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## Improving spatio-temporal benefit transfers for pest control by generalist predators in cotton in the southwestern US

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### ABSTRACT

Given rapid changes in agricultural practice, it is critical to understand how alterations in ecological, technological, and economic conditions over time and space impact ecosystem services in agroecosystems. Here, we present a benefit transfer approach to quantify cotton pest-control services provided by a generalist predator, the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*), in the southwestern United States. We show that pest-control estimates derived using (1) a *compound spatial-temporal* model – which incorporates spatial and temporal variability in crop pest-control service values – are likely to exhibit less error than those derived using (2) a *simple-spatial* model (i.e., a model that extrapolates values derived for one area directly, without adjustment, to other areas) or (3) a *simple-temporal* model (i.e., a model that extrapolates data from a few points in time over longer time periods). Using our compound spatial-temporal approach, the annualized pest-control value was \$12.2 million, in contrast to an estimate of \$70.1 million (5.7 times greater), obtained from the simple-spatial approach. Using estimates from one year (simple-temporal approach) revealed large value differences (0.4 times smaller to 2 times greater). Finally, we present a detailed protocol for valuing pest-control services, which can be used to develop robust pest-control transfer functions for generalist predators in agroecosystems.

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## Introduction

Understanding how ecosystem services vary across space and time can aid the evaluation of environmental and social costs associated with changing land-use patterns and the estimation of regional ecosystem service values. However, such an understanding is challenged by a lack of knowledge about the spatial and temporal influences on the economic values of these services (Schägnier et al. 2013), especially in agroecosystems (which contains both the environment and organisms of an agricultural system) (López-Hoffman et al. 2014). For instance, amidst widespread concern about declining bat populations, a high-profile study extrapolated US nationwide pest-control values provided by bats based on a single eight-county study for Texas (Boyles et al. 2011). This study was quickly criticized for its high level of oversimplification – vocalized as economists' frequent concern that 'some number may be worse than no number' if it gives inaccurate information to

inform conservation policy (Fisher & Naidoo 2011). Since pest-control values can fluctuate over time, especially in rapidly changing agricultural landscapes (López-Hoffman et al. 2014), accounting for spatio-temporal changes in ecosystem service values is important if such values are to guide conservation.

Careful estimation of ecosystem service values is important for conservation and management decisions in agricultural settings, but more accurate approaches may require more time and effort (Loomis & Rosenberger 2006; Spash & Vatn 2006). Underestimated values may lead to insufficient conservation funding levels or potentially an undervaluing of the agents providing the service, while overestimated values may reduce voluntary participation in incentive-based programs. Values that appear inaccurate may generate disbelief and reduce their ability to inform policy (Plummer 2009; Fisher & Naidoo 2011). On the other hand, more accurate ecosystem service valuations can be used to promote conservation actions. For instance, Bat Conservation

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International, Inc., the Nature Conservancy and the city of San Antonio, Texas, recently underwent an effective private fundraising campaign to purchase the land around a crucial Mexican free-tailed bat (*Tadarida brasiliensis mexicana*) roost, Bracken Cave, which was threatened by development. One argument used for the site's protection was the value of the pest-control services Mexican free-tailed bats provide to surrounding agricultural landscapes (Ralston 2015).

Using the pest-control services of Mexican free-tailed bats, we demonstrate the potential gain in accuracy in the estimation of pest-control service values when accounting for spatial and temporal influences on these values. We also discuss the types of ecological and economic data required for more accurately valuing the ecosystem services of generalist predators in agroecosystems and outline a protocol for doing so.

### **Pest-control services of generalist predators**

Bats and other generalist predators are part of a larger group of beneficial animals in agriculture systems worldwide that provide pollination and pest-control services (Kirk et al. 1996; Kremen et al. 2002; Losey & Vaughan 2006; Klein et al. 2007; Whelan et al. 2008; Colloff et al. 2013; Valencia-Aguilar et al. 2013; Wanger et al. 2014). Organisms that provide pest control include insectivorous bats and birds, pathogens, and a wide variety of predatory insect species including parasitoid wasps, spiders, beetles, and flies (Kirk et al. 1996; Hawkins et al. 1999; Cleveland et al. 2006; Losey & Vaughan 2006; Kunz et al. 2011; Colloff et al. 2013; Valencia-Aguilar et al. 2013; López-Hoffman et al. 2014). Pest-control services are crucial for food security and rural and national incomes, and stabilize agricultural systems by preventing pest outbreaks (Naylor & Ehrlich 1997). The vast majority of pests and diseases in agricultural systems are controlled by natural organisms (DeBach 1974). Worldwide 42% of crop yields are

estimated to be lost to pests; therefore, the value of pest control worldwide is significant, and could be valued at over \$100 billion USD (Pimentel et al. 1997).

However, ecological and socio-economic changes can lead to the decline of ecosystem service provision in agricultural settings. For instance, agricultural intensification can diminish the supply of ecosystem services in these systems (Sandhu et al. 2010a, 2010b; Spangenberg et al. 2014). Studies have found greater pest control and ecosystem service values on organic farms than conventional farms (Sandhu et al. 2008, 2010a, 2010b), and in conventional crops than genetically modified crops (Federico et al. 2008; López-Hoffman et al. 2014). Greater ecosystem service values on organic farms were linked to decreased private costs for fuel, labor, pesticides, and decreased social costs to human health and the environment (Sandhu et al. 2008). The genetically modified crops provide a substitute for natural pest control (in the form of *Bacillus thuringiensis*) cotton that is transgenically modified to express cry proteins that when eaten by lepidoptern pests can cause mortality; Federico et al. 2008; López-Hoffman et al. 2014). In addition, declines in generalist predators can lead to a reduction in pest-control services they provide (Boyles & Willis 2010; Boyles et al. 2011; Kunz et al. 2011). For instance, the population decline of the little brown bat (*Myotis lucifugus*) due to a fungus, white-nose syndrome, is estimated to have reduced insect consumption by 330 to 660 tons per year across its range (Boyles & Willis 2010; Boyles et al. 2011).

