Adoption of modern pest control systems associated with declines in butterfly abundance across Midwestern monitoring network

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Author contributions

BVD and SMS wrote the manuscript, under supervision and guidance of SMS, DAH and LR. BVD designed research, constructed final dataset, estimated models, and created figures. SMS and LR conceived research. LR curated butterfly survey data and DAH provided pesticide and seed trait survey data. All authors contributed ideas that shaped the direction of the research and edits for the final manuscript.

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Summary

Mounting evidence points to a global collapse in insect populations[1], with some of the best documented evidence among butterfly species[2]. While habitat loss, climate change, and agricultural pesticides have all been implicated[3], researchers have pointed to glyphosate herbicides and neonicotinoid insecticides specifically as potential causes of insect declines[4–6]. But the focus on individual pesticides or individual insect species or groups fails to grapple with the complex dynamics of how agricultural practices vary and correlate through time and space. By examining a comprehensive set of insecticide and herbicide classes from thousands of farm records over the years 1998-2014 and linking them with systematic butterfly abundance surveys across 60 Midwestern U.S. counties, this research disentangles correlated pesticide effects across butterfly species. For the median county in our sample, we find an 8% decline in total butterfly abundance due to changing pest control systems, with declines pronounced among forb-hosted specialist species including monarchs, for which populations declined 33.5% relative to predictions under historic pest control technologies. Neonicotinoid-treated seeds bear primary responsibility, while there appears to be no consistent negative effect from crop seed that incorporate *Bacillus thuringiensis* (*Bt*) proteins nor from glyphosate herbicide. Better public data are needed on pesticides applied to crop seed in order inform policy about environmental safety.

Introduction

Butterfly populations are in decline in the United States and globally. Total butterfly abundance in Ohio declined 33% from 1996 to 2016, a 2% decline per year[7]. The decline observed in the American Midwest conforms with the 35% global decline in the abundance of Lepidoptera, the taxonomic order including both butterflies and moths, from 1970 to 2010[2]. Declines in butterfly populations coincide with a 45% decline in insect abundance across all taxa during the same period[2]. Mounting evidence points to a risk of collapse in ecosystem services provided by insects[1], including the pollination, nutrient cycling, and aesthetic services provided by butterflies. Despite ample evidence that butterfly populations are in decline, direct evidence pointing to specific causes remains weak[8–10].

The scientific literature identifies three broad factors driving the decline of insects in general and butterflies in particular: habitat loss (i.e., land use change), climate change, and weed and insect control (hereafter, pesticide use) [1,8–10]. Loss of vegetative diversity to agricultural and urban land uses has harmed habitat and reduced floral resources for many insects[11–13]. Butterflies also require specific climate conditions during various life stages to facilitate overwintering, oviposition, development, and metamorphoses and, for some species, migration. There is growing evidence that, along with land-use, changing climate conditions are another cause of decreased butterfly populations across North America[6,14–16].

The third possible factor driving insect decline, change in agricultural pest control technology, has been hypothesized to harm butterfly populations both directly and indirectly. At least five mechanisms shape how pesticides and pest control practices more broadly might affect butterfly populations[3]. We distinguish between pest control practices targeting insects and

weeds, identify technologies which represent major shifts since the 1990s, and hypothesize how shifts between these technologies may affect butterfly abundance (Figure 1).

Insect control can be achieved via broadcast spray or via systemic toxins that are incorporated into plant tissue. Sprayed insecticides, including pyrethroids and organophosphates, are used reactively in response to detected insect infestations and pose an obvious direct threat when butterflies are exposed to spray or residues.

More recently, farmers have relied prophylactically on systemic pest control, wherein insect pests are exposed to toxins that are incorporated into crop tissue. This class of pest control includes neonicotinoid seed treatments and *Bacillus thuringiensis* (*Bt*) seed traits. Neonicotinoids are delivered into the crop tissue via chemical seed coatings from which toxins are absorbed throughout germination. *Bt* genes introduced via genetic engineering allow corn to produce insecticidal compounds directly in plant tissue.

Butterflies that feed directly on *Bt* crops in adult or caterpillar life stages could be harmed as the *Bt* toxins target lepidopteran pests. The same is true of butterflies that feed on crops treated with neonicotinoid-treated seed. Separate from exposure via crop tissue is exposure to insecticide residues (notably from neonicotinoid treated seeds) that persist in the soil and water and can contaminate the tissue of non-target plants which serve as forage or hosts for butterflies[17–19].

Weed control is most often achieved through herbicides, which are typically applied via broadcast spray on an annual basis and are not known to cause acute harm to insects. However, by killing weeds and other non-target plants near cropland, they may reduce butterfly habitat and forage resources[8,20]. The major technological shift in weed control since the 1990s has been the rise and continued dominance of glyphosate herbicides, commonly marketed as “Roundup®”. Since the introduction of corn and soybean seed genetically engineered to tolerate this broad-

spectrum herbicide, farmers have been able to rely primarily on glyphosate for their year-round weed control needs[21]. As a result, farmers have increased glyphosate use; yet after an initial period of reducing use of other herbicides, they returned to multiple herbicides targeted at specific weed species after about 2008, as more individual weed species developed resistance to glyphosate. The potential impact on butterflies of these changes is a simplification of the landscape in terms of available forage and hosts, particularly for specialist species such as monarchs[20].

Evidence is emerging that as American farmers substitute new pesticides, toxic threats to non-target insects, including bees, are increasing. By applying lab-based lethality measures to aggregate pesticide application volume data, DiBartolomeis et al. find a 48-fold increase in the average oral insect toxicity to bees of insecticides used in the United States from 1992 to 2014, driven largely by the large increase in the use of neonicotinoids[28]; Douglas et al. find a more conservative 9-fold increase through a similar analysis over the 1997 to 2012 period[29]. Perry and Moschini observe a decrease in ambient insecticide toxicity to bees between 1998 and 2006 as farmers replaced sprayed insecticides by *Bt* seed varieties, followed by a rise in acute bee toxicity as they adopted neonicotinoid-treated seed[25]. While these studies rely on lab-based measures of neonicotinoid toxicity to honeybees, field studies have found that neonicotinoid seed treatments in flowering crops are associated with detrimental effects on wild bee populations as well[30].

Prior empirical studies on the relationship between butterfly populations and pest control have generally examined the effects of a single pesticide active ingredient group at a time[9]. Saunders et al. find evidence of a negative association between glyphosate use and monarch abundance in areas of Illinois with heavily concentrated agriculture between 1994 to 2003[5].

Zylstra et al. find a negative relationship between glyphosate use and monarch abundance across the Midwest, although they find that summer and spring climate factors have considerably more relative influence[6]. Forister et al. find a negative association between neonicotinoid use and butterfly abundance in Northern California since neonicotinoid pesticides were first approved in 1995[4]. Gilburn et al. find a similar negative association between neonicotinoid use and butterfly abundance in the United Kingdom[22].

None of these studies account for trends in other pesticides, often citing data limitations. In the only study to our knowledge to directly link survey-based butterfly abundance and pest control use data for multiple technologies, Crone et al. use a partial-least squares approach that identifies glyphosate and neonicotinoid adoption as the primary drivers of western monarch decline in California, though whether these results are generalizable to other species or in other geographies remains an outstanding question[31].

Analyses of insect declines that focus on a single active ingredient can be misleading if they omit other correlated drivers of decline for two reasons. In the United States during 2004-12, corn and soybean farmers rapidly adopted glyphosate, *Bt* genetics, and neonicotinoid-treated seeds while use of other pest control technologies declined due to substitution effects[23,24]. As multiple pesticides may affect insect declines by one or more channels, each of these variables must be included if an analysis is to avoid omitted variable bias[25–27] or be useful for forecasting the potential impacts of pesticide regulations.

This research disentangles substitution effects behind how agricultural pesticides affect butterfly populations by exploiting a 17-year panel data across 60 counties of the U.S. Midwest. By modelling butterfly populations explicitly as a function of pesticide application measures, while controlling for weather and habitat, we capture effects of pesticides on abundance through

multiple mechanisms. Our models further allow comparison of impact size and direction between substitutes within widely recognized classes of pest control technologies. Finally, through a counter-factual analysis, our models are used to compare predicted annual butterfly abundance under observed pesticide-use trends compared with conditions in 1998, the difference between which we define as a "Net Pest Control Effect" on butterfly abundance.

