

# Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes

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**Increased demand for corn grain as an ethanol feedstock is altering U.S. agricultural landscapes and the ecosystem services they provide. From 2006 to 2007, corn acreage increased 19% nationally, resulting in reduced crop diversity in many areas. Biological control of insects is an ecosystem service that is strongly influenced by local landscape structure. Here, we estimate the value of natural biological control of the soybean aphid, a major pest in agricultural landscapes, and the economic impacts of reduced biocontrol caused by increased corn production in 4 U.S. states (Iowa, Michigan, Minnesota, and Wisconsin). For producers who use an integrated pest management strategy including insecticides as needed, natural suppression of soybean aphid in soybean is worth an average of \$33 ha<sup>-1</sup>. At 2007–2008 prices these services are worth at least \$239 million y<sup>-1</sup> in these 4 states. Recent biofuel-driven growth in corn planting results in lower landscape diversity, altering the supply of aphid natural enemies to soybean fields and reducing biocontrol services by 24%. This loss of biocontrol services cost soybean producers in these states an estimated \$58 million y<sup>-1</sup> in reduced yield and increased pesticide use. For producers who rely solely on biological control, the value of lost services is much greater. These findings from a single pest in 1 crop suggest that the value of biocontrol services to the U.S. economy may be underestimated. Furthermore, we suggest that development of cellulosic ethanol production processes that use a variety of feedstocks could foster increased diversity in agricultural landscapes and enhance arthropod-mediated ecosystem services.**

bioenergy | biological control | ecosystem services

High recent prices of oil and a growing interest in developing alternative liquid fuels has driven a rapid expansion of the corn ethanol industry in the United States. Continuing growth of ethanol production facilities in major corn-producing areas has significantly increased demand for corn grain (1) and is restructuring agricultural landscapes. In 2007, corn plantings in the U.S. totaled 37.9 million ha, a 19% increase over 2006 (ref. 2 and [http://usda.mannlib.cornell.edu/usda/nass/CropProd//2000s/2008/CropProd-08-12-2008\\_revision.pdf](http://usda.mannlib.cornell.edu/usda/nass/CropProd//2000s/2008/CropProd-08-12-2008_revision.pdf)). In 2008 corn plantings declined 7% from 2007 levels but still represent the second highest since 1946 (ref. 3 and <http://usda.mannlib.cornell.edu/usda/ers/FDS//2000s/2008/FDS-08-14-2008.pdf>). The Energy Independence and Security Act of 2007 mandates a nearly 5-fold expansion of biofuel production (4), which will likely drive further expansion of corn area. Increases in corn production are already having repercussions, driving up the prices of other major field crops that compete with corn for land. Increased corn acreage for biofuel production has raised concerns regarding the potential for increased food prices, fertilizer and pesticide pollution, soil erosion, biodiversity losses, and greenhouse gas emissions (5–7). Here, we consider a largely unrecognized impact, the effect of a change in landscape structure on arthropod-mediated ecosystem services and its implications for the sustainability of agricultural production systems (8).

It has been estimated that insects provide human society with ecosystem services valued at >\$57 billion yr<sup>-1</sup> in the United States (9). Of this, \$4.5 billion yr<sup>-1</sup> has been attributed to natural

pest control in agricultural crops. Much of this pest control service is provided by generalist natural enemies that suppress populations of a variety of native and exotic insect pests. Diverse, small-scale agricultural landscapes with a high proportion of noncrop habitats frequently support a greater abundance of natural enemies and lower pest populations than large-scale, monoculture landscapes with little noncrop habitat (10). Expansion of bioenergy crop production on arable lands is likely to change the habitat characteristics that enable these landscapes to support biological control. Increased planting of biofuel crops such as corn, that already dominate large areas in agricultural landscapes, may well reduce biocontrol services.

The soybean aphid (*Aphis glycines* Matsumura) is an invasive insect pest that has become the most significant threat to soybean production in the United States (11). Soybean aphid is consumed by a diversity of natural enemies, including predators and parasitoids (12, 13), that can provide strong top-down regulation of its populations (14), resulting in increased crop yields (15). The natural enemy complex of soybean aphid is currently dominated by generalist predators, in particular ladybird beetles (Coleoptera: Coccinellidae) (16, 17). The main effect of predation on aphid population growth occurs when aphid populations are still small and vulnerable to predation losses (18, 19). Our recent studies show that these predators are responsive to landscape structure and that habitat diversity at the 1.5-km scale surrounding a soybean field is strongly related to the level of soybean aphid suppression. Landscapes with high levels of corn and soybean production had low habitat diversity and significantly reduced biocontrol services in soybean fields (20). Here, we specifically examine how increasing amounts of corn production alters the value of arthropod biological control as an ecosystem service in agricultural landscapes.

