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Agricultural Production in the 21st Century: Land-use, Diversity, Pests and Pesticides

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Ecology, Evolution, and Marine Biology

by

Ashley Elizabeth Larsen

Committee in charge:

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September 2015

The dissertation of Ashley Elizabeth Larsen is approved.

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August 2015

Agricultural Production in the 21st Century: Land-use, Diversity, Pests and Pesticides

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by

Ashley Elizabeth Larsen

Here, on their own page, I thank my phenomenal family. I am forever grateful for my mother's infinite support, for my father encouraging science from an unreasonably young age, and for my siblings breaking trail. I also express my sincere appreciation for the understanding and support of my in-laws. Lastly, I would like to thank my husband, Andy MacDonald, for being the ideal partner in every conceivable way.

VITA OF ASHLEY ELIZABETH LARSEN
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PUBLICATIONS

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N.L. Gutiérrez, S.R. Valencia, T.A. Branch, D.J. Agnew, P. L. Bianchi, J. Cornejo-Donoso, C. Costello, O. Defeo, T.E. Essington, D.D. Hoggarth, **A. E. Larsen**, C. Ninnes, R. L. Selden, S.Sistla, A.D.M. Smith, A. Stern-Pirlot, S. J. Teck, J.T. Thorson, N.E.Williams. (2012). Eco-labels convey reliable information on stock status to seafood consumers. *PLoS One* 7 (8) e43765. doi:10.1371/journal.pone.0043765.

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ABSTRACT

Agricultural Production in the 21st Century: Land-use, Diversity, Pests and Pesticides

by

Ashley Elizabeth Larsen

Over the next 50 years, global food demand is forecast to double. Already it is estimated that agriculture covers about 40% of ice-free land, accounts for a third of greenhouse gas emissions, and contributes significantly to global biodiversity declines.

One means to reduce the impact of agriculture on humans and natural systems is to ensure the efficient use of pesticides. Pesticides, especially insecticides, have numerous negative externalities for human and environmental health, and their efficient use is an economic, ecological and public health priority. How land use patterns influence insect pests and insecticide demand is of special concern, because productive and efficient land use is key to meeting future food demand.

This research investigates the relationships between insecticide use and landscape configuration. It further investigates the importance of weather variability and data quality to understanding agriculture in the 21st Century. Finally, it explores ecological theory to understand how multiple natural enemies may coexist on a single resource species.

Specifically, I address the following questions: 1) is landscape simplification a consistent driver of insecticide use across time, 2) is landscape simplification a consistent driver of insecticide use across space and throughout the varied growing regions of the US,

and do annual weather patterns influence insecticide use? 3) Is satellite crop data sufficiently accurate to be applied to ecological and economic questions at the sub-county level? 4) Can coexistence be driven by non-consumptive ecological interactions?

To address these questions I integrate ecological and economic theory, and apply multivariate statistical techniques to multi-year national or regional databases.

I find that, contrary to expectations from ecological theory, landscape simplification does not consistently drive insecticide use over time (Chapter 1) or space (Chapter 2). This spatio-temporal variation helps explain the ambiguous results in the literature and implies that national land use policy will have very different effects on insecticide use if regional differences are ignored. To further understand the underlying mechanisms requires fine-scale spatial information of configuration and crop type. However, leveraging satellite data for sub-county information such as spatial configuration is well suited to simplified growing regions, but highly inaccurate elsewhere (Chapter 3). Lastly, I show natural enemies and other intermediate consumers can coexist with sufficiently strong non-consumptive effects of a top predator on the dominant consumer (Chapter 4).

In 2007 US farmers applied ~70 million pounds of insecticide active ingredients. While farmers pay the purchase price, society pays for degradation of natural systems and harm to human health. To minimize the cost of insecticides to both farmers and society, now and under future climate change, we must understand what drives variation in insecticide use and what enables persistence of natural enemy diversity. My dissertation research informs these key gaps in our understanding.

I. Does agricultural landscape simplification consistently drive insecticide use?

A. Introduction

Agricultural production has grown to meet the demands of an increasingly large and wealthy human population. The development of high yield crop varieties combined with the widespread use of irrigation, synthetic fertilizers, pesticides and land use changes that marked the "Green Revolution" have enabled an enormous increase in crop production per area (Tilman et al. 2002; Evenson and Gollin 2003; Soares and de Souza Porto 2009). As a result of these technologies, cereal production has doubled (Tilman et al. 2002). This increased production is credited with reducing poverty and improving nutrition intake for millions of people worldwide (Huang et al. 2002; Tilman et al. 2002).

This increase in production, however, also has costs. There are concerns that the loss of natural enemies and biodiversity caused by the increased size and connectivity of agricultural land, the trend towards monocultures and the conversion of natural habitat termed "landscape simplification" makes farms more susceptible to pest outbreaks (Tscharntke et al. 2005; Bianchi et al. 2006; Meehan et al. 2011; Tscharntke et al. 2012). With increased risk of pest outbreaks comes enhanced pesticide use. While other aspects of intensive farming also have negative externalities, such as synthetic fertilizers and eutrophication, pesticides have received some of the most widespread scrutiny and their

reduction (or at least efficient use) has become a priority for policy makers, as evidenced by Integrated Pest Management (IPM) (Sexton et al. 2007). The emphasis on pesticide use stems from serious human health concerns related to pesticide exposure in farm workers (Soares and de Souza Porto 2009; Weichenthal et al. 2010; Kouser and Qaim 2011) pesticide residues in food and water sources (Sexton et al. 2007; McKinlay et al. 2008), and bioaccumulation of pesticides in higher trophic levels (Hoekstra et al. 2003).

Despite popular ecological thinking that the connection between landscape simplification and pesticide use is clear, both theoretical and empirical studies have found ambiguous results. Agroecological theory holds that landscapes composed of a high proportion of cropland are more susceptible to pest outbreaks due to their habitat homogeneity and reduced natural enemy populations. Therefore more simplified landscapes would experience more pest problems and consequently use more pesticides. Conversely, economic theory of pesticide use suggests that the application of pesticides by a neighboring farm may have positive externalities for surrounding farms due to pesticide drift or pest suppression (Sexton et al. 2007). Additionally, as the amount of land in cropland increases, opportunities for invasion or refuge from pesticide applications may be reduced, thus leading to a negative effect of landscape simplification on pesticide use. Three recent reviews of empirical, landscape scale ecological studies evaluating the effect of landscape complexity on insect pests reported similarly equivocal results with some studies finding reduced pest pressure, pest abundance or pest diversity while others find no relationship or the opposite relationships (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Veres et al. 2011).

The variability in the literature may reflect the inadequacy of current study designs to disentangle the net effect of landscape simplification on pesticide use. Confounding variables such as crop type or endogenously determined variables such as farm size or income could

give misleading results if not properly controlled for. Alternatively studies that are small scale or over short time periods may miss important underlying drivers of pest abundance.

Many ecological processes governing agricultural pest abundance occur over a large spatial scale. Pests disperse large distances both naturally and aided by the movement of people and goods. Agricultural pests are thus likely governed in large part by metapopulation processes (i.e. immigration and extinction) (Levins 1969). Within an agricultural landscape pests may go locally extinct from crop patches due to pesticide use or due to stochasticity influencing small populations only to be recolonized from a persistent metapopulation existing in the surrounding agricultural matrix or from a new invasion into the system. Natural enemies too may require resources outside of individual crop fields for alternative prey and shelter for overwintering or from disturbances such as pesticide application or harvest (Landis et al. 2000). Furthermore, the periodic disturbance of crop fields may disrupt predator-prey dynamics by reducing natural enemies directly (Landis et al. 2000) or by temporarily reducing pest populations to the level below which predators can be supported. Due to pest and natural enemy dispersal and immigration, the effect of local processes on regional abundances may be small despite large effects on within-field abundances. Thus, small-scale studies that fail to account for the landscape scale dynamics of agricultural pests and their natural enemies could result in spurious associations of what promotes or limits pest abundance. For these reasons, landscape scale studies provide the best insight into the effect of habitat simplification on pests (Veres et al. 2011).

Beyond metapopulation dynamics and trophic interactions, invasion and spread of insect pests and natural enemies are partly stochastic processes influenced by yearly environmental conditions and by the timing of insect pest (Sexton et al. 2007) and natural enemy arrival (Ives and Settle 1997). Thus, temporal scale may be equally as important as

spatial scale to disentangle the effects of landscape simplification on pest abundance. For instance, a heat wave at the right time of the growing season may result in widespread pest mortality and high crop yields, whereas a heat wave at a different time of the season may stress crops making them more susceptible to pest outbreak while having little effect on the pests themselves. This variability over time could appear like ambivalent results of landscape simplification when it is instead the result of the interaction between insect pests and weather.

If we are to mitigate the effects of pesticide use on both human health and ecological systems, it is necessary to understand the underlying abiotic or biotic factors resulting in differences in pesticide use. Here I take advantage of longitudinal data from the USDA Census of Agriculture to revisit whether landscape simplification is a consistent driver of insecticide use. I perform cross-sectional analyses for five USDA census years (2007, 2002, 1997, 1992, 1987) in seven Midwestern U.S. states (IL, IN, IA, MI, MN, OH, WI) at the county level. I follow this with a panel data analysis using a fixed effects model, which identifies the effect of landscape simplification on insecticide use using year-to-year variation within counties. I specifically focus on insecticides in these states to compare this multi-year analysis with a recent single year study by Meehan et al. (2011). I check the robustness of these results by comparing data from the USDA Census of Agriculture[1] to the National Agricultural Statistics Service Cropland Data Layer (NASS CDL)[2], and check different selection criteria for included counties. I compare these results to that of Meehan et

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[1] USDA National Agricultural Statistics Service. *Census of Agriculture.* Available at http://www.agcensus.usda.gov/. 1997-2007 data is accessible online. 1987-1997 is accessible via CD-ROM (or in pdf online).

[2] USDA National Agricultural Statistics Service. *Cropland Data Layer.* Available at http://nassgeodata.gmu.edu/CropScape/ or http://www.nass.usda.gov/research/Cropland/SARS1a.htm.

al. (2011), who used the same data sources and model specifications for 2007 only, and find that incorporating multiple years of data as I do here provides insights impossible to glean from a single data year.

B. Methods

1. NASS Data

To first replicate Meehan et al. (2011), I obtained remotely sensed land cover data from the NASS 2007 Cropland Data Layer for the counties in the following states: Illinois, Indiana, Iowa, Michigan, Minnesota, Ohio and Wisconsin. Like Meehan et al. (2011), cropland was defined as the sum of all land in field crops (minus non-alfalfa hay), vegetable, fruit and nut crops. Fifty-six counties with proportion of cropland <0.01 were removed as were five counties that were missing data on the area treated with insecticides for the census year 2007, leaving 562 counties.

2. Census of Agriculture Data

Data on the total land in county, total harvested cropland, income, area treated with insecticides, area of corn (grain and silage), soybeans, small grains (barley, oats, wheat), vegetables, and fruit and nut orchards were obtained for the 1987, 1992, 1997, 2002, and 2007 Census' of Agriculture. Income was adjusted for inflation and reported in 2007 dollars. To extend the analysis beyond 2007, I needed to define "cropland" based on a census metric rather than on the NASS cropland data layer, which did not exist for the Midwest for years prior to 2007. I redefined "cropland" as total harvested acres and proportion of county in cropland as total harvested acres divided by total land in the county. Using this definition only 12 counties were excluded in 2007 for proportion of cropland <0.01, indicating total harvested cropland was greater than the remotely sensed cropland from the NASS Data Layer. Proportions of cropland treated with insecticide and proportion of cropland in a given

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crop type were calculated as insecticide (crop) area divided by total harvested cropland. Observations were dropped if they were missing data (or if data were withheld to avoid identifying individual farms) on the dependent variable (insecticide use) or the covariate of interest (harvested cropland). For the other covariates, I set withheld values to zero to avoid dropping a large number of counties (over 100 in 1987), which were missing one of the covariates[3].

I used the NASS Agricultural Pesticide Use Database (APUD)[4] to check that proportion of the cropland treated with insecticide reflected the amount (pounds of active ingredients) of insecticides applied at the state level (See Appendix, Fig A2).

3. Statistical Approach

To analyze whether landscape simplification drives insecticide use, I use both cross-sectional analyses for each of the five census years and fixed effects models on all five census years. Please see the appendix for additional information on these techniques. For both analyses the outcome variable was proportion of cropland treated with insecticide and the coefficient of interest was proportion of the county in cropland. Since insecticide use varies by crop type, I included covariates for proportion of the county in corn, proportion of the county in soybeans and small grains, and proportion of the county in fruit and vegetable orchards following Meehan et al. (2011). I also included a covariate for 2007 adjusted income to control for the possibility that higher income farms would use more insecticides (See SI text for additional model details).

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[3] Dropping all observation with missing data or with zero values for any covariate did not affect the patterns observed.

[4] USDA National Agricultural Statistics Service. *Agricultural Chemical Use Database.* Available at http://www.pestmanagement.info/nass/.

Cluster-robust standard errors are used to account for spatial autocorrelation in the above models. The USDA defines Agricultural Statistics Districts (ASD) within each state to reflect similarities in "geography, climate, and cropping practices" (USDA). There are roughly nine ASDs in each state (e.g. northwest, north central, northeast) composed of several counties. I chose to cluster on the ASD for the cross-sectional models allowing for covariance between counties in an ASD[5]. For the fixed-effects models there is an observation in each county for each year, and thus I take advantage of the repeated observations per county and cluster at the county level. I chose cluster-robust standard errors rather than heteroskedasticity-robust or spatial autoregressive errors to allow for arbitrary covariance between counties within an ASD or within counties over time (Moulton 1990; Wooldridge 2003). The choice of standard errors (SE) does not change the estimate of the coefficient but does change the range of the 95% confidence interval and thus whether or not the coefficient is considered statistically significant. All analyses were completed in Stata 12SE. I used Quantum GIS 1.8.0 to make figure 3, figure S3, and to obtain county centroid coordinates.

4. Model Robustness Checks

I checked the robustness of the cross-sectional results for different selection criteria and different definitions of cropland. For 2007, I first followed Meehan et al. (2011) and removed all counties that had less than 1% cropland based on the NASS CDL data. I repeated the analysis, again for 2007, using the census definition of cropland and removed counties whose census percent cropland was less than 1%. I repeated the analysis a final time not excluding any counties. Additionally, for 2007 I ran analyses with the NASS CDL

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[5] I checked for additional spatial correlation outside of ASDs using Conley standard errors (31,32), allowing for arbitrary correlation for counties within 100km and 150km of a given county centroid. Patterns of significance were largely the same.

definition of proportion of county in cropland and the census definition of proportion of county in cropland to see how the difference in definition influenced the magnitude of the coefficient. For years prior to 2007 the census definition of proportion of county in cropland was the only metric available and thus was the covariate included for 1987-2002 cross-sectional analyses and all fixed effects models. For selection in the cross-sectional years prior to 2007 I tried 1) removing all counties that were not included by the Meehan et al. selection criteria in 2007, 2) removing counties that were not included by the census selection criteria, 3) not removing any counties. For the fixed effects models I additionally tried only including counties that had data in all years (i.e. a balanced panel).

Finally, I addressed the possibility that these estimates suffer from endogeneity bias stemming from the income covariate. In other words if income drives insecticide use but the converse is also true, that insecticide use drives income, then the estimates of the slope coefficient on income and all of the other covariates will be biased (Wooldridge 2002). To evaluate this potential endogeneity problem, I re-ran the 2007 models excluding income. If endogeneity of income is biasing the estimates of the coefficients, I expected the coefficients on the other covariates to change when income is removed.

C. Results

1. Descriptive Analyses

Time trends for each covariate for each state were plotted to ensure no unexpectedly large changes in land use were present in the data. Within each state, proportion of the county in cropland, proportion of cropland in corn, soybeans and small grains, and fruit and vegetable orchards, and net income per harvested hectare (in 2007 dollars) remained similar over the study period, 1987-2007 (Fig.1; Fig. 2). The proportion of the cropland treated with insecticides averaged 0.191 across all states and time periods with the lowest average of

0.147 occurring in 1997 and the highest average of 0.259 occurring in 2007 (Fig. 2).

2. Econometric Analyses

The coefficient of interest was the metric for landscape simplification i.e. proportion of county in cropland, and thus these results focus on that coefficient. For all models, proportion of cropland in corn, soybeans and small grains, and fruit and vegetable orchards are included as covariates. Their coefficients and standard errors are reported in Table 1-2 and Table A1-A3.

Using the most recent census year available (2007) I tested the effect of data source, model specification and the potential for endogeneity of income. I first compared these results to that of Meehan et al. (2011) who, using the same model specification, found a significant positive effect of landscape simplification on insecticide use using data for 2007 from the Census of Agriculture and the NASS CDL. Since the NASS CDL data are only available for the census year 2007 and more recent years, I compared these results with similar data from the USDA Census of Agriculture to understand if differences in results could be attributable to differences in data sources. Regardless of data source or of the selection (exclusion) criteria of counties in the analysis (See Methods) I found a significant positive coefficient on proportion of county in cropland in 2007. The NASS data and selection criteria used by Meehan et al. (2011) provided the most conservative estimate while the census definition yielded the most liberal estimate of the effect of landscape simplification on insecticide use (Table 1).

To check whether the potential endogeneity of income was having an effect on the estimates, I reran the above regressions removing income per harvested hectare from the regression equations. In all specifications, the coefficients were similar, with or without income included in the regression (Table A1), indicating that income was not biasing the

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regression coefficients.

For the census years prior to 2007, all data were derived from the Census of Agriculture. For all model specifications I found the effect of landscape simplification to vary widely among census years (Table 2; Fig. 3; Table A2; Fig. A1). In 2002 and 1997, the coefficients on proportion of the county in cropland were generally negative and always non-significant, while in 1992 the estimates were negative and significant. Depending on the model specification, 1987 was either negative and significant or negative but not significant. Table 2 shows the results from the model that included all counties and Table A2 shows the results for all other selection criteria.

To determine whether either of the major crops was driving the variation in the results, I reran the above regressions for counties with more than half of cropland in corn, more than half of cropland in soybeans and more than one fifth of cropland in each corn and soybeans. Neither the counties with a high percentage of corn, soybeans nor the combination consistently reflected the results from the full model indicating that the variation observed was not simply reflecting variation driven by one crop type.

For the fixed effects models, I tested models with just county, just year or both county and year fixed effects. The fixed effects model exploits the year-to-year (census-to-census) variation in land-use at the county level to estimate how landscape simplification affects insecticide use, after controlling for year effects that are shared by all counties (see Methods, Appendix). Both year and county fixed effects were found to be statistically important. An F-test assuming homoskedastic standard errors (for computational feasibility) rejected the null hypothesis that year fixed effects were equal to zero ($F_{(4,3028)}$=97.223, P<0.0001) and that county effects were equal to zero ($F_{(619,2418)}$=5.035, P<0.0001) , indicating that unobserved heterogeneity in both year and county was present. Controlling for year effects proved very

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influential. Without year effects, the coefficient on proportion of county in cropland was negative and significant for all but one model specification (Table 2; Table A3). However, after controlling for year effects, I found no significant relationship between proportion of county in cropland and proportion of cropland treated with insecticides (Table 2; Table A3).

D. Discussion

Annual expenditure on insecticides is over 4 billion dollars in the United States (Grube et al. 2011), which equates to the use of almost one hundred million pounds of active ingredients (Grube et al. 2011). Given the many health and environmental consequences related to insecticide exposure, it is critical to understand what farm, landscape or environmental characteristics drive the insect pests that motivate insecticide use. It has long been thought that landscape simplification is one of these characteristics. Reviews of empirical evidence for this theory have been largely inconclusive (Bianchi et al. 2006; Chaplin-Kramer et al. 2011; Veres et al. 2011), though a recent statistical analysis of the Midwestern United States in 2007 found a strong, positive relationship between landscape simplification and insecticide use (Meehan et al. 2011).