Butterfly abundance data take the form of hourly counts by county-year during June, July, and August using citizen science observations from programs that are part of the North American Butterfly Monitoring Network, a loose network of formal survey programs run by multiple independent entities. To better understand how pesticide effects may vary by species, we apply our analysis to 15 common, easily identified species, total abundance of all identified butterflies, and species richness. We focus our discussion here on four species whose behavior affects their likely risk of pesticide exposure: monarch (*Danaus plexippus*) (migratory, grassland and disturbed area specialist feeders), silver-spotted skipper (*Epargyreus clarus*) (local and disturbed area grassland generalists that will feed on soybean), little wood satyr (*Megisto cymela*) (local, undisturbed grassland generalist feeder) and cabbage white (*Pieris rapae*) (local, an invasive, common grassland generalist feeder). Figure 2A shows evolving abundance of each focal species, as well as across all species and the number of distinct species observed in the 60 counties during 1998-2014. In addition to analysis for these four focal species, we present parallel results for 11 other species in the Supplementary Material.

We calculate county-level pest control use as area-treatments from detailed application data from corn and soybean farmers (details in Methods). Among the many distinct pest control practices that farmers apply, we categorize these into three classes with distinct modes of exposure and potential mechanisms of impact to butterflies: herbicides, reactive insect control,

and prophylactic insect control (Figure 1). Weed control is divided between glyphosate and non-glyphosate herbicides, due to the prevalence of glyphosate-based weed management systems and prior reports that it affects butterfly abundance[20]. Reactive insect control is comprised of pyrethroids and organophosphates, the two dominant sprayed insecticides by U.S. corn and soybean growers. Prophylactic insect control includes neonicotinoid-treated and *Bt*-traited seeds.

We measure each pest control product class as area-treatments, defined as the annual number of treatments applied across a county's land area. We use field-level survey data from farmers across the Midwest to estimate the annual number of applications on the average planted acre of soybean and corn at the U.S. Crop Reporting Districts (CRDs) level and link this measure to county-level cropland land cover data to derive an annual county-level area-treatment metric. The area-treatment measure based on broad practice classes is consistent with recent empirical results on patterns of substitution and complementarity in pest control markets [24,32,33], allowing deeper insights into how changes in pesticide markets or policy might affect the overall threat to specific insect populations.

The 1998-2014 analysis period includes important trends of rising adoption of glyphosate-tolerant and *Bt*-traited crop seed, introduction and rapid adoption of neonicotinoid-treated crop seed, and decline followed by increase in non-glyphosate herbicide use (Figure 2B). The specific timing of adoption and disadoption of these practices varies over our study region, allowing us to tease apart the differential impacts on butterfly populations. While the long timeframe and large-spatial scale with county-level grain allow us to tease apart the effects of different pest control practices, it is important to note that our analysis period is limited to years for which comprehensive pest control data is available. Because of changes in the data collection methods for these data, analysis beyond 2014 is not possible[34].

Other variables that drive butterfly abundance include spatiotemporal measures of weather and land cover. Daily weather data from the NASA Daymet spatial grid includes accumulated precipitation (mm) and temperature as summarized by growing degree days (GDDs), a thermal metric tied to insect growth[35]. Each is divided into three seasons, early (March-April), mid (May-June) and late (July-August), for six weather variables in total. For land cover, we create pooled measures of cropland, forest, and urban land cover in the counties where we have butterfly abundance data (Figure 2C) by calculating the proportion of each within county borders from the latest available version of the National Land Cover Database (NLCD), leaving all other land covers, primarily pasture and unmanaged grassland, as the baseline.

Results

Neonicotinoid insecticides are strongly associated with the decline of monarch and silver-spotted skipper butterfly species, as well as general butterfly species diversity. A one standard deviation increase in neonicotinoid seed treatment area-treatments is associated with 22% and 25% lower county-wide abundance for monarchs and silver-spotted skippers respectively, and 7% fewer distinct species observed (Figure 3). The negative binomial regression models, estimated with county and year fixed effects to account for unobserved variation, explain 68% to 82% of data variation (measured as adjusted R^2), indicating a good statistical fit (full parameter estimates for focal species, aggregate counts, and 11 additional species available in Supplementary Tables S1-3).

No insecticide groups other than neonicotinoids show a significant negative effect on butterfly populations. Indeed, *Bt*-traited seed is associated with higher abundances of silver-spotted skipper and little wood satyr and slightly higher numbers of monarchs (Figure 3).

Glyphosate herbicide use shows no harm to any of the four focal butterfly species or to total abundance and is positively associated with overall butterfly species diversity (Figure 3). Other non-glyphosate herbicides are associated with higher abundances of silver-spotted skipper and cabbage white butterflies but reduced species diversity (Figure 3).

Changes in land cover are also associated with changes in butterfly abundance. In counties where forest or cropland expanded relative to grassland, our models indicate reduced abundance of silver-spotted skippers and little wood satyrs, both of which rely on grassland habitat. In counties where forestland expanded during the study period, marginal increases in the number of distinct butterfly species are observed. Cropland expansion is marginally associated with higher observed numbers of monarchs (Figure 3).

Weather variables are also associated with butterfly abundance. Warmer early springs (measured by GDD in March-April) are associated with reduced total annual abundance. Warmer May-June months are associated with reduced monarch numbers, but not those of other species, while warmer July-August months are linked with higher counts of cabbage whites and overall butterfly species diversity. Rainfall has strongest effects in May-June, when increased rainfall is positively associated with monarch numbers but negatively linked with total butterfly abundance, as well as numbers of silver-spotted skippers and little wood satyrs (Figure 3).

The dynamic effects of evolving pesticide use are captured by calculating the Net Pest Control Effect: the difference in model predictions of butterfly abundance (or number of distinct species) between observed pesticide use patterns and a counter-factual where the pesticide use patterns of 1998 are continued through 2014. Changes in pesticide use were associated with reduced total butterfly abundance in every one of the 60 counties in our sample by 2014, with total butterfly abundance declining nearly 8% in the median county, including major declines in

the abundance of monarchs (34%), silver spotted skippers (36%), and cabbage whites (18%) (Figure 4). These three species are among the most affected by agricultural pesticides among the 15 species examined, likely because all three frequent disturbed grassland habitats such as those near agricultural fields.

The dynamics of the Net Pest Control Effect for these three focal species varies by habitat use. As systemic, prophylactic neonicotinoid seed treatments became standard for insect control, the change particularly affected butterfly species that prefer disturbed habitats (e.g., monarchs and silver-spotted skippers). In contrast, the shift away from sprayed insecticides, which can drift to nearby habitat, to prophylactic systemics has alleviated toxic risks to species like little wood satyrs that most often reside in undisturbed grassland near forest (Figure 4).

Changing weed control, chiefly the run-up in glyphosate herbicide use prior to reaching a plateau in 2008, has harmed silver spotted skippers and cabbage whites, generalist feeders in disturbed cropland areas. Monarchs, who are specialist feeders, show no evidence of harm from changes in herbicide use; similarly, we find no evidence of linkages between changing agricultural weed control and little wood satyr abundance (Figure 4).

Discussion

The results from this 17-year analysis of how farm-level U.S. agricultural pest control practices affect butterfly abundance highlight the harmful effects of neonicotinoid insecticides, particularly as contrasted with the negligible evidence of negative effects of glyphosate herbicide and other insecticides.

The harmful effect of neonicotinoid seed treatments on butterfly abundance generally, as well as on monarchs and silver spotted skippers specifically, is broadly consistent with previous

studies that examined neonicotinoids without accounting for trends in other pesticide groups [4,22]. We find that this result for butterflies persists even when other pesticides are accounted for. The greater rates of decline among butterfly species that prefer forbs and disturbed habitats (Figure 4) are consistent with greater exposure to neonicotinoids, as is the lack of neonicotinoid effect on little wood satyrs, which occupy undisturbed grassland habitat often further from where neonicotinoid treated seeds are planted. The connection between declining butterfly abundance and neonicotinoids use conforms with the geometric increase in acute insecticide toxic loading faced by honeybees that has also been linked with rising neonicotinoid use during 2004-14 [28,29]. Neonicotinoids are also implicated in the decline of grassland birds[36,37]; if our results are generalizable to other insects, then the neonicotinoid-induced decline in insect prey may be a channel through which this observed bird decline occurs.

