RESEARCH ARTICLE SUMMARY

ECOLOGICAL ECONOMICS

The economic impacts of ecosystem disruptions: Costs from substituting biological pest control

Eyal G. Frank

INTRODUCTION: Scientists have long theorized that declines in biodiversity and continued degradation of ecosystem functioning would lead to meaningful negative impacts on human well-being. Quantifying those impacts is challenging because of the limited measurements available on wildlife and plant populations as well as the ethical and feasibility constraints involved with randomly manipulating ecosystems at scales that would allow for the testing of key theoretical predictions. This work makes a contribution to our understanding of the relationship between ecosystem functioning and human well-being by using a natural experiment—an occurrence resulting from unexpected changes in environmental conditions that approximates a randomized control trial. Specifically, I use the sudden emergence of a deadly wildlife disease in insect-eating bats—known as white-nose syndrome—to quantify the benefits from their provision of biological pest control. I validate previous theoretical predictions that farmers respond by substituting bats with insecticides; however, because those are toxic compounds, by design, this substitution leads to higher human infant mortality rates in the areas affected by the bat die-offs.

RATIONALE: Ecologists have established, through experimental and observational studies, that insect-eating bats can limit crop pest populations. A long-standing prediction has been that if bat populations were to decline, so would their provision of biological pest control, and farmers would have to compensate with insecticides. Epidemiologists and public health experts have been concerned about the health impacts of pesticides even before Rachel Carson's seminal work in *Silent Spring*. The wildlife disease that is killing bats, with mortality rates averaging at above 70%, began spreading in the United States in 2006 as a result of an invasive fungus species. The gradual expansion of the disease provides a setting that approximates random manipulation of bat population levels, which allowed me to estimate how farm operations and human health change differentially before and after a location experiences a negative shock to biological pest control.

RESULTS: I used annual data at the county level on insecticide use and estimated that after the onset of bat die-offs, farmers in the county increase their insecticide use by 31.1%, on average. This demonstrates the substitution between a declining natural input and a human-made input—providing the first empirical validation of a fundamental theoretical prediction in environmental economics. I proceeded to document that infant mortality rates due to internal causes of death (i.e., not due to accidents or homicides) increased by 7.9%, on average, in the affected counties. This result highlights that real-world use levels of insecticides have a detrimental impact on health, even when used within regulatory limits, which highlights the difficulties of assessing the public health impacts of pesticides when regula
them individually.

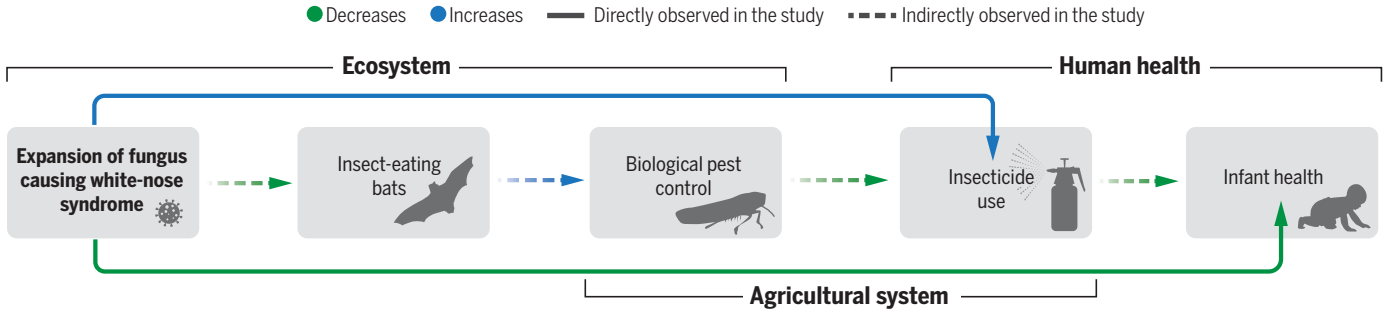
The staggered expansion of the wildlife disease supports the causal interpretation of the results. Any additional alternative explanation would need to change along the expansion path of the wildlife disease around the same timing of its expansion. In additional analyses, I demonstrate that changes in crop composition, in other types of mortality, or in economic conditions fail to explain the observed results, even when controlling for fine-scaled and flexible time trends.

CONCLUSION: These findings help validate previous theoretical predictions regarding well-functioning ecosystems, where interactions between natural enemies—insect-eating bats and crop pests—allow farmers to use lower amounts of toxic substitutes. Not only are these results informative about natural enemy interactions generally, and biological pest control more specifically, they also highlight the direct agricultural and health benefits that bats provide. White-nose syndrome is but one of many threats that bats face, including those that are shared with multiple other species, such as habitat loss and climate change.