Here I analyzed data from five USDA Census of Agriculture years using cross-sectional and fixed effects models. The cross-sectional results show that landscape simplification does not consistently drive higher insecticide use. While the coefficient on proportion of county in cropland, my metric for landscape simplification, is positive and significant in the 2007 analyses, that relationship is absent or reversed in prior census years. Further, adjacent census years such as 2002 to 2007 and 1992 to 1997 show large changes in the magnitude and changes in significance of the landscape simplification coefficient.

It is evident that the drivers of insecticide use may not be easily or reliably identified using single time period studies. Using a fixed effects model to remove unobserved

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characteristics, I find a non-significant relationship between landscape simplification and proportion of county in cropland. Counterintuitively, these results suggest that as cropland increases, the proportion of the county sprayed with insecticides is unaffected.

The existence of a null relationship between landscape simplification and insecticide use is not unlike the results of Hutchison et al. (2010), who reported large reductions in the European corn borer in non-Bt corn as a positive externality from Bt corn plantings. While pesticides may have negative effects on public health, biodiversity, and ecosystem services, the application of pesticides by a nearby farm may reduce pest incidence on surrounding farms due to pesticide drift or pest suppression (Sexton et al. 2007).

Additionally, as the amount of land in cropland increases, opportunities for invasion from natural or untreated areas may be reduced. As a result of landscape simplification, natural lands have been isolated to farm boundaries, fallow lands, or wood lots (Bianchi et al. 2006). Numerous ecological studies have found that these fragmented natural or less intensively managed areas can act as a source for natural enemies (e.g. Philpott et al. 2008) and pest species (Veres et al. 2011) that recolonize species poor crop fields (Tscharntke et al. 2005). If the cost of pest invasion is greater than the benefits of natural enemy pest suppression stemming from non-cropland, these habitats can have a net negative impact on the farmer in terms of pest control.

The above mechanisms may explain why a null relationship is observed in the fixed effects model, however they do not account for the importance of year. What could explain the wild variation in the landscape simplification coefficient in the cross-sectional analyses and why year fixed effects are so important? There are a number of drivers that could be behind the year-to-year variability and deciphering which mechanism is at play is critical since different policy measures are needed to address different types of drivers.

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For instance, a stochastic driver such as weather could be the culprit. Insect development is strongly influenced by weather conditions such as temperature and precipitation, and thus yearly differences in these or other environmental conditions could have an important effect on insecticide demand and the relationship between landscape simplification and insecticide use. Preliminary analysis[6] indicates that the effect of weather on this relationship is complex. This may be because the timing of pest arrival relative to the growing season may determine the likelihood of pest outbreaks and the benefits of applying insecticides (Sexton et al. 2007). Furthermore, temperature and precipitation affect the survival and development of different pests (and their enemies) differently, and thus which pests and enemies are present may determine the effect of weather on the relationship between landscape simplification and insecticide use. Refined data on pest outbreaks or type and timing of insecticide use are currently not available for the study area examined. However the development of such data or further empirical study focusing on abiotic conditions would greatly increase our understanding of the link between weather events and insect outbreaks, and thus increase our ability forecast variation in insecticide use both now and under future climate change.

It is also conceivable that the change in the relationship between landscape simplification and insecticide use between 2007 and all previous years reflects a systematic and predictable trend in insecticide use. For example, in 1996 there was a major change in the regulation of pesticides in the form of the Food Quality Protection Act (FQPA). FQPA prompted the re-evaluation of all (and restriction of many) registered pesticides, and

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[6] Preliminary analysis using growing season weather (precipitation and degree days) based on the National Climatic Data Center Global Historical Climatology Network-Daily file does not explain the variation in the cross-sectional relationship between landscape simplification and insecticide use.

promoted the use of more selective, less persistent "reduced-risk" pesticides via a fast-track registration process (EPA).

FQPA could affect the relationship between landscape simplification and insecticide use because insecticides that are effective against a multitude of insect pests and persist in the environment for longer periods of time may have provided higher positive externalities to surrounding crop fields thus necessitating less insecticide use in landscapes dominated by agricultural fields. The implementation of FQPA and the resulting use restrictions took ten years, and phasing out of certain chemicals is still in progress (EPA). Since changes in available insecticides were occurring between 1996 and 2007 it is difficult to statistically evaluate the effect of FQPA on the results reported here. Future Census' of Agriculture (i.e. 2012, 2017) or more refined insecticide data that include information on the active ingredient in use could elucidate how policy changes are interacting with the relationship between landscape simplification and insecticide use.

Agriculture has vast impacts on the Earth's environment and these impacts are only expected to grow as demand increases in the coming decades (Tilman et al. 2011). The challenge, as Balmford et al. (2012) discuss, is how to meet the increasing demand with the least effect on native biodiversity and the ecosystem services intact ecosystems provide. There are various advantages and disadvantages to whether increased demand should be met by increased intensity of farming on current agricultural land (land sparing) or by increased land conversion to agriculture to be farmed with more biologically harmonious farming methods (land sharing) (Vandermeer and Perfecto 2006; Godfray et al. 2010; Balmford et al. 2012; Phelps et al. 2013). In the Midwestern U.S., it appears that land sparing at the county level (i.e. more simplified landscapes) does not lead to consistent increases in the proportion of cropland treated with insecticides. However, without understanding what is behind the

year-to-year variation in the relationship between landscape simplification and insecticide use it is impossible to predict how land sharing or land sparing as a policy initiative would affect insecticide use in the future. As suggested by this study and recent empirical reviews (Chaplin-Kramer et al. 2011; Veres et al. 2011), the presence and direction of the relationship between landscape simplification and insecticide use can be positive, negative or null. If this variation is driven by variation in yearly weather, whether simplified landscapes cause more or less insecticide use could flip flop unpredictably. If the variation is driven by extreme weather or weather characteristics that will be altered with climate change, perhaps there will be some directionality. If the relationship between landscape simplification and insecticide use is an indirect consequence of management policies, perhaps 2007 is a glimpse of the future. The data available are currently inadequate to decipher the underlying mechanisms. However, given the different policy implications of a stochastic driver, such as weather, versus to a predictable driver such as regulatory change, developing the necessary data sources to tease apart the underlying causes is imperative.

Perhaps most importantly, this study emphasizes the need for longer-term research agendas, especially when investigating a politically, economically and ecologically important question such as insecticide or pesticide use. Analyses of single census years provide wildly varying estimates of the effect of land simplification on insecticide use. It is evident that the relationship between landscape simplification and insecticide use is spatially and temporally context dependent and that there are a number of ways that context could be determined. While it remains unclear what underlying mechanisms are providing the context, it is abundantly clear that the relationship between landscape simplification and insecticide use observed in 2007 does not hold for previous census years. It is time to move beyond simply asking whether landscape simplification drives insecticide use and instead focus on what

factors may explain the variability in this relationship over time and space.

E. Acknowledgements

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G. Appendix
1. Statistical Models

The cross-sectional approach, which uses one time period, attempts to directly quantify the effect of landscape simplification on insecticide use using a multiple linear regression. Its advantage is that it accounts for substitution behavior of the farmers when pest problems occur.   However, the cross-sectional approach is only valid if the effect of landscape simplification on insecticide use is consistently estimated (Wooldridge 2002). Unmeasured or unobserved characteristics such as soil quality are important determinants of land-use patterns in agricultural settings (Deschenes & Greenstone 2007). Thus, the cross-sectional approach may confound landscape simplification with other unobserved characteristics. Since the omitted variable is, as the name suggests, omitted from the regression, the magnitude and sign of the omitted variable bias is generally unknown (Wooldridge 2002).

The advantage of the fixed effects approach is that it removes the time invariant unobserved effects unique to individual counties that may otherwise bias the estimates derived from cross-sectional analyses (Wooldridge 2002). Rather, the fixed effects model exploits the year-to-year (census-to-census) variation in land-use at the county level to estimate how landscape simplification affects insecticide use. Analysis of within-county variation in cropland revealed sufficient year-to-year variation for the fixed-effects estimation to be reasonably statistically precise.

Mathematically, the cross-sectional analysis is represented by the following equation:

$Y_i = X_i'\beta + u_i$ where Y_i is the response variable, the proportion of harvested cropland sprayed with insecticides in county i. X represents the vector of covariates including proportion of county in cropland, income per harvested ha, and proportion of cropland in

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corn, soybeans and small grains, vegetables, and fruit and nut orchards in each county i, and

u represents the random error term for each county, i. This model is analyzed for each USDA

Census of Agriculture[7] year using data from the Census, and from the National Agriculture

Statistics Service Cropland Data Layer (CDL)[8] for one 2007 specification.

The fixed-effects estimation is represented by the following equation:

$Y_{it}=X_{it}'\beta+ c_i + u_{it}$ for county i in year t. Again, Y_{it} is the proportion of cropland treated

with insecticides and X is a vector of covariates as described above, indexed for each time

period t. c is the unobserved effects (or individual heterogeneity) term for each county i, that

is assumed roughly time invariant over the period of analysis (Wooldridge 2002). By de-

meaning the data, this time invariant unobserved effect drops out of the above equation and

the model is identified from the variation of observations for a given county, i, away from

that county's mean. If the model also includes year fixed effects, then the model is identified

from year-to-year variation within a county, after controlling for time trends shared by all

counties in the study. If the model is estimated by assuming c_i is uncorrelated with the

observable covariates (i.e. a random effects model or pooled ordinary least squares model), c_i

is effectively put in the error term. Thus, if c_i is in fact correlated with the observed

covariates (e.g. if unobserved soil quality is correlated with the observed proportion of

county in cropland), the coefficient on proportion of county in cropland and other

coefficients in the model will be inconsistent (Wooldridge 2002).

2. Insecticide Use Trends

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[7] USDA National Agricultural Statistics Service. *Census of Agriculture.* Available at
http://www.agcensus.usda.gov/. 1997-2007 data is accessible online. 1987-1997 is accessible
via CD-ROM (or in pdf online).

I used the NASS Agricultural Pesticide Use Database (APUD)[9] to check that proportion of cropland treated with insecticide from the Census of Agriculture reflected the amount of insecticides applied. The APUD is available for participating states, reporting a limited number of crops. I chose to examine the relationship between acres treated and active ingredients (AI/acre) applied to corn because 1) corn is reported in the APUD for most of the states in this study for two of the most recently available census years (1997, 2002), 2) it represents a large proportion of the cropland in the Midwest and 3) other crops such as soybeans are not reported for most of the Midwest for both 1997 and 2002. Only state-level data is available and thus I assumed that state-level trends hold at the county level.

I find a strong linear relationship between acres treated and AI/acre for both years (Fig. S2). The slope of the relationship is different between years, possibly reflecting differences in the rate (lb/acre/yr) of insecticides available. For instance, in Iowa in 1997 chlorpyrifos was applied at a rate of 1.730 lb/acre/yr to 6% of corn while cyfluthrin was applied at a rate of 0.006 lb/acre/yr to 3% of corn. In 1992 chlorpyrifos was applied to 9% of corn and cyfluthrin was not used. Despite changes in concentrations or chemicals in 1997 compared to 2002, it is clear that there is a linear relationship between acres treated and active ingredients used in each year.

3. References

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[8] USDA National Agricultural Statistics Service. *Cropland Data Layer.* Available at http://nassgeodata.gmu.edu/CropScape/ or http://www.nass.usda.gov/research/Cropland/SARS1a.htm.

[9] USDA National Agricultural Statistics Service. *Agricultural Chemical Use Database.* Available at http://www.pestmanagement.info/nass/.

H. Figure Captions

Figure 1. Time trends for covariates for Illinois. County is abbreviated "Cty" and "Prop. (crop type)" indicates proportion of cropland in (crop type). Covariates remained similar over the period from 1987-2007 indicating that the counties were comparable over this time frame. Other states displayed a similar pattern over time.

Figure 2. Time trends in dependent variable, proportion of cropland treated with insecticides, and the landscape simplification metric, proportion of the county in cropland, for all states and all years. Proportion of cropland treated with insecticides and proportion of the county in cropland are roughly similar within each state across all time periods, though all states had at least a small increase in proportion of treated area in 2007.
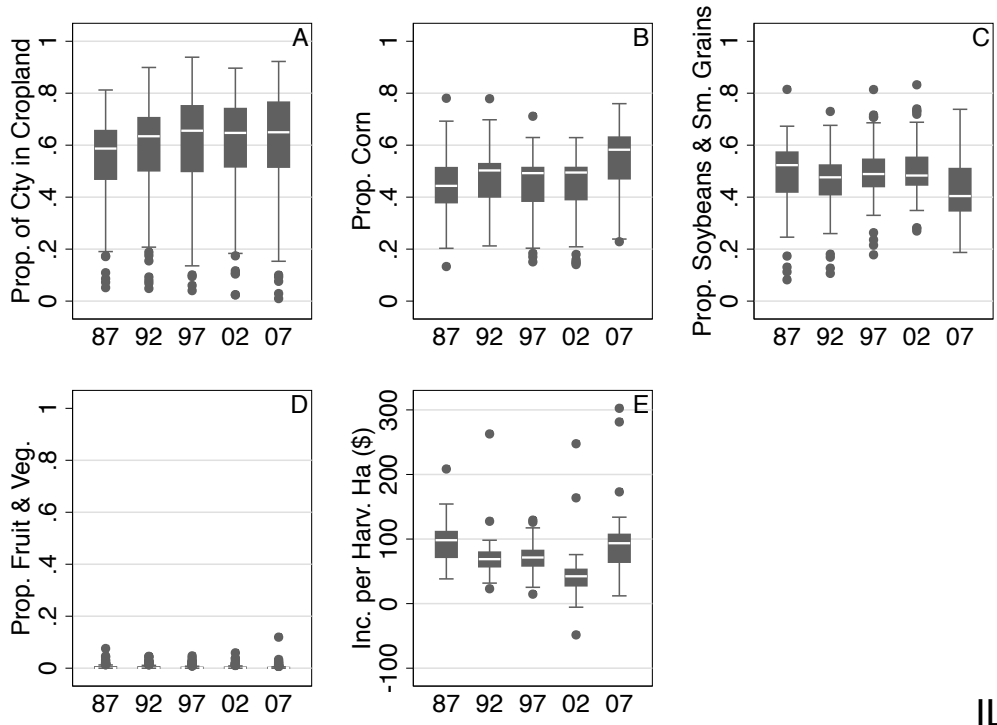
Figure 3. Map of proportion of cropland treated with insecticides (A-C) and proportion of the county in cropland (D-F) for 2007, 1997, and 1992 (see Fig. S3 for 2002 and 1987). The within- and between-county proportion of cropland treated with insecticides varies greatly between years. A positive correlation between cropland and insecticides is visually evident in 2007 and is absent in 1997 and reversed in 1992. The legend is based on 2007 quintiles with the range of the first and last quintile extended to incorporate the lowest (highest) values of the other years.

Figure A1. Partial residual plots of the effect of proportion of the county in cropland on proportion of cropland treated with insecticides over time from 2007-1987, including all counties. The coefficient on proportion of county in cropland (i.e. land simplification) is not a consistent driver of insecticide use. The number of points plotted in each year plot corresponds to the number of observations in table 2. The slopes and standard errors for proportion of county in cropland for each year also correspond to table 2.

Figure A2. Area treated with insecticides is linearly related to mass of insecticides applied at the state level. Points represent individual state data for 1997 (filled circle) and 2002 (diamond) with data for insecticides use in corn from the NASS Agricultural Pesticide Use Database. The difference in slope is likely due to different rates and different levels of application between years (see SI text).

Figure A3. Map of proportion of cropland treated with insecticides (A-B) and proportion of the county in cropland (C-D) for 2002 and 1987. The proportion of cropland treated with insecticides varies greatly between years both within the same county and between counties. The legend is based on 2007 quintiles with the range of the first and last quintile extended to incorporate the lowest (highest) values of the other years.

Figure 1.

Figure 2.

Figure 3.

Insecticides		Cropland	
☐	0/Missing	☐	0/ Missing
☐	0.0001–0.13	☐	0.0001 – 0.17
☐	0.13 – 0.22	☐	0.17 – 0.39
☐	0.22 – 0.29	☐	0.39 – 0.58
☐	0.29 – 0.37	☐	0.58 – 0.74
☐	0.37 – 0.67	☐	0.74 – 1.0

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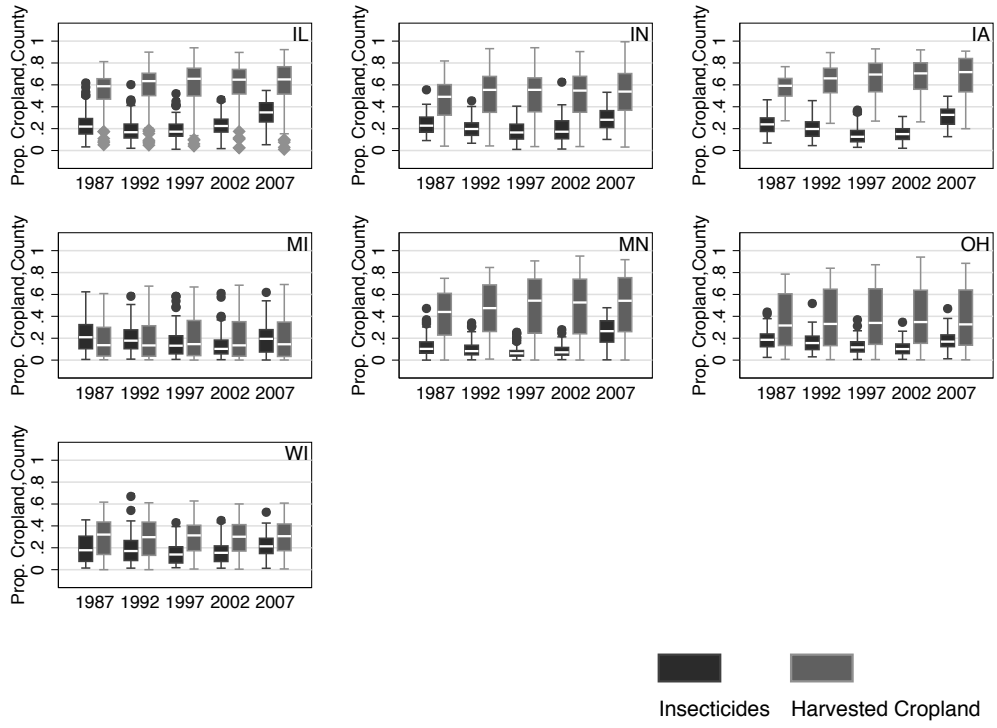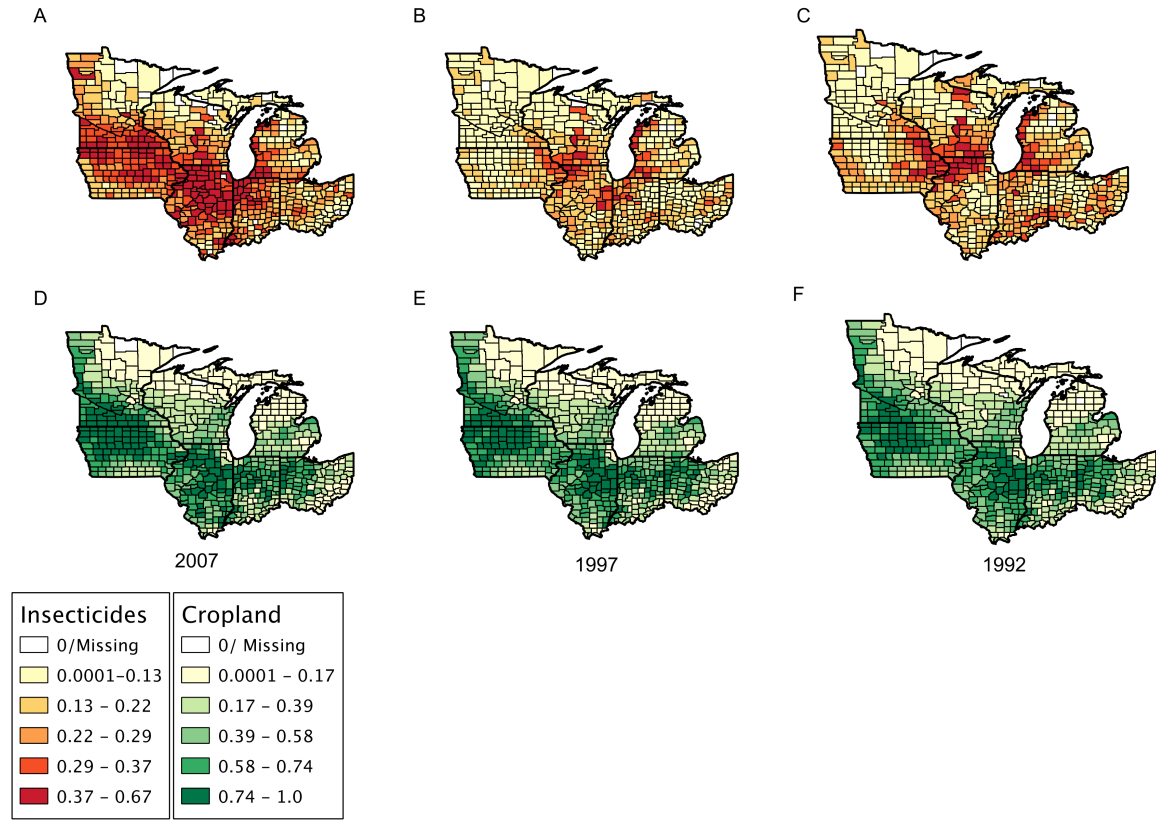
Figure A1.