The harmful effect of neonicotinoids contrasts with the largely benign effects of sprayed insecticides and farmers' other systemic pesticide option: *Bt* seed. *Bt* seed use is associated with greater abundance of silver spotted skippers and little wood satyrs. Although *Bacillus thuringiensis* is toxic to butterflies, direct feeding on *Bt* crops is the most obvious mechanism of potential exposure; unlike neonicotinoid dust from seed treatments which has been found in non-crop settings in adjacent habitat[17]. Otherwise, *Bt* seed adoption is linked to sharp reductions in the use of sprayed insecticides[24,38,]. Although any quantity substitution of *Bt* seed for sprayed insecticides would likely be identified statistically in this analysis, it is possible that *Bt* seed shifts the timing of insecticide spraying so that it reduces butterfly exposure, as the protection *Bt* provides allows planting crops earlier in the growing season[39]. The key result is that *Bt* seed adoption lacks the harmful effect on butterflies that is associated with neonicotinoids, farmers'

primary systemic insect control alternative, suggesting ecological value in promoting its use and protecting its efficacy from evolved resistance in target pests[40].

We fail to detect a noticeable glyphosate herbicide effect on butterfly abundance, a finding somewhat at odds with several previous lines of research that focused on glyphosate without accounting for other pesticides. Focusing on the role of milkweed as monarchs' preferred breeding habitat, Pleasants and Oberhauser linked the decline in numbers of monarchs overwintering in Mexico during 1999-2010 to decline in milkweed in the U.S. Midwest during a period of rising glyphosate use[20]. Haan and Landis report that monarchs prefer to lay eggs on milkweed plants in disturbed crop fields, where glyphosate may have made milkweed plants scarcer[12]. Saunders et al. find a negative relationship between county-level glyphosate purchases and site-level monarch abundance during 1994-2003, after which monarch numbers levelled off[5].

In focusing on the role of glyphosate while omitting consideration of other pesticides, these studies may have missed potential effects from similar trends occurring in the broader pesticide market, including the rise of neonicotinoid treated and *Bt* traited crop seeds, the reduced levels of sprayed insecticides, and the fall and subsequent resurgence in non-glyphosate herbicide use (Figure 2B). Omitting correlated causal variables from a regression analysis can bias the estimated effect of an included variable[25,26]. The omission of pesticides other than glyphosate limits the policy usefulness of previous studies that fail to capture the relevant range of pesticides farmers may elect to use. Such previous empirical findings may have mistakenly attributed negative pesticide effects on butterfly abundance to glyphosate when unobserved trends in neonicotinoid seed treatment are instead responsible. Such misattributions may lead to unrealistically high expectations for the prospects of regulatory measures to improve biodiversity, such as restrictions or taxes on specific chemicals. In contrast, this study jointly

accounts for the main trends in commercialized pest control technologies over the previous two decades, avoiding these concerns.

The direction and magnitude of the net pesticide effects we estimate fit with observed declines in the abundance of Midwestern butterfly populations reported elsewhere. Total butterfly abundance estimates in Ohio declined 33% from 1996 to 2016 [7]. In comparison, our findings of an 8% decline in total abundance attributable to changes in pest control practices suggest that agricultural pesticide use accounts for about a quarter of the total decline in abundance over the same period. Because our effect size is considerably smaller than the overall observed decline, our study supports previous research suggesting that recent declines of insect fauna are multicausal. Just as our methods allow a decomposition of the effects of multiple pest control technologies over time, future research can extend these techniques to other potential drivers of decline such as climate and land cover in order to identify which and where certain drivers are more or less dominate.

The strength of this study lies in linking of detailed, farm-level pesticide records with systematic observation of butterfly abundance by species across 60 counties of the U.S. Midwest and 17 years. Covering a period of rapid technological change in pesticides and crop genetics, the study offers deeper scrutiny of pesticide by species effects than has heretofore been possible. We also note that our study period ends in 2014 because the data provider, which also provides the raw data underlying USGS estimates, ceased to collect survey data on pesticidal seed treatments in that year, citing concerns over respondent knowledge of the technologies used. A recent follow-up survey conducted by USDA finds that farmers are generally knowledgeable about the products applied to their seed, particularly for insecticides[34]. Our results highlight an

urgent need for reliable, consistently reported, and publicly available pesticide use data, particularly for neonicotinoid seed treatments.

As is often the case when linking datasets that were gathered for different purposes, the county-level data matching is imperfect. The farm input data were sampled to be statistically representative only at the multi-county level of a U.S. Crop Reporting District, and the butterfly surveys are available based largely on citizen scientist willingness to make voluntary observations. Capable, willing butterfly enthusiasts are not randomly distributed across the landscape; instead, they cluster in population centers as people do generally. To capture local level effects of agricultural inputs on butterfly populations, an ideal designed study would observe over space and time both agricultural input use and nearby butterfly abundance. Such detail would, in turn, strengthen the ability to distinguish between local habitat, weather, and management effects.

Methods

Data construction

We bring together data from several sources to construct a unique panel dataset. The unit of observation is a county-year: the base geographic unit in the panel is a county and the base temporal unit is a year. The panel includes observations from 60 counties and 17 years (1998-2014). The annual number of monitored counties ranges from 15 to 37 based on data availability.

Butterfly abundance data

For butterfly abundance, we use county-year aggregates of monitoring surveys conducted by four volunteer programs associated with the North American Butterfly Monitoring Network.

Both the Illinois Butterfly Monitoring Network and the Ohio Lepidopterists provide data throughout the period of study, while the Iowa Butterfly Survey Network and Michigan Butterfly Network provide data beginning in 2006 and 2011, respectively. At approximately weekly to bi-weekly intervals during the months in which butterflies are active, citizen-scientist volunteers travelled along a fixed path, counting individuals by species within a 5-meter buffer of the path[41]. Subsets of these data have been previously analyzed to assess overall butterfly population trends in Ohio[7,42] and Monarch population trends in Illinois[5,43].

Each butterfly monitoring network makes use of methods known as Pollard surveys[44]. Routes are designed by volunteers in coordination with network coordinators to (a) transect a variety of habitat types, (b) follow existing pathways so as not to disturb habitat, (c) be easily located by other volunteers, and (d) take between 30 minutes to two hours to complete. For each route, a single volunteer walks at a consistent pace along routes with most programs suggesting a minimum of six visits per year during the months of June and, July, and August, with additional runs during these months or others if possible. Runs are conducted between 10:00am and 3:30pm on days with (a) less than 50% cloud cover and (b) light to moderate winds. During the run, the volunteer records all individuals by species sighted within roughly 20 feet to each side of the route. Volunteers are instructed to include only species-level identifications when they are certain and not to guess.

Counts by species and in total (across all individuals identified to the species level) are summed across surveys conducted during June through August for each county-year and then offset by the total survey time for each route. To better understand how pesticide effects may vary by species, we consider four specific butterfly species: monarchs (*Danaus plexippus*), silver-spotted skippers (*Epargyreus clarus*), cabbage whites (*Pieris rapae*), and little wood satyr

(*Megisto cymela*). These species are selected for specific examination because they are all consistently observed throughout the study region and timeframe while representing a range of life histories and functional traits. We expand our analysis to a total of 15 distinct species for the purpose of comparing pesticide effects across a wider range of life histories and functional traits.

Pesticide Use Data

We purchased pesticide application data collected via paid phone interviews by Kynetec USA, Inc., a market research company. These data were collected via computer-assisted telephone interviews of soybean and corn growers. Lists of eligible growers were constructed from lists of growers who receive federal payments, membership lists of state and national growers' associations, and subscription lists to agricultural periodicals. Sampling lists were constructed to ensure representativeness of applications at the level of the crop reporting district (CRD), USDA-designated groupings of counties in each state with similar geography, climate, and cropping practices. Non-respondents were recontacted at least eight times to reduce non-response error. Respondents were asked to detail their field-level pesticide, tillage, and seed choices during the previous growing season. Respondents were compensated monetarily upon survey completion, and responses were crosschecked against realistic application rates and consistency with other reported practices.

Pesticide use is measured in county-level area-treatments for each pesticide group. Area-treatments are defined as the average number of times a pesticide within a group is applied over a defined region (e.g., a field or a county) in a season[45]. Area-treatment measures are preferred over volumetric measures because their construction accounts for sometimes dramatic differences in application rates between different products[38,45]. By accounting for both the

geographic extent and frequency of application, area-treatments better capture the degree to which a population may have been exposed to a particular chemical.