Improving our understanding of how changes in biodiversity affect human well-being will be important when designing and implementing conservation policies. These findings inform ongoing efforts, such as pursuing the ambitious goal to place 30% of land and marine areas under protection by 2030, and highlight the importance of continued monitoring of biodiversity levels, as in the assessments released by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. ■

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Schematic framework linking the ecosystem and human health as being intermediated by the agricultural system. The figure depicts the main elements in the study and the theoretical predictions made regarding how (i) bat die-offs due to an invasive fungus species lead to lower provision of biological pest control, (ii) in turn causing farmers to compensate with higher insecticide use, and (iii) resulting in negative impacts on human infant health. The two solid lines highlight the observed relationships examined in this study.

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RESEARCH ARTICLE

ECOLOGICAL ECONOMICS

The economic impacts of ecosystem disruptions: Costs from substituting biological pest control

Eyal G. Frank[1,2,3]

Biodiversity loss is accelerating, yet we know little about how these ecosystem disruptions affect human well-being. Ecologists have documented both the importance of bats as natural predators of insects as well as their population declines after the emergence of a wildlife disease, resulting in a potential decline in biological pest control. In this work, I study how species interactions can extend beyond an ecosystem and affect agriculture and human health. I find that farmers compensated for bat decline by increasing their insecticide use by 31.1%. The compensatory increase in insecticide use by farmers adversely affected health—human infant mortality increased by 7.9% in the counties that experienced bat die-offs. These findings provide empirical validation to previous theoretical predictions about how ecosystem disruptions can have meaningful social costs.

Recent research has documented increases in biodiversity losses (*1*, *2*), which are suggested to have dire consequences on par with climate change (*3*–*5*). Economists and ecologists have repeatedly theorized that the reductions in the abundance and diversity of animals and plants (*6*–*11*) will result in large social costs (*11*–*15*), but well-established empirical estimates for these costs are sorely lacking. Despite growing interest in assessing the economic impacts of ecosystem degradation (*16*–*18*), efforts to quantify these costs are complicated by the difficulties in establishing changes in biodiversity as the cause of economic losses (*19*, *20*). Economic theory on sustainability emphasizes the importance of being able to compensate for the decline in natural capital with human-made substitutes (*21*–*24*). However, it remains empirically unknown whether such substitutions occur and whether they are equivalent to natural inputs in their intended and unintended consequences.

In the absence of rigorous quantitative evidence on the social costs of biodiversity losses, we risk making ill-informed policy decisions regarding the tension between preserving nature or allowing additional economic development at its expense. The vast scale of ecosystems makes it challenging to isolate the effect of a change in ecosystem functioning on human well-being. An ideal experiment would involve randomly manipulating wildlife populations; however, this would rarely be feasible or ethical in practice. As a result, valuations of ecosystems have mostly relied on nonexperimental settings (*16*, *25*). The lack of experimental or quasi-experimental variation limits our ability to interpret valuation studies, even in terms of orders of magnitude.

In this work, I test whether substitutions between natural and human-made capital occur in the context of biodiversity losses. To do so, I quantify the extent to which insecticides can provide an economically viable substitute for natural enemies as biological control agents for insect pests. Bats are widely known to consume large numbers of pest insects, such that in the absence of pest control by bats, farmers might face crop losses unless they compensate with insecticides (*26*, *27*). However, farmers might not experience a decline in biological pest control if other, unaffected species, such as birds, can fill the role, and farmers might not need to increase their insecticide use if they respond by switching to less-vulnerable crops or increasing plot diversity (*27*, *28*). Although the substitution from one form of pest control to another—from bats to insecticides—might allow farmers to compensate for the loss of biological pest control, it might also cause several knock-on effects, such as detrimental health consequences, because agrichemicals, of which insecticides are a subset, have been linked to negative health effects (*29*–*32*).

My empirical approach relies on a natural experiment to recover credible estimates for the role that insect-eating bats perform in agroecosystems and the benefits that they provide. In my analysis, I use the 2006 emergence of white-nose syndrome (WNS)—a fatal disease caused by an invasive fungus species, which has resulted in extremely high mortality rates in bat populations in North America—as a natural experiment. Specifically, I compare how insecticide use, infant health, and farm operations evolve after counties experience bat die-offs relative to counties that have yet to experience them.