Figure A2.

Figure A3.

Insecticides
- 0/Missing
- 0.0001 – 0.13
- 0.13 – 0.22
- 0.22 – 0.29
- 0.29– 0.37
- 0.37 – 0.67

Cropland
- 0/Missing
- 0.0001 – 0.17
- 0.17 – 0.39
- 0.39– 0.58
- 0.58 – 0.74
- 0.74– 1.0

2002   1987
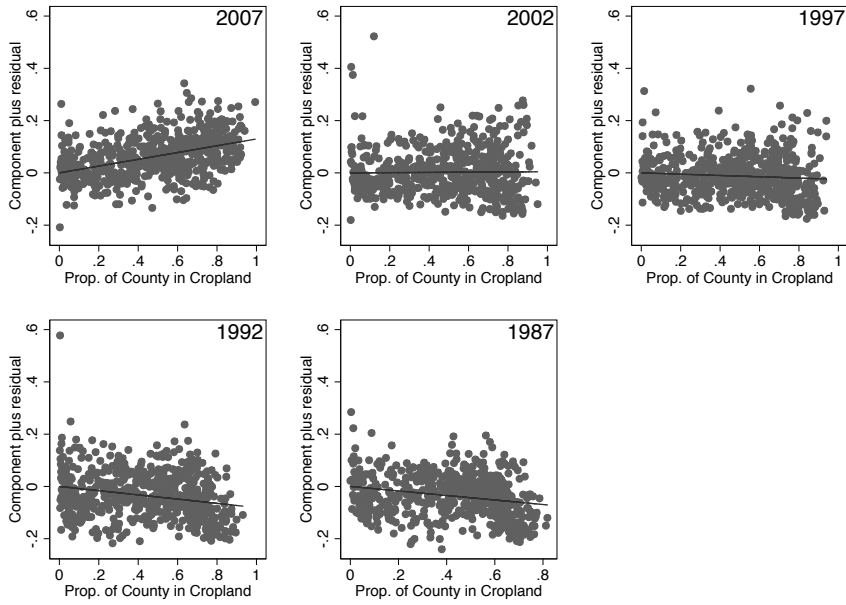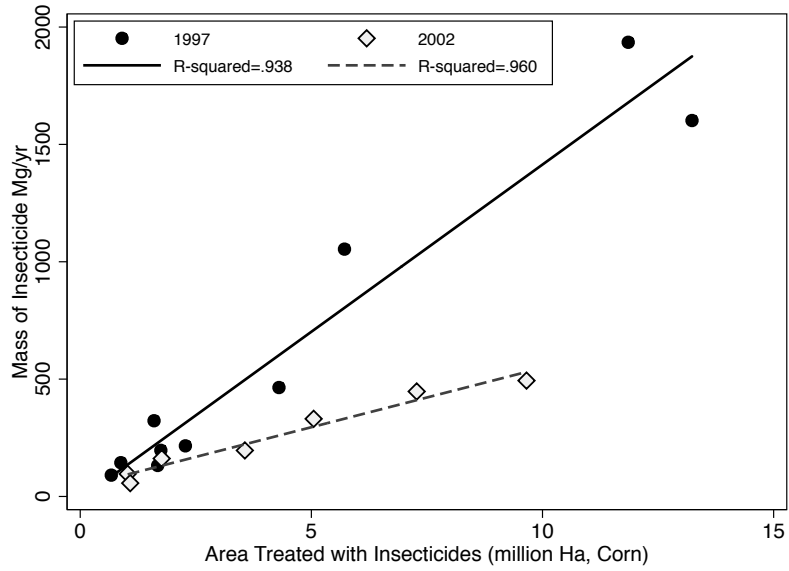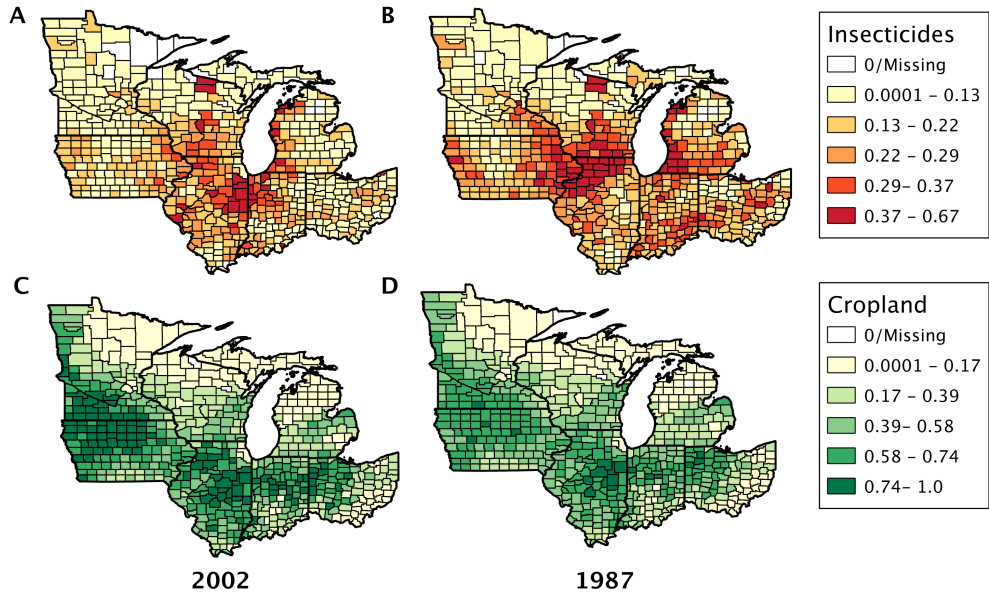
Table 1. Landscape simplification has a positive effect on insecticide use in 2007, regardless of data source or selection criteria.

	(1)	(2)	(3)
Prop. County in Cropland	0.0975** (0.0343)	0.1362** (0.0293)	0.1297** (0.0296)
Income per Harv. ha	0.0001 (0.0001)	0.0002** (0.0000)	0.0001* (0.0000)
Prop. Corn	0.4957** (0.0962)	0.4008** (0.0697)	0.4100** (0.0671)
Prop. Soybeans and small grains	0.0508 (0.0386)	-0.0029 (0.0356)	-0.0000 (0.0367)
Prop. Fruit & Veg.	0.9549** (0.0790)	0.8928** (0.0545)	0.8546** (0.0631)
Constant	-0.0450 (0.0335)	-0.0134 (0.0147)	-0.0095 (0.0139)
Observations	562	596	603
R-Squared	0.59	0.65	0.65
SE Clusters	ASD	ASD	ASD
No. Clusters	62	63	63
NASS Cropland	X		
Census Cropland		X	X
NASS Selection	X		
Census Selection		X	

Notes: In column (1) cropland was defined based on the NASS cropland data layer (CDL; see text). In columns (2) and (3) cropland was defined as total harvested acres based on the Census of Agriculture. All three specifications used cluster robust standard errors, clustering on the agricultural statistical districts (ASD) within each state. In Columns (1) and (2) counties were excluded if the respective definition of proportion of county in cropland < 0.01. In column (3) no counties were excluded. For all tables **,* indicates $p<0.01$, $p<0.05$, respectively.

Table 2. Cross-sectional analysis of census years 2007-1987 and fixed effects analysis.

	2007	2002	1997	1992	1987	A	B	C
Prop. County in	0.1297**	0.0044	-0.0249	-0.0810*	-0.0865*	-0.0080	-0.1379**	-0.0133
Cropland	(0.0296)	(0.0438)	(0.0391)	(0.0394)	(0.0391)	(0.0164)	(0.0409)	(0.0397)
Inc. per Harv. ha	0.0001*	0.0000	0.0001	0.0001*	0.0002*	0.0001*	0.0001	0.0000
	(0.0000)	(0.0000)	(0.0000)	(0.0001)	(0.0001)	(0.0000)	(0.0001)	(0.0000)
Prop. Corn	0.4100**	0.3256**	0.3412**	0.3897**	0.5873**	0.4269**	0.6936**	0.4830**
	(0.0671)	(0.0544)	(0.0617)	(0.0744)	(0.0695)	(0.0298)	(0.0479)	(0.0575)
Prop. Soybeans &	-0.0000	-0.0073	-0.0324	-0.0694	0.0094	-0.0391*	-0.3525**	-0.3875**
Sm.grains	(0.0367)	(0.0362)	(0.0386)	(0.0482)	(0.0446)	(0.0184)	(0.0468)	(0.0502)
Prop. Fruit & Veg.	0.8546**	0.7998**	0.8568**	0.7018**	0.8202**	0.7914**	0.4733**	0.3305**
	(0.0631)	(0.0895)	(0.0618)	(0.0752)	(0.0566)	(0.0452)	(0.0962)	(0.0973)
Constant	-0.0095	0.0226	0.0214	0.0585*	-0.0209	0.0181	0.0904*	0.1638**
	(0.0139)	(0.0159)	(0.0138)	(0.0241)	(0.0199)	(0.0100)	(0.0374)	(0.0415)
Observations	603	604	612	613	606	3,038	3,038	3,038
R-Squared	0.65	0.29	0.36	0.38	0.56	0.48	0.75	0.79
SE Clusters	ASD	ASD	ASD	ASD	ASD	County	County	County
No. Clusters	63	62	63	63	63	620	620	620
Year Effects						Y	N	Y
County Effects						N	Y	Y

Notes: Cropland was defined using the census metric, total harvested acres. All counties were included in each analysis. Column (A) includes year fixed effects, column (B) includes county fixed effects and column (C) includes both. The number of counties varies year-to-year because counties missing data on insecticide use or cropland in a given year were dropped.

Table A1. Evaluating the endogeneity of income.

	A: 2007 Model Specifications			B: 2007 Model Specifications Excluding Income		
	1	2	3	1	2	3
Prop. County in Cropland	0.0975** (0.0343)	0.1362** (0.0293)	0.1297** (0.0296)	0.0989** (0.0348)	0.1408** (0.0296)	0.1353** (0.0302)
Inc. per Harv. ha.	0.0001 (0.0001)	0.0002** (0.0000)	0.0001* (0.0000)			
Prop. Corn	0.4957** (0.0962)	0.4008** (0.0697)	0.4100** (0.0671)	0.5027** (0.0926)	0.4122** (0.0701)	0.4115** (0.0681)
Prop. Soybeans & Sm. grains	0.0508 (0.0386)	-0.0029 (0.0356)	-0.0000 (0.0367)	0.0472 (0.0376)	-0.0121 (0.0363)	-0.0078 (0.0380)
Prop. Fruit & Veg.	0.9549** (0.0790)	0.8928** (0.0545)	0.8546** (0.0631)	0.9612** (0.0802)	0.9121** (0.0605)	0.9102** (0.0610)
Constant	-0.0450 (0.0335)	-0.0134 (0.0147)	-0.0095 (0.0139)	-0.0406 (0.0344)	-0.0031 (0.0162)	-0.0010 (0.0156)
Observations	562	596	603	562	596	603
R-squared	0.59	0.65	0.65	0.59	0.64	0.64
SE Clusters	ASD	ASD	ASD	ASD	ASD	ASD
No. Clusters	62	63	63	62	63	63
NASS Cropland	X			X		
Census Cropland		X	X		X	X
NASS Selection	X			X		
Census Selection		X			X	

Notes: Column descriptions apply to both panels A and B. In column (1) cropland was defined based on the NASS cropland data layer (CDL; see text). In column (2) cropland was defined as total harvested acres based on the Census of Agriculture. Counties were excluded if the proportion of county in cropland was less than 0.01. Column (3) maintained the census definition of cropland but did not exclude any counties regardless of the proportion of the county in cropland. Panel B excludes the income covariate to evaluate potential endogeneity between income and insecticide use. Cluster-robust standard errors were used for all models, clustering on the agricultural statistical district within a state for single-year models and clustering on the county for multi-year models.

Table A2. Cross-sectional analysis of census years 2007-1987 for NASS (A) and Census (B) specifications.

	A					B				
	2007	2002	1997	1992	1987	2007	2002	1997	1992	1987
Prop. County in Cropland	0.1176**	-0.0134	-0.0320	-0.1151**	-0.0653	0.1362**	-0.0024	-0.0282	-0.1012**	-0.0847*
	(0.0367)	(0.0452)	(0.0411)	(0.0392)	(0.0372)	(0.0293)	(0.0444)	(0.0403)	(0.0377)	(0.0372)
Inc. per Harv. ha	0.0001	-0.0002	-0.0001	0.0000	-0.0002	0.0002**	0.0000	0.0002*	0.0003	0.0001
	(0.0001)	(0.0001)	(0.0001)	(0.0002)	(0.0001)	(0.0000)	(0.0001)	(0.0001)	(0.0002)	(0.0001)
Prop. Corn	0.4612**	0.4073**	0.3907**	0.5158**	0.6852**	0.4008**	0.3533**	0.3350**	0.4263**	0.6167**
	(0.1014)	(0.0732)	(0.0860)	(0.0970)	(0.0944)	(0.0697)	(0.0544)	(0.0655)	(0.0747)	(0.0721)
Prop. Soybeans & Sm.grains	0.0331	0.0206	-0.0184	0.0025	0.0100	-0.0029	0.0125	-0.0239	-0.0364	0.0128
	(0.0393)	(0.0415)	(0.0411)	(0.0448)	(0.0463)	(0.0356)	(0.0358)	(0.0390)	(0.0472)	(0.0442)
Prop. Fruit & Veg.	0.9515**	0.9486**	0.9116**	0.8053**	0.8843**	0.8928**	0.8853**	0.8419**	0.7404**	0.8484**
	(0.0795)	(0.0863)	(0.0754)	(0.0971)	(0.0741)	(0.0545)	(0.0656)	(0.0586)	(0.0748)	(0.0657)
Constant	-0.0404	-0.0052	0.0070	-0.0052	-0.0366	-0.0134	0.0038	0.0096	0.0285	-0.0256
	(0.0337)	(0.0275)	(0.0300)	(0.0337)	(0.0323)	(0.0147)	(0.0142)	(0.0145)	(0.0244)	(0.0204)
Observations	562	563	565	566	564	596	596	603	603	600
R-squared	0.59	0.31	0.33	0.41	0.54	0.65	0.32	0.37	0.41	0.56
SE Clusters	ASD	ASD	ASD	ASD	ASD	ASD	ASD	ASD	ASD	ASD
No. Clusters	62	62	62	62	62	63	62	63	63	63

Notes: For all specifications cropland was defined using the census metric, total harvested acres. In (A), counties were included if they met the NASS selection criteria (NASS proportion cropland >0.01) in 2007. In (B), counties were included if they met the census selection criteria. The number of counties in each year varies because of counties missing data on insecticides or cropland were dropped from the regression in that year. For both specifications, the relationship between proportion of county in cropland and proportion of cropland treated with insecticides is absent or reversed compared to the 2007 results.

Table A3. Fixed effects analysis for different model specifications with, year, county and year and county fixed effects.

	1	2	3	4	5	6	7	8	9
Prop. County in Cropland	-0.0212 (0.0171)	-0.0691 (0.0455)	-0.0126 (0.0411)	-0.0136 (0.0165)	-0.0967* (0.0434)	-0.0079 (0.0400)	-0.0164 (0.0169)	-0.1021* (0.0420)	-0.0089 (0.0401)
Inc. per Harv. ha	-0.0001 (0.0001)	0.0004** (0.0001)	0.0000 (0.0001)	0.0002* (0.0001)	0.0003** (0.0001)	0.0000 (0.0001)	0.0001 (0.0001)	0.0003** (0.0001)	0.0001 (0.0001)
Prop. Corn	0.5041** (0.0378)	0.6447** (0.0530)	0.4126** (0.0648)	0.4411** (0.0300)	0.6718** (0.0494)	0.4782** (0.0591)	0.4484** (0.0323)	0.6844** (0.0488)	0.4764** (0.0585)
Prop. Soybeans & Sm.grains	-0.0032 (0.0200)	-0.3531** (0.0501)	-0.4522** (0.0546)	-0.0234 (0.0177)	-0.3464** (0.0479)	-0.3984** (0.0513)	-0.0256 (0.0185)	-0.3401** (0.0484)	-0.4037** (0.0513)
Prop. Fruit & Veg.	0.8876** (0.0460)	0.4571** (0.1051)	0.4152** (0.1126)	0.8302** (0.0368)	0.3698** (0.1024)	0.3022* (0.1188)	0.8122** (0.0435)	0.4013** (0.0850)	0.3069** (0.0969)
Constant	-0.0160 (0.0150)	0.0580 (0.0434)	0.2192** (0.0494)	0.0017 (0.0091)	0.0659 (0.0392)	0.1641** (0.0432)	0.0068 (0.0113)	0.0607 (0.0400)	0.1683** (0.0446)
Observations	2,820	2,820	2,820	2,998	2,998	2,998	2,930	2,930	2,930
R-squared	0.49	0.74	0.79	0.50	0.75	0.80	0.49	0.74	0.79
No. Clusters	567	567	567	610	610	610	586	586	586
Year Effects	Y	N	Y	Y	N	Y	Y	N	Y
County Effects	N	Y	Y	N	Y	Y	N	Y	Y
Selection rule	NASS	NASS	NASS	Census	Census	Census	All, Balanced	All, Balanced	All, Balanced

Notes: For columns 1-3 counties were included if they met the NASS section criteria in 2007. In 4-6 counties were included if they met the census selection criteria. I repeated the analysis including all counties that had observations in all time periods, creating a balanced panel (7-9). All models used cluster robust standard errors, clustering on individual counties.

