Environmental Science & Technology
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Economic Dependence and Vulnerability of United States Agricultural Sector on Insect-Mediated Pollination Service

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Cite This: Environ. Sci. Technol. 2021, 55, 2243−2253

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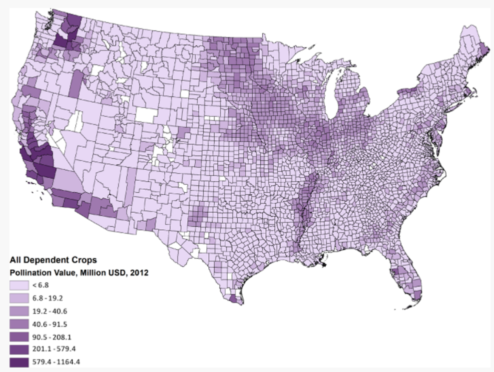
ABSTRACT: Deficits in insect-mediated pollination service undermine ecosystem biodiversity and function, human nutrition, and economic welfare. Global pollinator supply continues to decline, while production of pollination-dependent crops increases. Using publicly available price and production data and existing pollination field studies, we quantify economic dependence of United States crops on insect-mediated pollination service at the county level and update existing coefficients of insect dependence of sample crops when possible. Economic value dependent on pollination service totals 34.0 billion USD in 2012. Twenty percent of US counties produce 80% of total economic value attributable to insect pollinators. We compile county-level data and consider the spatial relationship between economic value dependent on insect-mediated pollination, region-specific forage suitability, and crop-specific agricultural areas within US landscapes. We identify vulnerable, highly dependent areas where habitat for wild pollinators has been reduced. These results can help inform future efforts to conserve and bolster managed and wild pollinator populations to ensure sustainable production of key agricultural crops.



■ INTRODUCTION

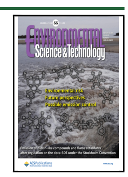
Ecosystem goods and services (derived from the world's natural capital) are critically important in sustaining human and industrial activity, yet remain consistently undervalued and underappreciated. One of these crucial ecosystem services is pollination mediated by animals, including both wild and managed species. Often considered to be inexhaustible, natural systems can be limited and degraded, and services can indeed be exhausted beyond their rate of replenishment.[1−3] More than 75% of global food crops depend on animal-mediated pollination, in some capacity, for yield and/or quality.[4,5] This accounts for a little more than one-third of global crops by production volume, but perhaps even more critically, these crops are some of the most nutritionally rich foods, including many fruits, vegetables, seeds, nuts, and oils.[5,6]

The majority of pollination service by animals is performed by insects including widely managed *Apis mellifera* and *Apis cerana* (honey bees), bumble bees, and solitary bees as well as unmanaged pollinators such as wild bees, flies, butterflies, moths, beetles, wasps, thrips, ants, and midges.[5] Crop yield (of both fruit and seed) and quality (such as color, nutrition, and shape) depend on pollinator abundance as well as pollinator species diversity. While the demand for pollinator-dependent crops has increased by 300% in fifty years,[7] populations of insect pollinators have exhibited extensive decline in many regions because of interacting stress factors including loss in habitat, poor nutrition (due to lack of abundance and diversity of flowering plant species), climate change, pests, parasites, pesticide use,[8] as well as management and transport practices.[5]

In addition, declines in insect populations have been recorded across the globe,[9] including in protected natural areas,[10] with nearly half of all evaluated insect species declining rapidly and a third facing threat of extinction.[11] Furthermore, the yield of pollination-dependent crops has been unstable compared to pollination-independent crops.[5,12] In addition to farming sectors, numerous other industry sectors depend upon pollination by insects indirectly (e.g., medicine, biofuels, processed food, fibers), potentially making them vulnerable to decline of insect pollinators.[6,13] Furthermore, insect pollinators support other vital ecosystem functions such as structuring ecological communities to support biodiversity and disease control as well as provide cultural and recreational benefits.[5,14,15]

Economically, the value of insect pollinators is apparent in the agricultural sector where there is a well-established connection to the beekeeping industry through buying or renting colonies of bee species and where the management or upkeep of those colonies is a common agricultural production practice. In previous research, crop dependence on insect pollinators and the economic value of insect pollination has

Received: July 18, 2020
Revised: January 13, 2021
Accepted: January 14, 2021
Published: January 26, 2021



https://dx.doi.org/10.1021/acs.est.0c04786
Environ. Sci. Technol. 2021, 55, 2243−2253

been calculated using limited field data.[16] In the case of Klein et al., global crop dependence on insect pollinators was determined broadly, assigning categorical values of essential, high, modest, little, no, or unknown insect dependence [based on a proportion of crop (fruit or seed) yield or fruit set and expert opinion].[4] These proportion values are referred to as dependence coefficients. In the cases of Free[17] and Delaplane and Mayer,[18] the mechanics and biology of crop pollination were described without quantification of dependence. Dependence coefficients were determined as point estimates by Robinson, Southwick and Southwick, and Calderone.[19−21] Overall, the data used in these studies were not necessarily generated from detailed assessment of pollination biology of a specific crop system (meaning, how pollinator visits or activity correlates with fruit or seed set) nor did they consider variation in crop cultivar, crop growth conditions, pollinator density, or surrounding landscape and weather conditions. Thus, these evaluations lack uncertainty estimates and are largely qualitative. Moreover, most previous estimates often focused on managed honey bees,[19,21,22] neglecting significant contributions of wild insects whose conservation stabilizes pollination efficacy and reduces demand from the honey bee industry. Others have applied a similar production value methodology to estimate the economic production value that depends on wild pollinators.[14,23] Alternative value methodologies based on the cost of replacement of pollination service by manual or hand pollination[24] or based on the change of consumer and producer surpluses of pollination-dependent crops have also been utilized.[21,25]

