Bats initiate vital agroecological interactions in corn

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In agroecosystems worldwide, bats are voracious predators of crop pests and may provide services to farmers worth billions of U.S. dollars. However, such valuations make untested assumptions about the ecological effect of bats in agroecosystems. Specifically, estimates of the value of pest suppression services assume bats consume sufficient numbers of crop pests to affect impact pest reproduction and subsequent damage to crops. Corn is an essential crop for farmers, and is grown on more than 150 million hectares worldwide. Using large exclosures in corn fields, we show that bats exert sufficient pressure on crop pests to suppress larval densities and damage in this cosmopolitan crop. In addition, we show that bats suppress pest-associated fungal growth and mycotoxin in corn. We estimate the suppression of herbivory by insectivorous bats is worth more than 1 billion USD globally on this crop alone, and bats may further benefit farmers by indirectly suppressing pest-associated fungal growth and toxic compounds on corn. Bats face a variety of threats globally, but their relevance as predators of insects in ubiquitous corn-dominated landscapes underlines the economic and ecological importance of conserving biodiversity.

agriculture | biological control | ecosystem service | predator–prey | trophic cascade

Humans currently sequester more than one third of terrestrial primary productivity to agriculture, and production is expected to further intensify to meet the demands of an expanding human population (1). Although agricultural production tends to degrade biodiversity, intact ecological communities also provide valuable ecological services to humans, such as regulation of crop pests (2). These agricultural ecosystems are characterized by simplified food webs with distinct trophic levels (3, 4), and thus may be particularly prone to trophic cascades wherein predators release plants from herbivory (5), suppressing crop damage and bolstering yields. In many countries, these services may be important for food security (6); thus, assessment of pest-regulating services provides key knowledge that can benefit human well-being.

In many agroecosystems, insectivorous bats are voracious predators of economically relevant crop pest species (7). As such, bats are assumed to facilitate crop production through pest suppression (8). Geographic extrapolation of small-scale models (6, 9, 10) suggests pest suppression by insectivorous bats in the continental United States alone is worth more than 3 billion USD annually (11). Although these studies have garnered considerable attention from public and scientific communities, all such studies have been based on estimates of bat population size, rate of pest consumption by bats, and damage by pests. These studies have advanced our understanding and appreciation of the economic impact of bats, but to date, all such estimates have relied on untested assumptions about the trophic effect of bats in row-crop agriculture (12). Specifically, herbivory by many crop pest species takes place at the larval stage, whereas bats feed on the adult stage. Therefore, to suppress crop pest populations, bats must consume enough adult crop pests to affect the number of eggs laid on crops. Also, many crop pests lay far more eggs than survive (13), and some larvae are known to cannibalize one another (14), so suppression of oviposition by bats does not necessarily equate to suppression of larvae or suppression of herbivory (12).

Recent attempts to experimentally test the effectiveness of bats as pest suppressors have focused on tropical agroforestry (15–17), where bats glean insects from vegetation. No such study has been conducted in ubiquitous and cosmopolitan row crops such as corn, where bats hawk insects from the air. Corn is one of the most widely grown row crops, with more than one billion metric tons produced globally (18). However, crop pest insects substantially suppress corn yields, reduce crop quality, and necessitate the use of costly insecticides. Corn earworms (*Helicoverpa zea*) are moths that cause significant damage to crops by feeding on leaves and ears during their larval life stage. In addition to direct herbivory, corn earworm larvae diminish crop value indirectly by creating avenues for infection by detrimental fungi, such as *Aspergillus flavus* and *Fusarium graminear* (19). These fungi produce toxic and carcinogenic metabolic by-products, such as aflatoxin and fumonisin, that represent serious health hazards to livestock (20) and can greatly affect the value of grain. Bats commonly feed on adult corn earworms, and thus may provide an important service to agriculture.

Here, we conducted an unprecedented experiment using large nocturnal exclosures and paired control plots in corn fields to provide the first experimental test of the trophic effect of bats in a widespread row crop. We conducted the experiment over the course of two growing seasons, with six treatment-control pairs each year, and evaluated larval and adult corn earworm abundance, crop damage, and bat activity over time. We further evaluated the presence of fungal pathogens and concentrations of mycotoxins on the corn, which are associated with damage by crop pests.