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Importance of bats in the provision of biological pest control

Existing research in ecology documents that bats provide biological pest control through their high population size and predation rates on a variety of insects, many of which are crop pests. Insectivorous bats consume 40% and above of their body weight in insects each night (*27*). The contribution of insect-eating bats to biological pest control has been well documented across several settings, where studies have demonstrated that bats limit the growth of insect populations in forests (*33*, *34*) and agricultural plots (*35*), in particular limiting insects that damage produce (*36*). Results from field experiments that prevented bats from accessing treatment plots showed an increase in the densities of arthropods by 59 to 84% in pantropical forests, a 66% increase in fungal growth, and a 56 to 68% increase in leaf damage from moth pests in corn fields in the US "Corn Belt" (*33*–*35*). Studies that mimic bat presence through acoustic signals have documented lower infestation of insects on maize plots and that insects sought fewer mating opportunities, had lowered pheromone excretion, and produced fewer larvae—validating the capacity of bats to limit insect populations beyond direct predatory pressure (*27*).

Damages from crop pests can substantially reduce agricultural productivity. In the US, about 13% of crops are estimated to be destroyed by insects each year (*37*), which represents a loss of $27.6 billion a year. Previous work has extrapolated estimates for single crop types, small geographic areas, and a small number of bat species to suggest that the value of avoided costs due to the pest control provided by bats in the US is between $3.7 billion and $53 billion a year (*26*). Although it provides a rough order of magnitude, the extrapolation assumes that out of the variety of management practices (*27*), farmers will compensate for the decline in bats by using more insecticides; however, the study does not empirically validate this crucial assumption.

Emergence of WNS and its validity as a natural experiment

WNS is an infectious wildlife disease that develops in certain bat species after exposure to an invasive cold-loving fungus species (*Pseudogymnoascus destructans*). The disease receives its name because the fungus grows around the nose of the bat and creates a cluster of white flakes (*38*). The main threat that WNS presents to bats is premature awakening from their hibernation. Facing scarce food supplies and a need for an increased calorie intake because of the low temperatures, infected bats generally do not survive the winter (*39*). By 2010, mortality rates of infected populations were between 30 and 99%, with a mean of 73%, characterized by rapid disease dynamics that

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can lead to local extinctions within 5 to 6 years (*38*). The earliest evidence of WNS in the US, from Albany, New York, dates to February of 2006 (*39*). As of 2024, 12 of the roughly 50 insectivorous bat species in the US are negatively affected by WNS [see (*40*) for the most up-to-date details about affected species and the spatial extent of WNS]. Sequencing the fungus's DNA, researchers have determined that it originated in Europe and was likely introduced accidentally by trade or travel (e.g., brought over on the shoes or backpacks of hikers) (*38*, *39*, *41*).

After the initial detection of WNS, every year, new counties become classified as WNS counties (Fig. 1). The pattern of county contagion appears to follow the migration path of bats as well as hiking trails along the Appalachian Mountains. The expansion of WNS remains a complex function of environmental conditions, host genetics, and behavioral responses of both bats and people (*42*), which makes it difficult for ecologists to predict its expansion. Because the fungus can survive even without an available bat host, an exposed county remains in exposed status even when bat populations have been extirpated. However, because the fungus has an upper temperature limit of 20°C (*43*) and is extremely sensitive to ultraviolet light (*44*), it is unlikely to survive outside the caves that bats use during the day and throughout the winter.

The sudden and unexpected emergence of WNS provides a natural experiment that approximates an ideal experiment where counties get fully randomly assigned to high or low bat population levels (*45*). In this setting, the natural experiment plausibly provides "good as random" assignment with respect to county and farm characteristics, but the spatial configuration of counties plays a role in determining WNS status. This approach builds on previous use of natural experiments in environmental settings (*46*) as well as their suitability in studying keystone species (*6*, *47*). As the fungus expands its range each year, more counties become affected by WNS (fig. S1 summarizes the number of WNS-susceptible bat species across counties, and fig. S4 summarizes the growth in the number of WNS counties each year). This allowed me to estimate the effects of declining bat populations on the outcomes of insecticide use, infant mortality, and farm operations (hereafter, outcomes of interest) as a function of time since exposure to WNS (see Materials and methods summary section for more details).

The effects of declining biological pest control after bat population losses

Evidence for higher insecticide use after bat population losses

Insecticide use increased in the years after WNS detection relative to that in non-WNS counties (Fig. 2A, positive event-time coefficients; to the right of the dashed line). Insecticide use in WNS-confirmed and non-WNS counties did not trend differently in the years before the emergence of WNS (Fig. 2A, negative event-time coefficients; to the left of the dashed line). The unexpected invasion of the fungus and difficulties in predicting where WNS will develop—approximating random perturbations to bat population levels—support a causal interpretation of these findings. Focusing on the post-WNS period and pooling event-time coefficients in 2-year intervals allowed me to increase the precision of the estimates (table S3), which allowed me to reject the null hypothesis of no change at the 95% confidence level for each of the estimated coefficients.