There is also considerable spatial variation in crop production systems and availability of pollination services from wild populations. Lonsdorf et al. developed a model informed by landcover data estimating wild bee relative abundance across the United States and demonstrated considerable variation.[26] Koh et al. utilized this bee abundance model to spatially evaluate demand for wild bees in the US.[27] Not an economic analysis, the "demand" component of the Koh et al. study is based on acreage of pollination-dependent crops grown in the US available in the United States Department of Agriculture (USDA) Cropland Data Layer (CDL), which gives high-quality spatial resolution. However, previous studies of the economic valuation of pollinators have not been conducted at this spatial resolution. Studies instead have an aggregated value at an international or national scale (which can dilute region-specific information) or at a finer scale with limited scope within local ecosystems, farms, or states (which can be impractical for assessment in other locations).[23,28]

Here, we build on previous work on economic valuation of pollination systems by including more detailed analyses of economic dependence on pollinators, supported by data reported in the scientific literature. Through extensive literature review, we update existing dependence coefficients when possible with quantitative estimates of crop dependence and associated uncertainty of the estimate, determined using robust statistical methods. We take a rigorous approach to determining the national economic value of pollination in terms of production value using publicly available USDA Census of Agriculture acreage data and National Agricultural Statistics Service (NASS) survey yield and price data. We provide high spatial resolution (county-level) of the economic value to agriculture dependent on pollinators and report uncertainty for this value derived from thorough simulations. Moreover, we integrate this information with the CDL and evaluate pollinator dependence and value with previous published model of wild pollinator abundance from Lonsdorf et al.[26] to identify counties in the United States especially vulnerable to pollinator decline. Overall, our studies considerably increase understanding of the economic dependence on pollination service by insects in terms of magnitude, spatial resolution, and commodity class. To the best of our knowledge, we report the first comprehensive estimates of economic dependence on insect-mediated pollination at the county-scale. Additionally, the integration of economic dependence for insect-mediated pollination with measures of bee abundance, thereby specifically highlighting areas of economic concern, is unprecedented in the literature.

■ MATERIALS AND METHODS

Accompanying this detailed outline of methodology is a flowchart of significant methodological steps for visual aid, available in the Supporting Information(Figure S2).

Calculating Dependence Coefficients. Approximately, 352 available crop commodity pollination studies were reviewed for the 25 most valuable pollination-dependent crops according to the Food and Agriculture Organization of the United Nations (FAO) 2012 United States Gross Production Value (GPV) estimates (Table S3). Data from 2012 was used as this is the most recently available Census of Agriculture year, and FAO data was used over USDA production estimates for their ease of reporting and compiling in this stage of research. Crops can be directly dependent on pollination service mediated by insects for yield and/or quality of the commodity of the crop such as the flesh of the apple for apples or the nut for almonds. Indirectly dependent crops are dependent on pollination for seed but not for the commodity of the crop. For example, alfalfa and onions are dependent on pollination for seed set, not for the growth of hay for alfalfa or bulb for onions. Indirectly dependent crops are represented as italicized in Table S3. The economic value of pollination for indirectly dependent crops is inherently more difficult to assess due to no direct measure of the commodity that is influenced by pollination. For example, fruit yield is measurable but not affected by pollination. Seed set is also measurable but not the basis for the economic value of the commodity. Thus, determining how much of subsequent fruit yield is dependent on seed dependence on pollination service is complex and indirect. We have chosen to remove alfalfa from analysis as an indirectly dependent crop with high economic value for alfalfa hay, which is not in one generation dependent upon insect-mediated pollination service. It is such a high value crop (18.6 billion USD, 2012[29]) that it overtakes the resulting analysis. The 17 crops represented in the data account for 82% of the total GPV of the 25 most valuable pollination-dependent crops.

To find field study data, we first searched the extensive EndNote database of pollination biology publications (more than 13,000 publications) compiled and continuously updated by Dr. David W. Inouye of the University of Maryland with each common and scientific crop name. Studies were retrieved from the database based on the title of the article when indicative of a field study of the crop and insect pollinators. We also searched the library system of the University of Pittsburgh using its online PittCAT interface using key terms of the crop name (common and scientific), "pollination," or "pollinator." For inclusion, articles must have had a comparison of fruit set

https://dx.doi.org/10.1021/acs.est.0c04786
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Table 1. Pollination Dependence Coefficient Estimates of Select Crops by Source[4,19,21,36−51a]

indirect/direct	commodity	no. studies	no. cultivars	no. estimates	bootstrap (this study)	SW	Cald	Klein et al.
D	apple	3 (1)	1+ (1+)	56 (46)	0.91 [0.87−0.94]	0.8	1.00	0.65 [0.41−0.89]
D	avocado	2 (1)	4 (3)	4 (3)	0.43 [0.18−0.73]	0.2	1.00	0.65 [0.41−0.89]
D	blueberry	6 (6)	∼11 (∼11)	18 (18)	0.73 [0.59−0.85]	0.7	1.00	0.65 [0.41−0.89]
I	onion	1 (1)	2 (2)	20 (20)	0.91 [0.87−0.94]	0.3	1.00	
D	soybean	1 (0)	1 (0)	3 (0)	0.37 [0.37−0.37]	0.01	0.10	0.25 [0.11−0.39]
D	strawberry	2 (1)	3+ (3)	15 (6)	0.37 [0.19−0.57]	0.3	0.20	0.25 [0.11−0.39]
D	sunflower[b]	1 (0)	1+ (0)	10 (0)	0.96 [0.89−0.99]	0.8	1.00	0.25 [0.11, 0.39]

[a]I: indirectly dependent crop (commodity of crop not dependent on insect-mediated pollination). D: directly dependent crop (commodity of crop not dependent on insect-mediated pollination). No. studies: number of studies represented in the estimate (US studies). No. cultivars: number of cultivars represented in studies used, + indicates unknown number of additional cultivars such as when "Various" reported (cultivars from US studies). No. estimates: number of dependence coefficient (D) estimates used in bootstrapping analysis; estimates of D come from paired fruit set values within the study composed of fruit set excluding pollinators and fruit set under open pollination circumstances. Bootstrap: derived by bootstrapping method using existing field study data mean (95% CI) (current study). SW: Southwick and Southwick, 1992. Cald: Calderone, 2012. Klein et al.: Klein et al., 2007; categorical estimate Monte-Carlo mean (95% CI). [b]Sunflower bootstrapped values were calculated using this methodology, but the Monte Carlo values were used in this study as described in the Materials and Methods section.

or crop yield under open pollination conditions with fruit set or crop yield under pollination exclusion conditions. It is not clear in each study that pollinators were abundant enough to suggest saturation (i.e., no pollinator limitation); however, open pollination conditions were that with a mix of both ambient pollinators (wild) and honey bees (managed) present (as is typical of an agricultural setting).