Pest-control values can be measured in agricultural settings using of a variety of techniques (Table 1). These include field experiments, meta analysis, avoided cost approaches, surveys, interviews, non-market valuation, replacement costs, simulation models, and benefit transfer (Cleveland et al. 2006; Gándara Fierro et al. 2006; Losey & Vaughan 2006; Federico et al. 2008; Kellermann et al. 2008; Sandhu et al. 2008, 2010a, 2010b; Power 2010; Boyles et al.

**Table 1.** Ecosystem service valuations of pest-control in a variety of agroecosystems.

Method	Crop(s)	Location	Citation
Avoided-cost approach	Cotton	Texas Winter Garden region, US	Cleveland et al. (2006)
Benefit transfer	Cotton	Nuevo Leon, Mexico	Gándara Fierro et al. (2006)
Avoided-cost approach	Multiple	US	Losey and Vaughan (2006)
Simulation model	Cotton	Texas Winter Garden region, US	Federico et al. (2008)
Field experiments, interviews	Coffee	Blue Mountains, Jamaica	Kellermann et al. (2008)
Field experiments	Multiple	Canterbury region, New Zealand	Sandhu et al. (2008)
Field experiments, interviews	Multiple	Canterbury region, New Zealand	Sandhu et al. (2010a, 2010b)
Benefit transfer	Multiple	US	Boyles et al. (2011)
Metanalysis	Multiple	Multiple	Chaplin-Kramer et al. (2011)
Surveys	Citrus	South Australia	Colloff et al. (2013)
Metanalysis	Multiple	Multiple	Shackelford et al. (2013)
Benefit transfer	Cotton	Southwestern US	López-Hoffman et al. (2014)
Field experiments, benefit transfer	Rice	Thailand	Wanger et al. (2014)
Field experiments	Corn	Illinois, US	Maine and Boyles (2015)

The method used to value the pest-control services, locations, and crop(s) are displayed.

2011; Chaplin-Kramer et al. 2011; Colloff et al. 2013; Shackelford et al. 2013; López-Hoffman et al. 2014; Wanger et al. 2014; Maine & Boyles 2015). One of the less effort- and cost-intensive methods of pest-control valuation is to conduct a simple benefit transfer. However, the estimation of ecosystem services in these settings using simple benefit transfer is problematic because of heterogeneity and rapid change in agricultural landscapes, such as the intensification of agricultural practices (Spangenberg et al. 2014) and the large-scale use of genetically modified crops (Tabashnik et al. 2013; López-Hoffman et al. 2014). While studies have examined ecological factors that influence predator densities and pest-control levels in agricultural systems (Bianchi et al. 2006, 2010; Chaplin-Kramer et al. 2011; Colloff et al. 2013; Shackelford et al. 2013; Veres et al. 2013), less is known about how market conditions for agricultural commodities, may cause spatial and temporal variation in monetary values for ecosystem services (López-Hoffman et al. 2014).

### **Valuation of Mexican free-tailed bat pest-control services**

Mexican free-tailed bats feed on insects from 35 families, making them an important source of pest suppression in agricultural settings in the southwestern United States and Mexico (Lee & McCracken 2005; Cleveland et al. 2006; Gándara Fierro et al. 2006; Federico et al. 2008), particularly for cotton, a globally significant crop (U.S. Department of Agriculture 2013). The bats emerge nightly to forage on pests and other insects in areas as far 50 km away from their roosts (Williams et al. 1973; Lee & McCracken 2005). Two studies of avoided predation cost in an eight-county region in south-central Texas (known as the Winter Garden) found that for cotton fields treated with insecticides, bats provide significant complementary pest-control services estimated at \$741,000 per year (Cleveland et al. 2006; Federico et al. 2008).

In another avoided-cost study spanning the southwestern US, López-Hoffman et al. (2014) determined that from 1990 to 2008 Mexican free-tailed bat pest-control values in cotton declined by 79% due to widespread adoption of Bt cotton, falling global cotton prices, and consequent reduction in the number of hectares of cotton planted in the United States (López-Hoffman et al. 2014). These researchers also found that fluctuations in market conditions caused temporal variation in ecosystem service values even when bat population sizes were held constant.

Finally, two additional studies used a simple benefit transfer to estimate pest-control values across the United States and Mexico. As mentioned previously, Boyles et al. (2011) applied estimates of ecosystem

service values from Cleveland et al. (2006) and Federico et al. (2008) to different regions across the United States and multiplied the two studies' per-acre cotton pest-control values by the total acreage of harvested cropland in the US – obtaining a nationwide estimate of more than \$3.7 billion for bat pest-control services (Boyles et al. 2011). Another study applied cotton ecosystem service estimates from Federico et al. (2008) to an agricultural region with a variety of crops in Nuevo Leon, Mexico and found the value to be from \$578,000 to \$1.47 million per year (Gándara Fierro et al. 2006).