After WNS detection, insecticide use was about 1 kg/km^2 higher in the WNS-confirmed counties compared with the non-WNS counties, relative to the year before WNS detection. After more than 5 years from initial exposure, insecticide use was, on average, more than 2 kg/km^2 higher. These results reflect substantial increases, above 25%, relative to a mean of ~8 kg/km^2. Increasing compensatory behavior by farmers is consistent with both increasing bat die-offs as well as farmers learning about the new pest pressure over time and adjusting to it.

The results hold when I control for weather controls or change the sample weights (table S4), when I allow time trends to change flexibly at the state level instead of the census region level (fig. S7), when I include substate linear trends (figs. S2, S3, and S8), or when I limit the sample to include non-WNS counties that are closer to the WNS counties and, as a result, are a potentially better comparison group. I verify that fungicide and herbicide use do not see a similar increase in WNS counties (fig. S10) because they do not directly substitute for biological pest control as insecticides do.

Evidence for higher infant mortality after bat population losses

Insecticide use is one source of agrichemical pollution that has been linked with negative health outcomes (*29*–*32*). Wind and water erosion can carry pesticides off of the target field, generating off-farm exposure (*48*, *49*). Insecticides are transported away from the farms, contributing to ambient levels of agrichemical pollution. Overall detections of insecticides in water samples across the US, including those not adjacent to farms, are higher during the agricultural production season of April to September (fig. S11), reflecting potential exposure to insecticides away from the targeted fields.

To test for the potential health consequences of increased insecticide use, I used county-level data on annual infant mortality—commonly

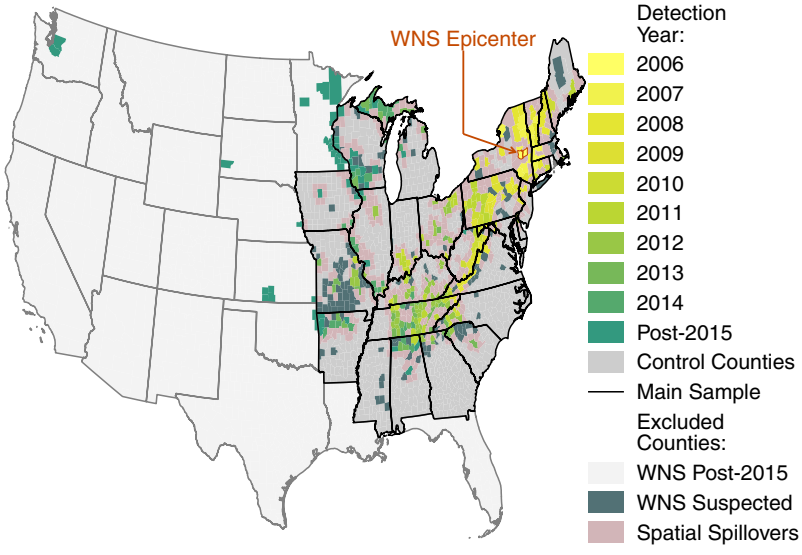


Fig. 1. Expansion of WNS across counties in the United States. This map (using the Lambert azimuthal equal-area projection) shows the official detection year, as classified by the Fish and Wildlife Service from 2006 to 2018, of WNS in each US county. The main sample (counties in states with a solid black line) in the analysis compares the counties that are classified as WNS-confirmed counties (highlighted in yellow to green) with counties in states that had at least one WNS-confirmed county by 2014 (shown in dark gray). The main analysis excludes counties in states with the first WNS detection after 2014, where only the fungus is detected and counties are WNS suspected, or the non-WNS counties that are adjacent to the WNS-confirmed counties where spatial spillovers might affect the counties. In total, the sample contains 1185 counties, in 27 states, where 245 counties ever become exposed to WNS.