In precise terms, area-treatments are calculated for each pesticide group as the sum of soybean and corn acres treated on respondent farms within each CRD, divided by the total planted acres of soybean and corn in each CRD for each year. To capture county-level variation in exposure potential, we multiply the CRD-scale field-level area-treatments by the percent of land area identified as planted/cultivated land cover in the National Land Cover Database (NLCD). The resulting product is a county-scale county-level annual area-treatment measure for each pesticide group of interest.

Farmers apply hundreds of distinct pesticide products to soybeans and corn. To simplify our analysis, we identify six groups of pesticides, divided into three classes, that together represent the majority and diversity of pesticide use on these crops. The first class is herbicides, represented by glyphosate and non-glyphosate herbicides. The second class is sprayed insecticides, which is comprised of pyrethroids and organophosphates. The final class is systemic insecticides, which includes neonicotinoids and *Bt* traited seed. We distinguish among three groups of pesticides: herbicides, sprayed insecticides, and systemic insecticides.

Glyphosate and non-glyphosate herbicides represent farmer use of herbicides. Our glyphosate variable measures all applications of herbicides containing glyphosate as an active ingredient, while non-glyphosate herbicides measure all other herbicide applications. Glyphosate is a broad-spectrum herbicide for which soybean and corn seed with genetically engineered resistance has been available since the late 1990s. Such seed increased the flexibility of glyphosate, allowing season-wide protection from any weed. Through the early period of our sample, glyphosate use rose while non-glyphosate use fell as farmers adopted glyphosate-

resistant soybean and corn seed. Since 2008, non-glyphosate herbicide use has risen, driven by responses to the spread of glyphosate-resistant weeds[32].

Pyrethroids and organophosphates constitute the two representative reactive insect control technologies. These pesticides represent the two primary sprayed insecticide groups used to control insect pests in corn and soybean[46]. Organophosphate use has declined since 2005 as neonicotinoid seed treatments and *Bt* traited seed has spread, while pyrethroid use has remained steady on average.

The final two pest control groups, neonicotinoids and *Bt* traited seed, represent the systemic insect controls available to farmers. Systemic insecticides remain present in crop tissue for many weeks post application. When pests feed on crops protected with systemic insecticides, they consume compounds toxic to insects. *Bt* traited seed is genetically modified to produce insecticidal proteins. Such seed has been available only in corn since 1996 and is targeted to European corn borer and, since 2003, corn rootworm and earworm. We observe increasing adoption over the period of our study. Neonicotinoids are most frequently applied via seed treatments in the form of an insecticidal dust coating on corn or soybean seed that is taken up by plant tissue as the crop develops. When neonicotinoids are present in plant tissue, they provide protection from a broad-spectrum of insect pests. Their use has grown dramatically since their introduction in 2004 in response to the appearance of soybean aphid and demand for additional systemic insecticides to supplement *Bt* traited corn, whose target insects were quickly evolving to resist[18].

Land Cover Data

We measure land cover at the county-level as the proportion of land within each county under three land cover groups: forest, urban, and cropland. We use county-level pixel counts from the USGS National Land Cover Database, which classifies the entire land area of the conterminous United States into one of several land cover classes at 30m resolution. The database is published for six calendar years over the course of our panel: 2001, 2004, 2006, 2008, 2011, and 2013. For years when the NLCD was not published, we assign the value from the nearest available year using a rolling join, assigning the value the nearest available year.

Weather Data

Local weather patterns have been previously shown to affect butterfly distributions, abundances, and the timing of life history stages, although the strength of such associations varies by species and land cover[5,13,42,43,47]. To control for potential weather effects on annual butterfly abundance, we generate county-level measures of precipitation and temperature that capture variation between years and within seasons.

Daily weather data were gathered from NASA Daymet, a 1km x 1km spatial grid of daily weather conditions using data from a network of weather stations[35]. To aggregate to the county-level, we average daily Daymet data over a rectangle centered at each county's centroid. Temperature is measured in growing degree days (GDDs), which measures the number of degrees Celsius within a range in which butterflies can develop (11.5°C to 33°C)[42]. Precipitation is measured in millimeters. We partition each season into three intervals: early (March and April), mid (May and June), and late (July and August) season. Daily accumulation of precipitation and GDD are summed over each interval. The resulting variables measure accumulated precipitation and GDDs for each county during each interval for each year.

Count models

We develop a negative binomial regression model to estimate expected butterfly counts, for each species-of-interest and in aggregate, in each county-year. For county i located in CRD $c(i)$ in year t, we treat the observed butterfly count (y_{it}) as a negative binomial random variable with covariates on the log-link scale.

$$\log(y_{it}) = \beta_0 + \boldsymbol{\beta_P} \cdot \boldsymbol{pest_{it}} + \boldsymbol{\beta_W} \cdot \boldsymbol{weather_{it}} + \boldsymbol{\beta_l} \cdot \boldsymbol{landcover_{it}} + \boldsymbol{\beta_i} + \boldsymbol{\beta_t} + \log(minutes_{it}) \qquad (1)$$

For covariates, we include the vector of weather variables ($\boldsymbol{weather_{it}}$), land cover ($\boldsymbol{landcover_{it}}$), and the vector of pest control group area-treatments ($\boldsymbol{pest_{it}}$). We also include vectors of fixed effects for county ($\boldsymbol{\beta_i}$) and year ($\boldsymbol{\beta_t}$) to control for unmeasured temporally invariant factors within each county and spatially invariant factors within each year[26]. Finally, we control for changes in sampling by including the summed duration of all surveys measured in minutes ($minutes_{it}$) as an offset. As a result, the exponentiated dependent variable can be interpreted as the rate of butterflies counted per minute.

We obtain quasi-maximum likelihood coefficient estimates via R 4.0.5[48]. We compute standard errors robust to violations of the assumed specific relationship between the conditional mean and the conditional variance specified by the negative binomial distribution[26]. We assess model fits via McFadden's pseudo R-squared. We use our robust standard errors[49] to perform z-tests ($\alpha = 0.05$) against the null hypotheses that each coefficient is equal to zero, and to compute confidence intervals for parameter estimates.

Pesticide, Weather, and Land Cover Effects by Group

To compare the strengths of the associations between weather, land cover, and pest control variables and species counts, we transform our coefficient estimates and associated confidence intervals into standardized incidence rate ratios. For each variable, we compute the mean of the interannual standard deviation across counties, representing the typical variation observed for a given observation over the period of the panel. The product of this value and the associated coefficient is exponentiated to compute the standardized incidence rate ratio, which can be interpreted as the ratio of expected butterfly counts for two observations separated by a standard deviation change in the given variable but otherwise equal.

Note that when land cover variables, measured as proportions, are included in multivariate regression, the implicit baseline land cover category is the average of all land cover categories not explicitly included in the regression. For the counties included in our sample, land cover categories not accounted for by our three groups are mainly natural open spaces such as prairie, grassland, or pasture. Therefore, effects should be interpreted in comparison to a county where such land covers are more or less dominant.

Net Pest Control Effects

To estimate the cumulative impact of all changes in pest control over the course the study period, we compare predictions in expected values between two pest control use scenarios for each county-year observation in our panel. We compute the difference between predicted population values computed using observed pesticide values ($\hat{y}_{it}$) and predictions computed using pest control values observed for each county in 1998 ($\hat{y}_{it}^{98}$), the first year of the period of study. With $f(\cdot)$ as the exponentiated right-hand side of Equation (1), $\boldsymbol{x_{it}}$ as a vector of all

covariates other than $\boldsymbol{pest_{it}}$, and $\widehat{\boldsymbol{\beta}}$ as the vector of estimated coefficients, these predicted values are calculated as:

$$\hat{y}_{it} = f(\boldsymbol{pest_{it}}, \boldsymbol{x_{it}};\ \widehat{\boldsymbol{\beta}}); \text{ and} \qquad (2)$$

$$\hat{y}_{it}^{98} = f(\boldsymbol{pest_{i,t=1998}}, \boldsymbol{x_{it}};\ \widehat{\boldsymbol{\beta}}). \qquad (3)$$

This difference is divided by $\hat{y}_{it}^{98}$ to compute proportional change:

$$\frac{\hat{y}_{it} - \hat{y}_{it}^{98}}{\hat{y}_{it}^{98}}. \qquad (4)$$

This metric is computed for all 15 observed species, the total across all species, and the count of distinct species. We further distinguish between insect control and weed control effects by holding only specific pest control classes at their 1998 values during calculations. We compute the median net pest control effect across counties for each species in each year to observe trends over time.