Results

Effect of Bats on Crop Pests. During 2014, when corn was planted on a normal schedule, we found 59% more corn earworm larvae/ ear where bats were excluded (mean $\pm$ SEM, 0.303 $\pm$ 0.020) than in paired controls (0.191 $\pm$ 0.020) (Fig. 1*A*; $F_{1,82}$ = 9.80; *P* = 0.0024). Larval infestation also varied significantly across time

Significance

Bats are thought to provide valuable services to agriculture by suppressing crop pests, but their ecological role in agricultural systems remains unclear. We implemented a unique field experiment to assess the ecological and economic effect of bats in corn agriculture and found that bats initiated strong and surprising ecological interactions in corn fields. Bats not only suppressed crop pest numbers and crop damage but also indirectly suppressed the presence of pest-associated fungus and a toxic compound produced by the fungus. As nocturnal flying insectivores, bats occupy unique ecological roles and provide valuable services to society, and it is therefore essential that we conserve this often-maligned group.
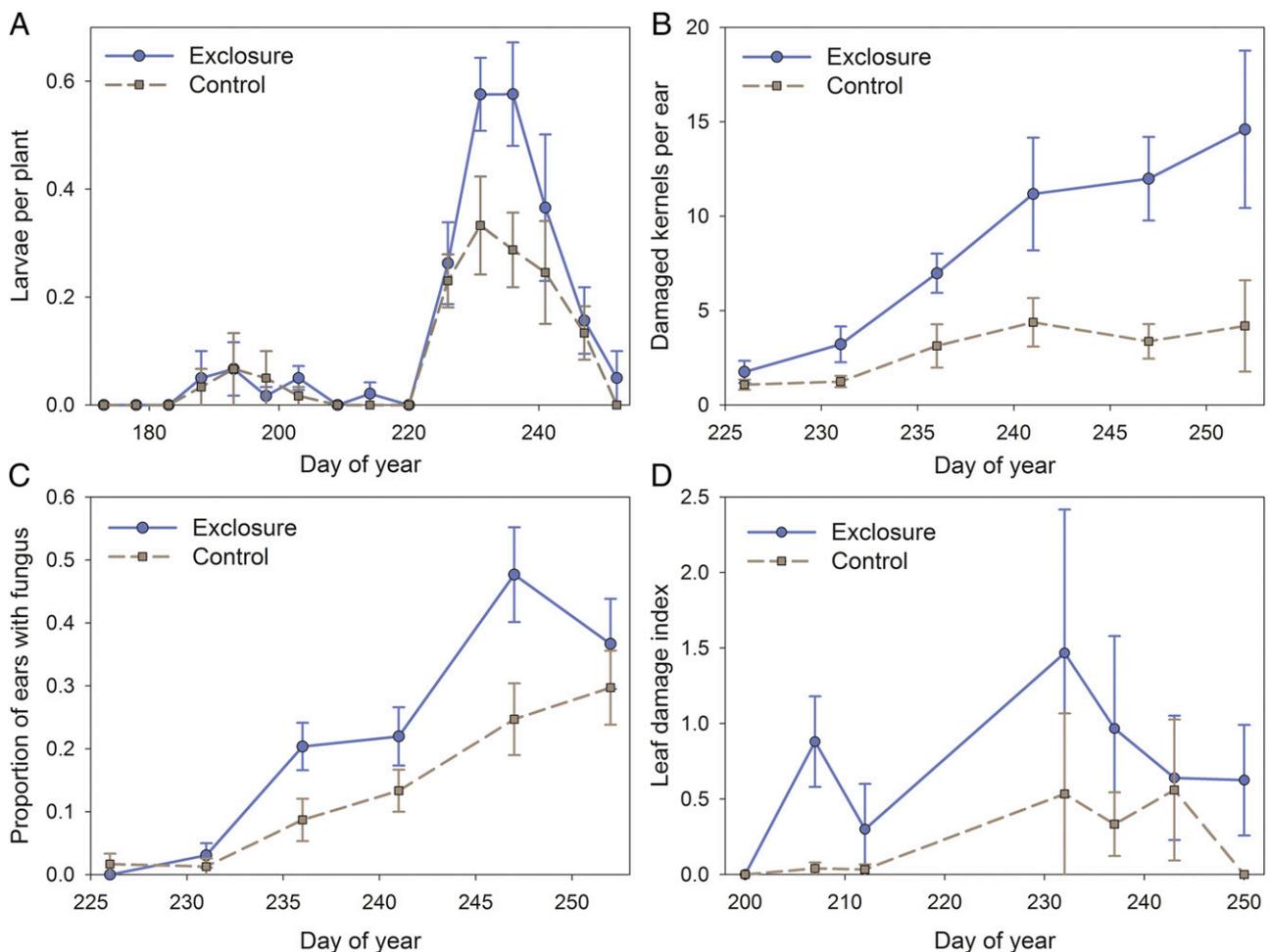
Fig. 1. Top-down effect of bats in corn agroecosystems. In 2014, bats suppressed corn earworm larvae across the six replicates (*A*) ($F_{1,60} = 10.45$; $P = 0.0022$), suppressing herbivory on corn ears (*B*) ($F_{1,5} = 34.64$; $P = 0.0020$), and decreasing the proportion of ears with pest-associated fungal growth (*C*) ($F_{1,60} = 10.84$; $P = 0.0017$). In 2013, larvae were abundant and feeding on vegetative-stage corn, and bats suppressed leaf damage (*D*) ($F_{1,59} = 6.74$; $P = 0.012$). In *A*, the two peaks in larvae represent separate generations: a small first generation, followed by a much larger second generation. The first generation was mainly found in one replicate and did relatively little damage, so it was excluded from analysis. *B* and *C* show ear damage and fungal growth, beginning when ears were present in the fields. All error bars represent SEM.

