Long-term expansion of cereal crops promotes regional population increase of polyphagous Helicoverpa armigera

Long Yang
  State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences

Minlong Li
  State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences

Jie Liu
  National Agro-Technical Extension and Service Center

Juan Zeng
  National Agro-Technical Extension and Service Center

Yanhui Lu (✉ luyanhui@caas.cn)
  State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences

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Abstract

Changes in land use is an important driver of insect pest population dynamics, but the long-term effects of land use may be contingent on changes in some factors. To identify potential effects of change in cropping pattern on agricultural pest population trends, data from large temporal and spatial scales are needed but are rarely available. Here, we use long-term pest monitoring data across a regional scale and across independent gradients of land-use intensity at the landscape level, to investigate the effects of the expansion of area devoted to major cereal crops on population trends of polyphagous *Helicoverpa armigera* in northern China. We found that an increased proportion of the land planted to maize and wheat in the landscape had an indirectly positive effect on the abundance of the summer population of *H. armigera* by increasing the population abundance of the preceding spring generations. Stable carbon isotope analysis suggested that maize acted as the source habitat for *H. armigera* population in the growing season. At the regional level, long-term expansion of maize and wheat production, as well as the contraction of cotton area, were associated with an increased density of *H. armigera* in spring generations across years, although temperature and precipitation factors also had significant effects on pest population sizes. These results across both temporal and spatial scales indicated that, in addition to Bt cotton contraction, increased cereal crops cultivation was an important driver of the *H. armigera* population increases in recent decades in northern China.

Key messages

- Increased maize and wheat in the landscape promoted summer population of cotton bollworm indirectly
- Maize acted as the source habitat for cotton bollworm population in the growing season
- Regional long-term expansion of maize and wheat increased cotton bollworm spring populations
- Results across spatial-temporal scales confirmed the role of cropping patterns in pest population

Introduction

Crop plants are the main host for many key pests of agricultural ecosystems, and plant characteristics such as nutritional quality, spatial distribution, and abundance could modulate the fitness of insect herbivores (i.e., bottom-up effects) (Han et al., 2021; Kennedy and Storer, 2000). Land use change is an important factor most often expected to affect pest access to food resources and influence pest population dynamics both within a season and over years (Clair and Gassmann, 2021; Madeira et al., 2021; Paredes et al., 2022a). For polyphagous pests that feed on multiple crops species, changes in cropping patterns can affect the pest's occurrence in multi-crops beyond the crop whose abundance has changed (Downes et al., 2017; Hutchison et al., 2010; Kennedy and Storer, 2000). For multivoltine species that have several generations during a single growing season and usually feed on different host plants in different generations, cropping pattern changes can affect the availability of alternative host plants and influence pest population densities at multiple time points across the pest's generations (Iuliano and

Gratton, 2020; Schellhorn et al., 2015). The preceding generation's population is the source of subsequent founders of the next generation, land use changes usually have a carryover effect on pest population density, where land use at prior time points remains influential through long-lasting effects (Kheirodin et al., 2020; Marrec et al., 2015). Therefore, long-term land-use trends (e.g., multi-year increases or decreases of planting areas of particular crops) may drive variation in pest population density at broad scales (both temporal and spatial scales). For instance, cropland loss in Shanghai and Jiangsu provinces in China over the last two decades have resulted in a consistent population decline for three farmland pest species (i.e., striped stem borer, *Chilo suppressalis* Walker; yellow stem borer, *Scirpophaga incertulas* Walker; and pink stem borer, *Sesamia inferens* Walker) (Wan et al., 2021).

Identification through field trials of landscape-level elements that influence pest occurrence can provide insights into the effects of land use changes on "source-sink" processes and population dynamics of pests (Paredes et al., 2022b; Tabuchi et al., 2017). In general, the abundance of herbivore pests should be highest in landscapes with the most suitable host crops or with the highest connectivity between host habitats, which makes it easier for pests to access continuous food resources (i.e., resource concentration hypothesis) (Peirce et al., 2021; Rand et al., 2014). Nevertheless, sometimes a high concentration of host habitat can cause dilution effects on pest populations, especially when pests immigrate into fields from other habitats; in such cases, immigrating pests may become distributed over a greater area, resulting in a reduced density per unit area (Parsa et al., 2011; Yang et al., 2019a). Additionally, crop rotation, plant phenology, and crop management during the growing season generally have extensive impacts on the quality of host crops, which contribute to vary intra-annual responses of different generations of the pest to the surrounding landscape (Claflin et al., 2019; Karp et al., 2018). For polyphagous, multivoltine pests whose host crops vary among different generations, current pest population size is directly related to the pest density in the preceding generation, as well as land-use patterns in the preceding season (Le Provost et al., 2020; Marrec et al., 2015). However, most studies at the landscape level have overlooked these time lag effects, especially indirect effects via preceding generations.

Changes in land use and climate are widely viewed as the two main drivers of pest population dynamics; however, the latter factor has rarely been taken account in landscape level studies, which are often restricted by limited climate gradients (Courson et al., 2022; Kammerer et al., 2021; Newbold, 2018; Sun et al., 2022). In such cases, landscape level results may not accurately predict trends in a pest's regional population dynamics at a broad temporal scale because the impact of land use changes on pest population may be contingent on climate changes (Ganuza et al., 2022; Oliver and Morecroft, 2014). Direct and indirect impacts of climate changes on pests' demographic parameters (i.e., birth rate, death rate, and immigration or emigration) can alter their ability to cope with land use changes (Oliver and Morecroft, 2014). At the regional level, long-term ecological monitoring data at broad geographic scales provide opportunities to separate the impacts of climate factors and land use changes on pest populations (Neff et al., 2022). For example, Dively et al. (2018) found that populations of European corn borer (*Ostrinia nubilalis* [Hübner]) and corn earworm (*Helicoverpa zea* [Boddie]) significantly declined in association with the regional expansion of the cropping area of Bt (*Bacillus thuringiensis*) maize, even as

increased temperatures buffered the population reduction, over four decades in the mid-Atlantic region of the United States.

Helicoverpa armigera (Hübner) (Lepidoptera: Noctuidae) is a highly polyphagous pest that feeds on many crops and completes four generations per year in the North China Plain (Guo, 1998). Overwintering generation larvae develop to pupae in September and October, diapausing pupae overwinter in the soil, and adults emerge in early May of the following year. First generation larvae feed mainly on spring crops in May, and adults emerge in June; July and August, producing the second and third generations, whose larvae feed on various summer crops (Guo, 1998). In recent decades, the cropping system in the region has changed due to widespread adoption of Bt cotton starting in the late 1990s and replacement of some cotton acreage by maize and wheat beginning in the early 2010s. Correspondingly, the regional population of *H. armigera* remained high during the early 1990s, declined markedly by around 2000, and then recovered again after 2010 (Lu et al., 2018). Earlier studies have demonstrated that the decrease in regional outbreaks of *H. armigera* (year 1997–2006) was associated with the commercial planting of Bt cotton, as Bt cotton can trap and kill the second and third generations in northern China (Wu et al., 2008). But the suppressive effect on this target pest was weakened when the area planted to cotton decreased (2007–2019) (Lu et al., 2021).A later expansion of maize and wheat in the region coincided with a gradual reduction in cotton acreage in recent decades; however, the roles of these cereal crops in *H. armigera* population dynamics are still unknown, especially their potential effects on the overwintering and first generations, which are the source of the summer populations.