Of the more than 325 studies reviewed, 16 studies spanning 7 crops met these criteria and were used for analysis. N estimates of dependence coefficients (Table 1) per each crop were used to resample for uncertainty analysis. Each of the N estimates are derived from a pair of yield/fruit set (open pollination, pollination exclusion) for a given crop from which a dependence coefficient could be calculated using the equation[16]

$$D = 1 - \frac{f_{pe}}{f_{op}} \tag{1}$$

D: dependence coefficient; f_{pe}: fruit set of commodity under pollinator exclusion conditions; f_{op}: fruit set of commodity under open pollination conditions.

Dependence was not estimated for crops for which there was insufficient field study data (<3 estimates) available in the literature. The dependence of at least one representative crop from each classification group (Supporting Information, Table S2) was determined. The main cultivars of rapeseed and soybean grown in the US are autogamous and therefore do not need insect-mediated pollination service; however, there is some controversy on this topic as both crops have shown some yield benefits in specific settings and as both remain important forage for insect pollinators.[18,30−33] With large field crops like these, the edge of the field benefits from the ecosystem service while the center of the field receives little if any benefit. This can cause smaller field studies on open pollination to give an inflated estimate of fruit set effects and subsequently our dependence calculation. Others have adjusted for this common overestimation.[27] Not wanting to make a capricious adjustment of dependence, our study makes no adjustment and instead cautions the reader when reviewing the analysis.

Crops with $N \geq 3$ estimates of dependence coefficients (six crops) underwent bootstrapping analysis to derive a mean dependence coefficient and two-sided 95% confidence interval (CI) after 10,000 resamples with replacement. For crops with $N < 3$ estimates of dependence coefficients and crops with limited field study literature (56 crops), the range of dependence described in Klein et al. for that crop was treated as a uniform distribution for Monte Carlo estimation of the mean dependence, and the two-sided 95% CI was calculated sampling 1000 times with replacement. For crops with no dependence coefficient described by Klein et al. but described by either Calderone (2012, six crops) or Southwick and Southwick (1992, five crops), a point estimate of dependence coefficient from these sources was used, using the most recent estimation[19] first (Supporting Information, Table S4).

Economic Valuation of Crops. This work uses a production value method to calculate the economic value of the crop production dependent upon insect-mediated pollination. Using Python scripting, acreage data were obtained from the 2012 USDA Agricultural Census, and yield and price data were obtained from the 2012 NASS survey. The agricultural census data gives a more rigorous, county-level estimate than the yearly NASS survey, which therefore leads to a representation of that crop's value at a higher spatial acuity. Acreage harvested (vegetables) or bearing (fruit), yield, and price data for pollination-dependent crops for the 2012 year were compiled for each county (acreage and yield) or state (price) when available. When unavailable, values were estimated using state-level, other states, or national-level data for 2012 in that order. If 2012 price or yield data were not available, data from a previous year up to 2007 were used with several exceptions utilizing 2001 data. The product of the harvested or bearing acreage, yield, and price data were used as the total economic value for each pollination-dependent crop for a given county in the US.

Valuation of Economic Dependence on Insect Pollination. The pollination value was calculated using a bootstrapping method modified from that described in the previous section. The product of the total economic value (previous section) and the dependence coefficient of the crop sampled randomly with replacement from either the field data pool (6 crops), a uniform distribution between the range estimated by Klein et al. (56 crops), or the point estimates given by either Calderone (6 crops) or Southwick and Southwick (5 crops) was used to calculate the pollination value for the crop in this county. The sum of the pollination value for each crop grown in the county is the total pollination value for that county. This total pollination value was calculated 1000 times for each county, state, and the national value, and the mean and CI of each pollination value were