## Results

**Biocontrol Services in Changing Agricultural Landscapes.** Annual crop production dominates agricultural landscapes in our study area of Iowa, Michigan, Minnesota, and Wisconsin, and the composition of these landscapes is rapidly changing because of increased demand for corn as a biofuel feedstock (Table 1). In 2007, harvested corn acreage increased by 12%, 20%, 14%, and 17% in Iowa, Michigan, Minnesota, and Wisconsin, respectively, compared with 2006 acreage (2). This increase was primarily at the expense of harvested soybean acreage, which declined by 16%, 13%, 15%, and 20%, respectively. We found that the proportion of corn ( $R^2 = 0.66$ ,  $P < 0.0001$ ) and soybean ( $R^2 =$

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**Table 1. Corn and soybean plantings in Iowa, Michigan, Minnesota, and Wisconsin showing changes in ha harvested from 2006 to 2007 and state average soybean yields**

State	Corn ha harvested			Soybean ha harvested			Soybean yield, Mg ha <sup>-1</sup> *
	2007, thousands ha	Change from 2006, %	Percentage of national	2007, thousands ha	Change from 2006, %	Percentage of national	
Iowa	5,604.9	+12	16	3,447.9	-16	14	3.16
Michigan	951.0	+20	3	704.2	-13	3	2.59
Minnesota	3,156.4	+14	9	2,488.9	-15	10	2.79
Wisconsin	1,327.4	+17	4	538.2	-19	2	2.96
Total	11,039.8	+14	32	7,179.2	-18	28	—

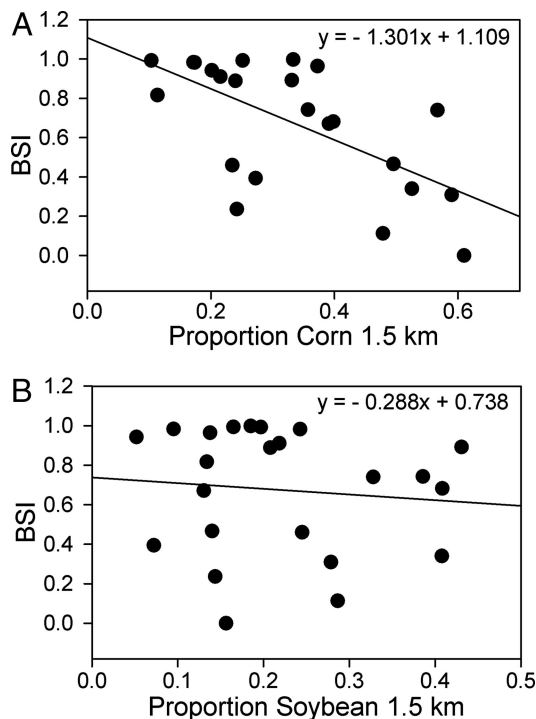
\*Ten-year median soybean yield, 1997–2006 from U.S. Department of Agriculture crop production summary reports (1999, 2002, 2005, 2008)

0.20,  $P < 0.0327$ ) in the local landscape (1.5-km scale) were both negatively associated with landscape diversity; however, these crops had differing impacts on biocontrol services. Using data from 23 site-year combinations on the growth of soybean aphid populations in treatments with and without natural enemies, we calculated a biocontrol services index (BSI) defined as the proportional decrease in aphid population growth in the presence of natural enemies. We found that BSI declined significantly with increasing proportion of corn in the landscape (Fig. 1A;  $R^2 = 0.39$ ,  $P = 0.001$ ) but BSI was not significantly related to the proportion of soybean (Fig. 1B;  $R^2 = 0.01$ ,  $P = 0.646$ ). Thus, exchanging corn for soybean does not have a neutral effect on biocontrol services. Rather, as corn area increased in the local landscape, biological control services to soybean decline.

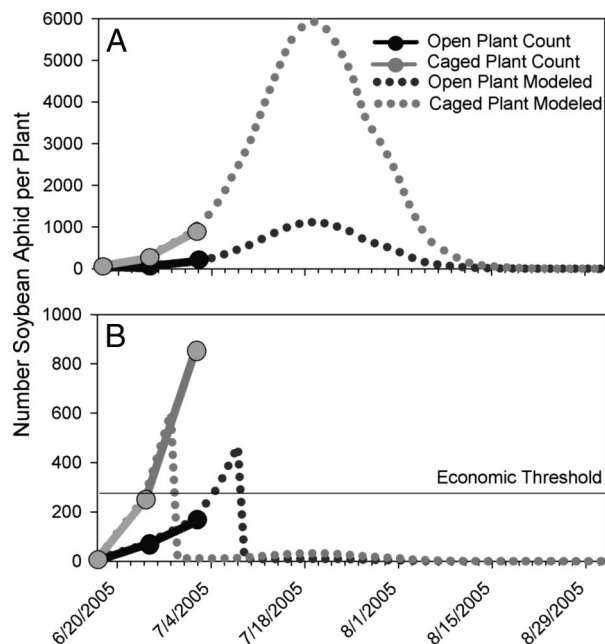
To estimate the economic impact of these landscape changes on biocontrol services, we used the estimated relationship between area of corn and BSI (Fig. 1A), in conjunction with established models for soybean aphid population dynamics (21) and aphid-induced yield loss (11), to project the effect of changes