For a multivoltine pest like *H. armigera*, current pest population size is directly related to pest density in the preceding generation and availability of food resources for the current generation, adult population dynamic is usually determined by the combined effect of these factors. In this study, we investigated the effects of wheat and maize expansion on abundance of the overwintering and first generations of *H. armigera* adults at the landscape and regional levels, based on a 4-year field trial and 15 years of regional monitoring. Specifically, at the landscape level, we monitored the population abundance of *H. armigera* at 61 sites selected across landscape composition gradients, over 4 consecutive years, to test the effects of cereal crop proportion in the landscape on overwintering and first generation *H. armigera* abundance, as well as the cascading effect on the second generation population abundance. At the regional level, we tested the effects of long-term changes in the area of landscape devoted to cereal crops and of climate factors on trends of *H. armigera* abundance using monitoring data from 29 counties in three provinces from 2007 to 2021 in northern China.

Materials and methods

Study area and experimental design

The North China Plain is one of the major grain-producing areas of China, accounting for approximately 23% of the agricultural land area of China. The winter wheat-summer maize rotation cropping system is commonly used in this area, and the region produces more than 75% and 32% of the nation's total wheat

and maize, respectively. Wheat and vegetables are the major spring crops, while the major summer crops are maize, soybean, peanut, and vegetables. Here, we combined studies at landscape and regional levels to determine the effect of cereal crops expansion on *H. armigera* abundance.

At the landscape level, we monitored the overwintering, first, and second generations of *H. armigera* adults in landscapes with varying levels of cereal crops cultivation (as % of landscape in maize for the overwintering and second generations, in wheat for the first generation) to detect the direct and indirect (via the previous generation) effects of the landscape proportion in cereal crops on pest abundance. Plants with different photosynthetic pathways (C_3 versus C_4 plants) have distinctly different carbon isotope ratios that leave isotopic signatures in the inert tissues (such as wings) of herbivores feeding on them. Stable carbon isotopes can be used to identify the category of the natal host plant (i.e., the larval diet) of *H. armigera* adults, discriminating individuals that fed on C_3 plants from those that fed on C_4 plants (Gould et al., 2002; Tsafack et al., 2016). For larvae of the overwintering generation of *H. armigera*, both C_3 (mainly vegetables, peanut, and soybean) and C_4 (mainly maize) host plants are available in the study agroecosystem. We determined the host plants used by this generation larvae by analyzing the stable carbon isotope composition of moth wings to give a direct support to the landscape-level results.

At the regional level, we used long-term monitoring data across three provinces (Henan, Hebei, and Shandong provinces, which account for 65% of the area of the North China Plain) to assess the regional effects of changes in the area of cereal crops (maize for the overwintering generation and wheat for the first generation) on the trends in *H. armigera* adult abundance, took the main local climate factors into account.

Helicoverpa armigera population dynamics across landscapes

Study sites. The landscape-level study was carried out at 61 winter wheat-summer maize rotation fields (12 fields in 2016, 16 in 2017, 18 in 2018, and 15 in 2019) in Hebei Province and the cities areas of Beijing and Tianjin in northern China. Fields were selected along a gradient proportion of cereal crops area within 2.0 km around the selected wheat/maize fields, and the minimum distance between any two sites was not less than 4.0 km within a given year (**Fig. 1**).

Sampling of H. armigera adults. Species-specific sex pheromone trapping was used to monitor adult moths of the overwintering, first, and second *H. armigera* generations in the selected fields. We used pheromone bucket traps baited with a commercial pheromone lure for trapping moths during the population peak of each generation. Five bucket traps (bottom of the bucket about 15 cm above the plant foliage) were randomly arranged in each wheat or maize field, with trap at least 20 m from each other. For the overwintering generation, there were 2 consecutive monitoring rounds (each round lasted one week) of trapping in 2016 and 2017 and 3 rounds for 2018 and 2019, from early to late May. For the first generation, there was one round of trapping in 2016, two rounds in 2017 and 2019, three rounds in 2018, between late June to early July. For the second generation, there were three rounds of trapping, from late July to mid-August in 2016–2019. During each round, the numbers of *H. armigera* moths in each bucket

were counted, trapped moths were collected, and pheromone lures were replaced. For each generation, the numbers of moths captured in buckets in different rounds were averaged (as moths per trap for each week) to represent the population abundance of *H. armigera* in each field for the further analysis.

Stable carbon isotope analysis. The ratio of stable carbon isotopes (δC) ^{13}C and ^{12}C (^{13}C/^{12}C) in the forewings of *H. armigera* were used as markers of the moth's natal host plant because this ratio undergoes little change in the adult stage. During the sampling period in mid-May, 10 moths of the overwintering generation were randomly collected at each of the 15 landscape study sites in 2019 (150 individuals total) and stored at -20 °C until used in stable isotope analysis. Small numbers of moths were analyzed because of the high cost of analysis. Forewings of each moth were removed and dried at 60 °C for 3 days. Dried wings were placed in pressed tin cups and then combusted to CO_2 in an EA-HT Elemental Analyzer (Thermo Fisher Scientific, Inc., Bremen, Germany). The CO_2 emitted was trapped cryogenically and used to determine δ^{13}C values with a DELTA V Advantage Isotope Ratio Mass Spectrometer. The stable carbon isotope ratios were calculated as follow:

δ^{13}C‰ = (R-sample / PDB − 1) × 1000,

where R-sample is the ^{13}C/ ^{12}C ratio of each sample, and PDB is the carbon element isotopic ratio of the international standard. Precision in the determination of δ^{13}C values was ± < 0.1‰.

Land use investigation and analysis. Land use information around the selected wheat/maize fields was quantified within a radius buffer of 2.0 km. This scale has been shown to be a relevant spatial extent to study the response of pests to landscape characters (Karp et al., 2018). For each site, we recorded the site's geographical coordinates and then obtained open-access satellite imagery for the surrounding area outward to a radius of 2.0 km from Google Earth maps. To eliminate inaccuracies caused by changes in crop land use between the image date and the date of the larval feeding period for each generation, we printed maps (1.0 × 1.0 m) and confirmed all land cover types through ground verification in last September, May, and July of each study year to corroborate landscape classifications corresponding to the overwintering, first and second generations *H. armigera* populations. After that we digitized the maps in ArcGIS 10.5 and calculated the proportion of each land use category within the landscape in FRAGSTATS 4.2. We did not take the effects of cotton into consideration as its area in the study landscape was low (cotton was noted only in 2016 and the proportion was less than 1%), although cotton is a dead-end trap for *H. armigera*. Land use cover was divided into several categories for each generation *H. armigera*, and the summed proportion of each category in landscapes was calculated and used in analyses as the landscape composition parameter. For the overwintering and second generations, land cover was divided into (1) semi-natural habitats (mainly poplar trees, reforested areas, and small areas of grassland), (2) dwellings (including dwellings, roads, and water bodies areas), (3) maize, and (4) other summer crops, i.e., vegetables, peanut, soybean, and the other summer crops. For the first generation, land use was divided into (1) semi-natural habitats, (2) dwellings, (3) wheat, (4) other spring crops, i.e., vegetables, pea, and the other spring crops, and (5) fallow lands.