($F_{7,82} = 21.99$; $P < 0.0001$). These data show that bats provide sufficient predation pressure on adult corn earworms to affect larval numbers. This case becomes more compelling considering that bats appeared to track adult corn earworm abundance. Although correlative, activity of both bats and moths followed the same temporal trend (Fig. 2).

Effect of Bats on Crop Damage. The suppression of corn earworm larvae was also sufficient to reduce crop damage: there were 56% more damaged kernels/ear in exclosures (5.82 ± 0.04) than controls (3.74 ± 0.04) (Fig. 1*B*; $F_{1,82} = 9.42$; $P = 0.0029$). The number of damaged kernels per ear varied across time ($F_{7,82} = 54.72$; $P < 0.0001$). The differences in larval density and damage did not result in statistically significant differences in yield weight ($F_{1,5} = 2.69$; $P = 0.162$) between controls (150.12 ± 11.43 bu/ha) and exclosures (123.63 ± 11.43 bu/ha), despite what would be considered an agriculturally significant difference (i.e., >20%) by most farmers. The lack of statistical significance was related to the large variation between replicates ($F_{5,5} = 10.71$; $P = 0.011$), and a retrospective power analysis suggested that 11 treatment–control pairs would be needed to detect a significant difference in yield, assuming the same means and variance. Although there was too much variation to detect an effect on yield by weight, we

also calculated difference in yield by determining the percentage difference in undamaged kernels between exclosures and controls and estimated that bats increased corn yields by 1.4%.

Corn earworm larvae also feed on corn foliage when no ears are present. The largest outbreak of corn earworm larvae occurred at similar times in 2013 and 2014 (Fig. 3). However, in 2013, corn was planted later than normal because of heavy spring rains, and was therefore in a vegetative state when corn earworm larvae were active. The altered climate in 2013 created a unique opportunity to evaluate the effect of bats on vegetative damage to corn. We found higher levels of leaf damage in exclosures than in paired control plots, showing that bats suppress herbivory even when pests are less abundant (Fig. 1*D*; $F_{1,59} = 6.73$; $P = 0.0120$). Leaf damage did not vary significantly over time ($F_{6,59} = 1.68$; $P = 0.1408$).

