural pest control. *P Royal Soc B* **273**: 1715–27.
- Butler SJ, Vickery JA, and Norris K. 2007. Farmland biodiversity and the footprint of agriculture. *Science* **315**: 381–84.
- Cardinale BJ, Harvey CT, Gross K, and Ives AR. 2003. Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecol Lett* **6**: 857–65.
- Cardinale BJ, Srivastava DS, Duffey JE, *et al.* 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature* **443**: 989–92.
- Casula P, Wilby A, and Thomas MB. 2006. Understanding biodiversity effects on prey in multi-energy systems. *Ecol Lett* **9**: 995–1004.
- Costamagna AC, Landis DA, and Difonzo C. 2007. Suppression of soybean aphid by generalist predators results in a trophic cascade in soybeans. *Ecol Appl* **17**: 441–51.
- Denoth M, Frid L, and Myers JH. 2002. Multiple agents in biological control: improving the odds? *Biol Control* **24**: 20–30.
- Dimitri C and Greene C. 2002. Recent growth patterns in the US organic food market. Washington, DC: USDA Economic Research Service.
- Drinkwater LE, Letourneau DK, Wroblek F, *et al.* 1995. Fundamental differences between conventional and organic tomato agroecosystems in California. *Ecol Appl* **5**: 1098–12.
- Dyer LA and Stireman JO. 2003. Community-wide trophic cascades and other indirect interactions in an agricultural community. *Basic Appl Ecol* **4**: 423–32.
- FAO (Food and Agriculture Organisation). 1999. Organic agriculture. Rome, Italy: Food and Agriculture Organisation.
- Finke DL and Denno RF. 2004. Predator diversity dampens trophic cascades. *Nature* **429**: 407–10.
- Frank SD, Wratten SD, Sandhu HS, and Shrewsbury PM. 2007. Video analysis to determine how habitat strata affects predator diversity and predation of *Epiphyas postvittana* (Lepidoptera: Tortricidae) in a vineyard. *Biol Control* **41**: 230–36.
- Gabriel D, Roschewitz I, Tscharntke T, and Thies C. 2006. Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. *Ecol Appl* **16**: 2011–21.
- Gliessman SR. 1989. Ecological basis for sustainable agriculture. In: Gliessman S (Ed). Agroecology: researching the ecological basis for sustainable agriculture. New York, NY: Springer-Verlag.

- Gove AD. 2007. Ant biodiversity and the predatory function (a response to Philpott and Armbrrecht, 2006). *Ecol Entomol* **32**: 435–36.
- Gurr GM, Wratten SD, and Altieri MA. 2004. Ecological engineering for pest management: advances in habitat management for arthropods. Ithaca, NY: Comstock Publishing Associates.
- Hole DG, Perkins AJ, Wilson JD, et al. 2005. Does organic farming benefit biodiversity? *Biol Conserv* **122**: 113–30.
- Hooper DU, Chapin FS, Ewel JJ, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* **75**: 3–35.
- Jones GA, Sieving KE, and Jacobson SK. 2005. Avian diversity and functional insectivory on north-central Florida farmlands. *Conserv Biol* **19**: 1234–45.
- Kasparczyk N and Knickel K. 2006. Environmental impacts of organic farming. In: Kristiansen P, Taji A, and Reganold J (Eds). *Organic agriculture: a global perspective*. Collingwood, Australia: CSIRO Publishing.
- Kleijn D, Baquero RA, Clough Y, et al. 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecol Lett* **9**: 243–54.
- Koellner T and Schmitz OJ. 2006. Biodiversity, ecosystem function, and investment risk. *BioScience* **56**: 977–85.
- Kristiansen P. 2006. Overview of organic agriculture. In: Kristiansen P, Taji A, and Reganold J (Eds). *Organic agriculture: a global perspective*. Collingwood, Australia: CSIRO Publishing.
- Landis DA, Wratten SD, and Gurr GM. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu Rev Entomol* **45**: 175–201.
- Letourneau DK and van Bruggen A. 2006. Crop protection in organic agriculture. In: Kristiansen P, Taji A, and Reganold J (Eds). *Organic agriculture: a global perspective*. Collingwood, Australia: CSIRO Publishing.