II. Spatiotemporal variation in the relationship between landscape simplification and insecticide use

This chapter is forthcoming in the November 2015 volume of Ecological Applications. Authorship on the published manuscript is as follows: Ashley E. Larsen, Steven D. Gaines, Olivier Deschenes

A. Introduction

Agriculture has an enormous influence on ecosystems across the globe. Cropland and pasture cover almost 40% of ice-free land (Ramankutty et al. 2008), account for roughly 1/3 of green house gas emissions (Foley et al. 2011), and contribute significantly to biodiversity declines in both temperate and tropical regions (Foley et al. 2005). Over the next 50 years, global food demand is forecast to double (Tilman et al. 2011). Simultaneously, policy initiatives for higher biofuel targets (Mehaffey et al. 2012) and increasing urban development are putting immense pressure on already limited land resources (Moilanen et al. 2011). The challenge for scientists and policy makers is to meet the increased agricultural demand while balancing alternative needs and minimizing damage to humans, natural systems, and the important services natural systems provide (DeFries et al. 2012).

One means to increase production on current agricultural land is to decrease crop loss to pests. Pre-harvest pests destroy between 15 and 60% of crops globally (Oerke 2006) and contribute to uncertainty in the supply and prices of food (Waterfield and Zilberman 2012). Although agricultural pesticides can reduce these losses, they also have a range of negative effects on human (Alavanja et al. 2004) and ecosystem health (Koleva and Schneider 2010; Beketov et al. 2013). Many of the negative externalities associated with pesticide use are

determined by the intensity of exposure (Kamel and Hoppin 2004). Therefore, reducing pesticide demand is an important ecological, economic, and policy goal.

Insect pest dynamics are often tied to land use practices (Landis et al. 2000), although competing theories make opposing predictions. Agroecological theory suggests that a more complex agricultural landscape should reduce insect pest incidence directly by limiting the size and connectivity of crop resources (O'Rourke and Jones 2011; O'Rourke et a. 2011; Martin et al. 2013) and indirectly by promoting the abundance and diversity of natural enemies (Altieri 1999; Philpott and Armbrecht 2006; Vandermeer et al. 2010; Martin et al. 2013). Based on this theory, simplified landscapes should harbor more pests and consequently promote increased insecticide use. Alternatively, economic theory suggests that simplified landscapes with high connectivity and homogeneity of cropland could enable positive externalities from pesticide application in the form of pesticide drift (and thus pest suppression) to surrounding farms and more limited refuges from pesticide application (Sexton et al. 2007). Field-level characteristics such as the quality of non-crop habitat for pests and natural enemies (Landis et al. 2000; Bianchi et al. 2006b) or the presence of resistant or novel pests can alter predictions from either theory (Sexton et al. 2007).

Reflecting the ambiguity of the competing theoretical predictions, recent empirical reviews have found equivocal relationships between landscape simplification and insect pests that ranged from positive (landscape simplification increases insecticides), to null, to negative relationships (Chaplin-Kramer et al. 2011; Meehan et al. 2011; Larsen 2013; Veres et al. 2013). Effective management would benefit from resolving the underlying mechanisms behind changes in the consequences of landscape simplification, yet many potential factors

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could correlate with variation in insect pest pressure or insecticide use at a single point in space or time.

Ecoinformatics approaches, taking advantage of longitudinal data at large spatial scales, can provide unique insight into complex agricultural pest dynamics (Rosenheim 2013). To the extent farmers modify treatment above or below baseline (or manufacturer recommended) applications in response to pest damage, insecticide use data reflect insect pest risk. An extensive economics literature provides evidence that pesticide use decisions balance the farmer's private costs of spraying with the benefits of pest control (Saphores 2000; Waterfield and Zilberman 2012), while empirical and statistical ecological studies suggest more pest management in response to higher pest pressure (Meehan et al. 2011).

Here, we leverage comprehensive, national-scale crop and insecticide use data over 25 years in order to clarify the context under which landscape complexity influences insect pests. By exploring consistencies and inconsistencies in the relationship between landscape simplification and insecticide use among crop regions, we statistically evaluated several hypothetical mechanisms (e.g., regional climates, changes in regulations, interannual variation in weather, non-linear effects of simplification and individual farm size) that could drive variation in the relationship between landscape simplification and insecticide use in ways that are infeasible to address in smaller empirical studies. Specifically we addressed five potential drivers of variable responses: (1) Are there consistent regional differences in the relationship between landscape simplification and insecticide use? (2) Can national pesticide legislation modify the temporal relationship between landscape simplification and insecticide use? (3) Does interannual variation in weather (growing season degree-days, precipitation, frosts) drive predictable variation in the landscape simplification coefficient

across time? (4) Is the relationship between landscape simplification and insecticide use driven by larger individual farms applying disproportionately more insecticides? (5) Are there non-linearities in the effects of land simplification (e.g., saturation at moderate simplification) and does accounting for a non-linear relationship explain the inconsistent outcomes in the linear analyses?

B. Methods

1. Data

For all analyses we were interested in predicting how the landscape simplification drives insecticide use. Following Meehan et al. (2011), we defined landscape simplification (i.e. the covariate of interest) as the proportion of a county in cropland, which was calculated using total harvested acres scaled by total land area in the county. The proportion of harvested cropland treated with insecticides was the dependent variable. Since different crops generally receive different amounts of insecticides, we included covariates for the proportion of the cropland in corn (grain and silage), soybeans and small grains (barley, oats, wheat), fruit and vegetable orchards, and cotton (in cotton growing regions). We also included a covariate for income per harvested hectare in 2007 dollars. County level data for all agricultural variables came from the bi-decadal USDA Census of Agriculture for the years 2012, 2007, 2002, 1997, 1992, 1987 (USDA).

We included counties in the contiguous US whose official boundaries remained constant over the study period, and that reported values for insecticides, total harvested cropland, and weather variables. For other covariates, we set missing or withheld values to zero to avoid dropping a large proportion of counties that were missing fruits and vegetables

or cotton. Counties missing approximate land area in 1987 or 1992 were filled in from the next census' data.

We calculated county-level degree-days and precipitation using weather station data on daily temperature and precipitation from the National Climatic Data Center (NCDC) Global Historical Climatology Network-Daily database. We used an inverse-distance weighted average of stations located within 300km of each county's centroid where weights were proportional to the squared distance of a station from the county centroid (Barreca et al. 2013). We calculated degree-days following (Deschênes and Greenstone 2007) and summed precipitation and degree-days over the growing season defined as April 1-September 30 (Deschênes and Greenstone 2007; USDA 2010).

We used the USDA Economic Research Service (ERS) Farm Resource Regions to group counties with similar growing conditions and growing practices. There are 9 ERS regions with varying farm characteristics (Table A1) and varying size, ranging from 165 counties in the Mississippi Portal to over 500 counties in the Heartland region (Fig. 1). County and county-equivalents were based on the USDA Census of Agriculture.

2. Econometric Approach

To evaluate the relationship between landscape simplification and insecticide use, we used a panel data approach pooling all data and including state and year fixed effects, or state and region-by-year fixed effects. We used fixed effects to control for time invariant unobserved effects unique to a state (e.g. historic legislation), shocks unique to a year (e.g. technological improvements), or time trends shared by counties within region (Wooldridge 2002).

The fixed effects model allowed for unique intercepts for each state, year or region-by-year. To allow for a different slope of the relationships between landscape simplification and insecticides between different years or regions, we reran the state and region-by-year fixed effects model including interaction terms between landscape simplification and year (region). For all models that include year (region) interaction terms, we interacted crop and income covariates with year (region) to allow their coefficients to also change by year (region). This accounted for the possibility the relationship between, for instance, corn and insecticides may differ from one year (region) to another due to different pest needs in different years (regions).

Due to the variation observed both across years and among regions, we investigated the variation by year within each region. To do so, we interacted proportion of county in cropland as well as crop and income covariates with both region and year, again including state and region-by-year fixed effects. This allowed the relationship between landscape simplification and insecticide use to vary for each year within each region after accounting for state-specific heterogeneity and year-specific heterogeneity shared by counties within a region.

3. Additional Model Specifications

We tested three additional hypotheses regarding landscape simplification and insecticide use. First, we investigated if yearly weather influenced the relationship between landscape simplification and insecticide use. We included growing season degree-days, growing season precipitation, date of first fall frost (contemporaneous and one-year lagged terms), date of last spring frost, and mean temperatures in January, April, and July in the region-by-year models. Second, we evaluated whether landscape simplification operates at

multiple scales by including a covariate for proportion of harvested cropland in large farms, which we defined as farms greater than 500 acres (data from the Census). Finally, we investigated if the effect of landscape simplification on insecticide use was nonlinear and if so, if including a quadratic term for proportion of county in cropland reduced within or between region heterogeneity.

For all models, we used F-tests to evaluate equality over time or regions. We used cluster-robust standard errors to allow for arbitrary spatial autocorrelation within Agricultural Statistics Districts (ASDs; Appendix). The USDA defines ASDs within each state to reflect similarities in "geography, climate, and cropping practices" (USDA). All analyses were completed in Stata 12SE and the map figure was completed in Quantum GIS 2.4.

C. Results

Including proportion of harvested cropland in large farms was highly influential, and thus, we show results with this covariate included in all models (See Tables A2 and A3 for results with this covariate omitted). Landscape simplification had no significant effect on proportion of cropland treated in either of the fixed effects models with all counties and years pooled (Table 1), or in the year interaction model, except in 2012 when simplification led to an increase in proportion of cropland treated (Table 1). Interannual variability in the landscape simplification coefficient was significant ($F_{(5,302)}=2.36$, $p<0.05$).

In the region interaction model with all years pooled, the landscape simplification-insecticide use relationship was regionally heterogeneous ($F_{(8,302)}=3.60$, $p<0.01$). Landscape simplification increased ($p<0.05$) the proportion of cropland treated in the Eastern Uplands, Southern Seaboard, Fruitful Rim, and Basin and Range regions. By contrast, landscape simplification lead to a decrease in insecticide use in the Mississippi Portal ($p<0.05$; Table 2).

The estimated coefficients were not significantly different from zero in the remaining regions.

Including region-by-year interaction terms, the landscape simplification-insecticide use relationship was highly variable across time within regions (Table 2). In the Fruitful Rim, and Basin and Range landscape simplification consistently led to an increase in insecticide use, although this relationship was not always significant. In the Mississippi Portal, simplification generally decreased insecticide use. In the Eastern Uplands, Southern Seaboard, and Prairie Gateway landscape simplification resulted in an increase in insecticides in early censuses, but trended towards a non-significant or negative effect by 2012. The Heartland, Northern Crescent, and Northern Great Plains were the opposite, with non-significant or negative relationships in early census' and trending towards positive relationships in 2007 and 2012.

We found similar regional and temporal patterns when we included weather covariates or a quadratic term on proportion of county in cropland in the region-by-year interaction model.

D. Discussion

The relationship between landscape simplification and insecticide use is fundamentally, but predictably heterogeneous over space and time. The patterns of heterogeneity present challenges for ecologists and opportunities for policymakers.

For ecologists, deciphering the mechanisms underlying the spatial and temporal variability is paramount to understanding how diversity in agricultural landscapes affects the dynamics of higher trophic levels. Two fundamentally different predictions derived from ecological theory can apparently both be true under different conditions. We see three

potential classes of explanations for how these divergent mechanisms arise that warrant more attention and exploration.

First, regions where landscape simplification results in increased insecticide use, the Fruitful Rim and Basin and Range, experience different climate conditions than their counterparts in the central and northern US. For example, the Fruitful Rim and Basin and Range regions are subject to seasonal summer droughts, which could result in natural habitat becoming a pest sink. In this case, landscapes with more cropland may maintain higher pest abundance due to a greater proportion of suitable habitat. Alternatively if mild winters enable generalist natural enemies to persist year-round, complex landscapes could provide higher relative pest control benefits in warmer regions such as the Fruitful Rim, than they do in regions experiencing greater seasonal change, such as the Northern Great Plains.

A second mechanism that may explain the between region variation is differences in crop types or cropping practices. The regions in which landscape simplification leads to increased insecticide use are also regions with higher crop and non-crop habitat diversity. While crop diversity is thought to reduce pest outbreaks by limiting the abundance of homogenous resources (Jactel et al. 2005; O'Rourke et al. 2011), diversity of crops may also reduce the positive spillover benefits of insecticide use by neighbouring farms or provide alternative hosts for crop pests (O'Rourke and Jones 2011) during large scale disturbances such as harvest. Therefore an increase in cropland may result in a higher proportional increase in insecticide use in high diversity counties than in low crop diversity counties. The lack of detailed pesticide use data makes investigating this relationship difficult, although new empirical studies that include regional crop or non-crop plant diversity could provide key insight.

Third, regional variability could also reflect unaccounted for differences in landscape characteristics that confound the identification of a consistent relationship. For instance, if the effect of cropland on insecticide use was important up to a threshold level of simplification, but unimportant thereafter, a different statistical relationship would be observed in regions with high average cropland and regions with low average cropland (Ricketts and Lonsdorf 2013). In empirical research on cropland and ecosystem services that have reported spatially-context dependent relationships (Riseng et al. 2011; Thies et al. 2011), the regionally disparate results could reflect a saturating effect. However, between and within regional variability in the relationship between landscape simplification and insecticide use was robust to a nonlinear effect of cropland.

Interestingly we found landscape simplification to operate on both the field and county scale. The proportion of harvested cropland in large farms led to significantly higher proportion of cropland treated in all regions except the Heartland and Eastern Uplands. There is both human behavior and ecological explanations for field level insecticide use. It is possible that large farms use more industrialized methods, and that economies of scale reduce the cost of insecticide use resulting in more frequent applications on large farms (Dasgupta et al. 2001). It is also conceivable that if farmers spray an entire crop when crop pests are observed in their field, a large area under one manager would be sprayed more extensively than the same area under multiple managers. Alternatively, it is possible that pests and natural enemies interact over multiple spatial scales (O'Rourke and Jones 2011; Chaplin-Kramer and Kremen 2012). There is a rich ecological literature suggesting field scale interactions may be especially important for parasitoids and other specialist natural enemies, and thus large contiguous areas of cropland may reduce the ability of these natural enemies

to control pests in large crop fields (Landis et al. 2000; Bianchi et al. 2006a). Like simplification at the county scale, the importance of large farms is regionally heterogeneous. This variability could reflect differences in cultural attitudes towards risk or pesticide use, or could reflect differences in the suite of natural enemies and pests that may be affected by large farms. Empirical research that includes measures of farmer behavior as well as pest density will be instrumental to deciphering the relative importance of human behavior and ecological factors to pesticide application on large farms.

In addition to regional heterogeneity, we found statistically significant within-region temporal variation, with the relationship between landscape simplification and insecticide use changing in opposing directions for different regions. These opposing trends between 1987-2012 are clearly inconsistent with the hypothesis that changes in national pesticide legislation such as the Food Quality Protection Act of 1996 modified the relationship between landscape simplification and insecticide use by modifying the persistence and selectivity of available chemicals. Additionally, controlling for a range of yearly weather realizations did little to explain the within-region temporal variation in the landscape simplification-insecticide use relationship. Time trends, which reflect changes in the interaction of insect pests and land use over the 25-year time frame, could result from changes in non-crop habitat or pest and natural enemy characteristics that appear to be shared at larger regional scales. Further research on changes in land use or pest community composition (e.g. novel pest invasions) could provide insight into the mechanisms underlying the observed time trends.

Understanding the mechanisms driving variability in the relationship between landscape simplification and insecticide use is important for the advancement of ecological understanding and may be key to forecasting the consequences of large-scale changes in

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environmental conditions such as those predicted under climate change. However, characteristics separating regions are likely predictable factors such as crop type or diversity, cropping practices or climate regimes that are more persistent through time. Thus, while ecologists continue to investigate the mechanistic drivers, land use planners can make more immediate use of the patterns to implement more effective land use policies.

The policy implications of this analysis suggest national land use policy should have very different impacts in different growing regions. Policy promoting land sparing could significantly increase insect pest burden and insecticide use in the Fruitful Rim and Basin and Range. In these regions, increasingly simplified landscapes consistently correspond to large increases in the proportion of cropland treated with insecticides. Other regions, such as the Prairie Gateway do not have similarly large and consistent insecticide responses to landscape simplification. Since the same policy action can have strikingly disparate consequences regionally, regional land use policies could more effectively address the impacts of land use on insecticides.

In practice there are existing policy mechanisms, which if informed by science, could be used to affect agricultural insecticide use. For instance, there are agricultural policies, currently at the field level, to incentivize the maintenance of agricultural land (i.e. agricultural conservation easements), to remove land from agriculture (e.g. Conservation Reserve Program; CRP), and to prevent the conversion of grazing land to cropland (e.g. Grassland Reserve Program). For regions such as the Mississippi Portal, where proportion of cropland in large farms has a dramatic effect on the proportion of cropland treated, field level incentives that fragment large farms with natural areas may be most appropriate. However, given that agricultural insect pests are governed in part by metapopulation processes such as

invasion and extinction (Levins 1969), these agricultural policies could be differentially applied regionally to incentivize landscape scale coordination of reserve lands to enhance insecticide reduction efforts in regions with large effects of county level simplification. Our findings demonstrate that the value of such programs to reduced insecticide use would be regionally specific. On average, reducing the proportion of cropland in an Oregon county would reduce insecticide use per area cropland by an order of magnitude more than the same reduction in a Kansas county, holding all else equal.

To minimize the costs of insecticides to both farmers and society, we must continue to improve upon the efficiency of insecticide use. While landscape simplification can be an important driver of insecticide use, its effect is heterogeneous and the underlying causes of this heterogeneity require further research. While ecologists investigate the mechanisms, policymakers can take advantage of regional patterns in the insecticide-land use relationship to better target land use policy that meets agricultural production needs while improving human health, preserving intact ecosystems and maintaining the ecosystem services on which we rely.

E. Acknowledgements

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G. Appendix

1. Fixed Effects Model Background

The pooled model is represented by the following equation:

$Y_i = X_i'\beta + u_i$ where Y_i is the response variable, the proportion of the county i treated with insecticides. X represents the vector of covariates including proportion of county in cropland, proportion of cropland in corn, soybeans and small grains, vegetables, fruit and nut orchards, and income per harvested hectare in each county i, and u represents the random error term for each county, i. In order to obtain an unbiased estimate of the vector β, the error must be uncorrelated with the vector of covariates X (Wooldridge 2002). If an unobserved variable is not included in the regression it is in effect is incorporated into the error term. Thus if that unobserved variable is correlated with one or more variables in X and the dependent variable, the estimate of the vector β will be biased (Wooldridge 2002).

The fixed effects model can greatly reduce omitted variable bias by controlling for time invariant unobserved effects unique to an area (e.g. soil quality) or shocks unique to a year (e.g. technological improvements) (Wooldridge 2002). Omitted variable bias occurs when variables that are predictive of the outcome and correlated with other covariates are not included in the regression. For instance, characteristics such as soil fertility or cultural practices are important determinants of agricultural land-use decisions (Deschênes and Greenstone 2007), but are not easily measured. Locational fixed effects, such as state or county fixed effects, isolate variation in land use to that which occurs within an individual location over time and thus can be very powerful when omitted variable bias is suspected. Due to low levels of within-county variation in the proportion of county in cropland in some ERS regions, we use state and region-by-year fixed effects rather than the county and year

fixed effects. State fixed effects control for time invariant characteristics shared by counties within a state such as soil quality or farming practices, and region-by-year effects control for time trends or year shocks shared by all counties in a region, and thus will lead to more reliable estimates and inference. However, to the extent that the unobserved factors that cause omitted variables bias are not distributed evenly across counties, the state fixed effects model remains inferior to a model with county fixed effects. As noted above, the county fixed effect model is not possible in the current setting. State fixed effects still remove potentially important sources of unobserved variation such as state farming practices and historical legislation, and in this case preserve sufficient year-to-year variation in cropland at the state level for the fixed-effects estimation to be reasonably statistically precise.