Effect of Bats on Pest-Associated Fungi. In our experiment, more ears had fungal growth in exclosures ($20\% \pm 1.4$) than controls ($12\% \pm 1.4$) (Fig. 1*C*; $F_{1,60} = 17.15$; $P = 0.0001$). Fungal infection also varied across time ($F_{5,60} = 13.78$; $P < 0.0001$). In addition to higher levels of fungal infection, we found significantly higher concentrations of fumonisin in exclosures (4.82 ± 0.17 ppm) than controls (4.15 ± 0.17 ppm) ($F_{1,29} = 7.67$; $P = 0.0097$), demonstrating
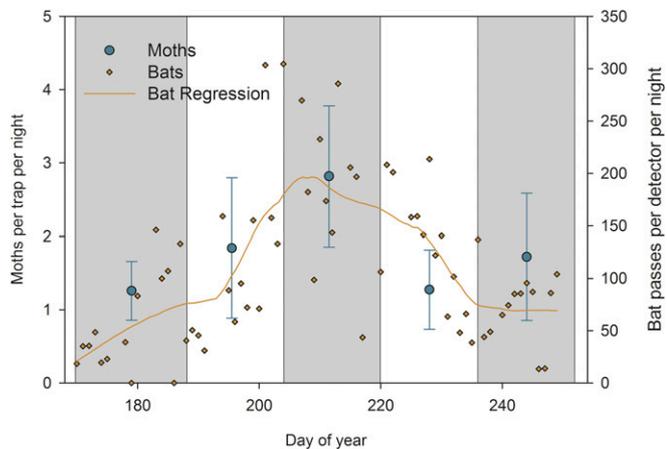
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Fig. 2. Corn earworm moth captures (± SEM) on the area and bat activity near the experimental pairs in 2014. Moth captures were averaged across the five traps each time the lures were replaced, represented by the gray and white bands. Bat call data were averaged between the two acoustic detectors and smoothed using a LOESS regression to discern the pattern of activity across time.

a previously unknown function of bats in agroecosystems. Levels of aflatoxin were not significantly different ($F_{1,29} = 0.30$; $P = 0.586$) between exclosures (2.68 ± 0.96 ppb) and controls (1.94 ± 0.96 ppb), but the fungus that produces aflatoxin (*A. flavus*) was rare in our fields.

Discussion

Our findings show conclusively that bat consumption of crop pests initiates a trophic cascade, suppressing damage to economically valuable row crops during both reproductive and vegetative stages. In addition, we demonstrate that this top-down effect of bats extends to pathogens and mycotoxins as well (Fig. 4). Although fumonisin levels in our corn were below maximum recommended levels for consumption by livestock (21), under optimum conditions for fungal growth, bats could substantially bolster the value of the grain by indirectly limiting fungal infection and associated mycotoxin concentrations, particularly when grain is stored long-term. Further, because our exclosures were small relative to the potential foraging height of bats, the effects we measured represent a fraction of the potential effect of insectivorous bats in agroecosystems.

The mechanisms by which bats effect these changes in larval density could include direct effects on adult moth populations or indirect effects on moth behavior. Many crop pests, including corn earworm, fall armyworm, and European corn borer, have evolved tympanate organs to detect echolocation calls produced by bats (22), suggesting moths may live in a "landscape of fear." Our experiment protected moths from direct predation and may have also protected them from perceived predation risk (i.e., echolocation). Given that our exclosures, although large, only excluded bats from relatively small areas of fields, it may be that differences we measured point to shifts in egg-laying behavior by moths, rather than overall differences in moth mortality. This landscape of fear could affect our experiment by shifting the distribution of adult moths from other areas of the field to exclosures, or by suppressing oviposition by moths. Bat-like ultrasound played in fields does not decrease adult corn earworm abundance (23), but does suppress oviposition and larval abundance of other eared-moths (24, 25). This suggests the landscape of fear created by bats may suppress reproductive behavior of corn earworm moths, rather than shifting their distribution in the fields. Such a strong behavioral response of moths to reduced

bat predation highlights the ability of bats to affect pest insect reproduction, even if they do so indirectly.

The effect of bats on crop pests and herbivory is thought to be economically beneficial to agriculture globally. The value of this service likely varies globally as a result of recent advances in pest management. In particular, corn genetically modified with insecticidal properties from *Bacillus thuringiensis* (*Bt* corn) has been widely adopted in some countries to manage corn earworm larvae. The corn in our plots was non-*Bt*, which represents 16% of the corn grown in the United States, or 9 million ha (26). Non-*Bt* corn is still predominant in much of the world, representing about 68% of corn planted globally in 2011, or 108 million ha (27). At our yield and current corn price, we estimate that the value of bats to non-*Bt* corn farmers is 7.88 USD/ha. Across 108 million ha of non-*Bt* corn grown globally, we estimate bats' direct value to this crop at 851 million USD. Ecological models suggest the value of bats in *Bt* cotton to be 38% of their value in conventional cotton (10). Using this to adjust our value for the effect of *Bt* crops, we estimate that bats provide an additional 150 million USD in *Bt* corn, for a total global value more than 1 billion USD in corn alone. Because the estimate is based on farm gate prices, the value represents a change in total revenue, rather than direct profit, and farmers may bear additional costs to collect and process the additional yield. This estimate also does not account for the indirect effects of suppressed mycotoxins or reduced use of pesticides, which may still be substantial (10, 28).