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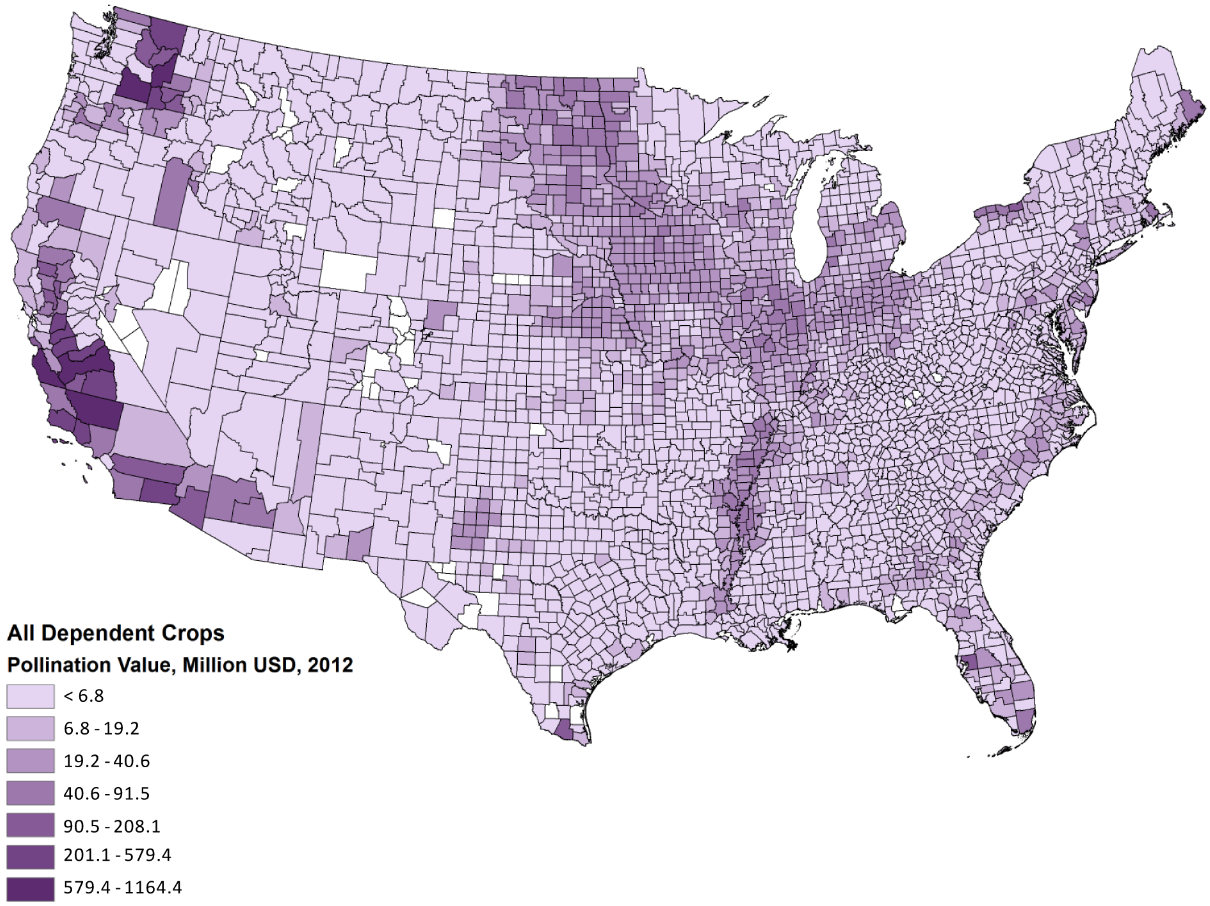

Figure 1. Average total pollination value mediated by insects both directly and indirectly, in billions USD (2012) per county. White counties indicate a pollination value calculated from values that are lower than USDA reporting thresholds.

derived from the empirical distribution of the sample mean. Coefficient of variation (CV %) is reported for the pollination value at the county level (Supporting Information, Figure S3). Crop economic data for directly dependent crops was aggregated for each county according to FAO crop classification into four categories, fruits and nuts, vegetables and melons, oilseed, and other (Supporting Information, Table S2) by the same bootstrapping methodology (1000 times with replacement). The economic value dependent on pollination service by insects was plotted spatially using ArcMap and GIS with an Albers Conical projection (Figures 1 and 2).

Determining Regions of Economic Vulnerability. The spatial model of relative wild bee abundance used in this study combines expert knowledge with spatial land cover data, nesting, and floral resource assumptions and was used to make assessments of regional vulnerability.[26] The relative bee abundance given by this model was compared with economic dependence to identify US regions with low relative bee abundance that also have high direct economic dependence on pollination services. These areas have high vulnerability to pollinator declines and losses.

RESULTS AND DISCUSSION

Identification of Published Studies Quantifying Pollination Dependence Coefficients. One of our goals was to develop estimates of the pollination dependence of US crops using data generated from the scientific literature and a statistically explicit method of calculation. Though the methodology used to achieve these estimates is broadly useful, there is a general lack of data for many crop cultivars that limit our understanding of pollination dynamics and complicate significant improvement of existing dependence coefficients. Using a systematic approach to screening the scientific literature, we identified field studies which provided quantitative comparison of fruit or seed set of pollination-dependent crops grown in the absence of pollinators and in circumstances of open pollination (as is typical of an agricultural setting). Of 75 insect pollination-dependent crops, only 7 had available field studies with information for quantitative estimation of crop dependence coefficients (Table 1). This highlights the lack of systematic field studies to understand crop dependence on insect pollination and underscores the need for additional studies, a trend common in entomological science[34] in order to fully understand crop dependence, although these field studies can be temporally and financially expensive. The incorporation of computational research methodology and more cost-effective data-driven approaches with quantification of uncertainty may enhance the practicality of this level of understanding. In addition, focusing systematic field study efforts on a select, highly valuable (in terms of pollination value) subset of crops would mitigate some temporal and financial cost while being highly informative for the uncertainty associated with the total pollination value.[35] The crop dependence coefficients determined using field study data showed no distinct pattern compared to previous estimates; in some cases, coefficients