### **Background on accuracy of benefit transfer in agroecosystems**

The economic approach known as benefit transfer offers a method for estimating ecosystem service values. Benefit transfer involves applying an ecosystem service value that has been estimated at an existing study site to a new, unstudied site where its value has not been previously estimated (Wilson & Hoehn 2006). Benefit transfers can take two forms – a simpler, often less accurate transfer of mean or median values from one site to another, or a function transfer that uses explanatory variables in regression models to predict values in a new context. Simple benefit transfer approaches can be problematic in that they typically yield large error rates (generalization error). This occurs when there is a lack of correspondence in biophysical and socioeconomic factors when extrapolating ecosystem service values from one area to another (Rosenberger & Stanley 2006; Plummer 2009; Eigenbrod et al. 2010; Schägner et al. 2013), or, as we show here and previously, when a few estimates over a short period of time are used to extrapolate over longer time frames (López-Hoffman et al. 2014).

To improve the accuracy of benefit transfer in agricultural systems, factors causing variation in ecosystem service values must be considered. To date, much of the concern about benefit transfer error has revolved around the inadequate consideration of factors causing spatial variation. These include shifting ecological and human social conditions such as proximity to human populations (Ricketts et al. 2004; Boyd 2008; Eigenbrod et al. 2009, 2011; Bianchi et al. 2010; Barbier 2012; Johnson et al. 2012; Spangenberg et al. 2014), as ecosystem service values depend highly on their location and on the demand of the surrounding community (Boyd 2008). For generalist insectivores such as bats, their location is important because they only provide pest-control services when they are near significant agricultural areas. In addition to population densities of generalist insectivores, ecosystem services in agricultural systems can vary spatially due to multiple factors

including insecticide use, technology adoption rates, economic forces, and environmental factors (e.g., soils, climate), making accurate evaluation of ecosystem services challenging.

In contrast to spatial variation, less attention has focused on the role of temporal variation of ecosystem service values. Ecosystem service values may vary according to dynamic ecological characteristics such as inter-annual climate fluctuations, landscape factors, crop phenology, agricultural management practices, prey availability, and species population dynamics determining service supply (Koch et al. 2009; Chaplin-Kramer et al. 2011; Veres et al. 2012; Vasseur et al. 2013; Schellhorn et al. 2015). They can also vary due to fluctuations in socioeconomic factors (Koch et al. 2009; Burkhard et al. 2012; Lautenbach et al. 2012; Yuan et al. 2012; López-Hoffman et al. 2014). Accounting for this temporal variability is critical. For example, López-Hoffman et al. (2014) found that changing agricultural practices and market conditions could cause substantial fluctuations in ecosystem services values.

Transfer functions, which develop a set of explanatory variables to predict ecosystem service values, can help better explain economic values and can account for this spatial and temporal variability in ecosystem services (Schägnier et al. 2013). Transfer functions with an appropriate set of explanatory variables reduce generalization errors often seen in simple benefit transfer approaches (Loomis 1992; Spash & Vatn 2006). Transfer functions have been developed for numerous ecosystem types (Brander et al. 2006, 2007; Zandersen & Tol 2009; Barrio & Loureiro 2010) and specific ecosystem services such as recreation and water quality (Smith & Kaoru 1990; Shrestha & Loomis 2003; Van Houtven et al. 2007). Like any regression model, transfer functions require an adequate sample size of primary valuation studies to draw upon, and the studies must be heterogeneous enough to account for the influence of a full range of explanatory variable values on the ecosystem service values they intend to predict.

For pest-control services, the diversity of studies needed to develop a transfer function is currently lacking. However, our pest-control results could be combined with future studies, particularly ecological, to develop such functions. Most economic data needed to value this service already exist (e.g., crop prices, private and social costs of pesticide use); so an improved understanding of crop-pest-predator dynamics can guide an improved understanding of the value of natural pest-control in rapidly changing agroecosystems.

### **A spatial-temporal approach to benefit transfer for valuing pest-control services**

Given the prevalent use of benefit transfer in ecosystem service valuation, we explore the consequences of

using simple benefit transfer on the estimation of pest-control values. We also provide recommendations on developing pest-control transfer functions for other generalist predators. First, we present a benefit transfer approach to extrapolate the value of crop pest-control services of a generalist predator, Mexican free-tailed bats (*Tadarida brasiliensis mexicana*), for cotton-producing areas of the southwest United States. What distinguishes our estimations is that we incorporate spatial and temporal variability of the factors that influence the value of crop pest-control services (López-Hoffman et al. 2014).

Second, we show that our compound spatial-temporal approach likely provides more accurate estimates for benefit transfer when compared to a *simple-spatial* approach (the most typical method for benefit transfer used by extrapolating values derived for one area directly to other areas) and a *simple-temporal* approach (i.e., incorporating data for one or a few points in time, which can introduce inaccuracy due to interannual variability in agroecological systems). In addition to presenting a detailed protocol for our compound spatial-temporal benefit transfer to estimate the cotton pest-control services of Mexican free-tailed bats, we suggest how to extend the approach to develop robust pest-control transfer functions for other generalist predators (insects, bats, birds, reptiles) by synthesizing ecological and economic data for agroecological systems.