Our experiment demonstrates strong top-down suppression of crop pests and damage by bats in row crops. Although the scale of the service provided by bats likely varies with crop type, pesticide use, pest abundance, and bat community structure, similar findings in our study and tropical agroforestry (15, 17) suggest that bats regulate crop pests across a variety of local and landscape management regimes. In fact, bats may be ideal biocontrol agents because they are highly mobile and long-lived, and thus can capitalize on the transient nature of pest outbreaks (12). The global importance of bats as pest insect suppressors demonstrates the significance of trophic interactions for ecosystem functions and services.

Insectivorous bats are abundant, although declining, in much of the world. Understanding bat–insect–crop trophic cascades has taken on new urgency as bats become increasingly threatened because of several synergistic threats. In North America, white-nose syndrome is a devastating epizootic threatening a
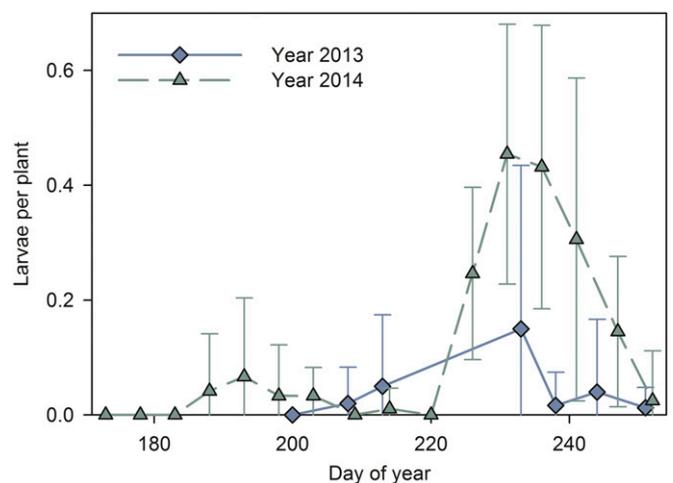

Fig. 3. Corn earworm larvae by year across six replicates. This shows a peak of mean larval abundance (± SEM) in mid-August in both years, despite a much later planting schedule in 2013. Corn earworms were less abundant in 2013, infesting two of six replicates.
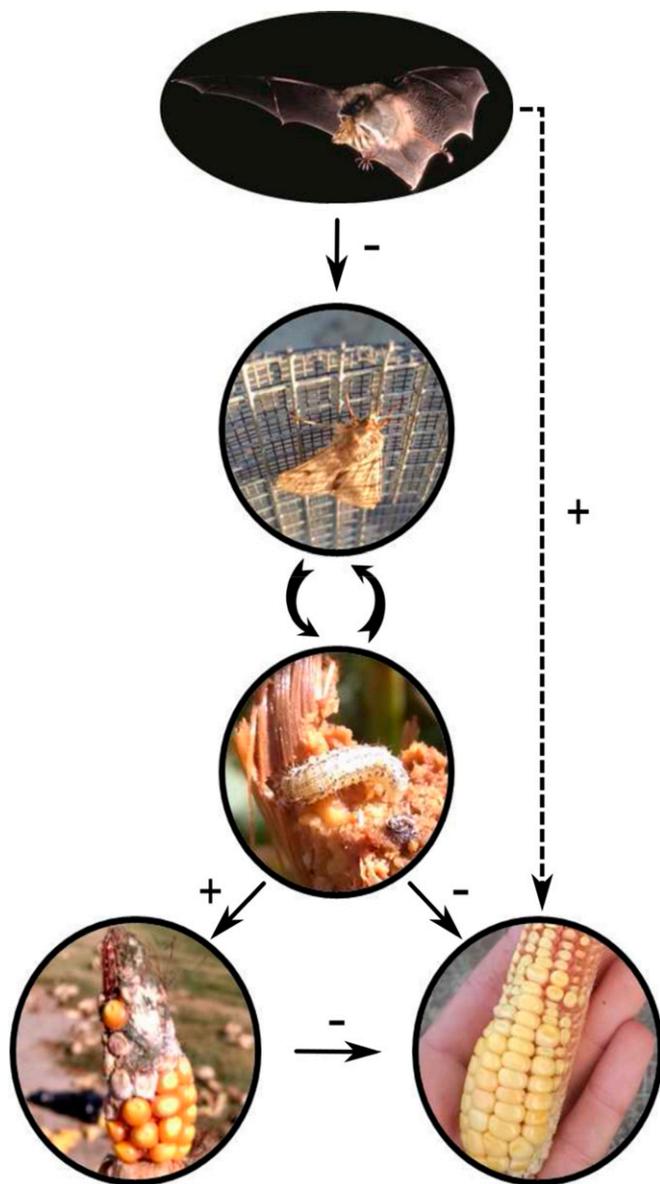
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Fig. 4. A conceptual diagram of the trophic effects initiated by bats in corn agroecosystems. Our experiment demonstrates that bats affect adult corn earworms sufficiently to suppress larvae, suppressing direct damage to corn, presence of pest-associated fungal growth on corn, and concentrations of mycotoxin produced by fungus on corn. Bats thereby bolster both quantity and quality one of the most widely produced crops globally. Bat photo by Merlin Tuttle and used with explicit permission of Bat Conservation International. All other photos by J. Maine.