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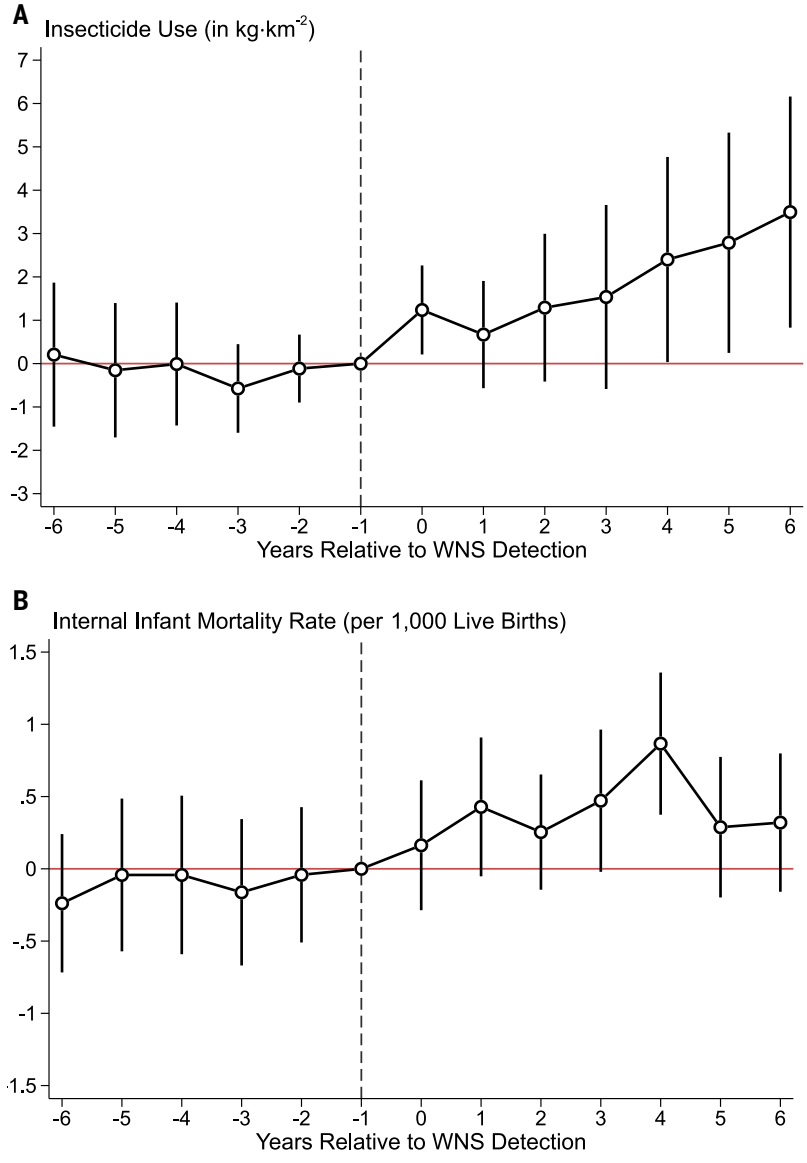


Fig. 2. Increase in insecticide use and infant mortality after WNS detection. (**A** and **B**) Each panel shows the regression results of comparing insecticide use (A) or IIMR (B) between counties that experience bat die-offs, before and after the bat mortality shocks, with counties that do not experience them. Each dot is a coefficient from the regression, and each line shows the 95% confidence interval. Insecticide use is weighted by the number of 2002 cropland acres, and the IIMR is weighted by the number of live births.

used to study negative health impacts of environmental pollution (*29*–*32*)—due to internal causes (not accidents or homicides). I found that the internal infant mortality rate (IIMR) increased in the years after WNS detection (Fig. 2B). As with the results on insecticide use, there does not appear to be a systematic difference between WNS-confirmed and non-WNS counties in the years before WNS detection (the coefficients to the left of the dashed line, pre-WNS years, are all close to zero, contain zero in their 95% confidence intervals, and do not appear to systematically increase as the counties approach their switch to confirmed WNS status). In addition, mothers giving birth before and after WNS emergence are similar in terms of a set of observable characteristics (fig. S12).

In additional analyses, I confirmed that the results hold when I control for weather, control for population shares in different age groups, and use different sample weights (table S5). For completeness, I also report nearly identical results for the infant mortality rate (IMR) that pools internal and external causes of death (table S6) and report that there is no difference in the IMR due to external causes of death (table S7). External causes of death (accidents and homicides) provide a placebo because we would have no reason to expect that bat die-offs and increased insecticide use would affect those outcomes. The fact that IMR due to external causes of death does not change in WNS counties also helps to alleviate any concerns about changes in vital statistics measurement that are somehow systematically correlated with the spread of WNS. Finally, I report no meaningful changes to other birth outcomes, such as birth weight, gestation, and other metrics of newborn health (table S8). This is in accordance with other studies that have detected higher IMR due to environmental pollution but saw no change in other birth outcomes (*50*, *51*). On average, insecticide use increased by 2.7 kg/km^2 (Fig. 3A), and the IIMR increased by 0.54 deaths per 1000 live births (Fig. 3B) after WNS emergence, reflecting increases of 31.1 and 7.9% relative to the mean levels in the population-weighted sample. This suggests that when insecticide use increased by 1%, the IIMR increased by 0.25%.

These findings agree with previous estimates on environmental pollution and infant health. Using the same data for infant health, earlier work has estimated that a 1% decline in ambient air pollution levels led to a 0.3% decline in the IIMR (*50*). Work focusing on agricultural water pollution in India found that a 1% increase in agrichemicals in the water led to a 0.46% increase in infant mortality (*28*). Recent studies examining the impacts of higher pesticide use have estimated increases in infant mortality, in deaths per 1000 live births, of 0.31 in the US and 0.93 in Brazil (*31*, *32*).