- Maeder P, Fliebach A, Dubois D, et al. 2002. Soil fertility and biodiversity in organic farming. *Science* **296**: 1694–97.
- MA (Millennium Ecosystem Assessment). 2003. *Ecosystems and human well-being: a framework for assessment*. Washington, DC: Island Press.
- Marino PC, Landis DA, and Hawkins BA. 2006. Conserving parasitoid assemblages of North American pest Lepidoptera: does biological control by native parasitoids depend on landscape complexity? *Biol Control* **37**: 173–85.
- Melnichuk NA, Olfert O, Youngs B, and Gillot C. 2003. Abundance and diversity of Carabidae (Coleoptera) in different farming systems. *Agr Ecosyst Environ* **95**: 69–72.
- Myers JH, Higgins C, and Kovacs E. 1989. How many insect species are necessary for the biological control of insects? *Environ Entomol* **18**: 541–47.
- Oehl F, Sieverding E, Mader P, et al. 2004. Impact of long-term conventional and organic farming on the diversity of arbuscular mycorrhizal fungi. *Oecologia* **138**: 574–83.
- Perez-Lachaud G, Batchelor TP, and Hardy ICW. 2004. Wasp eat wasp: facultative hyperparasitism and intra-guild predation by bethylid wasps. *Biol Control* **30**: 149–55.
- Pimentel D. 1961. Species diversity and insect population outbreaks. *Ann Entomol Soc Am* **54**: 76–86.
- Purtauf T, Roschewitz I, Dauber J, et al. 2005. Landscape context of organic and conventional farms: influence on carabid beetle diversity. *Agr Ecosyst Environ* **108**: 165–74.
- Resatarits WJ and Chalcraft DR. 2007. Functional diversity within a morphologically conservative genus of predators: implications for functional equivalence and redundancy in ecological communities. *Funct Ecol* **21**: 793–804.
- Root RB. 1973. Organization of a plant–arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol Monogr* **43**: 95–124.
- Rosenheim JA, Limburg DD, and Colfer RG. 1999. Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: direct observations. *Ecol Appl* **9**: 409–17.
- Ryden R. 2007. Smallholders, organic farmers, and agricultural policy: the case of Sweden compared with Denmark and Norway, from the 1970s to 2003. *Scand J Hist* **32**: 63–85.
- Schmidt MH, Roschewitz I, Thies C, and Tschamtk T. 2005. Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders. *J Appl Ecol* **42**: 281–87.
- Snyder WE, Chang GC, and Prasad RE. 2005. Conservation biological control: biodiversity influences the effectiveness of predators. In: Barbosa P and Castellanos I (Eds). *Ecology of predator–prey interactions*. New York, NY: Oxford University Press.
- Sooby J. 2001. State of the states: organic farming research at land grant institutions 2000–2001. Santa Cruz, CA: Organic Farming Research Foundation.
- Stireman J, Dyer LA, and Matlock R. 2005. Top-down forces in managed versus unmanaged habitats. In: Barbosa P and Castellanos I (Eds). *Ecology of predator–prey interactions*. New York, NY: Oxford University Press.
- Stoate C, Boatman ND, Borralho RJ, et al. 2001. Ecological impacts of arable intensification in Europe. *J Environ Manage* **63**: 337–65.
- Stoltz M. 2005. The current agri-policy context: the European action plan for organic farming and the current CAP reform. Nuremberg, Germany: Biofach Congress.
- Tschamtk T, Klein AM, Kruess A, et al. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecol Lett* **8**: 857–74.
- Tylianakis JM, Tschamtk T, and Lewis OT. 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* **445**: 202–05.
- Wickramasinghe LP, Harris S, Jones G, and Jennings NV. 2004. Abundance and species richness of nocturnal insects on organic and conventional farms: effects of agricultural intensification on bat foraging. *Conserv Biol* **18**: 1283–92.
- Wilby A and Thomas MB. 2002. Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecol Lett* **5**: 353–60.
- Zanoli R, Gambelli D, and Vitulano S. 2007. Conceptual framework on the assessment of the impact of organic agriculture on the economies of developing countries. Rome, Italy: Food and Agriculture Organisation.
- Zehnder G, Gurr OM, Kiehn S, et al. 2007. Arthropod pest management in organic crops. *Annu Rev Entomol* **52**: 57–80.