Trends in the H. armigera regional population

Area-wide population monitoring. *Helicoverpa armigera* moth numbers in the overwintering and first generations were monitored from 2007 to 2021 in 29 counties that belong to 21 cities (1 to 3 counties in each city) across Henan, Hebei and Shandong provinces in the North China Plain (**Fig. 1 and Table S1**). These monitoring sites belong to the nation area-wide monitoring network of *H. armigera*. At each county, a 20 W ultraviolet light trap was installed 1.5 m above the ground, and light trapping was done every night following the National Standards of the People's Republic of China (GB/T15800-1995). Trapping was conducted from sunset through sunrise, except during rain storms or power outages, carried out from May 1st to June 30th in each year. Each day, the total numbers of *H. armigera* adults in the traps were recorded. The total number of moths captured from May 1st to 31th was taken as the abundance of the overwintering generation, while captures from June 1st to 30th represent the abundance of the first generation.

Land use information and meteorological data. The annual acreages of wheat, maize and cotton in each city from 2006 to 2021 were obtained from the Statistical Yearbook of Henan, Hebei and Shandong provinces. Temperature (TEM) and precipitation (PRE) are two important climatic factors likely to affect egg and larval mortality and the pupal emergence rate of *H. armigera*. In general, temperature (TEM1) and precipitation (PRE1) in September and October are suggested to influence the egg and larval densities of the overwintering generation, these factors (TEM2, PRE2) during November to April may affect the survival of the overwintering pupae. During May of the following year, these same factors (TEM3, PRE3) could affect the emergence of the overwintered adults, as well as egg and larval density of the first spring generation. During June, these factors (TEM4, PRE4) may affect the emergence of the first generation adults. For each year, the mean daily temperature and precipitation data for each county were obtained from meteorological stations (China Meteorological Data Service Center, data.cma.cn). For two counties without a meteorological station, we used data collected at the nearest station.

Statistical analysis

At the landscape level, we fitted a piecewise structural equation model (SEM) to test for effects of landscape composition and the previous generation's population density on the number of *H. armigera* captures in the generation being modeled. The piecewise SEM was composed of three structural equations fitted using linear mixed-effects models (LMMs), with year as a random effect (**Table S2**). For the model describing abundance of the overwintering generation, we included the landscape proportions of maize, other minor crops, and dwellings in the previous year as explanatory variables. For the first generation, the landscape proportions of wheat, other spring crops, fallow lands, dwellings, and the abundance of the overwintering generation were treated as fixed factors. For the second generation, the landscape proportions of maize, other minor crops, dwellings, and the abundance of the first generation were used as fixed factors. For all LMMs, the counts of moths were $\log_{10}(x + 1)$ transformed to ensure the normality of model residuals. We did not include the proportion of semi-natural habitats as a fixed factor in these models, because our preliminary analyses and prior results showed that this variable was

strongly correlated (>|0.7|) with the other variables (wheat or maize proportions) for each generation. We tested for multicollinearity between remaining explanatory variables using variance inflation factors (VIFs) for complete models, and we found the VIFs were < 2.5, suggesting no evidence of multicollinearity. For all LMMs, we perform an automatic backward stepwise selection for model simplification, dropping non-significant predictors and the random effect as appropriate (Table S2). The overall fit of the path model was assessed using d-separation tests on Fisher's C statistic and AIC. For each LMM, marginal R^2 values (proportions of variation explained by fixed factors) and conditional R^2 values (total variation explained by fixed and random factors) were presented to provide an absolute value for the goodness-of-fit of the model. To detect relationships between the landscape area of semi-natural habitat and the *H. armigera* adult population, we used the proportion of semi-natural habitats in the landscape as the only fixed factor to explain the variation in adult abundance, keeping year as a random factor.

Based on the carbon isotope composition values of *H. armigera* adult wings, the abundance of captures that originated from maize was approximately calculated by multiplying the proportion of individuals originating from maize (as % from C_4 plants) by the total number of moths captured in the corresponding field. A simple linear model (LM) was fitted to the data to test effects of the proportion of maize in particular landscapes on the abundance of *H. armigera* moths that originated from maize.

At the regional level, LMMs were used to explain the variation in *H. armigera* moth captures, along with changes in cereal crop area across years. Here, we did also take the impacts of Bt cotton on spring populations into consideration, because cotton is supposed acts as a dead-trap trap for the second and third generations and may have indirect effect on the spring-generation via population dynamic processes. For the overwintering generation moths, the maize and cotton area in previous year in each city ($\log_{10}(x)$ transformed), together with temperature (TEM1, TEM2, and TEM3) and precipitation (PRE1, PRE2, and PRE3) factors corresponded to the different developmental stages (TEM1 and PRE1 for egg and larval stage, TEM2 and PRE2 for the overwintering pupal stage, TEM3 and PRE3 for adult emergence) of this generation were treated as fixed predictors, with county nested in city as a random effect. For the first generation, the model included the landscape area in wheat and cotton in each city ($\log_{10}(x)$ transformed) as well as temperature (TEM3, TEM4) and precipitation (PRE3, PRE4) factors (TEM3 and PRE3 affecting egg and larval development, TEM4 and PRE4 affecting adult emerge), and the overwintering generation population size as fixed effects and county nested in city as a random effect. For each linear mixed-effects model, the VIFs for mixed variables were < 2.5, and we included a temporal autoregressive structure of order1 (corAR1) to account for the temporal autocorrelation in the time series. Additionally, we did include random slope for cotton area since it did improve the goodness of fitting. The abundance of captures of the overwintering and first generations were $\log_{10}(x + 1)$ transformed to achieve a normal distribution of residuals and a better model fit, and all fixed variables were standardized to obtain comparable coefficients.

A multi-model inference procedure was used to reduce model selection bias and obtain robust results, which allowed us to derive coefficients for variables from a competing model set (Grueber et al., 2011).

We compared and ranked all alternative candidate models using a bias-corrected Akaike's information criterion (AICc) that corrects for small sample size, and we then used the 95% confidence model set that the summed Akaike weights from largest to smallest until reaching 0.95 to delineate a top model set for model averaging. The model selection process revealed the relative importance of explanatory variables and of relationships between the response and the explanatory factors. Relative importance values for variables were quantified by the sum of the Akaike weights associated with each variable in models in the selected model set. We also calculated marginal R^2 (R^2_m) and conditional R^2 (R^2_c) values for each model.

The residuals of all LMMs and LM models were graphically checked to ensure no violation of either normality or homoscedasticity assumptions. We also checked spatial correlation structure of these residuals and found no evidence of a correlation structure. All analyses were performed using R version 4.1.1(R Core Team, 2019). SEM was implemented with the package 'piecewiseSEM' (Lefcheck, 2015), and we used the 'nlme' package for linear mixed-effects models and simple linear models (Pinheiro et al., 2019), the 'MuMIn' package for multi-model inferences (Bartoń, 2017), the package 'spdep' for Moran's I statistics to test for spatial correlation structure in the residuals of models (Bivand and Wong, 2018), and the package 'car' for VIFs calculation and model validation (Fox and Weisberg, 2019).

Results

Effects of landscape composition on H. armigera captures

There was significant variation among weekly trap catches among different generations of *H. armigera* ($\chi2$ = 436.46, *P* < 0.001). The mean number of captures per bucket trap per week for moths of the overwintering generation was 75.26 (range from 8.20 to 288.70). For the first and second generations, the average catch of moths per trap per week were 111.80 (range from 4.20 to 402.60) and 11.70 (range from 1.60 to 39.54), respectively.