Evidence for lower farm profits after bat population losses

Changes in biological pest control could lead farmers to change the amount of land under cultivation. If the increase in insecticide use fails to fully substitute for the quality of pest control provided by bats, then crop quality might degrade, leading to lower crop revenue. To test for these impacts on farm operations, I estimated the effects of WNS emergence on chemical expenditures, land in agricultural production, and crop sales that aggregate agricultural crop production in dollar terms.

I did not find evidence that the percent of land used for cropland cultivation or the percent of harvested acres changed by a meaningful amount (Fig. 3C). However, although farmers might be planting and harvesting at levels similar to those before WNS emergence, the productivity and value of those crops might decline because of higher insect pest pressure.

Damages from insect pests could lower the quality of the agricultural output even when overall production does not decrease substantially, resulting in lower prices paid to the farmer and lower revenue. Documenting the effect of environmental conditions on crop quality is challenging because we often lack

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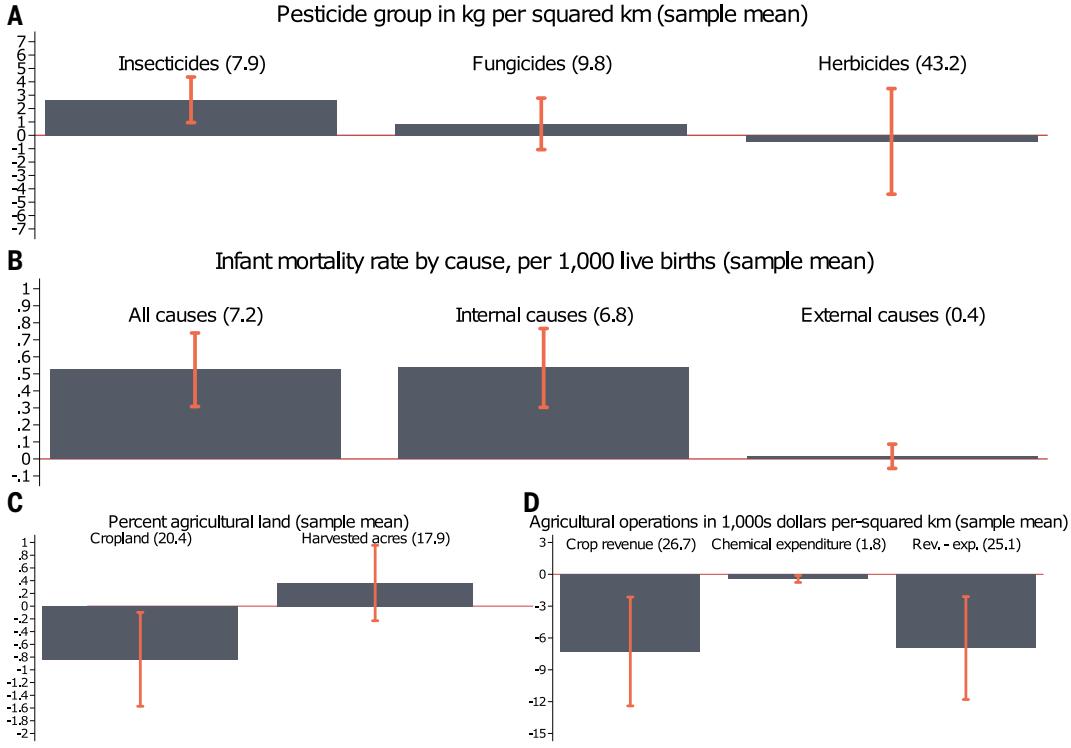


Fig. 3. Average changes in pesticide use, infant mortality, and farm operations between WNS and non-WNS counties before and after WNS introduction. This figure summarizes the differences between WNS counties and non-WNS counties after the exposure to WNS. Each panel reports the coefficient and 95% confidence interval from a separate regression. (**A**) Results for the different pesticide classes. (**B**) Results for IMRs by all causes, internal causes, or external causes. (**C**) Results for agricultural land areas. (**D**) Results for farm operations (total crop revenue, total chemical expenditure, and the difference between the two). All observations are population weighted.

detailed data on crop quality and prices paid to farmers. However, previous work has established that a decline in apple quality due to extreme weather conditions has led to a larger negative impact on farm revenue compared with a reduction in yield (*52*).