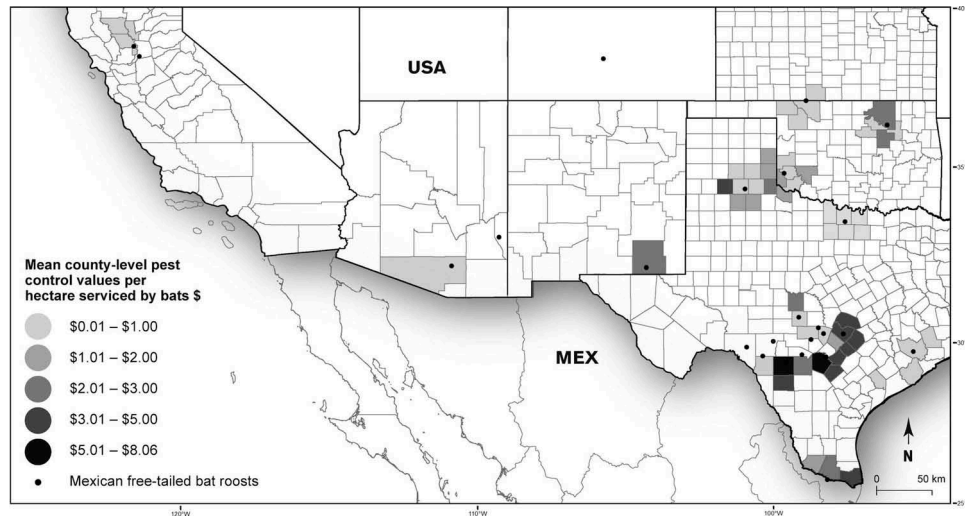
## **Materials and methods**

### **Compound spatial-temporal benefit transfer approach**

Economists typically have used an avoided-cost approach to value the pest-control services of species such as bats (DeFries et al. 2005; Cleveland et al. 2006). For Mexican free-tailed bats, this avoided-cost approach entails valuing (1) cotton spared by pest damage when bats are present, (2) the reduced private costs that farmers pay via fewer insecticide applications, and (3) reduced social costs to others aside from the farmer in the form of health impacts to farmworkers and consumers and reduced environmental impacts when less insecticide is used.

To estimate the avoided costs of crop damage in cotton we (a) estimated the number of bollworms (*Helicoverpa zea*), a major cotton pest, consumed nightly by individual bats, (b) determined the hectares of cotton fields in proximity to bat roosts, and (c) estimated the value of the crops that would have been damaged in the absence of bats. To determine the value of reduced insecticide use, we calculated (d) the reduced private costs for farmers of applying insecticides, and (e) the reduced cost to society of releasing fewer insecticides into the environment.





**Figure 1.** Spatial variability in US county-level pest-control values per hectare serviced by bats from the compound spatial-temporal approach (Tables 2 and 3). These values vary due to county-level differences in bat population size, area of cotton planted, variety of cotton, and the use of Bt cotton. Values are annual means from 1990 to 2008 in 2011 US dollars. Mexico is not considered.

Our study area includes all US counties in six states (Arizona, California, Kansas, New Mexico, Oklahoma, Texas) producing cotton within 50 km (conservatively, an individual bat's nightly foraging distance (Williams et al. 1973)) of a major Mexican free-tailed bat roost. We used roost location and bat population census data from the US Geological Survey's Bat Population Database (Ellison et al. 2003) and our own literature search (Supplementary material, Table A1 & A2; Figure 1). In our model, we assumed that 90% of the adult bats in each roost were female and 10% were male, which is consistent with field data from breeding roosts in the southern United States (Federico et al. 2008).

We considered both Pima and Upland cotton varieties in our calculations. We obtained data on the number of cotton hectares planted per county from the United States Department of Agriculture's National Agricultural Statistics Service (U.S. Department of Agriculture 2012) and the National Cotton Council (National Cotton Council 2012; Supplementary material, Table A2). Bt cotton was introduced for the Upland variety of cotton only in 1996. Data on the year of adoption of transgenic Bt Upland cotton was obtained from the Mississippi State University Department of Entomology and Plant Pathology's database on cotton crop losses (Supplementary material, Table A4; Mississippi State University Department of Entomology and Plant Pathology 2012). We used mean values over time, and our compound spatial-temporal analysis covers the two decades from 1990 through 2008 (López-Hoffman et al. 2014). Below we detail the calculations used to determine the value of the avoided crop damage and reduced insecticide use; see Supplementary material for more detailed pest-control valuation methodology.

### Comprehensive benefit transfer protocol

We start with the equations used to estimate the value of the avoided crop damage, and then detail the equations used to estimate the avoided insecticide use (i.e., the reduced private and social costs). While our equations produce county-level estimates, they could also be applied at finer spatial resolutions.

#### Avoided crop damage calculations

The avoided crop damage calculations estimate the value of the cotton bolls that would have been destroyed by pests if the bats' predation of these pests had not occurred.

$$\begin{aligned} \text{No. cotton bolls saved/night} &= \text{No. adult bats/county} \\ &\times \text{No. of larvae prevented from developing/bat/night} \\ &\times \text{No. of bolls eaten over larva's lifetime} \\ &\times \text{Bt or male adjustment factor*} \end{aligned} \quad (1)$$