Data and code availability

Kynetec data are proprietary; all code and remaining data are available in the attached repository.

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Competing interests

The authors declare no competing interests.

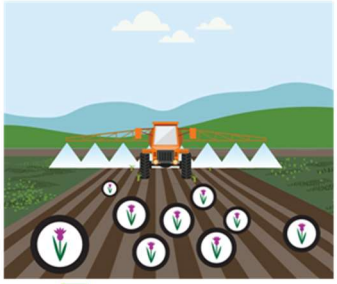
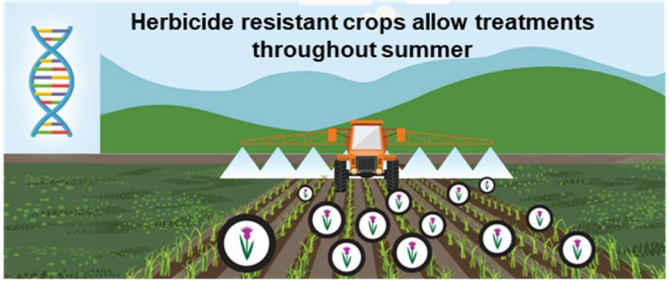
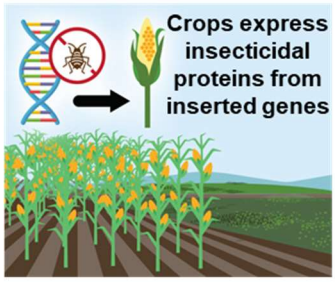
	Pre-1995 Technologies	Post-1995 Technologies	
Weed Control			
Representative Product(s)	Non-Glyphosate (various products)	Glyphosate (with resistant crops)	
Target Spectrum	Low – single weed class only	High – broad spectrum; nearly all plant species affected	
Within Season Frequency	High – before & after crop emergence	Low – mainly post-emergence	
Hypothesized Impact	Low	Low (High for certain specialist species)	
Insect Control			
Representative Product(s)	Pyrethroids Organophosphates	Bt-Traited Seed (Corn only)	Neonicotinoids
Spatial Spillover	High – broadcast spray	Low – in crop tissue only	Moderate to High – can wash off coats into environment
Between Season Frequency	Lowest – in response to pest outbreaks (reactive)	High – every year (prophylactic)	High – every year (prophylactic)
Persistence	Low	Low	High
Hypothesized Impact	Low	Low	High

Figure 1: Evolution of pest control technology in North American corn and soybean production.

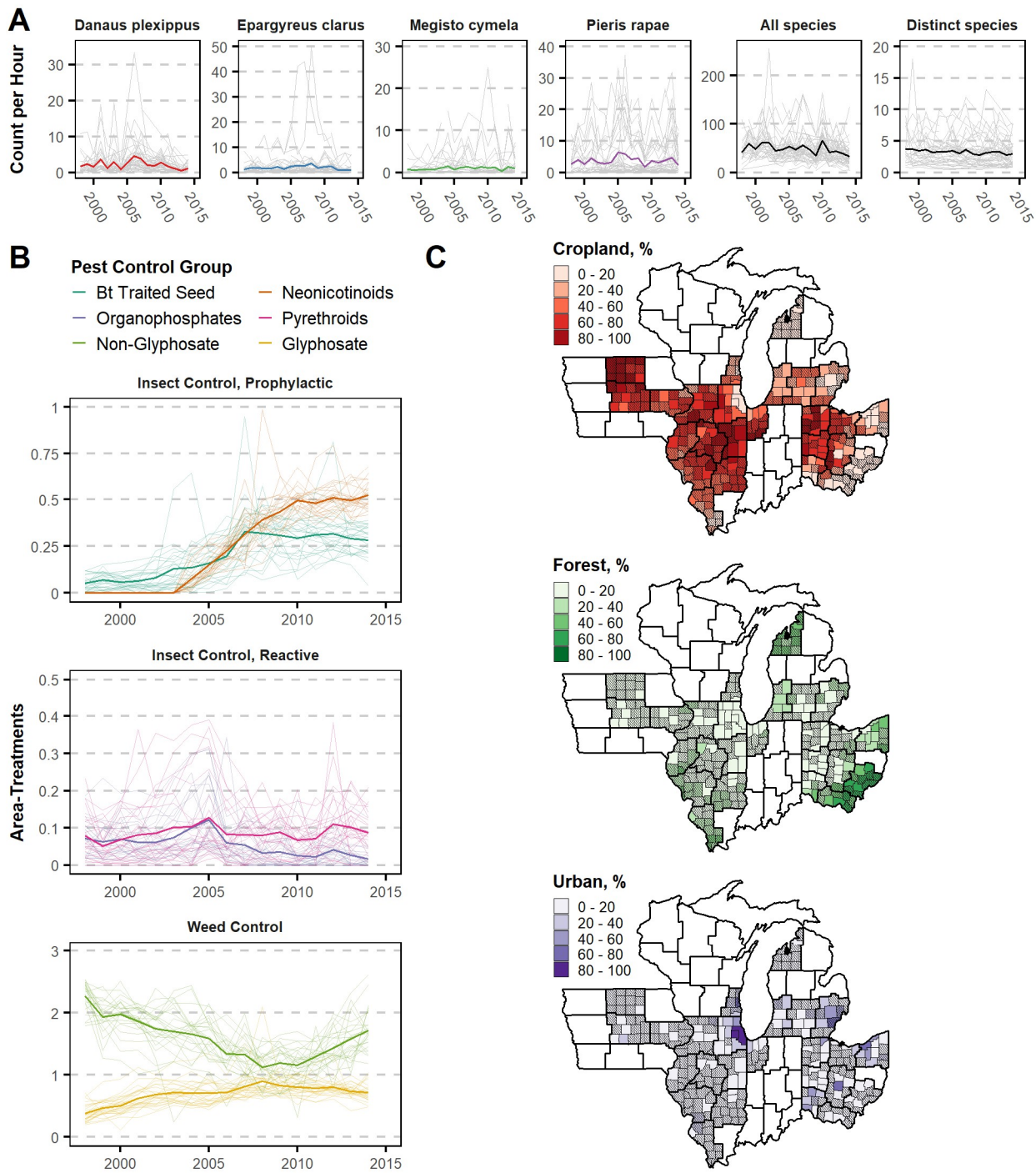


Figure 2: Data summaries for key variables. (A) shows incidence rates over time for four focal species, across all species, and for distinct species over time; smaller lines show county-level rates while bold lines show annual mean incidence rates across counties. (B) shows area-treatments over time for each pest control technology group; smaller lines show CRD-level rates while bold lines show annual mean area-treatments across CRDs. (C) shows land cover by county as percent of total land area in 2014; bold borders indicate CRD boundaries while hatching shows counties not included in analysis due to lack of butterfly survey data availability.