number of species of cave bats with extinction (29). Worldwide, the increased construction of wind-power facilities for production of clean energy also threatens many bat species (30). These acute threats, combined with the more diffuse effects of habitat destruction and increasing agricultural intensity, have potential to degrade the valuable ecosystem services provided by insectivorous bats (4). In just a few years, rapid decline of bat populations in the United States may create the largest bat exclusion experiment to date (12), but baseline data are necessary to make effective use of that experiment. It is imperative that we both implement conservation efforts to protect and restore the remaining bat community and document pest-regulating services provided by insectivorous bats before regional extinctions have occurred. Bats perform key functions in agricultural ecosystems,

and conservation efforts focusing on these vital trophic interactions have the potential to maintain ecosystem services beneficial for human well-being.

Materials and Methods

Study Site and System. We conducted this experiment at Horseshoe Lake State Fish and Wildlife Area in southern Illinois (37.109°, −89.333°). The area is dominated by bottomland hardwood forest fragments and corn, soybean, and millet fields flooded annually for waterfowl hunting. The corn (hybrid NK N68B-GT) was treated only with herbicides, and thus was likely to harbor a relatively large population of insect pests compared with more intensively managed fields. Bat populations in this area had been minimally affected by white-nose syndrome at the time of this study.

The bat community in the area is dominated by eastern red bats (*Lasiurus borealis*), evening bats (*Nycticeius humeralis*), tricolored bats (*Perimyotis subflavus*), and northern long-eared bats (*Myotis septentrionalis*). Eastern red bats feed on many species of moths, particularly noctuids (31), and thus may be the main chiropteran predator on common moth pests in the Midwestern United States. Evening bats at Horseshoe Lake feed heavily on spotted cucumber beetle (*Diabrotica undecimipunctata howardi*) (32), a common agricultural pest in both its adult and larval form. Tricolored bats in the area feed mainly on caddisflies (33). The northern long-eared bat may glean prey from vegetation, and occasionally consumes a high proportion of moths (34).

In North America, corn earworm (*Helicoverpa zea*) moth larvae cause widespread damage to common row crops such as corn, soybeans, and cotton. These crop pests feed on both leaves and ears of corn, decreasing corn yields in the southern United States by 1.5–16.7% (35). Corn earworms are typically managed with insecticides or *Bt* transgenic hybrids, which suppress larval densities. Bats in many areas feed heavily on adult corn earworms (7), but the effect on larval populations and crops is poorly understood.