Equation 1 estimates the number of cotton bolls saved per night per county. The first three factors consider female bats and conventional cotton; they estimate the number of adult bats per county, times the number of larvae the bats prevent from developing on cotton per night, times the number of cotton bolls one larva can eat over its lifetime. Each pregnant or lactating female bat consumes 5–10 female adult bollworms per night (Lee & McCracken 2005; Cleveland et al. 2006; McCracken et al. 2012). The consideration of predation by male and non-reproductive female bats also requires an adjustment as they eat fewer bollworms than lactating females due to the high metabolic costs of lactation; therefore

non-reproductive female and male bats were modeled as consuming 32% less bollworms (Cleveland et al. 2006; Federico et al. 2008). This consumption by pregnant and lactating bats in turn would prevent 5 larvae from developing and damaging cotton crops, when accounting for insect mortality during development and bollworm dispersal into cotton (Sansone & Smith 2001; Cleveland et al. 2006). Over its lifetime, a single bollworm larva can damage 2–3 bolls of cotton (Cleveland et al. 2006). When considering avoided crop damage for Bt cotton, an adjustment factor must be used as bats have less of an effect than they do for conventional cotton. We assumed that in Bt cotton bats prevented 52.6% of the number of larvae that would have in prevented in conventional cotton (Federico et al. 2008). All estimates of numbers of cotton bolls saved are summed.

$$\begin{aligned} & \text{Avoided crop damage value \$ / night} \\ & = \text{No. bolls saved / night} \times \text{Value of boll \$} \end{aligned} \quad (2)$$

Equation 2, the avoided crop damage value per night in US dollars (USD), is simply the number of cotton bolls saved times their value in USD (which varies according to the variety of cotton – i.e., Pima or Upland). Cotton prices were obtained from the National Cotton Council (National Cotton Council 2012); all values in this paper are in 2011 USD.

$$\begin{aligned} & \text{Avoided crop damage value \$ / season} \\ & = \text{Avoided crop damage value \$ / night} \\ & \times \text{Length of season (days)} \\ & \times \text{Decline boll value in season} \end{aligned} \quad (3)$$

Equation 3, the avoided crop damage value per season (early, mid, and late) in USD, accounts for the avoided crop damage value per night, times the length of the season, times an adjustment factor (to account for the fact that bolls earlier in the season contribute more to the harvest than bolls produced later in the season). Cotton bolls produced during the first third of the season generate about 50% of the harvest while bolls from the last third generate only 7% (Sansone et al. 2002).

$$\begin{aligned} & \text{Total avoided crop damage value \$ / year} \\ & = \text{Avoided crop damage value \$ / early season} \\ & + \text{Avoided crop damage value \$ / mid season} \\ & + \text{Avoided crop damage value \$ / late season} \end{aligned} \quad (4)$$

Equation 4, the total avoided crop damage value per year in USD, is a sum of the value over all three cotton seasons.

### **Avoided insecticide use calculations**

The avoided insecticide use calculations estimate the private and social costs of insecticides had the bats'

predation over the cotton not occurred. Insecticide applications are avoided early in the cotton season, from the first date of cotton flowering (the earliest economic significant susceptibility to bollworms) to the first date of insecticide application.

$$\begin{aligned} & \text{No. days to reach insecticide use threshold} \\ & = \text{Economic threshold for insecticide use (larvae/ha)} / \\ & \text{No. larvae developing per night/ha without bats} \end{aligned} \quad (5)$$

Equation 5 estimates how many days are needed to reach the economic threshold for insecticide use (20,000–25,000 larvae per hectare for bollworms) without bat predation (Sansone et al. 2002). The date at which the threshold is reached, which consequently triggers the first insecticide application, varies according to region.

$$\begin{aligned} & \text{No. of avoided insecticide applications} \\ & = \text{No. days between cotton flowering} \\ & \text{1st insecticide application /} \\ & \text{No. days to reach insecticide use threshold} \end{aligned} \quad (6)$$

Equation 6 estimates how many insecticide applications were avoided with bat predation by determining how many times the pest population would have reached the threshold for insecticide use during the early cotton season (without bat predation).

$$\begin{aligned} & \text{Private cost of avoided insecticide use} \\ & = \text{No. of avoided insecticide applications} \\ & \times \text{Ha of cropland} \\ & \times \text{Private cost \$ of insecticide/ha} \end{aligned} \quad (7)$$

Equation 7 estimates the private cost farmers would have incurred without bat predation. We used a uniform insecticide application rate of 0.29 kg/ha (Gianessi & Reigner 2006). Data on private costs of cotton insecticide applications from 1990 to 2008 were obtained from the Mississippi State University Department of Entomology and Plant Pathology's databases on cotton losses due to insects (Mississippi State University Department of Entomology and Plant Pathology 2012). Mean cotton insecticide costs per hectare for each state are reported.

$$\begin{aligned} & \text{Social cost of avoided insecticide use} \\ & = \text{No. of avoided insecticide applications} \\ & \times \text{Ha of cropland} \\ & \times \text{Social cost \$ of insecticide/ha} \end{aligned} \quad (8)$$

Equation 8 estimates the social cost (public health and environmental damage) that would have been incurred without bat predation. We determined the insecticides in the United States that are used predominantly on cotton bollworms (Gianessi & Reigner 2006), and used

data from Kovach et al. (1992) and Cornell University's Integrated Pest Management Program (Cornell University's Integrated Pest Management Program 2012) to estimate the environmental and toxicological impacts of these particular cotton insecticides. We then used a pesticide environmental accounting tool (Leach & Mumford 2008) to assign a social cost in dollars for each insecticide according to estimates of its degree of impact to human health, groundwater contamination, aquatic systems (fish), birds, bees, and other beneficial insects. We used a weighted mean cost of insecticide applications per hectare over time.

$$\begin{aligned} &\text{Total value \$ of avoided insecticide use/year} \\ &= \text{Private cost of avoided insecticide use} \quad (9) \\ &+ \text{Social cost of avoided insecticide use} \end{aligned}$$

Equation 9, the total value of the avoided insecticide use per year in USD, is simply the sum of the social and private costs of the avoided insecticide use.

$$\begin{aligned} &\text{Total pest – control value \$ /year} \\ &= \text{Total avoided crop damage value \$ /year} \quad (10) \\ &+ \text{Total value \$ of avoided insecticide use/year} \end{aligned}$$

Equation 10, the total pest-control value of bats per year per county in USD, is a sum of the annual value of the avoided insecticide use and annual value of the avoided crop damage.