in corn area on biocontrol services in soybean and the resulting effects on aphid population dynamics and crop damage. We considered 2 soybean aphid management strategies, integrated pest management (IPM) and biocontrol that encompass the range of management approaches currently used by producers. We defined IPM to include weekly field scouting with application of conventional insecticides when populations exceed the established economic threshold of 250 soybean aphids per plant (11). The biocontrol strategy relies solely on the capacity of the prevailing natural enemy complex to suppress soybean aphid. Data from predator exclusion experiments (20) were used to initialize and run the aphid population growth model and to project outcomes from the 2 management strategies.

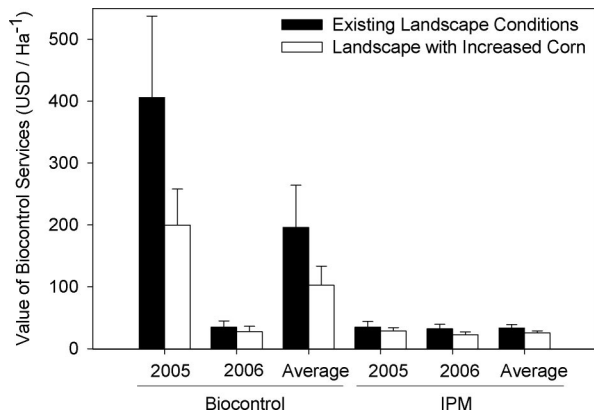
Output from the population dynamics model for 1 of the 23 site-year combinations is depicted in Fig. 2. Under biocontrol alone (Fig. 2A), the observed aphid population on the natural enemy-free plants grows rapidly over the 14-day experiment.



**Fig. 1.** Relationship between the BSI in soybean fields and proportion of corn (A) and soybean (B) in the local landscapes (1.5-km radius). BSI, the proportional decrease in aphid population growth in the presence of natural enemies, declines significantly with increasing corn ( $R^2 = 0.39$ ,  $P = 0.001$ ) but not soybean ( $R^2 = 0.01$ ,  $P = 0.6738$ ).



**Fig. 2.** Example model output of soybean aphid population growth with and without natural enemies under 2 management strategies biocontrol alone (A) and IPM (B). Solid lines represent observed data, and dotted lines indicate model projections. Caged plants are free of natural enemies that consume soybean aphid, while open plants have ambient levels of natural enemies present. Steep population declines simulate insecticide sprays triggered by the population exceeding the economic threshold of 250 aphids per plant. Sprays were applied 4 days after reaching threshold to simulate an average producer response time.



**Fig. 3.** Value (mean  $\pm$  SEM) of biocontrol services against soybean aphid in Iowa, Michigan, Minnesota, and Wisconsin in years of high (2005,  $n = 10$  sites) or low (2006,  $n = 13$  sites) aphid abundance. Average values represent means across the 2 years. Values shown are based on 2007–2008 projected soybean price of  $\$380 \text{ Mg}^{-1}$  for 2 aphid management strategies: biocontrol alone or IPM, under existing landscape conditions in each year and estimated with increased corn production for biofuel based on 2007 changes in corn acres harvested per state.

From this point the model projects continued population growth of aphids until changes in host plant quality cause their decline. By contrast, in the open field with natural enemies present, population growth is greatly suppressed. Using the same initial experimental data, the IPM example yields a markedly different result (Fig. 2B). Here, the observed aphid population on the natural enemy-free plants again rises throughout the initial 14 days, which in the model projection, triggers an insecticide application that reduces the population by 98%. In the presence of natural enemies, the open-field population grows more slowly but eventually exceeds the economic threshold, also triggering an insecticide treatment. The above 4 trajectory projections were replicated for each site-year combination under a landscape change scenario where corn area was increased to 2007 levels for each state. The resulting data were analyzed to determine the overall value of biocontrol services to soybean producers and the impact of landscape change on this ecosystem service under varying aphid infestations and management strategies.