The piecewise SEM based on mixed-effects models showed a good fit to the data (Fisher's C = 13.22, *P* = 0.778), none of the independence claims remained significant, indicating that no important links were missing in the model. Summary results for the best-fitting SEM showed that the best fitting model explained 71% (Marginal R^2) of variation in moth captures abundance of overwintering generation, 83% of the first generation, 80% of the second generation (**Table S2**). Increases in the landscape area planted to maize area in the previous year had an indirectly positive effect on moth captures of the following first-generation population, with the maize area in previous year being positively correlated with moth captures in the overwintering generation, which in turn was positively associated with moth captures in the first generation (**Fig. 2 and Fig. S1**). The landscape proportion of wheat and other spring crops area was positively associated with the moth trap catches in the first generation. The abundance (i.e., trap catch) of the second-generation population was positively correlated with that in the first generation population (**Fig. 2 and Fig. S1**). Conversely, landscape proportion increases in the area of other summer crops was negatively correlated with trap catches in the second moth generation, and the landscape area proportion of maize had no effect on second generation moth trap catches (**Fig. 2**). The proportion of

landscapes devoted to semi-natural habitats was negatively correlated with trap catches in both the first and second moth generations; however, this negative effect was not significant in the second generation (**Fig. S2**).

According to the $\delta^{13}C$ value ranges of *H. armigera* reared on C_4 or C_3 host plants in the laboratory in previous studies (Baker and Tann, 2012; Head et al., 2010) and the frequency distribution of $\delta^{13}C$ values for wings from 150 field-collected overwintering moths in this study, we classified any moth with a value less than − 20.0‰ as having fed on a C_3 plant (represents individuals that fed at the larval stage on C_3 host plants), and any moth with a value of more than − 16.0‰ as having fed on a C_4 plant (**Fig. S3**). We found that 59.6% (87 moths) had a C_4 natal host plant and 40.4% (59 moths) had a C_3 natal host plant. Four individuals had intermediate values that were not assignable to any group and were not used in subsequent analyses. These intermediate values may be caused by individual larvae feeding on both C_4 and C_3 plants in their larval stage. The proportion of individuals that originate from C_4 host plants at each site ranged from 40 to 80%. The result of the simple linear model showed that the proportion of maize area in landscapes had a significant positive impact on the number of trapped moths whose larvae had fed on C_4 plants (mainly maize), and the abundance of *H. armigera* moths whose larvae had fed on maize was much higher within landscapes dominated by maize (**Fig. 3**).

Trends of H. armigera abundance at the regional level

The area of land under cotton cultivation decreased significantly from 2006 to 2021 (*P* < 0.0001) (**Fig. 4 a**), while maize and wheat area both displayed a rising trend in recent decades at the regional scale (maize area: *P* < 0.0001; wheat area: *P* = 0.3859) (**Fig. 4 b, c**). These trends in cotton, maize and wheat production were associated with a significant increase in numbers of overwintering (*P* = 0.0002) and first (*P* = 0.0019) generations of *H. armigera* (**Fig. 4 d, e**).

Model averaging showed that the area of maize and cotton, the mean daily rainfall in September and October (PRE1) and during November to April (PRE2), mean daily temperature during November to April (TEM2) and in May (TEM3) had significant effects on the number of trap catches of the overwintering generation (**Tables S3 and S4**). The increase in maize area and the reduction of area planted to cotton had positive effects on moth captures (**Fig. 5 a, b**). But increased precipitation in September and October and during winter season had negative effects (**Fig. 4 and Fig. S4 a, b**). In addition, increases in mean daily temperature during winter and in May had positive effects on trap catches of overwintering moths (**Fig. S4 c, d**). For the first generation, averaging of the confidence model set showed that overwintering generation abundance and area planted to wheat had significant effects on first generation moth trap catches (**Tables S3 and S4**). The trap catches of first generation moths increased with greater areas of wheat and higher abundance of the preceding generation (**Fig. 5 c, d**). **Fig.** Climate factors such as the mean June temperature also significantly affected first generation moth abundance, with moth trap catch increasing as a function of temperature in June (**Fig. S4 e**). The area planted to cotton at the regional level had no significant effect on trap catch in the first generation of *H. armigera* (**Tables S3 and S4**).

Discussion

In northern China, *H. armigera* causes serious damage to summer crops, and higher spring populations of this multivoltine pest have been suggested to link to such summer pest problems (Guo, 1998). Here, we assessed contributions of land use changes coupled with climatic factors on the abundance of *H. armigera* in the overwintering and first generations in spring and the cascading effects of these early season impacts on the following summer generation, using long-term monitoring and studies at multiple spatial scales. At the landscape level, increased proportions of the landscape planted to maize and wheat within a given season had an indirect positive effect on the abundance of the summer generation by increasing the population abundance of earlier generations. At the regional level, in addition to Bt cotton area contraction, expansion of maize and wheat production was responsible for a trend of increasing abundance of *H. armigera* in the spring generations across years, although climate factors such as temperature or precipitations during key pest stages also significantly affected pest populations. In summary, the consistent positive relation between area devoted to cereal crops and the abundance of the spring *H. armigera* across temporal and spatial scales indicates that cropping patterns play an important role in determining densities of *H. armigera*, an economically important polyphagous pest in the North China Plain.

Crop fields in agricultural landscapes could serve as habitats for pests by providing various food resources. The availability, suitability, and accessibility of these alternative host plants can, over time, strongly alter the pest's population dynamics (Iuliano and Gratton, 2020; Jones et al., 2019). For many polyphagous pests that exploit, over the course of several generations, a sequence of crops during a single growing season, changes in host crops in the current or previous cropping season may determine the size of the pest population. In northern China, ear-stage wheat is the main spring host plant for overwintering *H. armigera* oviposition, but little management attention has been paid to *H. armigera* on wheat because of the high economic threshold, this crop area acts as the source habitat of the subsequent generations infesting summer crops (Xu et al., 2000). Our results from the landscape and regional levels also suggested that high concentrations of wheat area support larger numbers of first-generation *H. armigera* moths that could lead to higher densities of the second generation in the agroecosystem.

The abundance of the first-generation *H. armigera* was also indirectly increased by the high areas devoted to maize in the previous year at landscape and regional levels, which increased the number of overwintering moths to exploit wheat fields in the following year. Therefore, it is wheat that creates a bridge between spring emergence of moths and infestations of *H. armigera* in summer crops. In our study region, about 80% of summer maize is at the silking stage by late August (personal observation), corresponding to the peak of overwintering generation eggs and larvae of *H. armigera*. The silking stage of maize is highly favored as an oviposition and larval feeding site by *H. armigera*, summer maize therefore acts as a nursery crop, producing large numbers of overwintering generation *H. armigera*, whose moths then emerge in the following spring.. Here, we found that >60% of the overwintering moths trapping in spring had fed on C_4 plants (principally maize) as larvae, and the abundance of the C_4-derived

moths in spring increased with an increasing proportion of maize in the landscape of the preceding season. The consistent results obtained from landscape-level studies and from carbon isotope analysis supported the regional-level conclusions, that long-term expansion of maize was associated with an increase in density of *H. armigera* across years at the broad geographic scale, although Bt cotton area had a negative effect on the overwintering generation. These results confirmed the bottom-up effect on *H. armigera* population density of high concentrations of maize in agricultural ecosystems.