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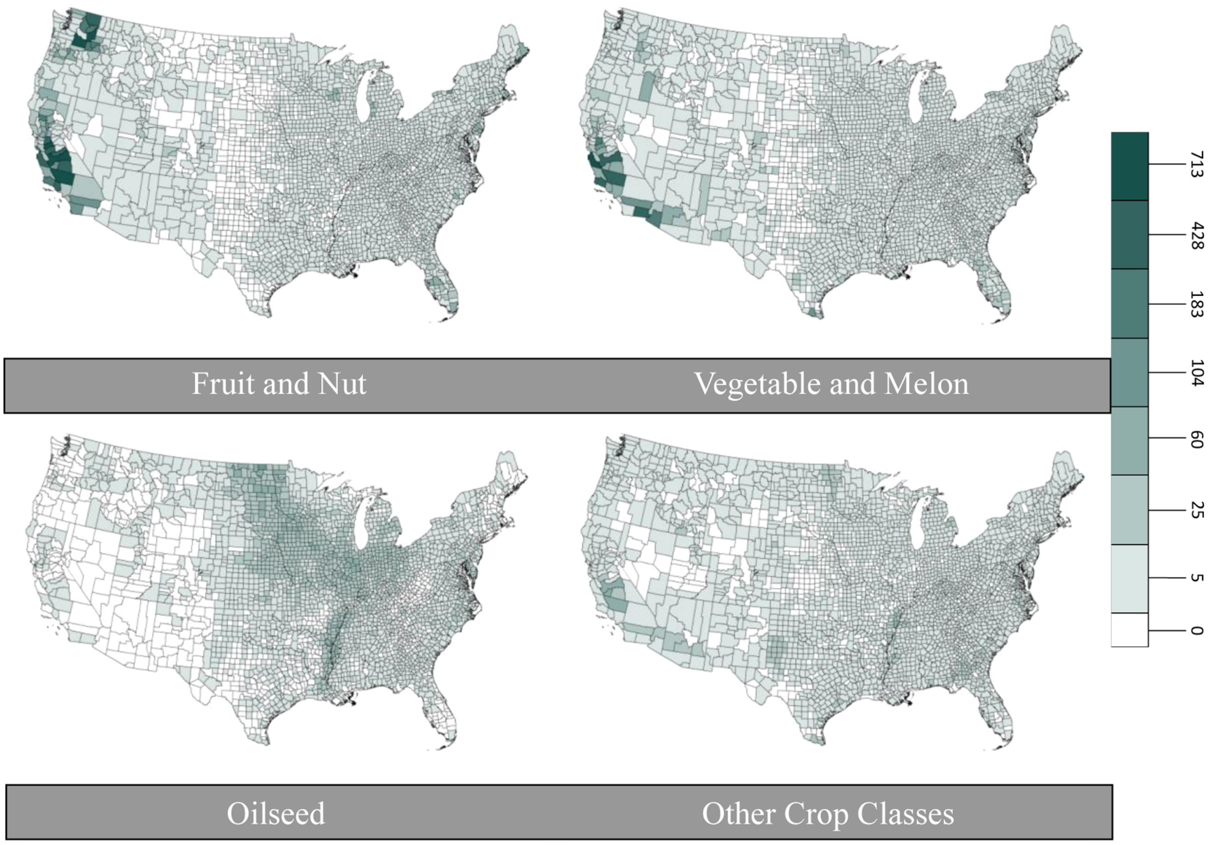

Figure 2. Regional economic value of crops dependent on insect-mediated pollination service by commodity class, in millions USD (2012).

were higher, and in others, coefficients were lower than previously estimated (Table 1).

Of the studies used for dependence coefficient estimates, 62% were US studies. Sunflower and soybean lacked any US studies that compared open pollination and pollinator exclusion effects on the production yield. Though climate, landscape, and cultivar choice may vary across different continents and influence pollination dependency, in the interests of using as large a data set as possible, we included data from all these studies in our analyses. However, compiling these studies demonstrates that information on crop pollination dependency across diverse landscapes is very limited. In studies where pollinator dependence coefficients were assessed for different cultivars or in different fields, we treated each of these assessments as separate estimates (see no. estimates in Table 1) rather than averaging to create a single value for one study. This allowed us to capture potential variation in environmental conditions.

Calculation of Pollination Dependence Coefficients for Representative Crops. It is important to note that studies on a wider variety of cultivars from a diverse range of US landscapes are necessary to fully understand the effects of pollination service on yield, fruit set, quality, and nutritional aspects of crops.[52] Furthermore, quantification of crop dependence through this methodology is a simplification of nature and farming systems, and dependence coefficients are derived from a formula (eq 1) that requires field studies comparing pollinator exclusion to open pollination. This contrast represents an extreme and uncommon case in nature; in reality, pollination service is provisioned on a gradient of pollinator activity. As an example, sunflower varieties have varying self-compatibility and therefore dependence, with hybrid seeds and confection varieties requiring pollination by insects completely (complete self-incompatibility) but oilseed cultivars having a wide range (17−90%) of self-compatibility.[4,38] While understanding crop dependence along a gradient of pollinator activity would provide a highly resolute image of pollination service dynamics and predictions for increasing pollination service, studies of this caliber for all pollination-dependent crops are impractical. Further, our use of a contrast between circumstances of open pollination and pollinator exclusion captures the full range of pollinator activity and provides a logical foundation for subsequent analysis regarding the economic value of insect-mediated pollination service.[53]

Pollination Value. To estimate the economic value of insect-mediated pollination services, we multiplied the production value of each crop by its dependence coefficient. Hereafter, this value will be referred to as pollination value in this article. The pollination value of crops which are directly dependent or indirectly dependent on crop pollination mediated by insects will be referred to as the direct-pollination value and the indirect-pollination value, respectively.

Combining USDA agricultural census (acreage) and NASS (price and yield) data resulted in a detailed representation of crop production value that utilizes the best of both datasets. Subsequently, a detailed and finely resolute spatial analysis of the economic value of crops which are both directly and indirectly dependent on pollination service by insects totals between 31.8 billion and 36.2 billion USD (average 34.0 billion USD) for 75 pollination-dependent crops in 2012 (Figure 1). Close to 87% (30.0 billion USD) of this production value represents direct-pollination value. These values are considerably higher than previous estimates and likely more accurately reflective of the current economic value since we