Below, we demonstrate the importance of both temporal and spatial variability in benefit transfers comparing three different approaches: compound spatial-temporal, simple-spatial, and simple-temporal benefit transfer approaches.

### ***Compound spatial-temporal approach vs. simple-spatial approach***

To explore spatial variability, we contrast estimates from the compound spatial-temporal approach (see the section above and Supplementary material), which accounted for temporal variability plus spatial variability in bat population sizes, insecticide costs, variety of cotton planted, and agricultural practices across the southwestern US, to estimates obtained from a simple-spatial approach, which ignored the above spatial factors. The simple-spatial approach is a unit value transfer extrapolating mean per-hectare pest-control estimates obtained in the Winter Garden region of Texas to all cotton growing areas in the southwestern United States. For both the compound and simple-spatial approaches, we used mean values (from 1990 to 2008) of bat pest-control estimates.

### ***Compound spatial-temporal approach vs. simple-temporal approach***

We next illustrate the importance of temporal variability in ecosystem service valuation based on estimates from the compound spatial-temporal approach across the southwestern United States as compared to a simple-temporal approach. We compare the annualized mean from 1990 to 2008 (compound approach) to a simple-temporal approach, in which we used spatially explicit factors estimated from compound approach, but extract point data from three different years encompassing both high and low values: 1990, 2005, and 2008. Both of these models accounted for spatial variability in bat population sizes, insecticide costs, variety of cotton planted, and agricultural practices.

## **Results**

### ***Spatial and temporal variation in the compound spatial-temporal approach***

Pest-control values calculated using the compound approach were spatially variable, reflecting county-level differences in bat population size, area of cotton planted, variety of cotton, and the use of Bt cotton (Figure 1). Estimates of the mean per hectare county-level ecosystem service value (annualized from 1990 to 2008) varied widely from \$0.01 to \$8.06; the highest values (>\$2.60) were all found in Texas (Figure 1). However, while Texas counties had the highest pest-control values, these counties also experienced the greatest mean annual declines in pest-control value from 1990 to 2008 (correlation test between annualized pest-control value per county and mean annual decline in pest-control value per county;  $r = -0.9$ ,  $p$ -value <0.001). From 1990 to 2008, the value of cotton pest-control services across the southwestern United States declined by 79% due to falling global cotton prices, the consequent reduction in the number of hectares planted with cotton, and the introduction and widespread adoption of Bt cotton (López-Hoffman et al. 2014). Thus, counties that had the highest initial pest-control values (mainly in Texas) also had more value available to be lost between 1990 and 2008. County-level variation in bat population sizes and the area planted with cotton were similar. County-level bat population sizes had a coefficient of variation of 1.84 (bat population sizes per county, range of <10 to 1.7 million individuals per county), while the coefficient of variation in mean annual cotton hectares planted over time was 1.81 (mean number of annual cotton hectares planted per county, range of <2000 to 3.47 million hectares planted).



**Table 2.** Annualized value differences in USD between a simple-spatial (extrapolation-based) approach on the Winter Garden region in Texas, and our compound spatial-temporal approach.

State	Compound approach	Simple-spatial approach
Arizona	4954	169,186
California	55,852	300,516
Kansas	0	3
New Mexico	27,500	190,145
Oklahoma	496,497	5,002,508
Texas	11,651,569	64,424,255
Sum	12,236,371	70,086,613

The latter approach accounted for spatial variation in bat population sizes, insecticide costs, variety of cotton planted, and agricultural practices. Values represent mean pest-control values in 2011 US dollars (from 1990 to 2008).

### Comparison of evaluation approaches

We found large differences in pest-control values estimated with our compound spatial-temporal approach as compared to values estimated with a simple-spatial approach extrapolated from one region (Table 2). Using the simple-spatial approach, the annualized pest-control value across the southwestern United States (from 1990 to 2008) was \$70.1 million, 5.7 times greater than that estimated using our compound approach (Table 2). The differences per county between our compound approach estimates and the simple-spatial approach estimates ranged from an underestimate of \$427,000 to an overestimate of \$13.9 million.

Using estimates from just one year (simple-temporal approach) revealed large value differences compared to the mean compound approach value from 1990 to 2008 (Table 3). Pest-control values from 1990 were nearly 2.0 times larger than the mean value. Using pest-control estimates from 2005 and 2008 underestimated values at 0.7 and 0.4 of the mean value, respectively. Such large differences are due to small sample sizes (i.e., number of years used to estimate values). Interestingly, the differences between the mean and single-year estimates were greatest in 1990, which had an above average extent of cotton planted and high cotton prices compared to

**Table 3.** Differences associated with benefit transfer based on compound spatial-temporal values comparing the mean pest-control values (from 1990 to 2008) to the simple-temporal approach (single year values).