In contrast, there were no significant effects of maize landscape area on the abundance of the second generation of *H. armigera* in the summer, perhaps because whorl-stage maize is not a suitable host for *H. armigera* due to high larval mortality. The first and second moth generations showed inconsistent responses to other minor crops in landscape, and variation in the intensity of field management among spring and summer crops is likely responsible for this difference. Minor spring crops are usually subject to less pesticide use, while intensive pesticide use is common in summer crops because of the greater pest pressure posed by a range of pests, including *H. armigera*. The negative effect of such insecticide use for pest management then reduces the number of moths captured in monitoring traps because of the suppression achieved of the pest's larvae. In this study we did not include other crops in the regional analysis because the accurate data on the planting areas for other crops in each city are not available in the statistical yearbook. However, most of the other crops are vegetables, and there was no obvious change in the area planted to these vegetables at the regional scale over recent decades according to government reports. The negative relationships between the proportion of land in semi-natural habitats and *H. armigera* abundance may be an indirect effect that more land in semi-natural habitats in the landscape usually corresponds to a smaller area in cereal crops. On the other hand, it is possible that such natural habitats are enhancing top-down suppression by natural enemies since such habitats often benefit insect predators or parasitoids (Yang et al., 2019b; Yang et al., 2018a). While, the previous multidecadal, county-level analysis in our study region found that semi-natural habitats such as forest and grassland displayed no significant effects on the severity of *H. armigera* (Zhang et al., 2019).

Across-years land use patterns affect pest population dynamics in conjunction with changes in pest management practices in crop habitats and climatic factors (Courson et al., 2022). Due to limitations imposed by small spatial-temporal scales, landscape-level results from short-term monitoring data sometimes fail to coincide with the trend of pest population at broad scales, although space-for-time substitution approaches have been widely used. For example, the long-term, widespread adoption of Bt cotton increased the population sizes of mirid bugs (dominated by polyphagous *Apolygus lucorum* Meyer-Dür) in the North China Plain, but landscape-level studies suggested that increases in the acreage planted to cotton had a negative effect on the landscape-level abundance of *A. lucorum* (Li et al., 2020a; Lu et al., 2010). Changes in the intensity of pesticide application in cotton fields accounted at least in part for this seeming paradox. Insecticide usage in cotton is still much higher than that in other crops even after the adoption of Bt cotton varieties. Deployment of Bt-cotton did reduce insecticide use in cotton fields, which often act as sink habitats and suppress *A. lucorum* populations in the landscape, but over the long-term Bt cotton reduced the manage intensity in cotton, weaking this crop as a dead-end trap for pests at the regional scale (Li et al., 2020a). Expansion of cereal crops may pose threats to biodiversity

and associated ecosystem services and tends to increase the use of insecticides in agricultural ecosystems (Meehan et al., 2011; Rosenheim et al., 2022). The negative impact of insecticide pressure on natural enemies can result in reduced pest suppression services and then increase pest population densities indirectly (Wu et al., 1992). In northern China, little attention has been paid to *H. armigera* damage on wheat because of the high economic threshold (Guo,1998). Most farmers apply insecticides one time to control aphids (the key pests in wheat) in the spring, and we found no trends in application frequency of insecticide in wheat cultivation over the study years. In our study region, the number of insecticide applications in local wheat fields displayed no correlations with the surrounding landscape complexity, but these two factors have mixed effects on in-field natural enemies (Yang et al., 2018b). A large area of maize in an agricultural landscape may have negative effects on natural enemies, by reducing landscape heterogeneity or increasing insecticide use (Schellhorn et al., 2015). However, carbon isotope values of *H. armigera* moths suggested that the bottom-up effect of host resources (maize) is a stronger driver of *H. armigera* populations compared with the top-down forces of natural enemies. At the regional level, resurgence of *H. armigera* led to an increase in insecticide applications in maize fields in recent decades (Lu et al., 2021), and the extent to which the cascading effects of this change on natural enemies and pest densities needs further study.

On the other hand, weather characteristics are also important drivers of regional pest population dynamics across years. However, the co-occurrence of land-use and climatic changes makes it difficult to separate the effects of these factors through using historical time-series data that lack independent gradients for land-use and climate elements, and this problem may cause different results to be obtained at different spatiotemporal scales (Forister et al., 2010; Lawton et al., 2022; Sun et al., 2022). We linked long-term monitoring data on *H. armigera* adult population to changes in the acreage of main cereal crops and climate factors that corresponded in time to development of specific stages of particular pest generations. Our results suggested that higher mean daily temperatures during *H. armigera* overwintering and emergence periods enhanced moth abundance, while heavy precipitation during the egg, larval stages and overwintering period was negatively associated with moth abundance. Increasing temperatures allow for a higher survival rate for pupae during the winter, and can also result in higher moth activity and the capture of more moths, but the heavy precipitation usually increase egg and larval mortality of *H. armigera* (Huang et al., 2020).

The long-term trend in a pest's population dynamics is the combined effect of many factors, performing controlled experiments in which all factors are held constant except for the one that we focused on is the best way to identify influence factors, but it's difficult to achieve at the regional scale. However, controlled experiments at a smaller scale (such as the landscape scale) are easier to realize, and the results can give supports or explanations to conclusions at the larger regional scale. Therefore, seeking evidence from different scales is an effective way to uncover drivers of long-term trends in pest densities. In this study, the increase in area planted to maize and wheat at regional level was associated with increases in trap catches of spring-generation adults, which promote the higher densities in the summer population (i.e., the second generation). To ensure that the correlations contributed by maize and wheat were true drivers of the pest population, controlled experiments and stable isotope analysis were carried out at the

landscape level, the results given a robust support to the hypothesis that regional increases in the area of maize and wheat across years has enhanced *H. armigera* spring populations by providing favorable food resources. Therefore, along with reductions in acreage of Bt cotton cultivars, a dead-end trap crop for *H. armigera* that can suppress its population levels in agroecosystems, cereal crop (maize and wheat) expansion has been an important driver of the population increase of *H. armigera* and higher damage to summer crops in recent decades in northern China (Lu et al., 2021; Wu et al., 2008).

Conclusion

In general, changes in cropping patterns have potential to profoundly influence pest population dynamics, crop yield loss, and pesticide use at a broad spatial scale (Baker and Tann, 2017; Lu et al., 2021; Wu et al., 2008; Zhang et al., 2018). For instance, expansion of acreage of maize planting at the state level in the United States contributed to the higher damage from soybean aphid (*Aphis glycines* Matsumura), lower yield, and greater pesticide use in soybeans (Landis et al., 2008). Understanding the impacts of intra- and inter-season changes in regional cropping patters on a pest's life system can enhance the predictability of its infestations across large changes in cropping patterns, provide early warnings of pest outbreaks and facilitate the design of more effective preventive management strategies. Most overwintering *H. armigera* in northern China originate from maize-feeding larvae, and, therefore, maize acts as the source habitat for *H. armigera* in both the current and the following growing season. Increased acreage of maize led to higher damage by *H. amigera*'s first generation on spring crops and by its subsequent generations on summer crops. Suppression of *H. armigera*'s overwintering population in maize would reduce its pest status for multiple crops in the following year. China's government has issued biosafety certificates for several genetically modified Bt maize hybrids in recent years (Li et al., 2021). We suspect that area-wide adaptation of such Bt maize would reduce *H. armigera* infestation across the growing season, both in maize and in various spring and summer crops the following year. To delay the evolution of Bt resistance in *H. armigera*, refuges of non-Bt maize should be planned and required, given that the other crops that are hosts for *H. armigera* produce only a few overwintering individuals (Li et al., 2020b; Yang et al., 2022).