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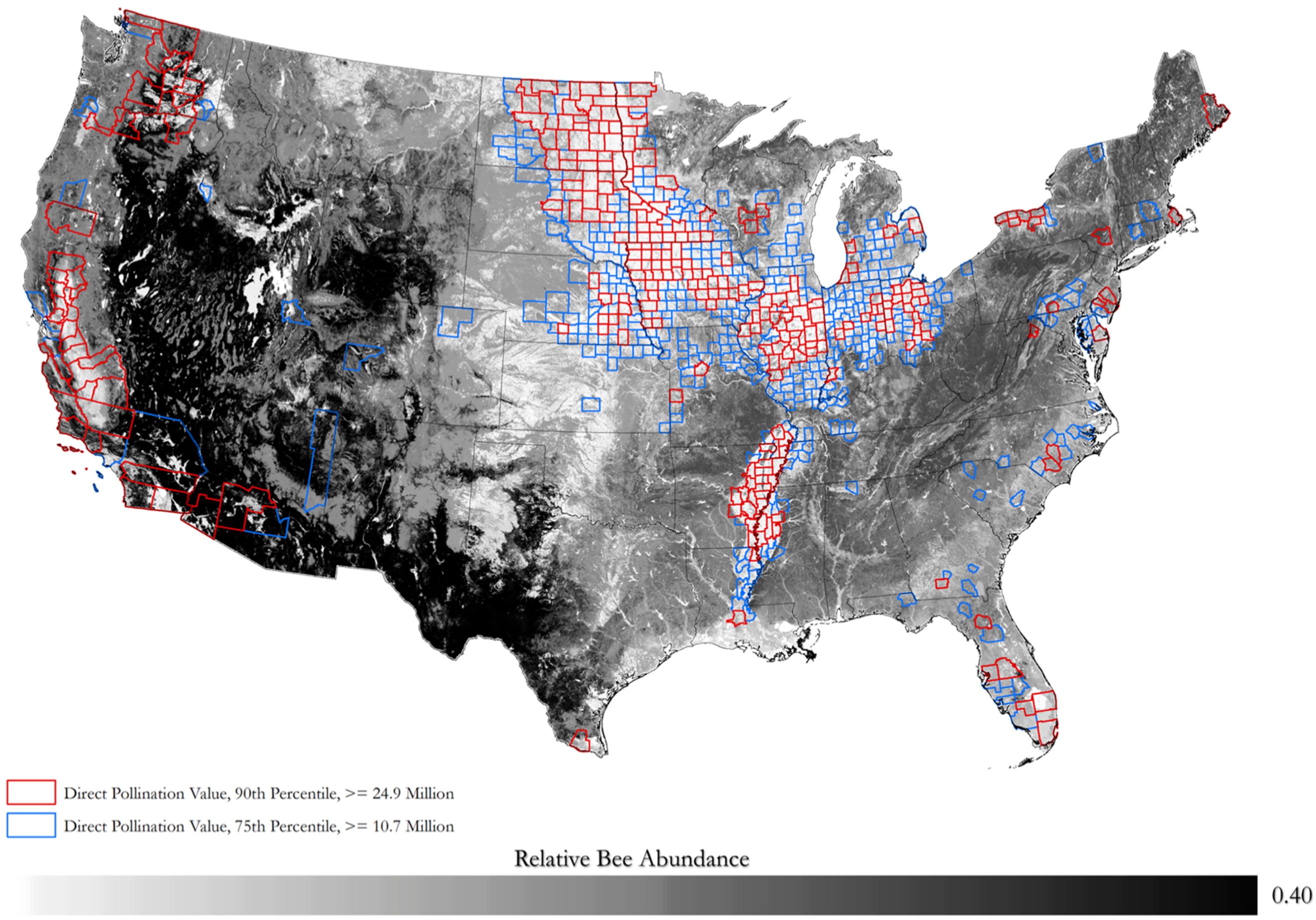

Figure 3. Counties of high direct economic dependence on insect-mediated pollination service highlighted over relative wild bee abundance.

used more recent production data (2012) and included more crops. For example, using a similar production value method, Chopra et al. estimated a dependence of 14.2 billion to 23.8 billion USD (mean of 19.0 billion USD) for 50 pollination-dependent crops on pollination mediated by all insects in 2007.[13] Calderone estimated dependence on all insects to be 29 billion[19] USD for 58 pollination-dependent crops in 2010. For crop dependence on honey bees alone, Calderone estimates 19.2 billion USD in 2010,[19] while Morse and Calderone estimate 14.6 billion USD for 45 crops in 2000.[22] For crop dependence on wild pollinators alone, Losey and Vaughan estimated 3.07 billion USD for 53 pollination-dependent crops in 2004 using an adaptation of this method.[14] In the same way, the referenced recent studies have developed the methods and valuations proposed in other, important prior work;[20,54] the results presented here update estimates for production conditions in the latest available crop year and expand previous work with the inclusion of a greater number of pollination-dependent crops grown in the US. The value of dependence is expected to continue to increase over time as our demand for pollination-dependent crops increases and is unevenly distributed throughout the country. Only 20 percent of US counties account for 80 percent of the total pollination value of directly dependent crops which is consistent with the Pareto principle (Supporting Information, Figures S5 and S6). Last, this estimate of pollination value of crops does not consider the 656.6 million USD that farmers paid for managed bee pollination services in 2012.[55]

The pollination value estimates described in this work are a conservative estimate of the magnitude of economic value dependent upon insect-mediated pollination service in a given area. They do not represent the economic value of what may be lost with decline of this service. That magnitude would be difficult to capture as many factors beyond the scope of this study could mitigate economic losses due to pollination decline including price adaptation[25] (increasing price of dependent crops to adapt to value loss resulting from lower yield), crop substitution (growth of an alternative crop with less or no dependence on insect-mediated pollination service), or increase of other inputs into production (fertilizers, water, and land).[56] Nonetheless, the estimates in this work serve as a conservative estimate of economic value provided by insect pollinators.

Regional differences in landscape suitability for crop growth are reflected in spatial heterogeneity in economic dependence of broad crop categories on insect-mediated pollination service (Figure 2). Along the east and west coasts, production of fruits, nuts, melons, and vegetables dominate the economic dependence, whereas in the Central and Midwestern US, the economic dependence stems from growth of oilseed crops. Pollinator deficiencies in these areas will have different implications on the national production of crops based on the composition of crop farming in these regions.

The total economic value of crops that is directly dependent on insect-mediated pollination service or direct-pollination service is the greatest in the oilseed class, which is predominantly attributable to soybean and canola production.