Experimental Design. We constructed six exclosures (20 m × 20 m × 7 m) and six paired control plots in corn fields during summer 2013 and 2014. The six replicates were spread over 2.5 km². Each replicate was in a separate field, although some replicates were as close as 0.1 km to each other. We had no existing estimates of variance, so a priori power analyses were not feasible. Logistics of building such exclosures limited us to six treatment-control pairs for practical reasons. To build exclosures, we suspended two steel cables (1/4 inch; breaking strength, 6,800 pounds) over 65 m of corn between steel masts. The cables were suspended 20 m apart (H50; ROHN Products), with 2-inch netting (3T Products) attached to 20 m of the cables. Two 20-m steel cables were attached perpendicular to the long cables to hold netting on the ends of the exclosure. The top of the netting was attached to metal clips, which slid on the cable. This allowed us to move all of the netting, using a rope-and-pulley system, during the day to allow access by diurnal birds and allow the farmer to maneuver equipment in the field. A plot of equal size under the net-free portion of the steel cables, 8 m from the exclosure, was designated as the control to ensure that any differences were not a result of birds using the cables as perches. Corn was removed 2 meters around the controls and exclosures to limit terrestrial dispersal of insect larvae. All necessary approval was obtained through the Southern Illinois University Institutional Animal Care and Use Committee. We began the experiment in early July 2013 and mid-June 2014 and removed the exclosures in mid-September.

Data Collection. During the vegetative stage of the corn, we counted larvae in the whorl and evaluated leaf damage, using a fall armyworm damage index ranging from 0 to 9 (36). Lepidopteran leaf damage is easily distinguished from other types of herbivory because of the orientation of feeding and large amounts of frass in the whorl or ear (36). Sampling regimes varied slightly between 2013 and 2014, but in both years, we selected plants by treating plots as a grid and used a random number generator to select a row and number of plants into each row. In 2013, we picked 3–10 plants from each plot every 5–20 d. Corn earworm larvae fed on vegetative structures of corn in both years, but as a result of a wet spring in 2013, corn was planted late, and larval populations peaked before ears had developed in the fields. Thus, leaf damage by corn earworm larvae was common in 2013, whereas it was nearly nonexistent in 2014. In 2014, corn was planted closer to the normal schedule for this region, so we used 2013 data to test the effect of bats on vegetative stage corn, and 2014 data for all other analyses.

To evaluate insect reproduction and herbivory in 2014, we randomly collected 10 plants from each plot every 5–6 d. Plants were sampled blindly; each plant was assigned a random number, removed from the plot, and assessed by a single researcher without knowledge of the associated

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treatment. To achieve random sampling in our plots, we treated plots as a grid and used a random number generator to select 10 combinations of a row and number of plants into each row for each sampling day. When ears were present, we removed the husks from each ear to count larvae and the number of damaged kernels. We also visually assessed the presence of fungal growth on each ear. During the 82 d of the experiment in 2014, we sampled 160 plants from each treatment within each replicate (1,920 total plants).

Three weeks after the end of the experiment in 2014, we collected 30 ears from each plot to determine yield and mycotoxin concentration. We estimated yield by shelling the ears, weighing the corn, and adjusting for moisture content, using a digital moisture tester (Burrows Digital Moisture Computer 700), to determine bushels per ear. We then multiplied the yield per ear by the estimated number of ears per plot and converted yield to bushels per hectare. To determine concentrations of fumonisin (a mycotoxin produced by *F. graminear*) and aflatoxin (produced by *A. flavus*), we used ELISA (fumonisin and aflatoxin plate kits; Beacon Analytical Systems, Inc.) on three random samples of shelled corn from each plot, each run in duplicate.

We evaluated bat activity in 2014 with two acoustic bat detectors (Model SM2, Wildlife Acoustics) placed on 3-m poles within 20 m of the plot pairs. We programed detectors to record for 9 h beginning at sunset and rotated detectors between the six replicates so that activity was measured in each treatment-control pair at least 16 nights throughout the experiment. We filtered noise from bat calls using Program Kaleidoscope (Wildlife Acoustics, Inc.) so bat passes could be counted for each night. Because of high variability in bat activity, we used a locally weighted scatterplot smoothing (LOESS) function (SigmaPlot Version 10.2) to describe changes in bat activity across time.

We monitored adult male corn earworm abundance in 2014, using five Hartstack traps with pheromone lures (Zealure; Hercon Environmental) scattered throughout the area at least 100 m from treatment-control pairs. Moths were removed and counted every 5–6 d, and pheromone lures were replaced every 15–18 d. Moth captures decreased substantially with days since lure replacement, so we represented moth captures graphically, using means of samples across the time frame for each lure.