State	Simple-temporal			Compound spatial-temporal
	1990	2005	2008	18 year mean
Arizona	9847	1548	809	4954
California	0	26,467	0	55,852
Kansas	0	0	0	0
New Mexico	61,813	12,942	7535	27,500
Oklahoma	1,258,808	315,971	90,128	496,497
Texas	22,634,299	8,006,800	4,781,257	11,651,569
Sum	23,964,768	8,363,728	4,879,729	12,236,371

Values are displayed in 2011 US dollars.

later years. The lowest overall value in our pest-control estimates was in 2008, and using values based on this year alone led to values much lower than the mean.

## Discussion

### Accuracy of ecosystem service valuation in agroecosystems

Inaccurate valuation of ecosystem services may complicate efforts to create incentives for protecting ecosystems and their functions. Accurate internalization of the external costs of ecosystem protection is unlikely to occur when ecosystem service values are significantly misestimated. For example, underestimated ecosystem service values may lead to inadequate conservation funding levels. Overestimated values may reduce participation in voluntary incentive-based conservation programs or create political resistance in efforts to create environmental markets due to high perceived costs. Finally, values must be seen as scientifically credible and accurate in order to be applied to policy (Plummer 2009; Fisher & Naidoo 2011). All these factors point toward the importance of accurate and timely estimation of changing ecosystem service values in dynamic agroecological systems (Ralston 2015).

Approaches such as ours that approximate a transfer function incorporating factors aimed at explaining temporal and spatial variation in pest-control services can help minimize generalization error (Loomis 1992; Spash & Vatn 2006). In contrast, simple benefit transfers may result in generalization error in a crop-pest-predator system by not accounting for these sources of variability. Simple benefit transfer can also potentially cause errors of uniformity, regionalization, or sampling that would reduce the accuracy of the valuation (Plummer 2009; Eigenbrod et al. 2010). Agricultural ecosystem services are likely to be sensitive to these types of errors, as temporal variability is common in agricultural practices, market forces, and ecological conditions affecting cropland, its extent, pest species dynamics, and those of the species providing the service (Zhang et al. 2007; Landis et al. 2008; Fisher & Naidoo 2011; Garibaldi et al. 2011; De Beenhouwer et al. 2013; Spangenberg et al. 2014).

Our study indicates that mean bat pest-control values varied spatially by a factor of 800 across different counties (Figure 1). A simple-spatial approach, extrapolating estimates from one region with high pest-control values (the Texas Winter Garden region), overestimated pest-control values across the southwestern United States by nearly six times (Table 2) compared to our compound spatial-temporal approach's estimates. These differences likely occurred because the simple-spatial extrapolation

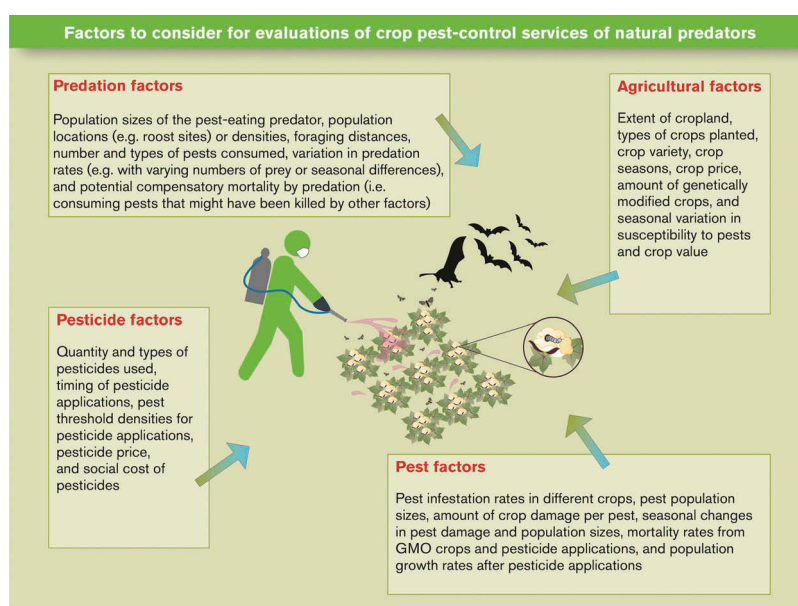
did not account for spatial variation in bat population sizes, insecticide costs, variety of cotton planted, or agricultural practices. Similarly, ignoring temporal variability by using single-year values caused large differences when compared to mean pest-control values (0.4 or two times their mean values; Table 3).

### General approach for valuing crop pest-control services

To help properly account for spatiotemporal context in a way that improves the accuracy of benefit transfers in agroecosystems, we suggest the factors to consider for the estimation of monetary ecosystem service values (Figure 2). These factors are specifically important for valuation of pest control by generalist predators, but could also be important for estimating other ecosystem service values in agroecosystems. The specific equations will vary according to the system in consideration (e.g., type of crop, species of generalist predator, degree of insecticide use, and usage of transgenic crop strains). Each variable should pertain to the local area considered and ideally include mean values over a range of time and space. First, agricultural factors should consider the extent of cropland, types of crops planted, including the use of genetically modified crops, and any other factors that affect crop susceptibility to pests. Second, pest factors should account for pest densities and crop damage rates, and how they vary over the season, as well as the effects of insecticides and genetically modified crops on pest survival and population growth rates. Predation factors should consider predator densities, their foraging distances and abilities, and other factors such as compensatory mortality that

could influence their predation rates and impact on pest populations. Finally, insecticide factors account for the types, quantity, and timing of insecticides used, rules for insecticide applications, private costs of insecticides to the farmer, and social costs of insecticide use to human health and the broader environment. Future studies may include additional factors that are not present in our study system.