Declarations

The authors declare no conflict of interest.

Author contributions

Acknowledgements

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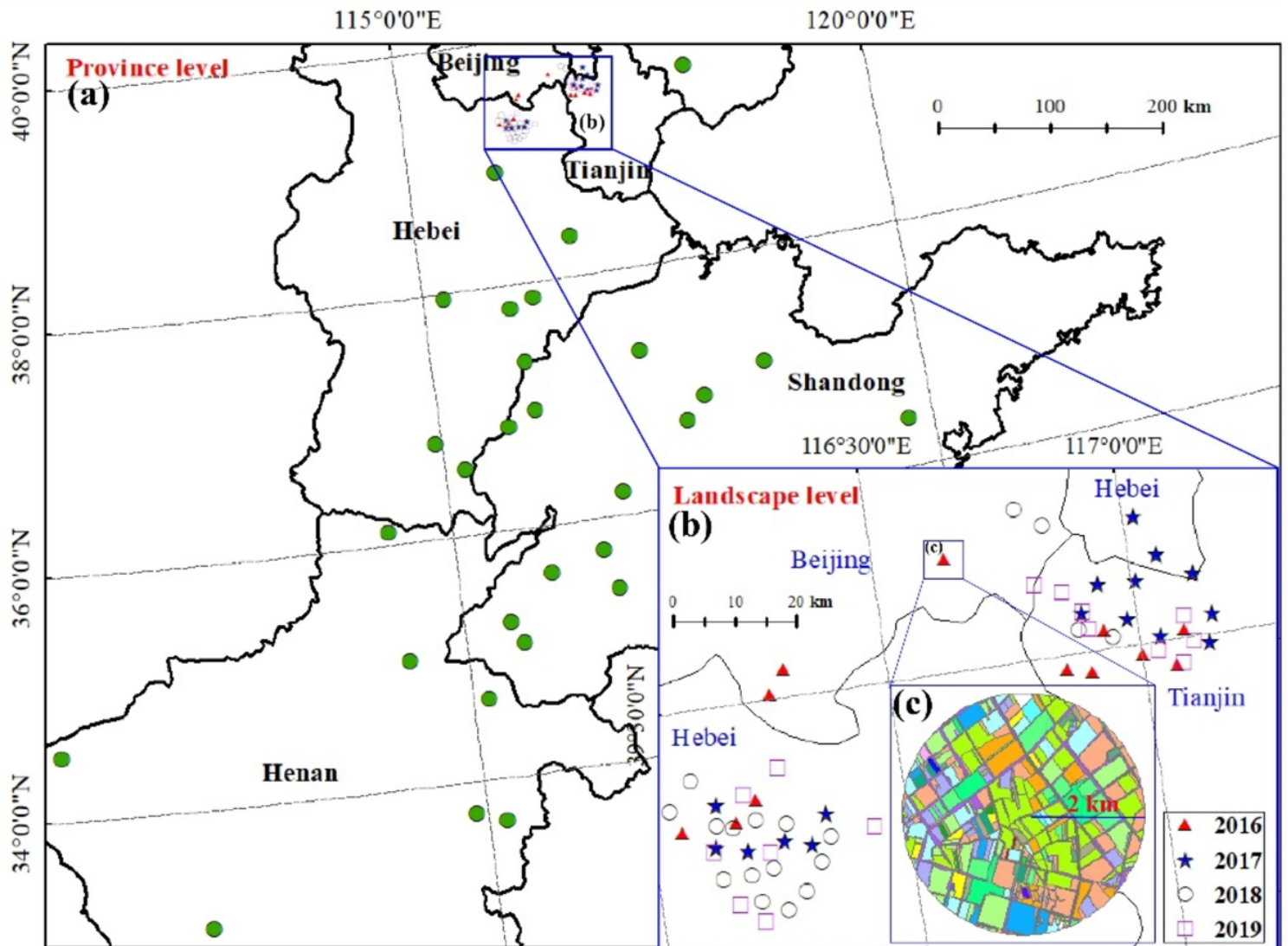
Figures

Figure 1

Geographical location of sampling sites in the North China Plain. (a) *Helicoverpa armigera* populations were monitored through light-trapping in 29 counties (7 counties belong to 6 cities in Henan, 13 counties belong to 9 cities in Shandong, and 9 counties belong to 6 cities in Hebei) from 2007 to 2021 at regional level, each monitoring station is represented by a green filled circle; (b) The distribution of 61 winter wheat-summer maize fields (12 fields in 2016, 16 in 2017, 18 in 2018, and 15 in 2019) that were sampled for landscape-level study in 2016-2019; (c) Detailed example of a landscape circle including the mapped land cover classifications within 2 km radius buffer around the sampling field
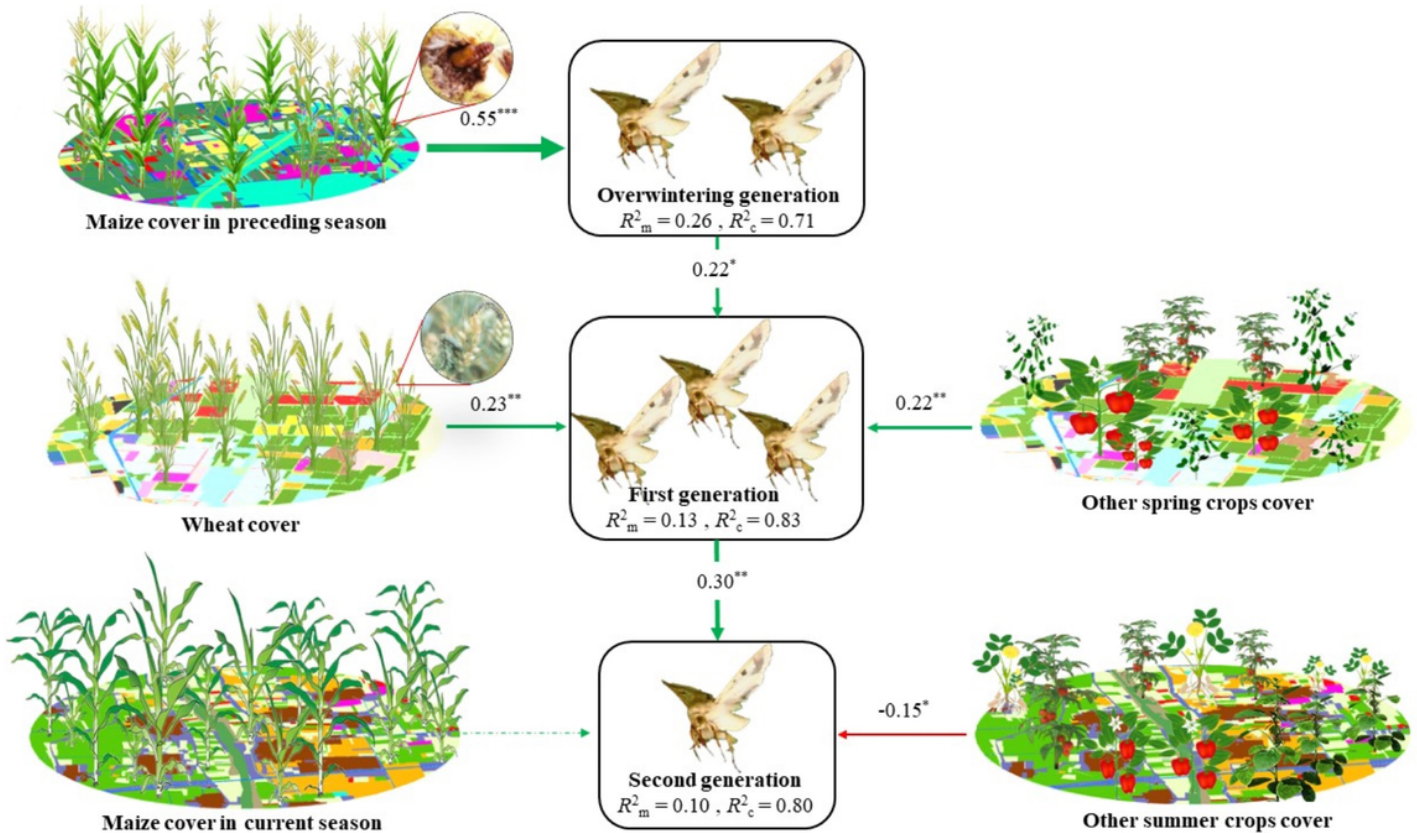
Figure 2