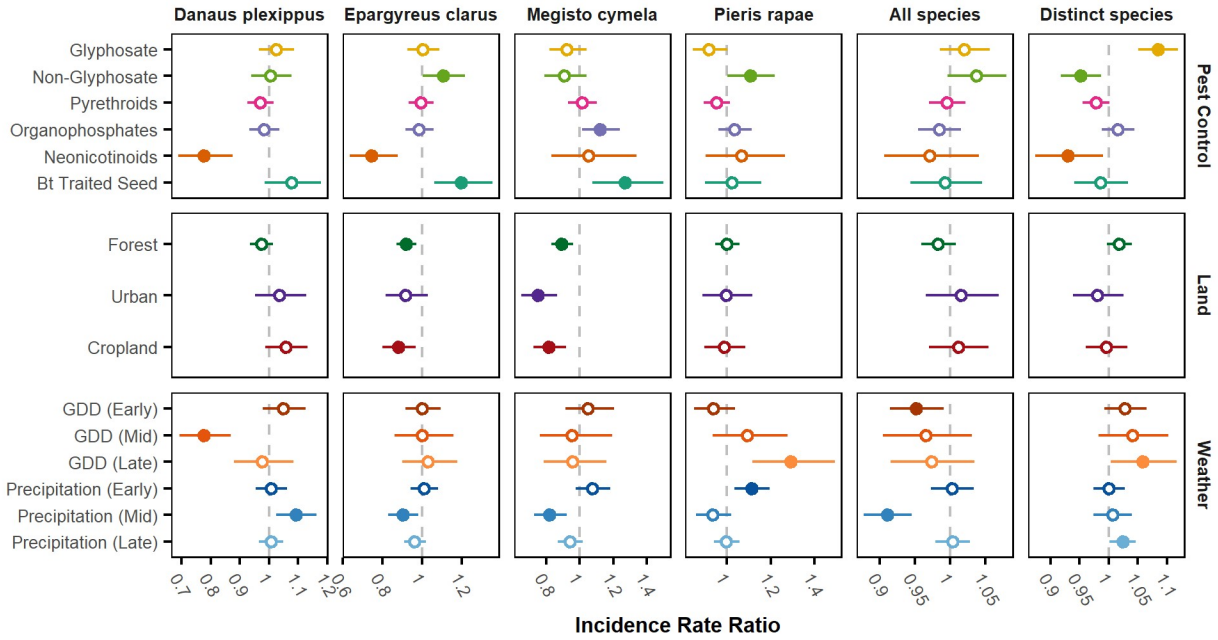


Figure 3: Incidence rate ratios (IRRs) for a standard deviation change in explanatory variables. IRRs are derived from negative binomial estimates by exponentiating the product of each coefficient and the mean of the interannual standard deviation of the associated variable for each county in the sample. For land use, categories are compared to an "open space" baseline. Lines show 95% confidence intervals based on heteroskedasticity-consistent standard errors (HC1). Solid points show statistically significant point estimates at the 95% level.

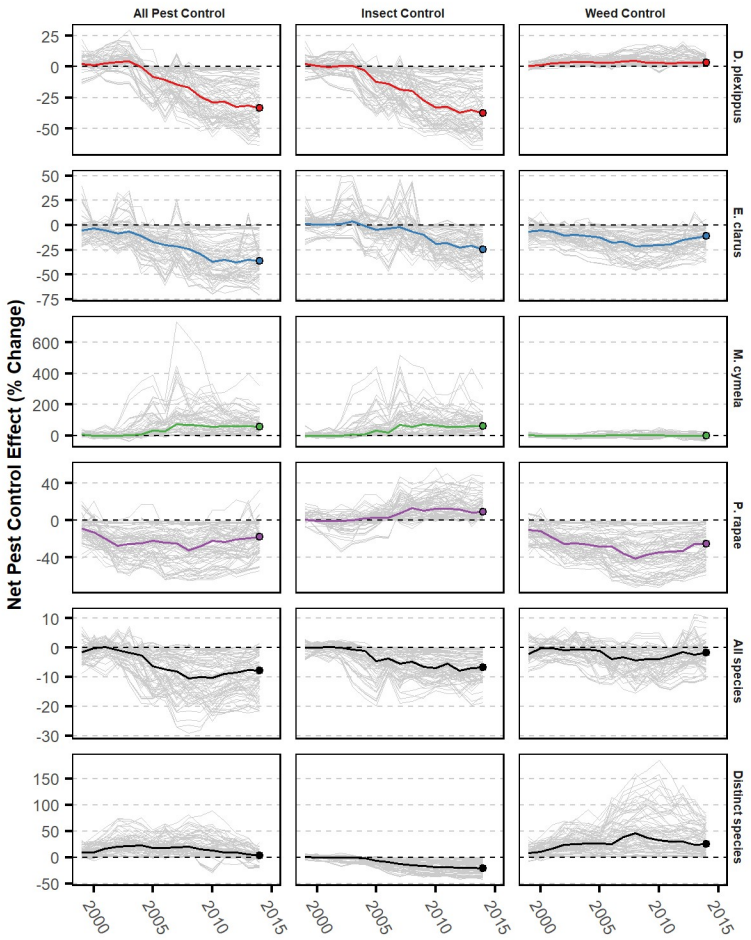


Figure 4: Net effect of pest control system change over time. Net pest control effect is the percent change between predicted incidence rates under observed pest control adoption and synthetic counties where pest control adoption is frozen at their 1998 levels. County-level net pest control effect over time are shown in grey lines and annual median net pest control effect in black lines; columns show effects computed holding all pest control, insect control, and weed control variables, respectively, at 1998 levels.

Supplementary tables

Table S1: Regression summaries.

Term	All species	Distinct species	Danaus plexippus	Epargyreus clarus	Megisto cymela	Pieris rapae
Intercept	-2.3	-2.12	-18.4	33.4*	73***	-0.704
	(9.05)	(9.21)	(12.5)	(17.8)	(24.4)	(20.1)
Glyphosate area-treatments	0.285	1.16***	0.339	0.0548	-1.13	-1.21
	(0.397)	(0.297)	(0.616)	(0.846)	(1.17)	(0.936)
Non-glyphosate area-treatments	0.205	-0.278*	0.033	0.557	-0.545	0.567
	(0.2)	(0.145)	(0.271)	(0.37)	(0.535)	(0.363)
Pyrethroid area-treatments	-0.177	-0.825	-1.16	-0.29	0.493	-1.91
	(0.721)	(0.627)	(1.25)	(1.7)	(1.87)	(1.76)
Organophosphate area-treatments	-0.752	0.757	-0.834	-0.775	5.48*	1.64
	(1.22)	(0.857)	(1.67)	(2.26)	(2.94)	(2.37)
Neonicotinoid area-treatments	-0.29	-0.714*	-2.51***	-2.9**	0.527	0.648
	(0.628)	(0.411)	(0.871)	(1.18)	(1.58)	(1.04)
Bt seed area-treatments	-0.133	-0.257	1.4	3.35**	4.47**	0.391
	(0.728)	(0.544)	(1.23)	(1.68)	(1.92)	(1.53)
Forest land cover	-11.6	12.3	-18.3	-56.9**	-75.6***	-0.0977
	(9.79)	(9.29)	(14.7)	(22.9)	(27.4)	(21.4)
Urban land cover	3.13	-3.93	7.33	-18.2	-58.4***	-0.902
	(6.44)	(6.82)	(9.4)	(16)	(16.9)	(14.8)
Cropland land cover	4.47	-1.53	21.9	-50.9**	-79.8***	-5.61
	(10.6)	(10.7)	(14.5)	(24.4)	(26.5)	(23.6)
GDD (Early)	-0.00127*	0.000718	0.00124	0.0000222	0.00127	-0.00168
	(0.000772)	(0.000639)	(0.00127)	(0.00163)	(0.0023)	(0.00186)
GDD (Mid)	-0.000394	0.000454	-0.00286***	-0.0000207	-0.00052	0.000995
	(0.000487)	(0.00043)	(0.000897)	(0.00104)	(0.00142)	(0.00107)
GDD (Late)	-0.000345	0.000729*	-0.000297	0.000352	-0.000575	0.00326**
	(0.000551)	(0.000432)	(0.00098)	(0.00116)	(0.00168)	(0.0014)
Precipitation (Early)	0.000042	0.0000147	0.00012	0.000142	0.00126	0.00186**
	(0.000353)	(0.000303)	(0.000617)	(0.000803)	(0.00123)	(0.000863)
Precipitation (Mid)	-0.00116***	0.0000815	0.00111**	-0.00129	-0.00249***	-0.000836
	(0.000333)	(0.000305)	(0.000557)	(0.000926)	(0.000912)	(0.000716)
Precipitation (Late)	0.0000491	0.000349	0.0000942	-0.000577	-0.000886	-0.0000475
	(0.00025)	(0.000218)	(0.000401)	(0.000565)	(0.000704)	(0.000627)
Fixed effects	County, Year	County, Year	County, Year	County, Year	County, Year	County, Year
Adj. R2	0.684	0.823	0.767	0.771	0.807	0.809
Dispersion (theta)	11.55	19.87	4.81	2.79	1.85	2.53
	(0.672)	(1.509)	(0.348)	(0.198)	(0.154)	(0.183)
AIC	9274.6	5593.7	5463.5	5086.3	3641.6	5574.7
BIC	9778.2	6097.3	5948.5	5547.6	4082.8	6058.1
N	637	637	632	624	609	623

* $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$; Heteroskedasticity-consistent standard errors in parentheses (HC1).