2. Additional Econometric Models

To account for the possibility large farms use more insecticides, we reran the region-by-year model including proportion of harvested cropland in large farms as a covariate. We allowed this variable to vary regionally, but not annually. To further parse the observed spatiotemporal variability we included growing season degree-days and precipitation, Julian date of first fall frost and last spring frost, as well as first fall frost of the previous year as covariates in the region-by-year model to assess the possibility that these weather variables modified the relationship between landscape simplification and insecticide use. We calculated degree-days as follows: days with mean temperature below 46.4F (8C) contributed zero degree-days, days with mean temperature between 46.4F and 89.6F (32C) contributed the difference between mean temperature and 46.4F degree-days and days above 89.6F contributed 43.2 degree-days (Deschênes and Greenstone 2007). We calculated Julian date of last spring frost as the last date the minimum temperature dropped to or below 32F prior to

July 1, and date of first fall frost as the first freezing temperature after July 1.We did not interact weather variables with region or year. Finally, we included a quadratic term on proportion of county in cropland allowing for a nonlinear relationship between landscape simplification and insecticide use. Again, we allowed this variable to vary regionally, but not annually.

To control for autocorrelation we used cluster robust standard errors clustered at the Agricultural Statistics District (ASD). We tested addition spatial autocorrelation models including Conley standard errors (Conley 2008, Hsiang 2010) as well as spatial error models at varying distances (300km, 400km). For computational ease, the spatial error models were run by individual region-year, using the same distance band for all regions and years. It is important to note there are limitations to this approach. In particular, using individual region models we cannot account for spatial autocorrelation between counties in different regions, even if counties are in close geographical proximity. Further, using a uniform distance band does not encapsulate differences in the extent of spatial autocorrelation known (from variograms) to be present in different regions. Despite these shortcomings, overall regional and temporal patterns were similar among the ASD, Conley and spatial error models. We leave it to future research to further investigate the nature of spatial autocorrelation in the landscape simplification-insecticide use relationship across regions.

3. References

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H. Figure Captions

Figure 1. US regions based on USDA Economic Research Service (ERS) Farm Resource Regions. Regions are based on farm and crop characteristics. Shading reflects the four different syndromes of the landscape simplification-insecticide use relationship. The hashed lines in the Heartland (R1), Northern Crescent (R2), and Northern Great Plains (R3), represents simplification having no effect or decreasing insecticide use in 1987-2002, trending towards simplification increasing insecticide use in 2007-2012. The light shading in the Prairie (R4), Eastern Uplands (R5) and Southern Seaboard (R6) indicates positive and significant relationship, simplification increases insecticide use, in 1987-1992 trending towards a null or negative relationship by 2007-2012. The dark shading in Fruitful Rim (R7), and Basin and Range (R8) indicates landscape simplification consistently leads to increased insecticide use. Finally, dotted shading in the Mississippi Portal (R9) indicates simplification generally decreases insecticide use.

Figure A1. Proportion of cropland treated with insecticides, proportion of county in cropland and covariates for the Heartland region. All crop variables were similar over the study period, 1987-2012. Other regions displayed similar patterns over time. "Cty" represents "county".
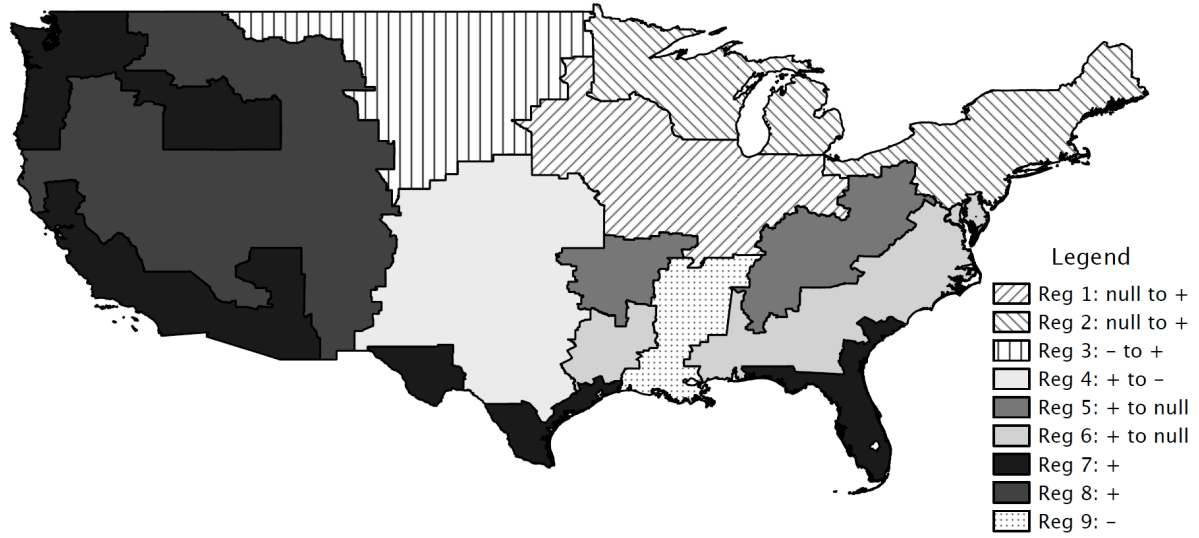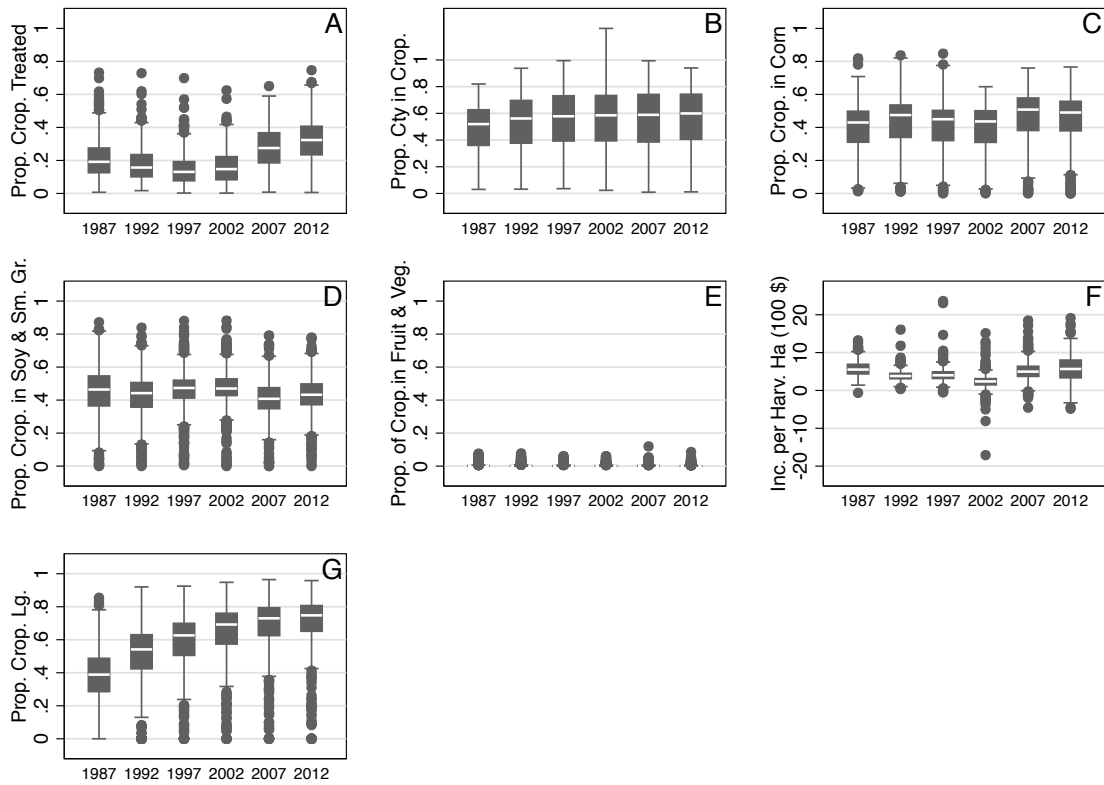
Figure 1.

Legend

Reg 1: null to +
Reg 2: null to +
Reg 3: − to +
Reg 4: + to −
Reg 5: + to null
Reg 6: + to null
Reg 7: +
Reg 8: +
Reg 9: −

Figure A1.

Table 1: Pooled model with fixed effects and year interactions.

VARIABLES	State & Year (1)	State, Yr* Reg. (2)	1987 (3)	1992 (4)	1997 (5)	2002 (6)	2007 (7)	2012 (8)
Prop. Cropland	-0.0045	0.0115	0.0085	0.0211	-0.0081	-0.0268	0.0296	0.0536~
	(0.0180)	(0.0174)	(0.0316)	(0.0281)	(0.0240)	(0.0238)	(0.0250)	(0.0281)
Inc. per Harv. Ha	0.0000*	0.0000~	0.0000	0.0000	-0.0000	0.0000	0.0000**	0.0000
	(0.0000)	(0.0000)	(0.0000)	(0.0000)	(0.0000)	(0.0000)	(0.0000)	(0.0000)
Prop. Corn	0.3425**	0.3394**	0.4622**	0.3007**	0.3566**	0.2873**	0.2996**	0.2908**
	(0.0298)	(0.0300)	(0.0371)	(0.0401)	(0.0351)	(0.0377)	(0.0347)	(0.0446)
Prop Soy. & Sm. Gr	-0.0562*	-0.0397~	-0.0118	-0.0918**	-0.0390	-0.0530~	-0.0556~	0.0187
	(0.0244)	(0.0230)	(0.0267)	(0.0248)	(0.0251)	(0.0310)	(0.0310)	(0.0311)
Prop. Fruit & Veg.	0.5590**	0.5380**	0.5292**	0.4785**	0.5159**	0.5708**	0.6581**	0.4532**
	(0.0509)	(0.0496)	(0.0565)	(0.0497)	(0.0504)	(0.0462)	(0.0547)	(0.0956)
Prop. Cotton	0.4888**	0.4816**	0.3740**	0.3223**	0.4230**	0.5712**	0.8045**	0.4026**
	(0.0646)	(0.0564)	(0.0756)	(0.0881)	(0.0879)	(0.0423)	(0.0399)	(0.0650)
Prop. Large	0.2086**	0.1920**			0.1921**			
	(0.0203)	(0.0187)			(0.0184)			
Constant	0.0795**	0.0474**			-0.0142			
	(0.0095)	(0.0172)			(0.0181)			
Observations	17,305	17,305			17,305			
R-squared	0.60	0.63			0.64			

Notes: Pooled national models with year and state fixed effects, state and region-by-year fixed effects, and year interaction models. Both fixed effects only (columns 1-2) and year interaction models (columns 3-8) generally resulted in a null relationship between landscape simplification and insecticides with the exception of 2012. This interannual variability in the landscape simplification coefficient was significant ($F_{(5,302)}$=2.36, P<0.05). For the all interaction models, state and region-by-year fixed effects were included. In all models, standard errors are below the coefficients in parentheses. We used cluster robust standard errors, clustering at the agricultural statistics district. For all tables **,*, ~ indicates p<0.01, p<0.05, p<0.1, respectively. Coefficients on landscape simplifications are shaded on a gradient to reflect their magnitude and sign. Green represents significant positive and red represents significant negative coefficients, and the intensity of the shading reflects the size of the coefficient. Coefficients <0.10 are light shading, coefficients 0.10< β < 0.20 are medium shading, coefficients 0.20< β <0.40 are dark and coefficients >0.40 are very dark.

Table 2. Region and region by year models including state and region-by-year fixed effects.

	Pool (1)	1987 (2)	1992 (3)	1997 (4)	2002 (5)	2007 (6)	2012 (7)	Prop. Lg Farms	$F(5,302)$ (9)
Heart. Prop. Crop.	0.0246 (0.0370)	0.0509 (0.0554)	-0.0427 (0.0473)	-0.0060 (0.0419)	0.0248 (0.0503)	0.1325** (0.0504)	0.0255 (0.0537)	0.0665 (0.0635)	9.43**
N.Cres. Prop. Crop.	0.0204 (0.0494)	-0.0318 (0.0462)	0.0273 (0.0551)	-0.0910 (0.0623)	-0.0070 (0.0622)	0.0475 (0.0601)	0.1670** (0.0574)	0.1684** (0.0386)	7.61**
N. Gr. Pl. Prop. Crop.	0.0652 (0.0448)	-0.2091* (0.0918)	0.0149 (0.0550)	0.1152** (0.0323)	0.0870 (0.0559)	0.1748** (0.0411)	0.2335** (0.0431)	0.0674* (0.0296)	6.24**
Prairie Prop. Crop	0.0262 (0.0412)	0.1126 (0.0729)	0.1142* (0.0554)	0.0302 (0.0593)	-0.0107 (0.0431)	-0.0790 (0.0703)	-0.0949 (0.0628)	0.2028** (0.0348)	2.71*
E. Up. Prop. Crop	0.1765** (0.0537)	0.4012** (0.0738)	0.3477** (0.0964)	0.3064** (0.0619)	0.0613 (0.0555)	0.0237 (0.0557)	-0.0177 (0.0919)	0.0528 (0.0374)	10.00**
S. Sea. Prop. Crop.	0.1235** (0.0445)	0.3648** (0.1090)	0.2463* (0.1025)	0.1704* (0.0800)	0.0072 (0.0963)	-0.1122 (0.0783)	0.0243 (0.1110)	0.1790** (0.0302)	3.18**
Fruit. Rim Prop. Crop.	0.2498** (0.0688)	0.3922** (0.0912)	0.2466* (0.0969)	0.3098** (0.0768)	0.1835* (0.0770)	0.1280 (0.0859)	0.2250 (0.1480)	0.1334** (0.0371)	4.03**
B & R Prop. Crop.	0.1730* (0.0776)	0.0792 (0.2243)	0.1926** (0.0736)	0.2624* (0.1124)	0.2741* (0.1311)	0.0688 (0.1394)	0.1843 (0.1583)	0.1010* (0.0429)	0.79
Miss.Port. Prop. Crop.	-0.1323* (0.0604)	-0.2044** (0.0680)	-0.1353** (0.0479)	-0.1937* (0.0823)	-0.0012 (0.1045)	-0.1228 (0.1263)	-0.1091~ (0.0648)	0.4669** (0.0464)	3.61**

Notes: The relationship between landscape simplification and insecticides varied both regionally (column 1; $F_{(8,302)}$=3.60**) and within region over time (column 2-7). This variability was significant in all regions except the Basin and Range (column 9, shading indicates significant F tests). Column 8 is the coefficient on proportion of harvested cropland in large farms. Other covariates included in the regressions were suppressed from the table for clarity. For all models, state and region-by-year fixed effects were included, N=17,305 and the R^2=0.66 and 0.69 for the pooled and interaction model, respectively.

Table A1. Summary statistics by region, pooling 1987-2012.

	Heartland	N. Crescent	N. Gr. Plains	Prairie	E. Uplands	S. Seaboard	Fruitful Rim	Basin & Range	Miss. Portal
Prop. Treated	0.22 (0.13)	0.19 (0.15)	0.12 (0.09)	0.24 (0.18)	0.11 (0.10)	0.31 (0.23)	0.44 (0.28)	0.20 (0.19)	0.36 (0.22)
Prop. Cropland	0.54 (0.22)	0.19 (0.18)	0.32 (0.21)	0.25 (0.18)	0.10 (0.08)	0.11 (0.10)	0.10 (0.12)	0.05 (0.08)	0.25 (0.22)
Prop. Corn	0.43 (0.15)	0.27 (0.15)	0.12 (0.13)	0.13 (0.17)	0.10 (0.10)	0.13 (0.12)	0.07 (0.10)	0.02 (0.05)	0.11 (0.12)
Prop Soy. & Sm. Gr	0.44 (0.13)	0.16 (0.16)	0.50 (0.25)	0.38 (0.26)	0.09 (0.13)	0.23 (0.25)	0.13 (0.19)	0.20 (0.26)	0.35 (0.24)
Prop. Fruit & Veg	0.00 (0.01)	0.06 (0.11)	0.00 (0.00)	0.02 (0.05)	0.01 (0.04)	0.04 (0.07)	0.21 (0.27)	0.05 (0.14)	0.01 (0.04)
Inc. per harv ha	451 (252)	1014 (4799)	292 (187)	359 (1519)	608 (984)	1191 (2262)	1765 (4989)	366 (1599)	614 (1750)
Prop. Cotton	0.00 (0.03)	0.00 (0.00)	0.00 (0.00)	0.08 (0.20)	0.01 (0.05)	0.08 (0.15)	0.05 (0.13)	0.00 (0.03)	0.13 (0.16)
Prop. Large	0.58 (0.21)	0.27 (0.22)	0.78 (0.16)	0.57 (0.28)	0.10 (0.16)	0.29 (0.31)	0.43 (0.32)	0.41 (0.32)	0.58 (0.33)
N	3240	2368	1012	2236	2326	2731	1520	909	963

Notes: Proportion of cropland treated with insecticides (Prop. Treated) and proportion of county in cropland (Prop. Cropland) vary greatly between regions, as do other covariates. Cotton growing regions were considered Prairie, Eastern Uplands, Southern Seaboard, Fruitful Rim and Mississippi Portal. Standard errors are below the mean, in parentheses.

Table A2. Pooled model with fixed effects and year interactions, not including a covariate for large farms.

VARIABLES	State & Year	State, Yr* Reg.	1987	1992	1997	2002	2007	2012
	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)
Prop. Cropland	0.0612**	0.0772**	0.0878*	0.0940**	0.0567*	0.0368	0.0825**	0.1119**
	(0.0212)	(0.0199)	(0.0347)	(0.0301)	(0.0263)	(0.0247)	(0.0261)	(0.0296)
Inc. per Harv. Ha	0.0000~	0.0000	0.0000	0.0000	-0.0000	0.0000	0.0000**	0.0000
	(0.0000)	(0.0000)	(0.0000)	(0.0000)	(0.0000)	(0.0000)	(0.0000)	(0.0000)
Prop. Corn	0.4134**	0.4119**	0.4791**	0.3550**	0.4210**	0.3698**	0.4007**	0.3906**
	(0.0301)	(0.0308)	(0.0393)	(0.0417)	(0.0384)	(0.0382)	(0.0342)	(0.0443)
Prop Soy. & Sm. Gr	0.0857**	0.0848**	0.0940**	0.0225	0.0828**	0.0766*	0.0826**	0.1527**
	(0.0189)	(0.0192)	(0.0228)	(0.0207)	(0.0232)	(0.0295)	(0.0269)	(0.0284)
Prop. Fruit & Veg.	0.6087**	0.5819**	0.5630**	0.5180**	0.5650**	0.6073**	0.7047**	0.5044**
	(0.0428)	(0.0428)	(0.0535)	(0.0472)	(0.0480)	(0.0395)	(0.0506)	(0.0841)
Prop. Cotton	0.6712**	0.6443**	0.4793**	0.4786**	0.5789**	0.7422**	0.9887**	0.5927**
	(0.0673)	(0.0584)	(0.0787)	(0.0882)	(0.0914)	(0.0403)	(0.0419)	(0.0706)
Constant	0.0813**	0.0229			-0.0112			
	(0.0098)	(0.0165)			(0.0186)			
Observations	17,305	17,305			17,305			
R-squared	0.57	0.61			0.62			

Notes: Proportion of harvested cropland in large farms was highly influential to the relationship between landscape simplification and insecticide use. Omitting this variable confounded the estimation of the relationship between landscape simplification and insecticide use resulting in generally different conclusions when this covariate was omitted. We used cluster robust standard errors, clustering at the agricultural statistics district. For all tables **, *, ~ indicates p<0.01, p<0.05, p<0.1, respectively. For all tables, coefficients on landscape simplifications are shaded on a gradient to reflect their magnitude and sign. Green represents significant positive and red represents significant negative coefficients, and the intensity of the shading reflects the size of the coefficient. Coefficients <0.10 are light shading, coefficients 0.10< β < 0.20 are medium shading, coefficients 0.20< β <0.40 are dark and coefficients >0.40 are very dark.