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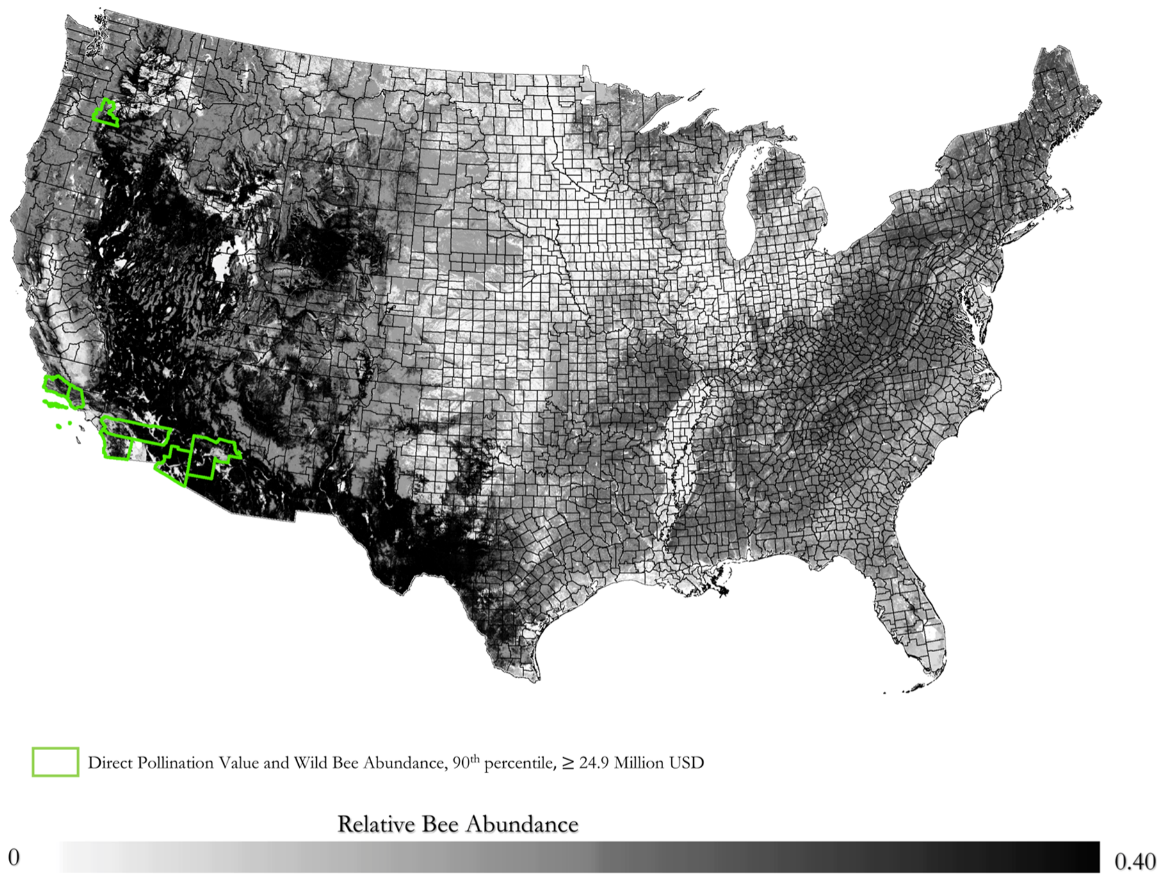

Figure 4. Counties of high direct economic dependence on insect-mediated pollination service (≥90th percentile) and high wild bee abundance (>90th percentile) highlighted over relative wild bee abundance.

In addition, the uncertainty associated with the pollination value is relatively low in these regions (Supporting Information, Figure S3). It is important to cautiously interpret such a large production value as it is primarily a result of the scale of production as opposed to the dependence of the crop on insect-mediated pollination service. These crops are also those with substantial economic value before crop dependence is considered. Specifically, the production value of soybean is $43 billion (2012). Thus, even a small fraction of that large production value being dependent on insect-mediated pollination service will cause the crop to dominate the commodity class. In addition, low uncertainty is expected as available soybean field study data used in bootstrapping is limited and homogeneous (Table 1). The field study data used to calculate soybean dependence is qualitatively inconsistent with the literature[18,30−33] and is further discussed in the Materials and Methods section. The necessity for thorough and systematic field studies to inform dependence is apparent here. While these field studies are expensive, as previously discussed, systematic field studies of the crops with the greatest pollination value can be highly informative for the uncertainty of pollination dependence and subsequently value, overall.[35]

It is also important to note that while there is monetary significance to crop dependence on insect-mediated pollination service, the value of pollination service can extend well beyond agricultural economics through versatile industrial and non-industrial uses of crops.[13] For example, cotton is used for fibers for many applications including clothing, cleaning, and personal care products. Also, many crops dependent on insect pollination are some of the most nutritionally rich crops (fruits, vegetables, nuts, oils, and seeds), thus highlighting their importance for human health.[57,58]

Economic Vulnerability. When compared with the index of relative bee abundance given by the wild bee abundance model,[26] there are regions in the US with high direct-pollination value that simultaneously are predicted to have relatively low wild pollinator abundance (Figure 3). Areas with high oilseed production (Central and Midwestern US) as well as central California and small areas along the Atlantic coast are predicted to have low wild pollinator abundance (≤10th percentile) while having a high (≥75th percentile) direct economic dependence on pollination service mediated by these insects. The direct-pollination value of those counties in the 75th percentile is greater than or equal to 10.7 million USD, 2012 and total 25.3 billion USD, 2012. The direct-pollination value of those counties in the 95th percentile is greater than or equal to 32.3 million USD, 2012 and total 13.9 billion USD, 2012. Of these counties, notable vulnerabilities with very high direct-pollination dependence (≥95th percentile) and very low wild bee abundance (≤10th percentile) include several counties in North Dakota (Cass, Stutsman), Illinois (McLean), Indiana (Benton), and Minnesota (Traverse). These results must be viewed cautiously because, as previously mentioned, the domination of oilseed crops, especially soybean, in the Midwest can inflate the economic dependence in those counties. The general ill-suited habitat in areas highlighted in Figure 3 may be due to these counties having a general lack of noncrop land cover that is supportive of pollinator forage and nesting such as deciduous and

https://dx.doi.org/10.1021/acs.est.0c04786
Environ. Sci. Technol. 2021, 55, 2243−2253

coniferous forests, shrublands, and grasslands and large areas of cultivated lands.[27]

While there are certainly areas of concern, there are also regions producing high direct-pollination value (≥90th percentile) while simultaneously having suitable forage and landscape supportive of wild pollinators (≥90th percentile wild bee abundance) (Figure 4). These include several counties in California (Ventura, Santa Barbara, Riverside, and San Diego), Arizona (Yuma, Maricopa), and Oregon (Wasco). The direct-pollination value of these counties in the 90th percentile is greater than or equal to 23.6 million USD, 2012 and total 18.0 billion USD, 2012. By contrast to those counties highlighted in Figure 3, the counties highlighted in Figure 4 grow pollination-dependent crops with a high economic value but also include large areas of noncrop land cover as well as cultivated crops such as orchard crops which are supportive of pollinator forage and nesting compared to other counties in the US.