Table S2: Regression summaries.

Term	Celastrina ladon	Cercyonis pegala	Colias eurytheme	Everes comyntas	Junonia coenia	Nymphalis antiopa
Intercept	19.1 (17.5)	86.6*** (22.3)	-13.1 (22.8)	-15.1 (17.1)	37.6 (31.9)	-25 (20.6)
Glyphosate area-treatments	1.3* (0.697)	-2.51*** (0.906)	0.71 (0.945)	-0.285 (0.847)	0.302 (1.37)	-0.0633 (0.868)
Non-glyphosate area-treatments	-0.0249 (0.319)	-0.119 (0.485)	1.08** (0.464)	0.832** (0.36)	-0.955* (0.56)	0.145 (0.348)
Pyrethroid area-treatments	-1.89 (1.49)	-1.81 (2.23)	0.401 (1.6)	1.96 (1.57)	0.326 (2.65)	0.386 (1.81)
Organophosphate area-treatments	-0.996 (1.93)	1.6 (3.19)	-1.4 (2.78)	-0.154 (2.29)	-3.89 (4.02)	-4.87* (2.58)
Neonicotinoid area-treatments	-0.282 (1.05)	3.26*** (1.25)	1.15 (1.39)	-1.25 (1.17)	0.242 (1.79)	-0.643 (1.06)
Bt seed area-treatments	-2.84** (1.44)	0.22 (1.68)	-4.41*** (1.47)	2.82* (1.56)	-9.14*** (2.84)	-1.15 (1.63)
Forest land cover	9.76 (18.3)	-124*** (24.7)	26.9 (23.2)	40.6* (22.5)	-8.94 (38.1)	18.8 (23)
Urban land cover	-10.9 (13.2)	-56*** (15.9)	11.9 (15.8)	2.2 (14.4)	-34.3 (22.9)	12.3 (14.9)
Cropland land cover	-29.5 (20.7)	-97.3*** (26.2)	9.15 (27.1)	0.544 (23.4)	-42.9 (34.1)	25.3 (23.5)
GDD (Early)	0.00124 (0.00152)	-0.00395** (0.00167)	-0.00355** (0.00149)	-0.00408*** (0.00151)	-0.012*** (0.00317)	-0.0000569 (0.00136)
GDD (Mid)	-0.000191 (0.000955)	0.00189* (0.00109)	-0.00128 (0.00112)	0.002* (0.00104)	0.00313 (0.00216)	-0.00203** (0.000988)
GDD (Late)	0.00159 (0.00114)	0.00183 (0.00135)	-0.000806 (0.00121)	0.0024** (0.00113)	-0.00183 (0.00193)	-0.00117 (0.00132)
Precipitation (Early)	-0.000575 (0.000757)	-0.000928 (0.000844)	-0.00116 (0.00088)	0.000521 (0.000826)	0.00218* (0.00133)	0.00278*** (0.000891)
Precipitation (Mid)	0.000623 (0.000648)	-0.000747 (0.000859)	0.000673 (0.000855)	-0.000495 (0.000759)	0.000288 (0.00122)	0.000142 (0.000879)
Precipitation (Late)	0.000762 (0.000493)	0.000459 (0.000644)	0.00147*** (0.000525)	-0.0000545 (0.000546)	-0.00229** (0.000928)	-0.000263 (0.000597)
Fixed effects	County, Year	County, Year	County, Year	County, Year	County, Year	County, Year
Adj. R2	0.636	0.724	0.637	0.691	0.758	0.822
Dispersion (theta)	2.97 (0.197)	2.33 (0.178)	2.30 (0.139)	2.37 (0.158)	1.49 (0.130)	4.17 (0.340)
AIC	6123.1	4746.9	6464.3	5674	3163.7	4204.7
BIC	6603.4	5183.2	6949.4	6131	3583	4659.4
N	631	606	633	624	610	611

* $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$; Heteroskedasticity-consistent standard errors in parentheses (HC1).

Table S3: Regression summaries.

Term	Papilio glaucus	Papilio polyxenes	Phyciodes tharos	Polites peckius	Speyeria cybele
Intercept	-37.1*	2.84	-38***	-84.7***	23.1
	(20.1)	(17.6)	(14.5)	(31.9)	(23.5)
Glyphosate area-treatments	0.327	-0.343	0.688	-3.39***	-0.122
	(0.779)	(0.618)	(0.688)	(1.14)	(0.774)
Non-glyphosate area-treatments	0.335	-0.809***	-0.0355	0.0362	0.936**
	(0.33)	(0.31)	(0.297)	(0.506)	(0.427)
Pyrethroid area-treatments	-0.069	-1.47	-3.41**	-4.37**	3.29**
	(1.68)	(1.48)	(1.41)	(2.03)	(1.59)
Organophosphate area-treatments	4.58**	5.18**	0.101	1.59	-1.38
	(2.23)	(2.08)	(2.17)	(3.3)	(2.54)
Neonicotinoid area-treatments	1.38	-0.783	-0.338	-0.578	-1.34
	(1.11)	(1.05)	(1.02)	(1.62)	(1.18)
Bt seed area-treatments	0.305	-0.903	-2.34*	4.5**	2.32
	(1.39)	(1.4)	(1.33)	(2.24)	(1.49)
Forest land cover	-25.4	-3.3	69.7***	65.5**	-20
	(24.9)	(19.5)	(20.5)	(29)	(24.7)
Urban land cover	21.3	-5.84	38.6***	58.9***	-13.1
	(15.1)	(13)	(13)	(22.2)	(17.1)
Cropland land cover	40.7*	-3.77	44.9**	87.9***	-30.3
	(23)	(20.7)	(19.8)	(33.9)	(27.6)
GDD (Early)	-0.00326*	-0.00225	-0.00561***	-0.00527***	0.000317
	(0.00193)	(0.00149)	(0.00133)	(0.00178)	(0.00153)
GDD (Mid)	0.000541	-0.00064	-0.00105	0.00115	0.000714
	(0.00123)	(0.00104)	(0.000955)	(0.00135)	(0.000917)
GDD (Late)	-0.0000121	-0.000221	-0.00348***	-0.00175	0.000735
	(0.00133)	(0.00109)	(0.00105)	(0.00137)	(0.000986)
Precipitation (Early)	-0.00297***	-0.000391	-0.000672	-0.0013	-0.0000751
	(0.000824)	(0.000736)	(0.000887)	(0.00099)	(0.000805)
Precipitation (Mid)	-0.000238	-0.000585	-0.00172***	-0.00000404	-0.00223***
	(0.000786)	(0.000714)	(0.000648)	(0.00114)	(0.000806)
Precipitation (Late)	-0.00068	-0.000353	-0.0000842	-0.00102	0.000773
	(0.000636)	(0.000476)	(0.000492)	(0.000675)	(0.000537)
Fixed effects	County, Year	County, Year	County, Year	County, Year	County, Year
Adj. R2	0.538	0.778	0.77	0.51	0.762
Dispersion (theta)	2.55	3.25	3.19	2.74	2.95
	(0.196)	(0.215)	(0.196)	(0.259)	(0.216)
AIC	4363.1	5986.7	7065	3258.7	5206.8
BIC	4848.2	6448.4	7540.2	3676	5686.1
N	633	626	627	597	625

* $p < 0.1$, ** $p < 0.05$, *** $p < 0.01$; Heteroskedasticity-consistent standard errors in parentheses (HC1).