Table A3. Region by year models not including proportion of harvested cropland in large farms.

	Pool (1)	1987 (2)	1992 (3)	1997 (4)	2002 (5)	2007 (6)	2012 (7)	F(5,302) (8)
Heart. Prop. Crop.	0.0365 (0.0515)	0.0614 (0.0624)	-0.0283 (0.0576)	0.0096 (0.0578)	0.0409 (0.0659)	0.1430* (0.0640)	0.0369 (0.0668)	9.70**
N.Cres. Prop. Crop.	0.0523 (0.0510)	-0.0024 (0.0492)	0.0447 (0.0560)	-0.0591 (0.0642)	0.0354 (0.0640)	0.0905 (0.0629)	0.2045** (0.0580)	6.78**
N. Gr. Pl. Prop. Crop.	0.0963* (0.0450)	-0.1840* (0.0924)	0.0440 (0.0559)	0.1435** (0.0326)	0.1197* (0.0566)	0.2019** (0.0439)	0.2600** (0.0451)	5.57**
Prairie Prop. Crop	0.0697~ (0.0419)	0.1934* (0.0765)	0.1785** (0.0529)	0.0623 (0.0596)	0.0191 (0.0425)	-0.0634 (0.0702)	-0.0632 (0.0619)	3.71**
E. Up. Prop. Crop	0.2124** (0.0545)	0.4340** (0.0763)	0.3740** (0.0970)	0.3422** (0.0637)	0.0992~ (0.0544)	0.0573 (0.0540)	0.0117 (0.0935)	10.33**
S. Sea. Prop. Crop.	0.3095** (0.0560)	0.6073** (0.1328)	0.4448** (0.1065)	0.3539** (0.0887)	0.1832 (0.1142)	0.0423 (0.0809)	0.1996* (0.0968)	3.26**
Fruit. Rim Prop. Crop.	0.3865** (0.0667)	0.5369** (0.0826)	0.3775** (0.0927)	0.4229** (0.0764)	0.3224** (0.0776)	0.2636** (0.0881)	0.3569* (0.1428)	3.50**
B & R Prop. Crop.	0.2429** (0.0809)	0.1663 (0.2315)	0.2598** (0.0779)	0.3320** (0.1179)	0.3399* (0.1412)	0.1261 (0.1386)	0.2458 (0.1568)	0.87
Miss.Port. Prop. Crop.	0.1049 (0.0889)	0.0531 (0.0873)	0.0472 (0.0801)	-0.0750 (0.1079)	0.2340~ (0.1320)	0.1188 (0.1284)	0.1553~ (0.0873)	3.24**

Notes: Proportion of cropland harvested in large farms is highly influential to the regional relationship between landscape simplification and insecticide use. As with the pooled region model (Table A1), omitting this variable confounded the estimation of the relationship between landscape simplification and insecticide use resulting in generally different conclusions when this covariate was omitted. N=17,305, R^2=0.64 and 0.67 for the pooled and region by year models respectively.

III. Taken as a Given: Evaluating the Accuracy of Remotely Sensed Crop Data

This chapter is in review. Authorship on the manuscript is as follows: Ashley E. Larsen, Brandon T. Hendrickson, Nicholas Dedeic, Andrew J. MacDonald.

A. Introduction

Beyond food production, the extent and spatial arrangement of agricultural land is important for biodiversity, management of agricultural pests and disease (Larsen, 2013; Rittenhouse et al. 2012; Tscharntke et al. 2012), carbon storage, bioenergy production, and agricultural policy (Lawler et al. 2014; Mosnier et al. 2013). Spatial arrangement of agricultural land has been shown to be particularly important for maintenance of on and off farm biodiversity (Landis et al. 2000), and for pest management in both ecological (Levins, 1969) and economic theory (Costello et al. 2014) . However, a dearth of refined, spatially explicit data on cropland arrangement has largely limited investigations to either field studies or general analytical models thus hampering consensus across heterogeneous regions or crop types.

With the recent explosion of satellite data, large-scale studies are just now becoming feasible. This is especially exciting for investigations of agricultural processes in developing countries where traditional agricultural statistics have historically been unavailable. Yet, in order to understand how satellite data can and should be applied, scientists must understand the accuracy of such data relative to other agricultural statistics. To do so necessitates focusing on regions where satellite data can be compared to high quality tabulated data. Here we take advantage of the simultaneous availability of the USDA Census of Agriculture, the most comprehensive agricultural statistics tabulated in the US (USDA, 2014), and the

National Agricultural Statistics Service (NASS) Cropland Data Layer (CDL), one of the only agriculture-focused satellite data layers available annually, to understand how satellite data may be employed more broadly in rigorous scientific investigations.

The purpose of the CDL is largely to produce seasonal acreage estimates for major crops or to inform the design of other NASS data products, such as the June Acreage Survey (Johnson, 2013). However, scientists have leveraged the disaggregated crop classification and refined spatial resolution of these data to address a much wider range of questions from grassland conversion to soy/corn (Wright and Wimberly, 2013), to predicting crop acreage in response to commodity price (Hendricks et al. 2014), to investigating land use change and conversion between specific crop types associated with the spatial location of ethanol refineries (Johnston, 2013). For these and similar studies, sub-county assessments, which rely on the accuracy of pixel data, are critical.

Area estimation from pixel counting, however, is thought to be biased downward, resulting in underestimates of cropland area (Johnson, 2013). While such bias in estimates of cropland extent could be corrected using a regression with other annual data (Boryan et al. 2011), spatial arrangement of different crop types could be distorted and is not easily corrected in such a manner. Furthermore, such corrective regression methods are not commonly used in scientific applications employing these data and would be impossible to replicate with other geospatial data in countries lacking accurate agricultural tabulations. Thus, understanding the accuracy of pixel counting is important for understanding the suitability of the CDL and other satellite data for the various applications to which they have been and could be employed.

To develop a comprehensive and scientifically relevant analysis of the accuracy of the CDL, we compare area estimates from the Cropland Data Layer to the USDA Census of

Agriculture for 2012, the first year both data products are simultaneously available for the coterminous US. Using these datasets we address, (1) how different are county-level estimates of cropland and crop groups derived from pixel counting from the Census and are these differences statistically significant? and (2) how often and where are county-level CDL and Census estimates statistically similar for individual crops such as soybeans and wheat?

B. Methods & Materials

1. Cropland Data Layer

The Cropland Data Layer was first produced for the Corn Belt in the late 1990s (USDA, n.d.). As satellite and computer technology increased in power and decreased in cost, NASS began to produce these high-resolution data freely available, annually, and for the contiguous US. The CDL dataset use as combination of satellite imagery (Deimos-1, UK-DMC2, and Landsat TM/ETM+) ground truthed by the USDA Farm Service Agency (FSA) Common Land Unit (CLU) Program data to produce a 30m data layer in 2012 (USDA, n.d.). An in-depth description of the program can be found in Boryan et al. (2011). State-level accuracy assessments are available in the metadata, but pixel accuracies for tilled crops are generally reported to be 70-95% at the state level (Boryan et al. 2011; Johnson, 2013).

2. USDA Census of Agriculture

The USDA Census of Agriculture is conducted every five years by the NASS, and is considered the most comprehensive agricultural data for every county in the US (USDA, 2014). The Census is conducted via questionnaires provided to every farm that produced or sold at least $1000 of agricultural products (or had the potential to) in a census year (USDA, 2014). The responses are generally tabulated at the county level. The Census provides extensive information regarding crop and livestock production, costs, inputs, and farmer demographics.

In 2012, the Census had a response rate of ~80% (USDA, 2014). The Census compensates for bias stemming from non-response or incomplete mailing lists at the country, state, and county level using a combination of weighted adjustments and other imputation measures to "produce agricultural census totals for publication that were fully adjusted for [mailing] list undercoverage, nonresponse and misclassification [of farm/nonfarm] at the county level" (USDA, 2014).

In 2012, the Census provides a measure of the uncertainty due to the above errors at the state and county level by means of a coefficient of variation. From the state level, generalized coefficient of variation, a 95% confidence interval around the census estimate can be easily computed (USDA, 2014).

3. Comparison

We compare the CDL to the Census of Agriculture for measures of total cropland area, and major crops and crop groups in the contiguous 48 US states (Table 1). To do so, we use CDL crop pixels converted to acres and aggregated at the county level. These data are provided by NASS on the CropScape FAQs website (USDA, n.d.). We compare the data sets using paired t-tests, and measure percent difference from the Census, provided the Census records at least 50 acres (~20ha) of a given crop. We include this lower benchmark to avoid enormous percent difference resulting from trivially small differences in area.

We map percent differences for corn, soybeans, small grains (wheat, oats, barley) and cropland. We define cropland in the Census to be "cropland harvested" and "cropland on which all crops failed". The Census definition of cropland harvested includes acres of hay, but not pasture. To construct as comparable a group as possible, our measure of cropland in the CDL includes crops as well as alfalfa and other hay, but not pasture or grassland (Table

1). We compute paired t-tests for each crop comparison to evaluate statistical significance of the observed differences in the two datasets.

Using the Census' coefficient of variation, we construct a 95% confidence interval for soybeans and wheat, and compare whether the CDL falls within this 95% confidence interval for these individual crops in individual counties.

C. Results

For aggregate cropland as well as most major crop groups evaluated, significant differences were observed between the USDA Census of Agriculture and the NASS Cropland Data Layer (Table 1). The CDL significantly over predicted Corn and small grains on average, and significantly under predicted soybeans and total cropland. Of the groups evaluated, only the aggregate of corn and soybeans was similar across datasets. While mean percent differences were modest (Table 1), there was very large variance around the mean, with the standard deviation of percent difference over 60% for all groups.

There were important regional differences in the accuracy of the CDL relative to the Census of Agriculture. Regions with high cropland area, such as the Midwest, Mississippi River Valley, and the Central Valley of California were generally within +/- 10% of the Census estimates for cumulative cropland, while regions with less cropland were often more than +/- 50% off (Fig 1A). Similarly for corn and soybeans, the CDL is most consistent (+/- 10%) with the Census in areas with a high proportion of these crops, particularly the upper Midwest (Figs. 1B, 1C), though significant differences between the datasets remain for all crop groups[10]. Outside of the Midwest, corn and soybeans are over or underestimated by more than 25% in many of the other corn growing counties. Small grains had a distinctly

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[10] When paired t-tests are evaluated for just counties in the "Heartland" region of the USDA Economic Research Service, Farm Resource Regions.

different pattern, with small differences in the CDL in the Northern Great Plains, but large

overestimates (50% or more) in much of the western and southwestern US and

underestimates of 25% or more in the Midwest as well as much of the eastern US (Fig. 1D).

To account for the potential inaccuracies embedded in the Census, we evaluated

whether soybeans and wheat measurements from the CDL were within or outside of the 95%

confidence interval around the Census estimates. Proportionally, soybean and wheat

estimates from the CDL fell outside the 95% CI of the Census in 51% and 62% of

observations, respectively. CDL estimates in high soybean growing regions generally were

within the 95% CI of the Census estimate (Fig. 2).

D. Discussion

Geospatial data hold great promise in providing extensive and detailed information on

agricultural activity. However, using these data for purposes that leverage information at the

pixel level should be done with great caution. Here we compared the extensively processed

and ground-truthed NASS Cropland Data Layer to the most accurate US agricultural data

available (Maxwell et al. 2008; USDA, 2014), and found large disparities across aggregated

measures of crops and cropland at the county level. Very large differences were particularly

commonplace outside of regions dominated by cropland or regions dominated by a small

number of crops.

Unsurprisingly given the CDL's original purpose within the NASS, accuracy for

individual crops is high within regions where that crop dominates. For example, the Midwest

Corn Belt generally had the highest accuracy relative to the Census for cropland, soybeans

and corn. This is likely due to the highly simplified agricultural habitat in these states in

combination with additional NASS effort to develop accurate production estimates in these

agriculturally dominated regions (Johnson, 2013). By contrast, for less common crops such

as small grains or wheat, the Midwest Corn Belt was just as inaccurate as less agriculturally dominated regions.

The importance of accuracy at the pixel level and/or disaggregated crop type depends on the scientific application. For assessing total cropland, the CDL is generally within 10% in cropland-dominated regions, and despite a statistically significant difference, that difference may not be biologically or economically important depending on the question. In contrast, using the CDL to decipher between specific crop pixels such as the conversion of land between different row crops, or between grassland and small grains, may present significant challenges depending on the location.

Satellite data are thought to perform poorly in distinguishing cropland from grassland in non-irrigated regions (Maxwell et al. 2008), and perform poorly in regions with multiple crop rotations (USDA, n.d.) or regions with forest interspersed with cropland (Maxwell et al. 2008). The cropland data layer displays these patterns of inaccuracy. For example, small grains are underestimated by the CDL in the Dakotas, where deciphering between grassland and dryland crops may be difficult (Maxwell et al. 2008), and in Minnesota and Pennsylvania, where broad-leaf forest canopy could result in misestimates of field size. In contrast, small grains are greatly overestimated in the Central Valley of California, which has numerous crop rotations.

Some error is inherent in geospatial data. Misclassification error can become a particular problem with high-resolution data and disaggregated pixel classifications, and the CDL is no exception (Kline et al. 2013). The appropriateness of the CDL for different scientific applications will thus be highly dependent on the region of focus and the demands placed on the data.

E. Conclusion

The NASS CDL has been produced annually since the late 1990s, with continuously improving satellite data and ground-truthing. As such, it is one of the best available geospatial datasets focused on agricultural production in the world, and its wide-use in several disciplines reflects its utility. Nonetheless, large differences were observed for major crops and aggregate crop groups relative to the USDA Census of Agriculture. We suggest caution should be applied when considering using the CDL for pixel level analyses, particularly in regions that are not dominated by cropland with relatively simple crop composition. Similar or greater caution should be applied to geospatial data from other regions of the world where satellite data may be less substantially developed, funded or ground-truthed, or where tabulated data is not available for comparison. Geospatial data are opening new directions of scientific exploration that would otherwise be infeasible. Yet, as with traditional tabulated or empirically derived data, it remains important to recognize the limitations of underlying data in the pursuit of rigorous scientific research.

F. Acknowledgements

G. References

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H. Figure Captions

Figure 1. Percent difference of CDL relative to Census of Agriculture for overall cropland (A) soybeans (B), corn (C) and small grains (D). Negative values indicate the CDL overestimated relative to the Census, while positive values indicate an underestimate. For all analyses, counties were excluded if the Census reported less than 50 acres for a given crop or crop group.

Figure 2. Evaluation of CDL estimate relative to 95% confidence interval (CI) of the Census of Agriculture for soybeans (A) and wheat (B). 0 indicates the CDL was within the 95% CI and 1 indicates it was outside of the Census' 95% CI.
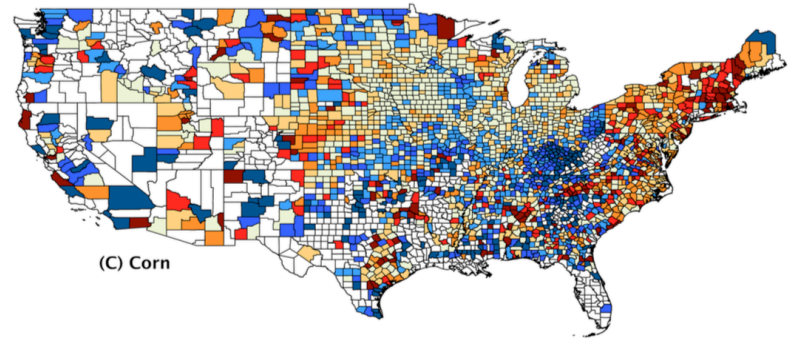
Figure 1.

(A) Cropland

(B) Soybeans

(C) Corn

(D) Small Grains

% Diff. from CoA

- −100 or less
- −100 to −50
- −50 to −25
- −25 to −10
- −10 to 10
- 10 to 25
- 25 to 50
- 50 to 100
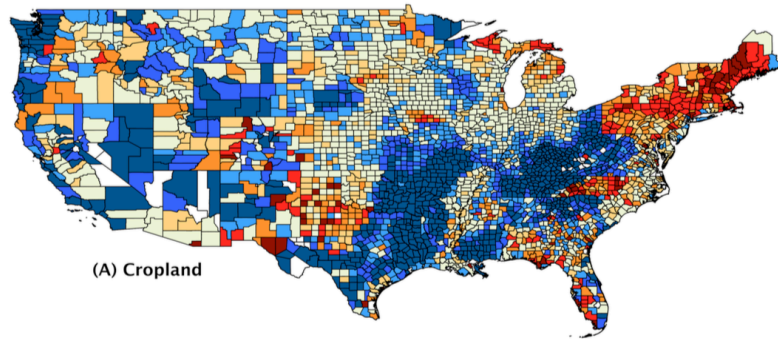- 100 or more

Figure 2.