**Value of Biocontrol Services.** The value of soybean aphid biocontrol services varies with soybean aphid abundance, management strategy, and amount of corn in the landscape. Soybean aphid populations fluctuate from year to year (22), resulting in different values of ecosystem services provided in years of high (2005) versus low (2006) soybean aphid abundance (Fig. 3). In 2005, yield losses were high for growers who relied solely on natural biocontrol. Consequently, the value of the ecosystem service of biological control mitigating these losses was also high, averaging  $\$406 \text{ ha}^{-1}$  across the 4 states. An increase of corn in these landscapes to 2007 levels reduced the value of the biocontrol service to an average of  $\$199 \text{ ha}^{-1}$ . Using the IPM strategy greatly reduced economic losses to soybean aphids; however, IPM users still received an average of  $\$35 \text{ ha}^{-1}$  in biocontrol services in 2005. This benefit decreased to an average of  $\$29 \text{ ha}^{-1}$  when corn was increased to 2007 levels.

In 2006, soybean aphid abundance was dramatically lower across the study region, resulting in similar biocontrol service values for the IPM and biocontrol approaches (Fig. 3). For growers who rely on biocontrol alone, the presence of natural enemies was worth an average of  $\$35 \text{ ha}^{-1}$  across the 4 states. Modeling an increase in corn in these landscapes to 2007 levels reduced the value of the biocontrol service to an average of  $\$28 \text{ ha}^{-1}$ . In 2006, IPM users received an average of  $\$32 \text{ ha}^{-1}$  in

biocontrol services, which decreased to an average of  $\$23 \text{ ha}^{-1}$  when corn was increased to 2007 levels.

The value of biocontrol services in soybean depends in part on the number of fields in which aphids exceed the economic threshold and thus trigger costly insecticide applications to protect yield. In 2005, model projections show that 100% of the fields where natural enemies were excluded exceeded the economic threshold. In contrast, where natural enemies were not excluded, 30% of these fields remained below the threshold. In 2006, 62% of fields reached threshold in the absence of natural enemies; however, in the presence of natural enemies no fields required insecticide sprays. Using typical pesticide and application costs of  $\$24.5 \text{ ha}^{-1}$  (11), it is clear that the action of natural enemies in preventing the need for insecticide applications is a major factor contributing to the value of the biocontrol service. Additional information on the range of biocontrol service values as influenced by aphid abundance, soybean price, management scenarios, and land-use change are given in *SI Text* and *Tables S1 and S2*.

**Aggregate Values.** Averaged over the 23 site-year combinations, the value of biocontrol services decreased from  $\$196 \text{ ha}^{-1}$  to  $\$103 \text{ ha}^{-1}$  as a result of increased corn in the landscape when biological control was the sole pest management strategy (Table S2). Under IPM, the average value of biocontrol services decreased from  $\$33 \text{ ha}^{-1}$  to  $\$25 \text{ ha}^{-1}$ . This change of  $\$8 \text{ ha}^{-1}$  amounts to nearly a quarter of average crop chemicals cost of  $\$35 \text{ ha}^{-1}$  or 3.4% of total operating costs of  $\$235 \text{ ha}^{-1}$  for conventional soybean farmers in the U.S. “heartland” and “northern crescent” states during 2006 (ref. 23 and [www.ers.usda.gov/Data/CostsAndReturns](http://www.ers.usda.gov/Data/CostsAndReturns)). The overall percentage of fields reaching threshold with natural enemies present increased from 30% under the 2005/2006 landscape conditions to an estimated 43% with an increase in corn acreage to the 2007 level.

If all producers used IPM, we estimate the value of natural biocontrol services against soybean aphid in the 4 target states at  $\$239 \text{ million y}^{-1}$  or  $\$1,620 \text{ farm}^{-1} \text{ y}^{-1}$  under 2007–2008 “biofuel-influenced” soybean prices of  $\$380 \text{ Mg}^{-1} = \$10.40 \text{ Bu}^{-1}$  (Table 2). With corn increased to 2007 levels, the value of biocontrol services in these states declines by an estimated 24%, equivalent to  $\$58 \text{ million y}^{-1}$  or  $\$390 \text{ farm}^{-1} \text{ y}^{-1}$ . Because of increased risk of yield loss, sole reliance on natural biocontrol is a much less common grower strategy. However, if followed by all growers, it would yield aggregate annual biocontrol services against soybean aphid exceeding  $\$1.4 \text{ billion y}^{-1}$  in the 4 target states. With corn increased to 2007 levels, the annual value of these services would be reduced by 48% or  $\$671 \text{ million y}^{-1}$ . Thus, in the world of corn ethanol-driven prices the IPM-based figure of  $\$239 \text{ million y}^{-1}$  is a lower bound for the value of these services in these 4 states as some growers realize greater gains by relying entirely on natural biocontrol.