I estimate that in the years after WNS detection, crop revenue—measured in thousands of dollars per square kilometer—dropped by 7.96 (Fig. 3C), reflecting a decline of 28.9% relative to the mean. The findings on lower crop sales agree with recent research that has documented a 2.5% decline in agricultural land rental rates in counties where bat populations were negatively affected by WNS (*53*). Chemical expenditure, which accounts for all agrichemical inputs, such as pesticides and fertilizer, dropped by 23.4%, but this is relative to a lower baseline amount relative to crop sales such that the change in levels is much smaller (a drop of less than 1000 dollars per square kilometer).

Although I would have expected to see an increase in chemical expenditure because of the increase in insecticide use, the net drop in chemical expenditure is consistent with the notion that farmers maximize profits not yields. In other words, farmers might increase their insecticide use until the point where the marginal benefit is at least as high as the marginal cost. Farmers could also substitute by reducing one chemical class and increasing another. Because marginal benefits are often assumed to be diminishing but marginal costs are increasing, and we observe declining revenues, the new optimal input use might be lower and, as a result, lower overall chemical expenditure. In additional analyses, I found inconclusive evidence for input substitution. I estimated a sharp decline in herbicide use in WNS-confirmed counites—consistent with farmers substituting one input for another to maintain costs constant—when weighting the sample by baseline acres (fig. S10B) but not when using population weights (Fig. 3A).

Through a variety of additional tests, I explored different dimensions of heterogeneity, such as species richness—where counties with more susceptible species might experience a larger reduction in biological pest control—and estimated WNS severity (tables S9 to S11) and examined the magnitude of the spatial spillovers (table S12) as well as the degree to which spatial correlation affects the precision of the estimates (table S13). I report results for changes in a variety of crop yields (fig. S13); yet, data limitations limit the interpretation of those results. I confirm that it is spatial proximity to a WNS-confirmed county and not the lagged values of the outcomes that have predictive power for the expansion of WNS (table S14), address potential confounders (figs. S14 and S15 and tables S15 to S23), and verify that the results are not sensitive to the composition of the sample (figs. S9 and S16) and that the results are not driven by spurious correlation (fig. S17) as well as using alternative estimators (fig. S18 and table S24). Finally, I report analysis for insecticide use that also incorporates toxicity indicators (figs. S19 to S21 and table S25).

Discussion

Disruption to biological pest control has a meaningful impact on human well-being. I demonstrate how declines in insect-eating bat population levels induce farmers to substitute with insecticides, consequently resulting in a negative health shock to infant mortality. These findings provide empirical validation to theoretical predictions in ecological, agronomic, and epidemiological studies. An important contribution I make relative to prior work is using an emergent wildlife disease, WNS, as an approximation to an experiment that would have randomly manipulated biological pest control by bats.

I evaluate the magnitude of the losses attributable to the decline in bat populations and estimate total agricultural losses, crop revenue, and chemical expenditure on the magnitude of $26.9 billion (2017 dollars) for the

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WNS-confirmed counties across the 2006-to-2017 period. To anchor this magnitude, consider that crop revenue across the entire US in 2017 alone was around $190 billion (2017 dollars). For the health damages, I use the US Environmental Protection Agency (EPA)'s recommended central mortality risk reduction value (also referred to as the value of statistical life) of $9.24 million (2017 dollars) and estimate that the additional 1334 infant deaths reflect damages valued at $12.4 billion. Combined, these amount to damages of $39.4 billion, or $1932.20 per capita, in the WNS-confirmed counties from 2006 to 2017 (see the supplementary materials for more detailed calculations). The findings in this Research Article highlight two policy implications: monitoring and regulating agrichemical pollution levels and the conservation funding and protections for bat populations.

Increasing the capacity to monitor chemical pollutants could allow for more precise research on the health effects of pesticide exposure. Currently, legislation around pesticides regulates compounds individually. This means that various permutations are not tested, and as a result, we have only observational data to alert us to the effects of agrichemical mixtures. Our ability to learn about these mixture effects could greatly improve if pesticide use data became more readily available at more fine-scaled spatiotemporal resolutions.

Bat populations face a combination of threats owing to land use changes that degrade their habitats, the expansion of onshore wind energy (*54*), and heightened sensitivity to the impacts of climate change (*55*). Because bats have a low fecundity, any losses that we experience today might require several years, if not decades, of efforts to rebuild bat populations. If the costs of conserving bat populations are low and damages from our currently best-available substitutes for their biological pest control—pesticides—are high, then conserving bats can be beneficial for society. Additional funding for wildlife population monitoring and evaluating mitigation strategies for the adverse effects detailed above could greatly contribute to stabilizing and recovering bat population levels.