Accounting for these variables for natural predators as described above would help increase the accuracy of benefit transfers in agroecosystems. Explicit inclusion of these variables can help improve the precision of estimates given varying levels of correspondence (similarity) between the sites, including the type of ecosystem service and the amount provided, market characteristics, institutional settings, geographical location, cultural norms and policy, and time between data collection and transfer (Loomis & Rosenberger 2006; Spash & Vatn 2006). If annual point estimates are not desired, a wide range of years ideally should be used to obtain long-term mean estimates of service values and their variance. The standardization and reporting of large-scale data over time would greatly facilitate the valuation of ecosystem service values. To address uncertainty in model parameters, sensitivity analyses should be conducted to understand the impact of individual parameters on service value estimates (see Supplementary materials). Finally, both ecological and socioeconomic factors should be taken into account in ecosystem service evaluation: in our study both factors had similar levels of variation between counties (C.V. of 1.84 vs. 1.81 for bat population size and cotton extent per county, respectively).



**Figure 2.** Factors we suggest be considered when estimating the ecosystem service values provided by generalist, insectivorous predators in agroecosystems.

A better approach than simple unit value transfers for estimating monetary values is a transfer function (developing a regression models where explanatory variables can predict ecosystem service values), based on multiple primary studies (Schägnier et al. 2013). Here, we illustrate the factors that would be needed to develop transfer functions in agricultural systems (Figure 2).

Our results could be combined with other studies to develop pest-control or other agricultural ecosystem services transfer functions by accounting for the role of shifting agricultural prices and practices. This is especially pertinent for agroecological systems where rapid change has been documented, such as the expansion in biofuels production (Landis et al. 2008), the widespread adoption of genetically modified crops (Tabashnik et al. 2013; López-Hoffman et al. 2014), and the intensification of agricultural practices (Spangenberg et al. 2014). The agricultural industry in the United States in particular has also been changing over the last two decades as, for example, cotton prices and hectares planted in cotton in the United States have declined. The declines are generally attributed to global market forces—including trade barriers falling in the 1990s and increased production of cotton in developing countries (U.S. Department of Agriculture 2013).

### **Fluctuating ecosystem services values**

Even though the value of bat pest-control services fluctuates across space and time, maintaining the ecological functions provided by bats is helpful to farmers. Our study evaluates the pest-control effects of only 1 of the 44 insectivorous bat species found within the US, and we considered only a single crop and a single crop pest. Thus, the pest-control value of bats is undoubtedly much greater, suggesting that the conservation of large bat populations plays an important role in lowering insecticide use, suppressing pest populations, and hedging against the rise of Bt resistance among pests in the future (Boyles et al. 2011; U.S. Department of Agriculture 2012).

Over the past few years, mounting evidence from around the world suggests that insect pests are evolving resistance to Bt-modified crops (Tabashnik et al. 2013). While not yet widespread, Bt-resistant pests have been found in fields in India, China, and the US, and in laboratory studies (Tabashnik et al. 2008, 2012; Bagla 2010; Kaur & Dilawari 2011; Gassmann 2012). The main strategy to delay the evolution of resistance is planting nearby refuges of host crops without Bt toxins in fields of genetically modified crops (Tabashnik et al. 2013). The objective is that susceptible pests (from refuges) will mate with those relatively few resistant individuals left after spraying. If inheritance of Bt resistance is recessive, the

offspring will die on Bt crops, thus slowing the evolution of resistance (Tabashnik et al. 2013). While refuges are an important strategy, resistance can still develop in their presence, and generalist predators such as bats offer another mechanism to slow resistance development. By preying on the individual insects surviving the Bt toxin – and preventing them from multiplying – bats can provide the additional service of slowing the evolution of resistance to Bt and other insecticides (Federico et al. 2008; Liu et al. 2014). Bats and other natural enemies can play an important role in integrated pest management at all times (Hagerty et al. 2005), regardless of temporal fluctuations in the value of their pest-control services. Importantly, these fluctuations in ecosystem service value do not imply that bat conservation or management efforts should wax or wane.

Given these rapid changes in agriculture and emerging threats to bats, an important taxon for natural pest-control (Arnett et al. 2008; Miller 2008; Cryan & Barclay 2009; Popa-Lisseanu & Voigt 2009; Piorkowski & O'Connell 2010), studies such as this are valuable in supporting development of agricultural transfer functions that can improve our understanding of pest-control value in agroecosystems.

### **Conclusion**

Scholars have recommended that assessments of ecosystem service values should include variance estimates and avoid simple-spatial extrapolations (Loomis 1992; Bergstrom & Taylor 2006); functions to estimate ecosystem service values in different areas are also recommended (Spash & Vatn 2006). Here we have outlined the necessary steps for developing these functions in agricultural systems, particularly for evaluating the pest-control values provided by generalist predators such as birds, bats, and insects. We also suggest more careful benefit transfer analyses should include a mean value over time and ensure a high level of correspondence between sites by accounting for the spatial effects of changes in technology, ecological conditions, and differences in social practices (e.g., extent of cropland). This is especially pertinent for valuations of ecosystem services in agricultural systems, where socioeconomic drivers such as transgenic crop adoption, agricultural intensification, and changing crop prices can greatly change agroecosystem dynamics across space and time.

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