The piecewise structural equation model (SEM) was used to test the direct and indirect (mediated through preceding generation population) effects of landscape composition on *Helicoverpa armigera* adult abundance. Green arrows indicate significant positive links; red arrows indicate significant negative links; dotted arrow indicate no significant causal correlation ([*]$P < 0.05$; [**]$P < 0.01$; [***]$P < 0.001$). Arrow thickness is proportional to the standardized effect sizes. Marginal R^2 (R^2_m) and Conditional R^2 (R^2_c) values are shown for response variables. Fisher's C = 13.22, *df* = 18, *P* = 0.778.
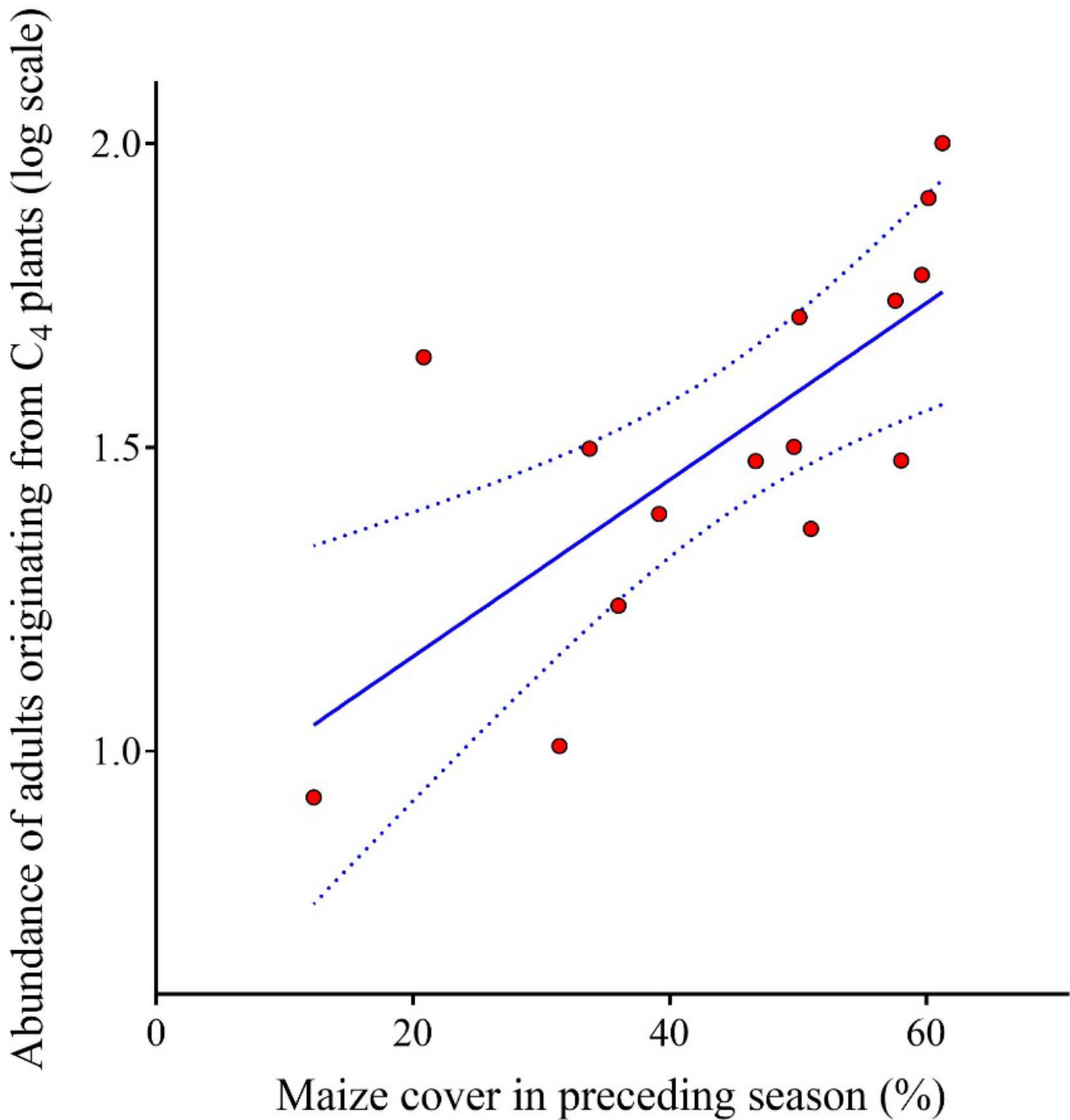
Figure 3