## Discussion

Increased corn prices and production provide an immediate profitability benefit to corn growers; however, many of these same growers incur hidden costs to their soybean production because of the attendant landscape change. These impacts extend to neighboring producers and society as a whole through an overall reduction in biocontrol services from these landscapes. From 2006 to 2007, U.S. corn acreage increased dramatically, primarily at the expense of soybean but also from reduced production of minor crops and cultivation of formerly fallow areas such as Conservation Reserve Program acreage. The overall impact of these changes is agricultural landscapes with lower habitat diversity, which has been associated with reduced biological control. A recent metaanalysis found that simple agricultural landscapes had lower abundance of natural enemies (76% of studies) and increased pest pressure (45% of studies)



crop production, and increased communication between scientists, policy makers and the biofuels industry, is critically needed to inform decisions on development of sustainable biofuel production technologies (33).

## Materials and Methods

**Biocontrol Services Data.** Gardiner *et al.* (20) measured the biocontrol service supplied by natural enemies of the soybean aphid, *A. glycines*, in soybean fields across 2 years (2005 and 2006) and 4 states (Iowa, Michigan, Minnesota, and Wisconsin). Within each state, 3–8 sites were studied over the 2 seasons, for a total of 23 site-year combinations. To determine the impact of natural enemies on soybean aphid populations, 2 treatments were compared: an open treatment where natural enemies had full access to aphid-infested soybean plants, and a caged treatment where exclusion cages prevented natural enemies from colonizing plants and consuming aphids. At each location, treatments ( $n = 4$  replications) were established when fields reached an average of 10 aphids per plant, and plants in both treatments were manipulated to start with this aphid density at day 0. Aphid counts were made 7 and 14 days after the treatments were established. We have previously established that this time period allows observation of the critical predator impacts while minimizing potential for cage effects (12). Based on these data, we calculated a BSI, which is the relative reduction in aphid density caused by predator access over a period of 14 days:

$$BSI = \frac{\left( \sum_{p=1}^4 \frac{(Ac_p - Ao_p)}{Ac_p} \right)}{n}, \quad [1]$$

where  $Ac$  is the number of aphids on the caged plant on day 14,  $Ao$  is the number of aphids on the open plant on day 14,  $p$  is plot, and  $n$  is the number of replicates for a given site.

**Evaluating Biofuel Landscapes.** From 2006 to 2007 harvested corn acreage increased by 12–20% in Iowa, Michigan, Minnesota, and Wisconsin (Table 1). To account for this shift in production, we first determined the corn acreage present within a 1.5-km radius surrounding each of the 23 soybean field sites where BSI was measured in 2005 and 2006. Next, we increased corn acreage for each of these landscapes by the proportional increase recorded for the state in which each individual site was located. Finally, we used the equation from the linear regression of corn and BSI ( $y = -1.301x + 1.109$ ) to determine new predicted BSI values for each site based on the increased corn acreage. These BSI values allow for the calculation of adjusted aphid abundance values for the open, i.e., predator-exposed treatment at 14 days of the experiment. We then compare the service provided by natural enemies under 2 landscape regimes, the 2005–2006 landscape (based on land cover data collected in 2005 and 2006) and a biofuels-influenced landscape (incorporating the 2007 corn increase).

**Predicting Aphid Population Growth.** To predict the value of biocontrol services obtained under both landscape regimes, it was necessary to project aphid population growth beyond the timeframe of the 14-day experiment. To accomplish this we used an aphid population growth model (21) that is based on the growth of natural enemy-free (i.e., caged) soybean aphid populations. We used a linear interpolation to estimate aphid populations during the experimental period 0–14 days then projected the population for the remainder of the season by using Eq. 2:

$$N_t = N_0 e^{rt \left( 1 - \frac{1}{2} at \right)}, \quad [2]$$

where  $N$  is the aphid population size,  $t$  is thermal time since sowing (degree days base = 10 °C),  $r$  is the intrinsic rate of increase of soybean aphid at thermal time 0, and  $a$  expresses the effect of plant age (thermal time) on the rate of population increase of soybean aphid on soybean plants (34). This model showed good to excellent predictions of soybean aphid population dynamics in the absence of predators with  $R^2_{\text{prediction}}$  from independent data ranging from 0.86 to 0.99 (21). The population projection after the 2-week period of the field measurements does not account for further predation effects and therefore provides a lower bound for predator impact.