Beyond the specific empirical setting in this study, we stand to gain a few broader insights. These findings will likely generalize to other locations that will become negatively affected by WNS—because it is still spreading—as long as those are similar in terms of their ecosystem and agricultural characteristics. Even outside of North America, the results of this analysis inform us about the value of biological pest control, namely from bats. More broadly, the evidence in this work demonstrates that natural enemy interactions in ecosystems can generate meaningful impacts on human well-being. However, broad applicability has clear limits. It is important to note that the estimates regarding how farmers respond to bat die-offs reflect short-term economic effects and responses, to which farmers might adapt differently over longer time horizons, especially if newer technologies become available. It would be almost impossible, and ill-advised, to use these results to evaluate how the vast patterns of changes in biodiversity—e.g., the declines in insect populations or the reintroduction of apex predators—create costs and benefits through socioecological channels.

Contributing to a growing body of work on quantifying the value of nature, this study demonstrates the usefulness of quasi-experimental methods to overcome the challenges in studying the importance of species and ecosystem functions. Disruptions to ecosystems and wildlife populations present us with an opportunity to learn more about what is lost in their absence. Given the limitations of field experiments, natural experiments allow us to gain an approximation of those ideal experimental conditions. The implementation of quasi-experimental methods in this work builds and extends on previous work by combining knowledge and tools from ecology and economics to provide credible estimates for the social costs of biodiversity losses and the pathways through which they operate.

Across many species and ecosystems, making informed decisions about conservation policies and priorities requires a rigorous evidence base. Even if manipulating wildlife populations across large areas is not feasible, we can still use other sources of disruptions to ecosystem functioning to learn about their importance to humanity.

Materials and methods summary

I used ordinary least squares regression to link the outcomes of interest at the county-year level (see table S2 for summary statistics and fig. S5 for a summary of the trends in each time series). In the main sample, I include counties that either get classified as WNS counties or counties that do not get classified as WNS counties and are at least one neighboring degree of separation from WNS counties. In other words, I exclude non-WNS counties adjacent to WNS counties. In addition, I restrict the sample to counties that reside in states that had counties classified as WNS counties by 2014. Finally, I exclude counties classified as suspected of being affected by WNS because their status is ambiguous.

To estimate how the outcomes develop in the years before and after the arrival of the fungus and the emergence of WNS in that specific county, I include binary variables that represent the leads and lags from the timing of WNS onset (see fig. S6 for results that examine delays in WNS detection). This research design is often referred to as staggered difference-in-differences. When counties switch from a non-WNS to a WNS county, they enter the treatment group, and they are compared with counties that never enter the treatment group or those that enter later in the sample. The regression captures how the outcomes evolve over time in two sets of counties (WNS and non-WNS) before and after the change in WNS status. Although counties have different spatial configurations in terms of how many neighboring counties are in WNS or non-WNS status, the regression focuses on the temporal switching from non-WNS to WNS status and does not adjust for the spatial structure of WNS in neighboring counties. Specifically, I report estimation results from a regression specification of the following form

$$y_{ct} = \Sigma\beta_{\tau}\mu_{ct} + \lambda_{c} + \delta_{rt} + \varepsilon_{it}$$

The dependent variable is at the county-year level, except for outcomes obtained from the agricultural census, which is available at the county level in 5-year intervals. The set of binary indicators μ_{ct} are equal to one when the county is τ years away from becoming classified as a WNS county; they are zero otherwise. This means that they are always zero for non-WNS counties. The regression performs a double-demeaning at the county- and census region–by-year levels. This is achieved by including a set of binary variables for each county- and census region–year pair, λ_{c} and δ_{rt}, respectively. The standard errors are clustered at the county level.

In the regression results, each coefficient, β_{τ}, represents the difference in means between WNS and non-WNS counties. These differences are interpreted relative to a reference level of the difference in means in the year immediately before WNS emergence. The interpretation here is that small and imprecise coefficients are capturing the pattern of WNS and non-WNS counties evolving along parallel trends (in other words, not having differential trends before the onset of WNS), but if the WNS counties begin to diverge from the non-WNS counties, those coefficients become significantly different from zero.

The key assumptions for causal interpretation of the coefficients obtained from this research design are that (i) counties would have had their outcomes evolve along parallel trends in the absence of WNS exposure, (ii) the ongoing expansion of WNS is quasi-random conditional on lagged outcomes, and (iii) non-WNS counties are not experiencing spillovers from the WNS counties. The first assumption is supported by, but cannot be directly tested, the coefficients on the leads being close to zero and not exhibiting a pretrend. The second assumption is supported by results that fail to find that lagged outcomes predict WNS status (table S14). The third assumption is more plausible after excluding the non-WNS counties

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that are adjacent to WNS counties (see table S12 for evidence of spatial spillover to adjacent counties). For more details, see the methods section in the supplementary materials.

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SUPPLEMENTARY MATERIALS

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