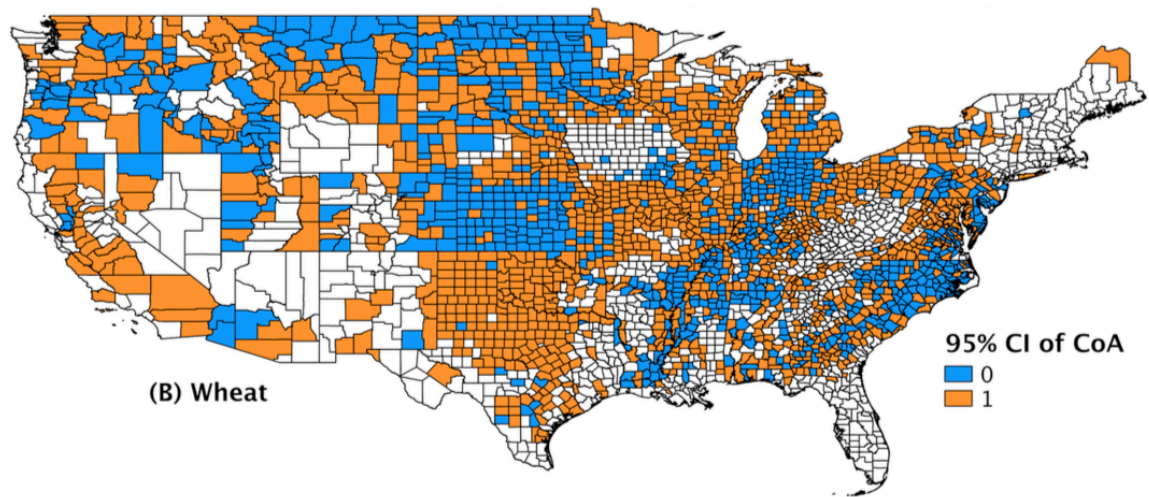(A) Soybeans
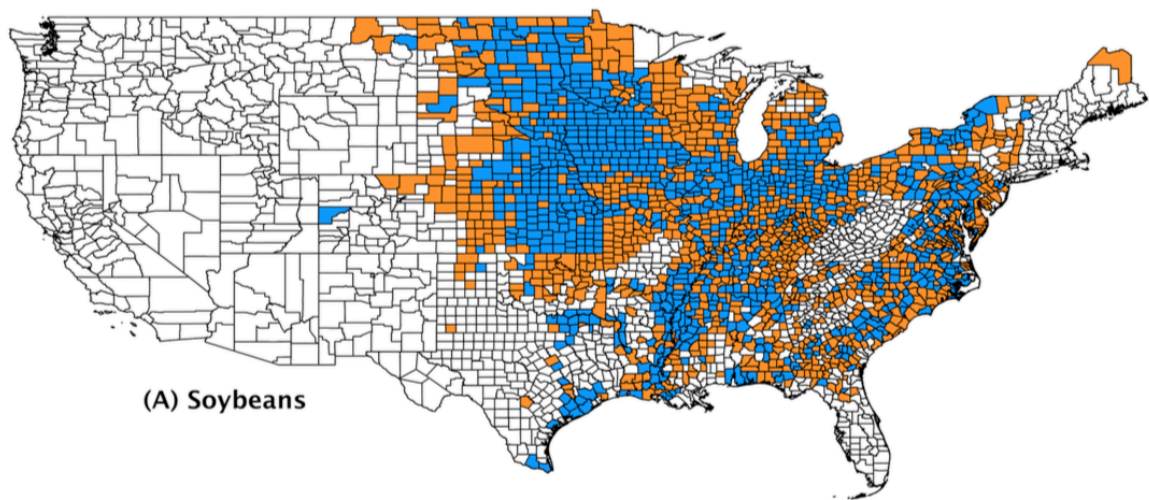
(B) Wheat

95% CI of CoA
0
1
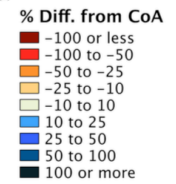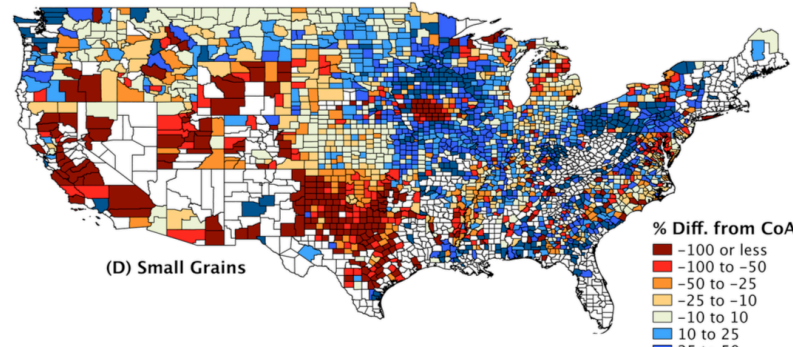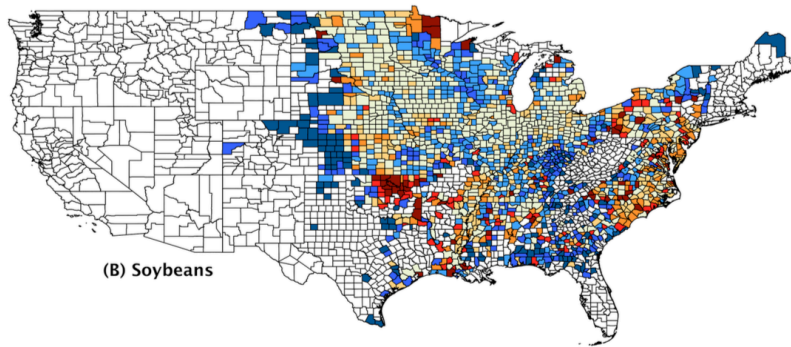
Table 1. CDL and comparable Census crop categories and metrics of difference for observations in the continental US with at least 50 acres reported in the Census.

	CDL Categories (grouped categories)	Census Tables	Avg. % diff. at County level (+/- SD)	Avg. acre diff. at County level
Corn	001, 225, 226, 237, 241 ("Corn all")	Corn grain (Table 25), Corn silage (Table 26)	-16 (207)	-423* (8825)
Soybean	005, 026, 239, 240, 241, 254 ("Soybeans all")	Soybeans (Table 25)	-3 (65)	474** (7964)
Corn & Soybeans	Corn + Soybeans	Corn + Soybeans	-23 (222)	-99 (13524)
Small Grains	021, 022, 023, 024, 026, 028, 225, 226, 230, 234, 235, 236, 237, 238, 240, 254 ("Wheat Durum all", "Wheat Winter all", Spring Wheat, "Oats all", "Barley all")	Barley for grain, Oats for grain, Wheat for grain (all) (Table 25)	-33 (165)	-2793** (15623)
Total Cropland	001-006, 010-014, 021-39, 041-057,059-060, 066-072, 074-077, 204-209, 211-214, 216-227, 229-232, 234-250, 254	Harvested cropland, Cropland on which all crops failed (Table 8)	9 (93)	5523** (28855)

Notes: The Census crops are measured in harvested acres. The Census counts acres for each crop harvested on the same plot of land as acres for each crop, but only counts the acres once in the overall cropland categories. To be consistent, we did the same for the CDL for grouped crops and overall cropland. **,* indicates significant differences between the two datasets at the 0.01 and 0.05 level, respectively, based on paired t-tests.

IV. Modeling multiple non-consumptive effects in simple food webs; a modified Lotka-Volterra approach

A. Introduction

Density mediated, or consumptive, effects, have long been known to be an important determinant of the distribution and abundance of species within an ecosystem. Reflecting this long history, most basic ecological theory is based on density dependent interactions (Werner and Peacor 2003; Pressier et al. 2005) among species in linear food webs (Polis 1991; Berlow et al. 2004; Agrawal et al. 2007) . The implicit assumptions of these models are that prey fail to respond behaviorally to predation risk (Schmitz et al. 2004; Pressier et al. 2005) and that changes in prey species density are solely a result of consumptive interactions, scramble competition, or natural mortality.

However, over the last two decades, empirical ecologists have demonstrated the widespread importance of non-consumptive effects (NCEs) in many communities (Lima 1998; Werner and Peacor 2003; Schmitz et al. 2004). Non-consumptive effects, or the non-lethal influence of a predator (or competitor), have been found to result in changes in foraging/mating behavior (Soluk and Collins 1988a), growth (Peckarsky and McIntosh 1998) and habitat choice (Turner and Mittelbach 1990) of the affected species, as well as higher order interactions such as trophic cascades (e.g. Schmitz 1998; Madin et al. 2010) that may influence the structure of entire communities (Liere and Larsen 2010). Similarly, non-consumptive effects may influence the success of conservation efforts, as illustrated by the

Yellowstone wolf-elk-aspen system (Fortin et al. 2005), the effectiveness of biocontrol in both positive (Walzer and Schausberger 2009) and negative (Eubanks and Styrsky 2006) ways, and the exacerbation of the ecosystem impacts of fishing down large marine predators (Madin et al. 2010). Yet, despite this wealth of empirical studies, there remains a dearth of empirically informed models of non-consumptive effects.

This lack of data-informed models is not due to a lack of theoretical work on non-consumptive effects. The theoretical research on NCEs to date has yielded insight into how dynamic traits may influence population dynamics (Abrams 1982; Holt 1984), the coexistence of prey with a shared predator (Abrams and Matsuda 1993), the relative strength of direct and indirect interactions (Abrams 1995), the distribution of prey in a patchy environment (Abrams 2007; Abrams et al. 2007), and the coevolution of predator and prey behavior (Brown et al. 1999; Fussman et al. 2007). However, most of the current models have been relatively abstract with little incorporation of empirical data or methods (Bolker et al. 2003). The resulting theoretical frameworks have made it difficult for empirical studies to design the experiments or observations necessary to test model predictions, which limits the collection of data necessary to evaluate the importance of NCEs on the longer-term system dynamics. Resolving these challenges may yield important insight into how susceptible a system might be to disturbance, invasion, or extraction (Sutherland 2006).

What is lacking is a simple framework for incorporating empirical results into ecological models in order to better understand the mechanism(s) driving the structure, diversity and function of simple food webs. Here I expand on the concept of predator interference (Beddington 1975; Crowley and Martin 1989) to depict a broad array of non-consumptive species interactions. I derive a simple 4 species Lotka-Volterra style model that can include multiple NCEs and interactions among them. The model is specified for a four

species food web assuming type II functional responses (Hollings 1959), but may be modifiable to study smaller or larger ecological networks that include type I, II, or III functional responses. I first derive the model, then illustrate the diverse uses of the model with two example systems: (1) the influence of a NCE on predation behavior of a non-dominant predatory stonefly in a stream community and (2) the coexistence of a weaker competitor on a shared resource via interacting NCEs. Lastly, I discuss the implications of the model to these systems and other systems where NCEs may be important. In the appendix, I briefly explain the empirical experiments and statistics necessary to parameterize the model.

B. Derivation of the model and its relation to predator interference models

This model expands on the pre-emption model of predator interference proposed by Crowley and Martin (1989). To be consistent, where possible I follow their notation and parameter definitions. The environment is assumed to be homogenous with the resource present at density H (resource individuals per area), dominant consumers present at density D (dominant consumers per area), competitors present at density C (competitors per area), and predators present at density P (predators per area). Because abundances are modeled as continuous variables, I use the actual density i rather than i-1 for all functional responses (Skalski and Gilliam 2001). I assume individuals of a species are identical, move randomly with respect to each other, and that depletion of prey is relatively insignificant and can be ignored.

The Crowley and Martin (1989) model assumes there are just two species, the predator and the prey.

$$\frac{dH}{dt} = rH(1 - \frac{H}{K}) - F_pP \qquad (1)$$

$$\frac{dP}{dt} = e_pF_pP - m_pP \qquad (2)$$

where r is the prey's intrinsic rate of growth, K is the prey carrying capacity, F_p is the *per capita* predation rate of the predator on the prey, e_p is the conversion efficiency of converting prey biomass to predator biomass and m_p is the density-independent mortality rate of the predator. Parameters used below and their units are listed in Table 1. A predator consumes the resource at the rate F_p, which is an increasing function of the attack coefficient a (area/predator/time) and the density of the prey species. This rate is reduced by the proportion of time spent handling the prey b_pF_p, where b_p is the time spent exclusively handling the attacked resource individual (Predator-time per prey individual attacked). Thus,

$$F_P = a_PH(1 - b_pF_P) \qquad (3)$$

Solving for per capita consumption rate yields

$$F_P = \frac{a_pH}{1 + a_pb_pH}. \qquad (4)$$

which is Holling's type II functional response (Holling 1959).

Crowley and Martin (1989) take this a step further by incorporating predator interference. Thus,

$$F_P = a_PH(1 - b_pF_P - \beta_PI_P) \qquad (5)$$

where the last term represents the proportion of total time spent encountering conspecifics where β_p is the amount of time wasted on each encounter. I_p is the per capita rate of interference (predators/predator/time) defined as:

$$I_P = \alpha_PP(1 - \beta_PI_P) \qquad (6)$$

where α_p is the area 'swept out' by a predator individual. Rearranging and plugging (6) into (5) and solving for F_p yields

$$F_P = \frac{a_P H}{(1 + a_P b_P H)(1 + \alpha_P \beta_P P)} \tag{7}$$

To broaden the array of NCEs that can be explored, I expand this approach to a 4 species diamond food web that includes one resource species (*H*), two intermediate consumers labeled for clarity as the dominant consumer (*D*) and the competitor (*C*) both of which consume the resource and are consumed by the top predator (*P*) (fig 1i). The predator in the food web has a multispecies type II functional response and can have separate intraspecific interference rates depending on which of the two prey species it is attacking (see Appendix 1 for discussion of type I, III functional responses). Following the approach above, the predator functional response becomes

$$F_{PD=} \frac{a_{PD} D}{(1 + a_{PC} b_{PC} C + a_{PD} b_{PD} D)(1 + \alpha_{PC} \beta_{PC} P + \alpha_{PD} \beta_{PD} P)} \tag{8}$$

for the dominant consumer prey, with a corresponding term for predation on the competitor (See Appendix 1 for detailed derivation). The dominant consumer and the competitor species face interference from interspecific interactions. The dominant consumer interferes with the competitor species and faces interference from the predator, reflecting the non-consumptive effect of the predator on the dominant consumer's behavior. The NCE influences the dominant consumer's functional response and the dominant consumer's ability to interfere with the competitor species (fig 1i). Thus for the dominant consumer that both interferes with the competitor and receives interference from the predator,

$$F_D = a_D H(1 - b_D F_D - \beta_{DC} I_{DC} - \gamma_{DP} W_{DP}) \tag{9}$$

where $\beta_{DC}I_{DC}$ is the proportion of time wasted by the dominant interfering with the competitor and $\gamma_{DP}W_{DP}$ is the corresponding term for interference on the dominant from the predator, defined as

$$I_{DC} = \alpha_{DC}C(1 - \beta_{DC}I_{DC} - \gamma_{DP}W_{DP}) \tag{10}$$

and

$$W_{DP} = \delta_{DP}P(1 - \gamma_{DP}W_{DP}) \tag{11}$$

Solving for I_{DC} and W_{DP}, and plugging into (9) yields

$$F_D = \frac{a_D H}{(1 + a_{DC}b_{DC}H)(1 + \alpha_{DC}\beta_{DC}C)(1 + \delta_{DP}\gamma_{DP}P)} \tag{12}$$

The competitor receives interference from the predator and the dominant consumer, and its functional response is initially similar. As above I define

$$F_C = a_C H(1 - b_C F_C - \gamma_{CP}W_{CP} - \gamma_{CD}W_{CD}) \tag{14}$$

where

$$W_{CP} = \delta_{CP}P(1 - \gamma_{CP}W_{CP} - \gamma_{CD}W_{CD}) \tag{15}$$

and

$$W_{CD} = \delta_{CD}D(1 - \gamma_{CP}W_{CP} - \gamma_{CD}W_{CD}) \tag{16}$$

However, the interference link from the dominant (W_{CD}) is modified by the interference of the predator on the dominant consumer. I define $\bar{\gamma}_{CD}$, the units of competitor time wasted on each encounter with the dominant, as

$$\bar{\gamma}_{CD} = \gamma_{CD}(1 - \gamma_{DP}W_{DP}) \tag{17}$$

where $\gamma_{DP}W_{DP}$, as before, is the proportion of total time wasted by dominant consumer encountering the predator. Simplifying and solving the above equations and plugging into (14) yields

$$F_C = \frac{a_C H}{(1 + a_C b_C H)(1 + (\frac{\gamma_{CD}}{1 + \delta_{DP}\gamma_{DP}P})\delta_{CD}D + \delta_{CP}\gamma_{CP}P)} \quad (18)$$

The above per capita predation rates can then be modified to reflect other three and four food webs that have mechanisms such as predator interference (fig 1a), trophic cascades (fig 1b), interference competition (fig 1c) and omnivory (fig 1d). This can be done by retaining only the parameters that are pertinent to the system being studied. For instance, to model a system structured like figure 1e the attack coefficients would be

$$F_P = \frac{a_P D}{(1 + a_P b_P D)(1 + \alpha_P \beta_P P)} \quad (19)$$

$$F_D = \frac{a_D H}{(1 + a_D b_D H)(1 + \alpha_{DP} \beta_{DP} P)} \quad (20)$$

$$F_C = \frac{a_C H}{(1 + a_C b_C H)}. \quad (21)$$

Additionally, NCE can have a positive effect on trophic interaction in the form of facilitation. For instance, if the above case encountering conspecifics is beneficial to the per capita predation rate of the predator then β_p, the time lost to intraspecific interference, is negative. Thus equation 19 becomes,

$$F_P = \frac{a_P D}{(1 + a_P b_P D)(1 - \alpha_P \beta_P P)}, (1 > \alpha_P \beta_P P) \quad (22)$$

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C. Example systems

1. Parameterization of Example Systems

Very few systems currently have the detailed data available to parameterize this model in full. Two systems for which there are significant data available are discussed below to illustrate the model's potential.

Parameter values for both example systems were derived from the literature (Table 2). In some cases parameter values from related species or related systems were used when data for the focal species were not available.

2. Multiple Non-consumptive Effects: Stream Community

I explore how multiple predators and multiple NCEs change the dynamics and population abundances of 3 and 4 species stream communities. The existence and strength of behavioral interactions have been well documented in stream communities involving fish, predatory stoneflies and mayfly prey (e.g. Peckarsky 1980; Soluk and Collins 1988b; Soluk and Collins 1988c; Soluk and Collins 1988a; Soluk 1993; McIntosh and Peckarsky 1999). The structure of the fish-stonefly-mayfly-algae food web is not exactly analogous to the food web used in the derivation above. Rather the food web takes on a "Y" shape with the two competitors sharing a single resource existing at the top trophic level. In relation to the above derivation, the stonefly can be thought of as the dominant consumer and the sculpin as the invading competitor. Both interfere with the grazing of their mayfly prey (fig 1f). I modeled the sculpin as the species invading the stonefly-mayfly-algae food web because most empirical observations and experiments focus on the community interactions and population abundances in streams with and without the sculpin present.

Empirical research has found that the presence of sculpin significantly reduces the movement of *Agentina* stonefly larvae (Soluk and Collins 1988c) and causes a decrease in

the mean number of *Baetis* mayfly consumed by stonefly larvae by over 50% in a 24h period (Soluk and Collins 1988a). When both predators are present, the total consumption of *Baetis* is lower than the additive consumption, with stoneflies bearing the brunt of the negative interaction (Soluk and Collins 1988c). Sculpin have also been found to have an increased capture success of an alternative prey in the presence of stoneflies (Soluk and Collins 1988c), indicating the potential for facilitation. Additionally, experiments involving brook trout, stoneflies, and mayfly prey demonstrated that the non-lethal presence of either or both predators caused a decrease in algal grazing and consequently, fecundity of mayflies (Peckarsky and McIntosh 1998). Using empirical results from this extensive literature, I modeled the interactions between the two competitors, sculpin and *Agentina* stonefly which both consume *Baetis* mayflies. The mayfly in turn consumes the algal resource. I incorporated the following NCEs:

(1) Stoneflies interfere intraspecifically

(2) Stoneflies facilitate sculpin foraging

(3) Stoneflies interfere with mayfly grazing

I address the following questions:

(1) Can the inclusion of NCEs enable sculpin to invade and both stonefly and sculpin to persist?

    (a) Without any non-consumptive effects, does the sculpin invade and displace the stonefly?

    (b) With intraspecific interference of the stonefly, does the sculpin invade and if so, does it displace the stonefly or do the two populations persist? Is the same result found with only positive interference (i.e. facilitation) of the stonefly on the sculpin?

(c) Does the inclusion of multiple non-consumptive effects change the outcome observed in (b)?

(2) What is the relative strength of non-consumptive effects to consumptive effects needed to produce comparable equilibrium population densities of the mayfly and algae?

a. Stream Community Simulation Results

For the estimated parameters, the sculpin could not invade when no interference terms were included in the model (fig 2a). Predator interference of the stonefly on itself could enable invasion of the sculpin and persistence of both predator species (fig 2b). If instead of stonefly intraspecific interference, a positive interference term of the stonefly facilitating sculpin predation was included, the sculpin could invade and both species again persisted (fig 2c). A combination of interference terms did not have a large influence on the long-run equilibrium abundances (fig 2d).

As can be seen in figure 2, the population abundances of the basal species and of mayflies did not change dramatically with or without the sculpin present. With one or both predators present, algal density was near carrying capacity, but with neither present, algal density and mayfly density oscillated in predator-prey cycles. However, the stabilizing influence of the predator was seen when only density-dependent effects were present. To isolate the NCE of the stonefly, I mimicked short-term empirical experimental designs that sew or glue mouthpieces to prevent consumptive attacks (e.g. Schmitz 1998) by setting the attack rate and mortality rate of the stonefly to zero with the sculpin absent. In this scenario, algal density stabilized and increased as the strength of the NCE coefficient of the stonefly predator increased. The effect, however, was much weaker than the consumptive effects at similar predator densities. In order to see a similar change in algal density with an extremely strong non-consumptive effect, the non-consumptive population of the predator had to be

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roughly 5 times greater than the consumptive population. The size of the corresponding

population depended on the strength of the interaction term such that an interaction term half

as strong requires a population of predators roughly twice as large.