**Soybean Aphid Pest Management Scenarios.** We used 2 scenarios to describe producer responses to soybean aphid infestations. The first was IPM, where

producers scout soybean aphid populations every 7 days and make insecticide applications 4 days after a population reaches the economic threshold. Our second strategy was a biocontrol-alone strategy, where producers rely completely on natural biocontrol. IPM strategies represent profit-maximizing behavior for those soybean growers that use pesticides. The economic threshold for pest control is the level at which a pest population will cause crop yield losses that exceed the cost of control, in this case, insecticide treatment. The established economic threshold is 250 aphids per soybean plant (11). Because many producers rely on custom applicators for field spraying services, the 4-day delay represents a realistic average response time. We assume insecticide applications induce 98% mortality and prevent aphid population growth for 7 days.

**Estimating Soybean Damage.** To estimate the damage caused by soybean aphid in the presence and absence of natural enemies, cumulative aphid days (CAD) were calculated by integrating the area under each curve (aphid population with and without predation) by application of the trapezoidal rule over daily time intervals. To translate CAD into yield loss, we applied a yield loss coefficient of 0.688% per 1,000 aphid days per plant, derived from yield loss studies from 19 location-year combinations in 6 Midwestern states, including all 4 states included in our study (linear regression of yield loss on CAD,  $R^2 = 0.665$ ) (11). To avoid crop loss >100%, the proportional crop loss was truncated at a value of 1.

**Calculation of Value of Biocontrol Services.** To calculate the monetary value of yield loss caused by soybean aphid we used the 10-year median yields in  $\text{Mg} \cdot \text{ha}^{-1}$  from 1997 to 2006 for Iowa (3.16), Michigan (2.59), Minnesota (2.79), and Wisconsin (2.96) (35). Pesticide application costs of  $\$24.5 \text{ ha}^{-1}$  represent a midrange control cost representative of hired ground application of a moderately-priced soybean aphid insecticide (11). For each year and field we estimated the value of income loss  $\text{ha}^{-1}$  caused by soybean aphid with or without natural enemies, including yield loss, insecticide, and scouting costs for IPM strategies ( $\$5 \text{ ha}^{-1}$ ) (36). We calculated the mean for each set of  $n = 23$  site-years per scenario. By subtracting the mean loss with natural enemies present from the loss in their absence, we obtained the value of biocontrol services (VBS) for that scenario. The loss  $\text{ha}^{-1}$  was multiplied by the area of soybean harvested in each state to provide a statewide estimate of VBS. The difference in VBS  $\text{ha}^{-1}$  between 2005–2006 and 2007 landscapes was used to calculate the reduced VBS in a biofuel landscape that was scaled to the state level.

**Monetary Valuation Method.** We adopted the production function approach to monetary valuation (37), which allows the value of biocontrol services to be inferred from their effects on the production of a marketed product, such as soybean. Critics of prior attempts to place monetary values on ecosystem services have highlighted the importance of focusing on marginal changes, consideration of most likely alternatives, and recognition of market price feedback effects (38, 39). For followers of the IPM strategy, the value of biocontrol services comes from both avoiding insecticide application costs and averting yield loss. For producers relying solely on biocontrol, the value of biocontrol services comes entirely from reduced yield loss. Although the relative size of these grower groups is not well known, U.S. Department of Agriculture surveys in 2005–2006 in the 4 states studied found the percentage of soybean acreage with insecticide use ranges from 4% (Wisconsin) to 56% (Minnesota), with a 2-year median of 23% (ref. 40 and <http://usda.mannlib.cornell.edu/MannUsda/viewDocumentInfo.do?documentID=1560>). In contrast, only 0.2% of U.S. soybean land is certified for organic production (ref. 41 and [www.ers.usda.gov/Data/Organic](http://www.ers.usda.gov/Data/Organic)) and hence committed to a strategy like sole reliance on biocontrol. Given the current situation, we judge the IPM scenario to be the most representative strategy for purposes of valuation of biocontrol as an ecosystem service.

The importance of market-price feedback effects is evident from the recent fluctuations in agricultural commodity prices. Soybean prices more than doubled from their recent historic levels of 1997–2006 to early 2008, when soybean futures market prices reached levels considerably higher than the 2007–2008 U.S. Department of Agriculture price projection of  $\$380 \text{ Mg}^{-1} = \$10.40 \text{ Bu}^{-1}$  (ref. 42 and <http://usda.mannlib.cornell.edu/usda/ers/OCS//2000s/2008/OCS-02-11-2008.pdf>). In response, U.S. farmers reduced corn planted area by 7% in 2008 (still the second-highest level since 1946) in favor of more soybean (2). To balance these positive and negative price feedback effects, we contrasted 2 market values for soybean, the current, biofuel-driven price (the U.S. Department of Agriculture 2007–2008 projection) and the recent past 10-year median U.S. soybean prices in 1997–2006 (ref. 42 and <http://usda.mannlib.cornell.edu/usda/ers/OCS//2000s/2008/OCS-02-11-2008.pdf>). Changes in the value of biocontrol services were also contrasted to chemical

and total operating cost for soybean producers in our region (ref. 23 and www.ers.usda.gov/Data/CostsAndReturns).