The abundance of overwintering *Helicoverpa armigera* adults originating from C_4 plants increased with the proportion of maize cover in the surrounding landscape in the preceding season, in 2019 landscape-level study. Predictions from LM is plotted (dark lines) along with upper and lower confidence levels (95% CI: dotted lines), while points represent moth originating from C_4 plants
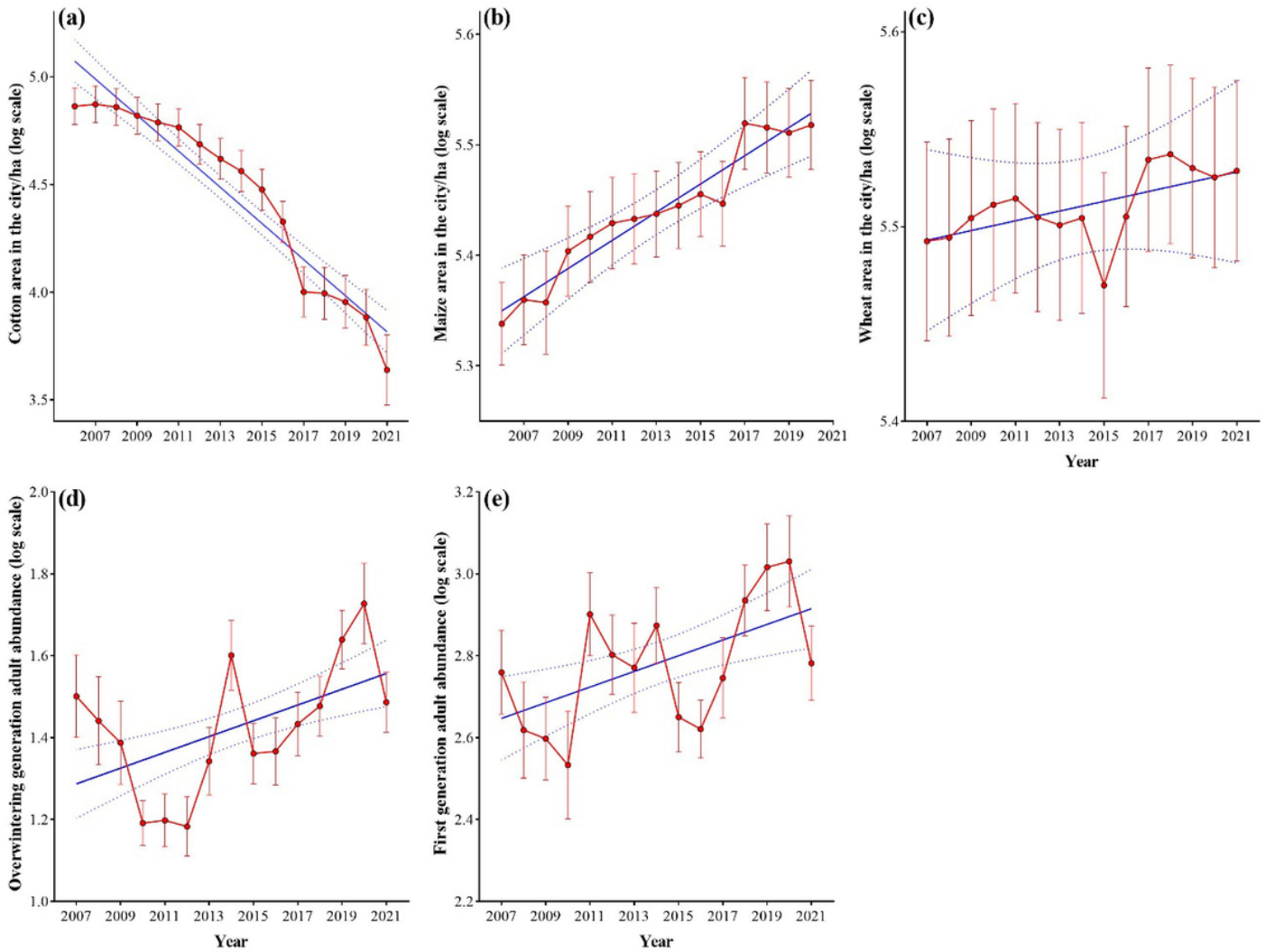
Figure 4

Trends in crop area and spring-generation *Helicoverpa armigera* moth captures in regional level from 2006 to 2021. (a) Cotton planting area decreased from 2006 to 2021; (b) Maize planting area increased from 2006 to 2020; (c) Wheat planting area increased from 2007 to 2021; (d) *H. armigera* overwintering adult abundance increased from 2007 to 2021; (e) *H. armigera* first generation adult abundance increased from 2007 to 2021. Predictions from LMs are plotted (dark lines) along with upper and lower confidence levels (95% CI: dotted lines)
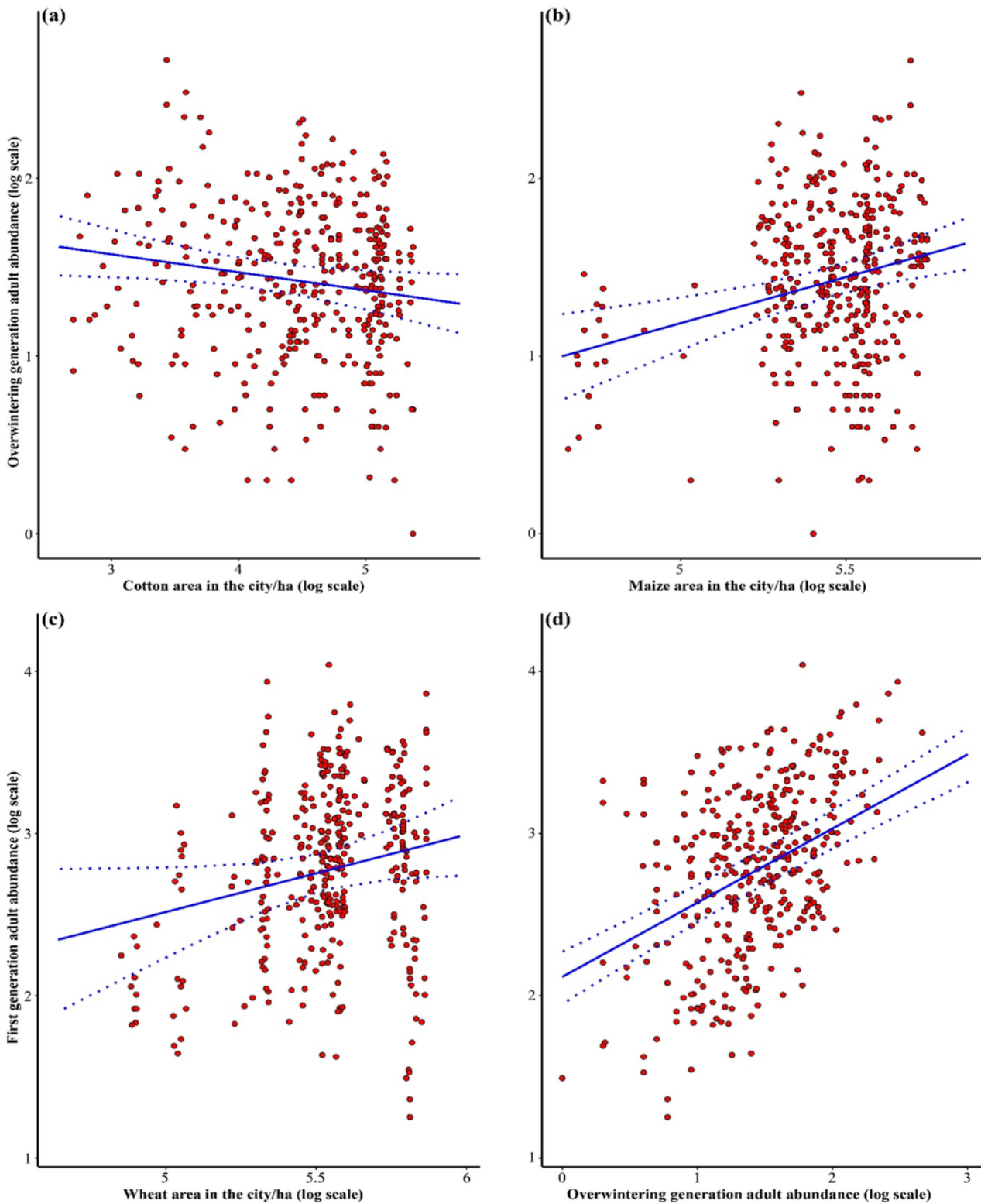
Figure 5

Relationships between crop area and *Helicoverpa armigera* moth captures at regional level across years. (a) Overwintering generation adult abundance of *H. armigera* decreased with the area of cotton; (b) Overwintering generation adult abundance of *H. armigera* increased with the area of maize; (c) First generation adult abundance of *H. armigera* increased with the area of wheat; (d) First generation adult

abundance of *H. armigera* increased with the abundance of overwintering adults. Predictions from LMMs are plotted (dark lines) along with upper and lower confidence levels (95% CI: dotted lines)

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