Supplementary figures

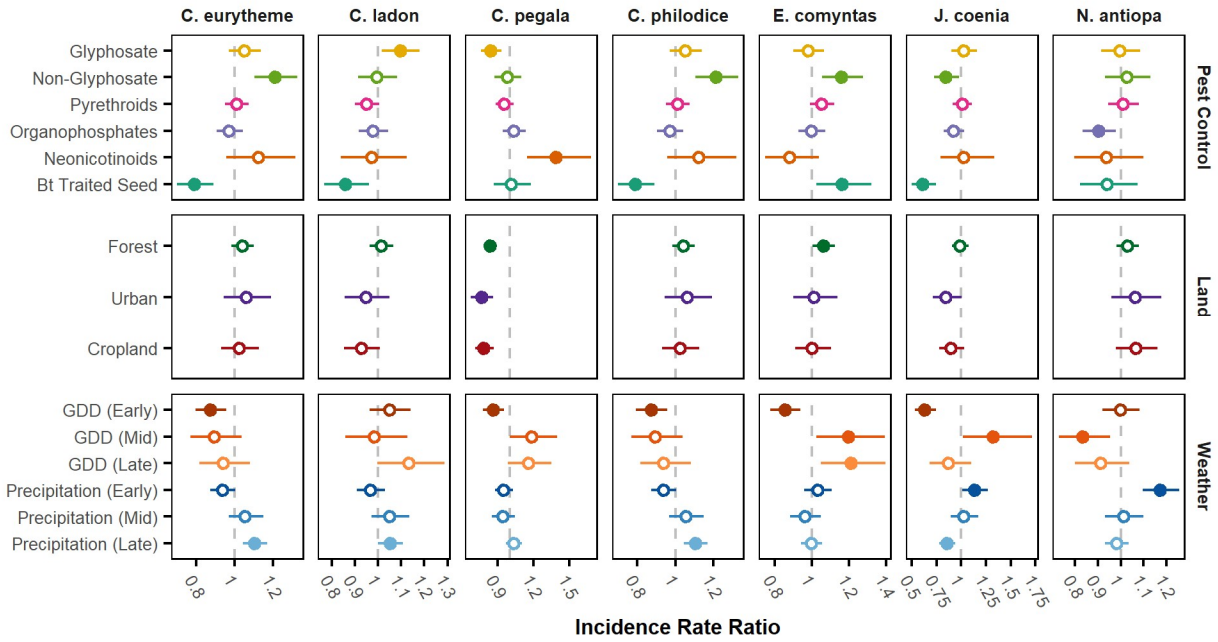


Figure S1: Incidence rate ratios (IRRs) for a standard deviation change in explanatory variables; additional species. See Figure 2 caption for details.

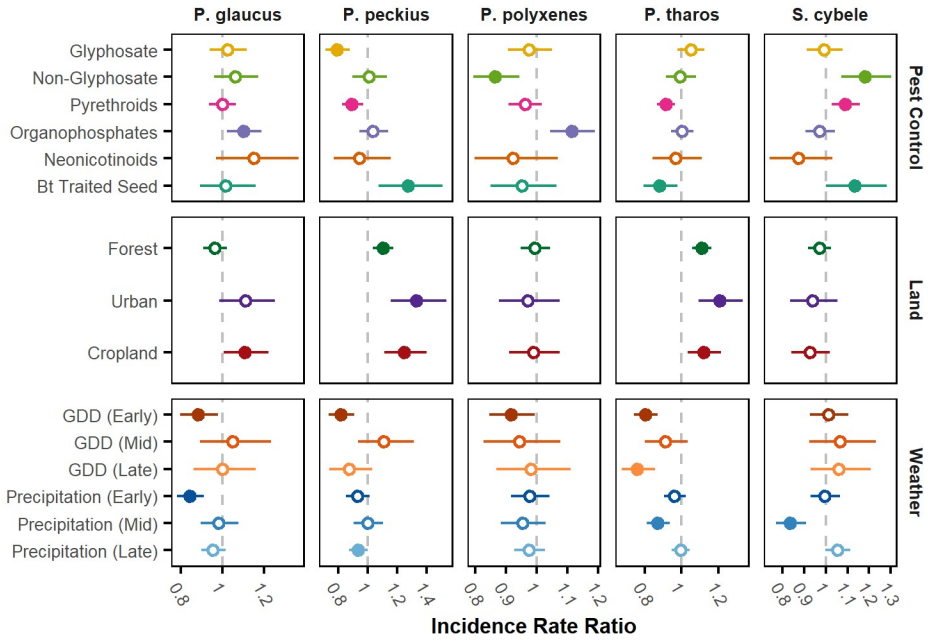


Figure S2: Incidence rate ratios (IRRs) for a standard deviation change in explanatory variables; additional species (cont.). See Figure 2 caption for details.

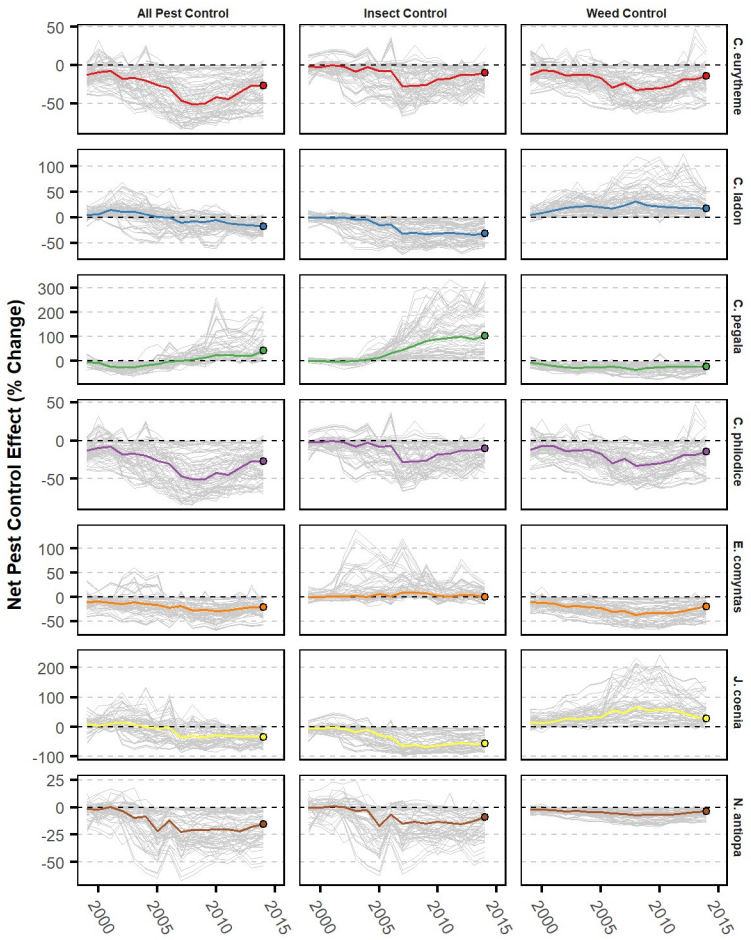


Figure S3: Net effect of pest control system change over time; additional species. See Figure 4 caption for details.

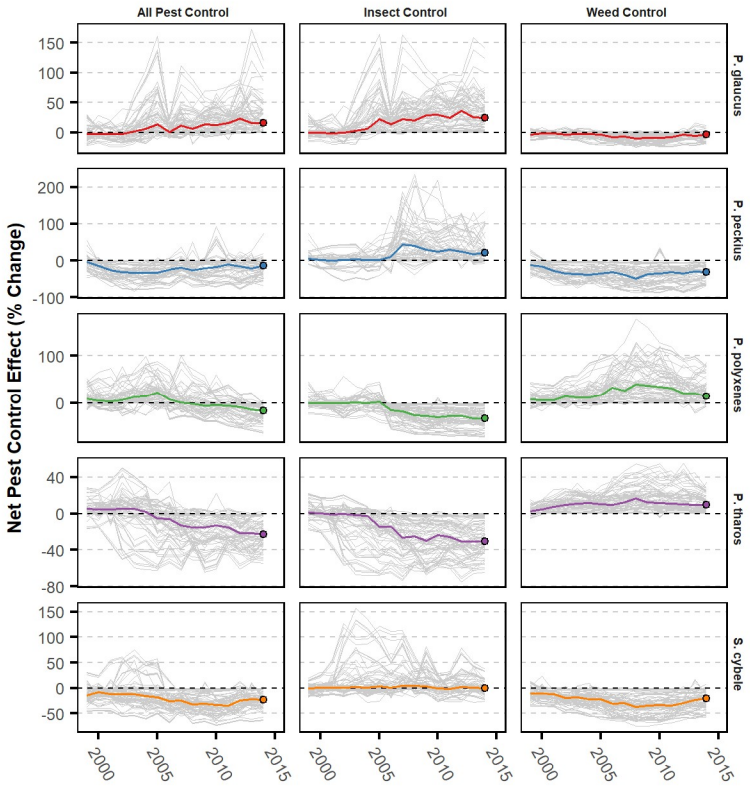


Figure S4: Net effect of pest control system change over time; additional species. See Figure 4 caption for details.