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# Supporting Information

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## SI Text

**Variability and Uncertainty in Value of Biocontrol Services.** Aphid abundance, management strategy, soybean price, and land-use change each influence the value of biocontrol services. Here, we explore the magnitude of these effects in further detail and assess relative uncertainties in outcomes.

**Aphid Abundance.** Soybean aphid abundance was high in 2005 but low in 2006, resulting in large differences in the value of biocontrol services. Using the 10-year median price for soybeans (1996–2007), the value of biocontrol service across the 4 states for soybean crops grown without pesticides was  $\$224 \pm 73 \text{ ha}^{-1}$  (mean  $\pm$  SEM) in 2005 but only  $\$19 \pm 6 \text{ ha}^{-1}$  in 2006, nearly a 12-fold difference (Table S1). This difference occurs because potential yield gains from the action of natural enemies are smaller in years of low aphid abundance. Since 2000, years of high and low aphid populations have frequently alternated, supporting our use of the mean estimates from 2005–2006 to project the value of biocontrol services to the landscape scale. If future studies determine that soybean aphid outbreaks occur with greater or lesser frequency, the overall value of biocontrol services will shift, becoming smaller with decreasing frequency of aphid outbreak.

**Management Strategy.** Under IPM and assuming the 10-year median price of soybean, the value of the ecosystem service is much lower than under biological control alone. For example, in 2005 the value of biocontrol services under IPM was  $\$23 \pm 6 \text{ ha}^{-1}$ ,  $\approx 10$ -fold less than the  $\$224 \pm 73 \text{ ha}^{-1}$  value under biocontrol alone (Table S1), because IPM producers limit the total potential for aphid damage to the crop by spraying at recommended thresholds. In 2006, when aphid populations were low, the ecosystem service value was more similar under both management strategies,  $\$24 \pm 5$  under IPM versus  $\$19 \pm 6 \text{ ha}^{-1}$  under biocontrol.

Under IPM, the variability in the value of biocontrol services between years is substantially less than under biocontrol alone. Part of the value comes from yield savings and part from a reduction in the number of required sprays. The presence of natural enemies reduced the proportion of sites requiring treatment from 100% to 70% in 2005 and from 62% to 0 in 2006. This reduction in sprays resulted in an average savings of  $\$7 \pm 4 \text{ ha}^{-1}$  (as a component of the total value of the ecosystem service) in the high aphid year of 2005 and  $\$15 \pm 3 \text{ ha}^{-1}$  in the low aphid year of 2006 when fewer sprays were required.

**Soybean Price.** The overall ecosystem service value is directly proportional to soybean price in the biocontrol scenarios where all value is caused by reduced yield loss. The 2007–2008 projected soybean price of  $\$380 \text{ Mg}^{-1}$  ( $\$10.40 \text{ bu}^{-1}$ ) is  $>80\%$  higher than the 10-year median price of  $\$210 \text{ Mg}^{-1}$  ( $\$5.60 \text{ bu}^{-1}$ ), so the calculated values of the ecosystem service are increased proportionately from  $\$224 \pm 73$  to  $\$406 \pm 132 \text{ ha}^{-1}$  in 2005 and from  $\$19 \pm 6$  to  $\$35 \pm 10 \text{ ha}^{-1}$  in 2006. The impact of increased soybean price is less than proportional in the IPM scenarios,

where a significant proportion of the value of ecosystem services is caused by saved pesticide sprays. In this scenario, the total value of the biocontrol service increased 52% to  $\$35 \pm 9 \text{ ha}^{-1}$  in 2005 and 33% to  $\$32 \pm 7 \text{ ha}^{-1}$  in 2006.

**Land Use Change.** Using 10-year median or 2007–2008 projected soybean prices, the value of biocontrol services with increased corn declined by 1.2- to 2-fold in relation to the corresponding 2005–2006 scenarios (Table S1). In the IPM scenarios under increased corn, the value of biocontrol services attributable to saved pesticide sprays was  $\$5 \pm 3 \text{ ha}^{-1}$  in 2005 and  $\$11 \pm 4 \text{ ha}^{-1}$  in 2006.