Statistical Analysis. We evaluated effects of bat predation on leaf damage, ear damage, larval corn earworm numbers, and the proportion of ears with visible fungal growth, using generalized linear mixed models with repeated measures. To model correlation within experimental units across time, we first determined the appropriate covariance structure (variance components) for ear damage and larval numbers based on Akaike Information Criterion adjusted for small sample sizes. Larvae and crop damage were rare for much of the experiment, so all dependent variables contained a high proportion of zeros. In 2014, we excluded data before the larger, second generation of larvae infested the plants because excess zeros heavily skewed the distributions of data. This left six samples from each of the six replicates for the three variables measured over time in 2014: number of larvae per ear, number of kernels damaged per ear, and proportion of ears with visible fungal growth. We transformed larvae and number of kernels damaged using a $\ln(x+1)$ transformation, and by doing so, obtained a near normal distribution. We analyzed fungal infection using logit link with a binomial distribution. We used diagnostic plots to check the assumptions of the generalized linear mixed model with repeated measures. We conducted our analysis with treatment as a fixed effect, replicate (treatment-control pair) as a random effect, and specified each plot as a subject for repeated measures across time. The effect of bat exclusion on yield (scaled to bushels per hectare) and mycotoxin concentration were analyzed using two-way ANOVA with treatment as a fixed effect, and with replicate and plot as random effects. Analyses of larvae, damaged kernels per ear,

mycotoxins, and yield were conducted using PROC MIXED, whereas analysis of fungal infection were conducted using PROC GLIMMIX in SAS (Version 9.3; SAS Inc.).

Economic Effect of Bats on Corn. Extrapolating from our field experiment to a detailed analysis of the global economic effect of bats in agroecosystems is difficult because of many unknown parameters. However, we used our data to provide a plausible estimate calculated through two different methods. We used yield weights from the 30 ears collected in each plot after the end of our experiment and also estimated the value of the difference in damage between treatments and controls based on the 10 ears collected in each plot on the final day of normal sampling. Although there was too much variation between replicates to detect a difference in yield weight between treatments, the observed damage by corn earworm larvae on the final day of the experiment in 2014 was higher in exclosures (14.6 kernels/ear) than controls (9.6 kernels/ear). We estimated the number of kernels on 10 ears from each plot at the end of the experiment in 2013, yielding a mean of 348.2 kernels per ear of corn in our area. We divided the mean number of damaged kernels in exclosures and controls by the mean kernels per ear to obtain percentage of kernels damaged by corn earworm larvae (4.2% in exclosures and 2.8% in controls). Thus, we estimate that bats increased corn yields by 1.4%.

The value of bats is also a function of corn yield and price, which vary widely across the world. In our control plots, yield was 150.12 bu/ha, which is less than half the mean yield in the United States, but is more representative of global mean yield (37). Corn price is currently near record lows for recent years, at $3.75/bu in the United States, and is also much lower than that of most other countries (38). In this sense, calculation of value from the yield in our control plots and the price of corn in the United States represents a conservative estimate of the value of bats. It is relevant to note that because our estimate is based on farm gate prices, we are calculating a change in total revenue, and farmers may bear additional costs to collect and process the additional yield. Further, our fields are unusual, at least compared with surrounding areas, because the farmers do not spray chemical insecticides. In fields not planted with *Bt* crops, insecticides are commonly used to manage corn earworm, but because of the high cost of this application, only when populations of adults or presence of eggs reach outbreak levels (35). Thus, bats may reduce the direct and environmental cost of insecticide use by suppressing adult moth populations below outbreak thresholds, but our economic estimate only addresses suppression of direct damage to crops. This estimate does not consider indirect value related to reduced fungal infestation and mycotoxin concentration, so it may be an underestimate. Conversely, it does not include the effects of pesticides sprayed on crops, which may decrease the estimated value of bats by suppressing pest density and damage. To our knowledge, there are no existing datasets showing the global area of corn managed for corn earworm with insecticides; thus, we did not account for this in our extrapolation. However, corn earworm is managed with *Bt* transgenic hybrids in 32% of corn grown globally, or about 50 million hectares. In cotton, the value of bats to *Bt* crops is estimated to be 38% of the value to non-*Bt* crops (10). We used this value to adjust the value of bats in our experiment for the 50 million hectares of *Bt* corn grown globally.

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