A model developed by Lonsdorf et al. estimates wild bee abundance and is being used as a proxy in this study for all wild insect pollinators.[26] These results do not show the quantity of managed pollinators in the US as it is beyond the scope of this study; however, the beekeeping industry (including migratory beekeeping) has struggled to mitigate losses in managed honey bee colonies.[59,60] While overall, the number of honey bee colonies in the US has been relatively stable in recent years, this is due to substantial work by beekeepers to recover from substantial annual winter losses. Each winter, 30−40% of honey bee colonies die in the United States, and a surprisingly large number of colony deaths are also recorded in the summer.[59,61−64] While some areas may have a sufficient supportive network of wild pollinators with which to pollinate their high density of pollination-dependent crops (Figure 4), aforementioned vulnerable counties (Figure 3) may have a higher reliance on managed species (predominantly honey bee colonies) that must be rented or purchased and maintained.[4,21] This can potentiate difficulties and assumes that pollination by wild pollinators is perfectly substitutable with that by managed species, which is not well understood.[65−67] It has been shown that although managed colonies of honey bees can help to mitigate wild insect pollinator losses and are themselves important pollinators to crops, honey bees are also less effective, generalist pollinators and are not a full replacement for many specialized species or the combination of several wild pollinators.[68] Evidence suggests that this occurs at varying degrees according to the crop being pollinated, and a mix of both wild and managed species of pollinators is optimal for pollination efficacy.[65,69] Thus, the beekeeping industry may mitigate some lack of supply of wild pollinators; however, it does so by generating other potential issues.

Economic valuation such as those presented in this work highlights the need to consider the role of ecosystem goods and services for agricultural and other products; however, the value must be considered with caution. For example, a production value approach indicates that changes in the production value of the crop indicate changes in the production (yield) of this crop; however, this is not necessarily true. Market fluctuations influence price, making it difficult to label the production value as purely yield-related. It follows that changes to yield may not be captured entirely by comparing time periods using a production value approach. In addition, this value represents the economic value dependent upon insect pollinators and does not reflect a value of potential loss by the agricultural sector. Realistically, were there to be a decline in pollinators and thus a decline in crop production or yield, the agricultural sector and downstream sectors may adjust prices to compensate for economic losses in the short-term.[70] Further, no approach to economic valuation can capture the true value of pollinators which is arguably infinite.[71] The results presented here are a representation of static dependence of the agricultural sector in economic terms on insect pollinators.

It could also be argued that from a consumption standpoint, if demand remains consistent while supply wanes, there may be compensation in other ways such as increased land, water, and fertilizer use.[56] Future investigations evaluating such trade-offs can improve valuation. In addition, one must consider how the value of a diverse body of pollinator resources creates long-term stability that is critically important for the longevity and sustainability of humans and the environment.[67] There are also other aspects to the value of pollination service in the form of nonagricultural plant and ecosystem biodiversity and reproduction, quality of fruits (which is positively correlated with the economic and nutritional value), and stability of food crop yields that are generally not captured.[12,15] Last, insect-mediated pollination service can also be a difficult subject to investigate as studies frequently combine service mediated by wild insects with service mediated by managed insects,[16] leaving important distinctions unexplored. While exploring these distinctions and incorporating other aspects of the value of pollination service can improve the economic valuation presented here, these improvements would require longitudinal studies which are not presently available but could be the directive of future work.

Here, we have demonstrated that there is high direct-economic dependence on insect-mediated pollination service in areas of the US which are lacking in wild pollinator abundance. This work updates existing estimates of dependence and provides a framework for improving estimates as more data become available. Results show substantially higher economic dependence on insect pollinators than prior estimates. Farmers in areas lacking wild pollinator abundance can target mitigation efforts to improve nesting and forage resources in these areas. While this work presents spatial analysis greater than previous publications with the latest available economic data, even greater spatial resolution of economic data in future work can enhance specific understanding of vulnerability by matching the resolution of current estimates of wild bee abundance at 30 m.[72] Importantly, the high direct-economic dependence of these regions is only intensified when one considers any indirect, downstream dependence of industry sectors beyond agriculture. The dependence of nonagricultural sectors is based on linkages to the directly and indirectly dependent crops within the agricultural sectors. The downstream dependence of nonagricultural sectors merits quantification in future work, and the current resolution of economic dependence allows for future quantification of downstream economic dependence at national and local scales. This work necessarily frames the discussion of the importance of pollinators to the welfare of farming sectors, and it provides foundational work for examining dependence of economic sectors outside of agriculture.

https://dx.doi.org/10.1021/acs.est.0c04786
Environ. Sci. Technol. 2021, 55, 2243−2253

■ ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.est.0c04786.

Crop selection, dependence coefficients, pollination value, spatial analysis, economic details, and bee abundance (PDF)

Relative wild bee abundance given by the model developed by Lonsdorf et al, 2015 for each pixel of the contiguous US averaged for each county (XLSX)

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Notes

The authors declare no competing financial interest.

The code and underlying data that supports the methodology of this study are available from the corresponding author upon reasonable request.

■ ACKNOWLEDGMENTS

The authors thank David Inouye, Insu Koh, Eric Lonsdorf, and Taylor Ricketts for useful data and resources, Margaret Douglas, Bernard Vaissière, and Andony Melathopoulos for useful comments and suggestions, and Brandon Rebholz and Robert Zupan for data processing and code assistance. This research was funded by the National Science Foundation (award number CBET 1603667).

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https://dx.doi.org/10.1021/acs.est.0c04786
Environ. Sci. Technol. 2021, 55, 2243−2253