Landscapes with increased corn acreage support sharply lower biological control, but this relationship is likely to vary over space and time. Hence, we conducted a sensitivity analysis to explore the value of biocontrol services if reductions in BSI caused by increased corn acreage were only half as large on average as those that we actually observed in 2005–2006 (i.e., a slope of  $-0.65$  versus  $-1.30$  from regression of BSI versus proportion corn; Fig. 1A). The 50% lower BSI-response scenario resulted in greater values of biocontrol service, which translate into smaller declines in biocontrol services under increased corn (Table S2). The greatest difference was in the 2005 biocontrol value estimate, which was 42% higher in the lower BSI-response scenario than our base scenario, i.e.,  $\$156 \pm 51 \text{ ha}^{-1}$  versus  $\$110 \pm 32 \text{ ha}^{-1}$  for the low price and  $\$283 \pm 93 \text{ ha}^{-1}$  versus  $\$199 \pm 58 \text{ ha}^{-1}$  for the high price. Under the lower BSI-response slope scenario, all other comparisons showed smaller increases in the value of biocontrol services ranging from 7% to 30%. Thus, even relatively large variation around our original estimate of the BSI to corn area relationship does not alter our core finding that increased corn decreases biocontrol services in the surrounding landscape.

**Summary.** Estimated values of the ecosystem service of biological control can vary sharply between years as a result of differing aphid abundance ( $\approx 12$ -fold) and differing management strategies ( $\approx 10$ -fold). In contrast, price sensitivity analysis led to 1.3- to 1.8-fold differences and landscape change to 1.2- to 2-fold differences in the value of biocontrol services. A 50% more conservative estimate of the effect of increased corn on BSI led to a 7–42% increase in the value of biocontrol services under landscape change. Given these sources of uncertainty and variability, our results should not be used as fixed predictions of the exact dollar value of this ecosystem service. Rather, they should be used to inform the direction and relative magnitude of landscape change on the economic value of biological control as an ecosystem service. Despite this caveat, the significance of the regression between corn acreage and biocontrol services, coupled with the strong empirical basis of the data and assumptions used in the model framework and the established predictive power of submodels, suggest that a negative impact of increased corn acreage on biocontrol in surrounding crops is highly likely and should be considered in the development of policy regarding the production and processing of biofuels.

**Table S1. Estimated value of soybean aphid biocontrol service for 2 management strategies under years of high (2005) and low (2006) aphid abundance in 4 states (Iowa, Michigan, Minnesota, and Wisconsin)**

Management strategy	Year	N	2005–2006 landscape		Projected landscape with increased corn	
			10-year median soybean price, \$ ha <sup>-1</sup> *	2007–2008 projected price, \$ ha <sup>-1</sup> †	10-year median soybean price, \$ ha <sup>-1</sup> *	2007–2008 projected price, \$ ha <sup>-1</sup> †
Biocontrol	2005	10	224 ± 73	406 ± 132	110 ± 32	199 ± 58
	2006	13	19 ± 6	35 ± 10	15 ± 5	28 ± 9
	Overall	23	108 ± 38	196 ± 68	57 ± 17	103 ± 31
IPM	2005	10	23 ± 6	35 ± 9	18 ± 3	29 ± 5
	2006	13	24 ± 5	32 ± 7	18 ± 4	23 ± 5
	Overall	23	24 ± 4	33 ± 6	18 ± 3	25 ± 3

Values are given for historic and 2007–2008 price levels of soybean and actual 2005–2006 and biofuel-influenced landscapes.

\*1996–2007 median soybean price \$210 Mg<sup>-1</sup> = \$5.60 Bu<sup>-1</sup> (U.S. Department of Agriculture Economic Research Service).

†2007–2008 projected soybean price \$380 Mg<sup>-1</sup> = \$10.40 Bu<sup>-1</sup> (U.S. Department of Agriculture Economic Research Service).



**Table S2. Sensitivity analysis showing estimated value of biocontrol services if reductions in BSI caused by increased corn acreage was only half as large on average as those observed in 2005–2006**

Management strategy	Year	N	Value of biocontrol service (mean $\pm$ SEM)	
			10-year median soybean price, \$ ha <sup>-1</sup> *	2007–2008 projected price, \$ ha <sup>-1</sup> †
Biocontrol	2005	10	156 $\pm$ 51	283 $\pm$ 93
	2006	13	18 $\pm$ 6	32 $\pm$ 10
	Overall	23	78 $\pm$ 26	141 $\pm$ 63
IPM	2005	10	19 $\pm$ 5	31 $\pm$ 7
	2006	13	23 $\pm$ 5	29 $\pm$ 7
	Overall	23	21 $\pm$ 4	30 $\pm$ 5

Results shown for 2 management strategies under years of high (2005) and low (2006) aphid abundance.

\*1996–2007 median soybean price \$210 Mg<sup>-1</sup> = \$5.60 Bu<sup>-1</sup> (U.S. Department of Agriculture Economic Research Service).

†2007–2008 projected soybean price \$380 Mg<sup>-1</sup> = \$10.40 Bu<sup>-1</sup> (U.S. Department of Agriculture Economic Research Service).