3. Interacting Non-Consumptive Effects: Coffee Insect Community

Here I model the dynamics of a 4-species food web present in a coffee agroecosystem

in Chiapas, Mexico as a motivator to study the effect of interacting non-consumptive effects.

Specific details of the study system and empirical experiments can be found in Liere and

Larsen (2010). In brief, this system is composed of a scale insect (*Coccus virdis*) that is

tended by a behaviorally dominant arboreal ant, *Azteca instabilis* that forages on the

honeydew excreted by the scale insect. In the process of tending, *Azteca* non-lethally deters

predators and parasites of the scale, most important of which is a coccinellid beetle.

However, in the presence of a specialist parasitic phorid fly, *Azteca* stops moving or seeks

shelter (Philpott et al. 2004; Philpott 2005; Liere and Larsen 2010). This reduces the ants'

exposure to parasitism (Mathis et al. 2010) but also interrupts the protection it provides to its

mutualistic scale partner for up to two hours (Philpott et al. 2004). In relation to the

derivation, the scale insect is the resource that is shared by the two consumers, Azteca ants—

the dominant consumer and coccinellid beetles—the competitor. Azteca ants were modeled

as the dominant consumer because they are behaviorally dominant to the beetle and inhibit

the beetles foraging ability (Liere & Larsen 2010). The phorid fly is the predator of the

dominant consumer, exerting both a consumptive and non-consumptive effect (fig 1g).

The break in ant activity due to the presence of the phorid fly enables the coccinellid

beetle to occupy coffee plants for a longer period of time, and to consume as many scales in

the presence of *Azteca* and phorids as when the beetle is foraging alone (Liere and Larsen

2010). It is hypothesized that the non-consumptive effect of the phorid on ant-activity that

interrupts the first non-consumptive effect of the ants on the beetle is responsible for the persistence of the coccinellid beetle within the system (Liere and Larsen 2010).

I incorporate the following NCEs:

Parasitoid: Intraspecific interference of the parasitoid stemming from the change in ant behavior in the presence of a phorid fly

Ant: (1) Interference by the phorid on ant foraging, (2) Interference by the ant on beetle foraging which is costly to ant foraging (i.e. opportunity cost lost to finding and removing the beetles)

Beetle: Interference by the ant on beetle, which is reduced by the interference the phorid exerts on ants (#1 above).

I address the following questions:

(1) Is invasion and persistence possible via the inclusion of one or more non-consumptive effects?

    a. Does the inclusion of any single non-consumptive effect enable coexistence of the two consumers, as seen in the stream system? If so, which link(s)? If not, are there combinations of links that enable invasion of the competitor and persistence of both consumers?

    b. Does the incorporation of additional NCE links change the outcome seen in (a)?

(2) What is the effect of the interacting non-consumptive effects term?

a. Coffee Community Simulation Results

In the coffee system simulation, invasion and persistence of the beetle was possible via NCEs. The inclusion of any single link did not result in invasion by the competitor

species (fig 3a). Very strong links between the two competitors or a combination of strong links between the two competitors and a modifying link from the parasitoid were necessary for invasion and persistence of the beetle competitor (fig 3 b,c). Again I found the long-term population abundances of the existing species were similar regardless of whether zero, one, or all non-consumptive terms were included. Once the competitor was capable of invading, the inclusion of additional or stronger NCE terms only moderately affected its long-term abundance (fig 3d).

The incorporation of an interacting non-consumptive effect was not critical for invasion and persistence if the interaction between the ant and the beetle was sufficiently strong. Due to the additional non-linearities in the system from this interaction term, the invasion of the beetle did not produce intuitive changes in the other species population densities. Rather, the invasion of the beetle led to a reduction in the phorid population while the ant and the scale population remained largely unchanged (fig 3). Thus, it appears that the phorid promotes the invasion of the beetle, which subsequently reduces the phorid population.

In both systems, coexistence of two competitors on one resource was sensitive to the demographic parameters of the invading competitor (attack rate, mortality, conversion efficiency, interference terms), and sensitivity increased substantially with interacting NCE terms.

As mentioned above, the parameters for these models were estimated from the literature. The data required to fully parameterize this model are not available for many, if any, systems. Thus, more detailed data collection is necessary to determine how widespread this mechanism may be, to robustly estimate parameters in systems displaying these mechanisms and to do thorough stability analysis on those estimated parameters.

D. Discussion

Ecologists are continually attempting to disentangle the biotic and abiotic interactions responsible for the complexity seen in nature to understand questions such as why species are distributed where they are, why biocontrol or invasion is successful in one location but not in another, or which species may have disproportionate influences on the community. Understanding these questions is critical not only to basic ecology but also to understanding questions of conservation and resource management.

Non-consumptive effects are one area where understanding could be improved with increased collaboration between empirical and theoretical ecologists (Bolker et al. 2003). Presently, there is a rich literature in both fields indicating NCEs exist and may be important, but understanding of how NCEs work and interact with each other in ecological communities remains poorly understood (Schmitz et al. 2004). I believe this is due, in part, to the lack of intuitive and accessible models that incorporate NCEs. The model I propose here is a simple mechanistic approach that can incorporate multiple non-consumptive effects and interacting non-consumptive effects.

Using two example systems I have shown that invasion and persistence of a competitor on a shared resource is possible in the presence of non-consumptive effects. Even at low predator densities where NCEs had only a small effect on population abundances, invasion and persistence was possible. This indicates two potentially important aspects of NCEs. First, depending on the system attributes, invasion of non-native species or coexistence of competitors via NCEs may be robust to external forcing. This may be of special importance in areas where predator populations or other behaviorally dominant species are being reduced. For instance, in fisheries, there is concern that removal of the top predator may have far reaching repercussions on biodiversity of lower trophic levels

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(Salomon et al. 2010). While this may still be the case in numerous contexts, it is possible that lower trophic levels that are strongly influenced by NCE stemming from predator species may be more robust to extinction of competing species than those only influenced by consumptive effects. Second, NCEs may be most important to population abundances in systems where equilibrium populations of the predator and the resource are high. This is evident based on the shape of the functional response curve of the consumer as prey density and predator density increase (See Appendix 1). At low predator density or low prey density, the curves with high and no NCE coefficient differ only slightly. However, as either prey density or predators increase, the separation becomes more apparent. In the two example systems, the equilibrium populations of the predator were low and thus, I found consumptive effects to be much stronger than non-consumptive effects with respect to population size even when it was clear that NCEs were reducing consumption rates.

Finer scale data on more systems are needed to better evaluate this and other models that attempt to achieve a more comprehensive understanding of the importance of NCEs in different ecological systems. While the mechanism proposed above may be important in numerous systems, whether or not this mechanism is the likely driver of coexistence in any given system will depend on the details of the system and the careful measurement of parameter values for systems displaying these mechanisms. Other considerations such as space and stage-structure have been ignored in this model. Extensions that include these and other system-specific attributes that may alter the impacts of NCEs would be insightful additions.

Non-consumptive effects, especially behavioral modification caused by the presence of predators, have been recognized empirically and theoretically for some time (Abrams 1990; Turner and Mittelbach 1990). However, to date only intraspecific NCEs have been

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incorporated into simple mechanistic models, and even then, popularity of these models has remained low despite evidence of their frequent superiority to the classic type II functional response (Skalski and Gilliam 2001). I hope the increased flexibility of this model will prove useful to empirical ecologists trying to quantify the importance of NCEs and will help bridge the gap between empirical and theoretical studies leading towards more data-driven models of these interactions.

E. Acknowledgements

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G. Appendix

1. Experiments and Statistics

Experiments required to parameterize this model are extensions of those required to parameterize type II functional responses and predator interference. As with the Holling type II functional response, feeding experiments are required that measure the number of prey consumed by an individual predator at several different densities of prey. To measure intraspecific interference, the same experiment must be repeated over several different numbers of conspecific predators (Crowley and Martin 1989). For each interference or non-consumptive relationship a similar experiment must be undertaken. For example in a predator-consumer-resource system, to measure the non-lethal effect of a predator on the consumer's intake rate of the resource, one needs a feeding experiment that measures an individual consumer's intake rate at different densities of the resource without any predators present (fig A1a), and experiments that measure that intake rate in the non-lethal presence of different numbers of predators (fig A1b). Care should be taken to replace prey during experiments to avoid complicating statistical approaches (Juliano 1999), and when addressing interference between species, to ensure the *non*-lethal presence of the second species.

Non-linear least squares (NLS) is then used to estimate the attack coefficient and handling time using the feeding experiment of density of prey versus number of prey eaten by an individual predator (Juliano 1999). Holding these two parameters constant, the predator interference coefficient is estimated using an NLS on the extended feeding experiment data that includes average number of prey eaten per predator individual with different predator numbers present (Crowley and Martin 1989). The coefficient of an interspecific NCE can be

estimated in a similar way using the data from feeding experiments that evaluate how consumption behavior of one species over a range of prey densities is modified when a second species is present in different numbers.

2. Detailed Model Derivation

The model presented here builds on the framework of Crowley and Martin (1989), which I outline in equations (1) through (7) in the main text. If I expand this to include four species, resource (H), dominant competitor (D), competitor (C), and predator (P) which consumes both competitors, the system of equations can be defined as,

$$\frac{\partial H}{\partial t} = rH(1 - \frac{H}{K}) - F_D D - F_C C \tag{A1}$$

$$\frac{\partial D}{\partial t} = e_D F_D D - F_{PD} D - m_D D \tag{A2}$$

$$\frac{\partial C}{\partial t} = e_C F_C C - F_{PC} C - m_C C \tag{A3}$$

$$\frac{\partial P}{\partial t} = e_{PD} F_{PD} P + e_{PC} F_{PC} P - m_P P \tag{A4}$$

where F_D is the per capita predation rate of the dominant consumer on H (its only prey resource), and F_{PD} is the per capita predation rate of the predator on the dominant consumer and F_{PC} is the per capita predation rate of the predator on the competitor. I maintain this subscript notation throughout (see Table 1).

The predator, P, consumes the dominant consumer, *D*, and the competitor, *C*. The predator can only handle one prey item at a time, thus the predators feeding rate on each species is reduced by the handling time for both species creating a multi-species type II function response. Additionally, if there is a cost of interference from conspecifics, that also reduces the predation rate on each prey item. Interference is allowed to differ for each prey

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species being attacked. In this case, the per capita feeding rate of the predator on the

dominant consumer is

$$F_{PD} = a_{PD}D(1 - b_{PD}F_{PD} - b_{PC}F_{PC} - \beta_{PD}I_{PD} - \beta_{PC}I_{PC}) \tag{A5}$$

and for the competitor is

$$F_{PC} = a_{PC}C(1 - b_{PD}F_{PD} - b_{PC}F_{PC} - \beta_{PD}I_{PD} - \beta_{PC}I_{PC}) \tag{A6}$$

with intraspecific interference of the predator when attacking the dominant prey defined

as,

$$I_{PD} = \alpha_{PD}P(1 - \beta_{PD}I_{PD} - \beta_{PC}I_{PC}) \tag{A7}$$

and the corresponding term when attacking the competitor. Solving (A5) and (A6) for

F_{PD}, setting them equal to each other and solving for F_{PC} yields

$$F_{PC} = \frac{a_{PC}C(1 - \beta_{PD}I_{PD} - \beta_{PC}I_{PC})}{(1 + a_{PC}b_{PC}C + a_{PD}b_{PD}D)}. \tag{A8}$$

Solving (A7) and the corresponding equation for I_{PC}, for I_{PD} and I_{PC} and plugging into

(A8),

$$F_{PC} = \frac{a_{PC}C}{(1 + a_{PC}b_{PC}C + a_{PD}b_{PD}D)(1 + \alpha_{PD}\beta_{PD}P + \alpha_{PC}\beta_{PC}P)}. \tag{A9}$$

The same procedure can be repeated to derive

$$F_{PD} = \frac{a_{PD}D}{(1 + a_{PC}b_{PC}C + a_{PD}b_{PD}D)(1 + \alpha_{PD}\beta_{PD}P + \alpha_{PC}\beta_{PC}P)}. \tag{A10}$$

Unlike the predator, the dominant consumer and the competitor face interference

costs to their per capita predation rates on the prey resource due to interactions with other

species. In fig. 1i, the costs reducing the dominant consumers per capita predation rate

include handling the prey item, interference from the predator (e.g. behavioral modifications

resulting from encounters), and interfering with the predation rate of the competitor (e.g.

contest competition). Thus, there must be three terms reducing the feeding rate;

$$F_D = a_D H(1 - b_D F_D - \beta_{DC} I_{DC} - \gamma_{DP} W_{DP})$$ (A11)

where $\beta_{DC} I_{DC}$ is the proportion of time wasted interfering with the competitor and $\gamma_{DP} W_{DP}$

is corresponding term for interference from the predator, defined as

$$I_{DC} = \alpha_{DC} C(1 - \beta_{DC} I_{DC} - \gamma_{DP} W_{DP})$$ (A12)

and

$$W_{DP} = \delta_{DP} P(1 - \gamma_{DP} W_{DP})$$ (A13)

Solving for I_{DC} and W_{DP}, and plugging W_{DP} into I_{DC} yields

$$I_{DC} = \frac{\alpha_{DC} C}{(1 + \beta_{DC} \alpha_{DC} C)(1 + \delta_{DP} \gamma_{DP} P)}$$ (A14)

Solving (A11) for F_D, plugging in (A14) and simplifying gives the per capita predation

rate of the dominant consumer,

$$F_D = \frac{a_D H}{(1 + a_D b_D H)(1 + \alpha_{DC} \beta_{DC} C)(1 + \delta_{DP} \gamma_{DP} P)}.$$ (A15)

Like the dominant consumer, the competitor faces several sources of interference—

interference from the predator, and interference from the dominant consumer, which is

modified by the effect of the predator on the dominant consumer. As above I define

$$F_C = a_C H(1 - b_C F_C - \gamma_{CP} W_{CP} - \gamma_{CD} W_{CD})$$ (A16)

where

$$W_{CP} = \delta_{CP} P(1 - \gamma_{CP} W_{CP} - \gamma_{CD} W_{CD})$$ (A17)

and

$$W_{CD} = \delta_{CD} D(1 - \gamma_{CP} W_{CP} - \gamma_{CD} W_{CD})$$ (A18)

However, the interference link from the dominant (W_{CD}) is modified by the interference

of the predator on the dominant competitor. I define $\bar{\gamma}_{CD}$, the units of competitor time wasted

on each encounter with the dominant, as

$$\bar{\gamma}_{CD} = \gamma_{CD}D(1 - \gamma_{DP}W_{DP})$$ (A19)

where $\gamma_{DP}W_{DP}$, as before, is the proportion of total time wasted by dominant consumer encountering the predator. Thus,

$$W_{DP} = \delta_{DP}P(1 - \gamma_{DP}W_{DP}) \Rightarrow W_{DP} = \frac{\delta_{DP}P}{(1 + \gamma_{DP}\delta_{DP}P)}$$ (A20)

and

$$\bar{\gamma}_{CD} = \gamma_{CD}(1 - \frac{\gamma_{DP}\delta_{DP}P}{1 + \gamma_{DP}\delta_{DP}P}) \Rightarrow \bar{\gamma}_{CD} = \frac{\gamma_{CD}}{1 + \gamma_{DP}\delta_{DP}P}.$$ (A21)

Thus, the units of competitor time wasted on each encounter with the dominant is a decreasing function of the proportion of time wasted by the dominant consumer as a result of encounters with the predator,

$$W_{CD} = \frac{\delta_{CD}D}{(1 + \bar{\gamma}_{CD}\delta_{CD}D + \gamma_{CP}\delta_{CP}P)}$$ (A22)

which, after plugging in (A21) it is clear,

$$W_{CD} = \frac{\delta_{CD}D}{(1 + (\frac{\gamma_{CD}}{1 + \gamma_{DP}\delta_{DP}P})\delta_{CD}D + \delta_{CP}\gamma_{CP}P)}$$ (A23)

and

$$W_{CP} = \frac{\delta_{CP}P}{(1 + (\frac{\gamma_{CD}}{1 + \gamma_{DP}\delta_{DP}P})\delta_{CD}D + \delta_{CP}\gamma_{CP}P)}.$$ (A24)

Solving (A16) for F_C, and plugging in (A23) and (A24) yields the per capita predation rate of the competitor on the prey,

$$F_C = \frac{a_C H}{(1 + a_C b_C H)(1 + (\frac{\gamma_{CD}}{1 + \gamma_{DP}\delta_{DP}P})\delta_{CD}D + \delta_{CP}\gamma_{CP}P)}.$$ (A25)

As discussed in the main text, the per capita predation rate equations can then be modified to reflect other simple food webs by retaining only the NCE parameters that are pertinent to the system being studied and setting the rest equal to zero.

It is important to note that these equations can be modified to account for other functional responses. Following Crowley and Martin (1989), I assumed an underlying type II functional response. However, if handling time for species i (b_i) is equal to zero then, in the absence of any interference, F_i is a linear function of prey density (i.e. a type I functional response). If instead, an underlying type III functional response is more appropriate, substitute $a_i = \dfrac{z + xH}{1 + yH}$ where z,x,y are constants, for the constant attack coefficient, a_i (Juliano 1999). While it is possible to modify the above model to different functional responses, how doing so influences the importance of NCE has not been explored here. However, changing the underlying functional response will likely change the dynamics and stability of a system whether or not the system includes non-consumptive effects.

H. Figure Captions

Figure 1. 3- and 4-species food webs that include non-consumptive effects. Solid lines indicate a trophic interaction with the arrow pointing in the direction of energy flow. Dotted lines indicate a non-consumptive interaction and the open circle indicates the disruption of a trophic link. Predator interference (a), trait-mediated trophic cascades (b), interference competition (c), omnivory with NCE (d), predator/NCE driven coexistence (e-i), stream example (f), coffee example (g), and the structure of the derived system (h).

Figure 2. Simulations of the stream system. Solid black line represents the algal population, black dotted line represents the stonefly population, grey dotted line represents the mayfly population and grey solid line represents the sculpin population. (A) no non-consumptive effects included, (B) stonefly intraspecific interference, (C) positive interference of stonefly on sculpin (D) incorporation of additional NCE terms do not greatly alter long term equilibrium abundances. Invasion of the sculpin and persistence of all four species is only possible with the inclusion of one or more non-consumptive effect. Additional non-consumptive effects do not greatly alter the long run equilibrium densities of the existing populations.

Figure 3. Simulations of coffee system. Black dotted line represents the scale insect population, grey dotted line represents the ant population, grey solid line represents the phorid population and black solid line represents the beetle population. (A) no non-consumptive effects included, (B) Extremely strong NCE between ant and beetle, (C) Strong NCE between ant and beetle with interacting NCE term from the phorid interfering with the ant, (D) incorporation of additional NCE terms do not greatly alter long term equilibrium abundances. Invasion of the beetle and persistence of all four species is only possible with strong interference between the ant and the beetle. Surprisingly, the invasion of the beetle results in a reduction in the phorid population.

Figure A1. Illustration of the effect of interference and facilitation on the shape of the function response, using stonefly (A) and sculpin (B) as examples. (A) Negative interference ("interference") reduces the amplitude of the functional response. From highest to lowest amplitude: (black, solid) no interference, type II functional response; (black, dashed) 1 intraspecific individual present; (grey, dot-dashed) 1 competing individual of 2 species present (e.g. an intraspecific and an interspecific individual); (black, dotted) 3 intraspecific individuals present; (grey, solid) 3 intraspecific, 3 interspecific interfering individuals. (B) Positive interference ("facilitation") increases amplitude of functional response. From highest to lowest amplitude: (black, dotted) 3 facilitating individuals; (grey, dashed) 1 facilitating individual; (black, solid) no facilitation, type II functional response.
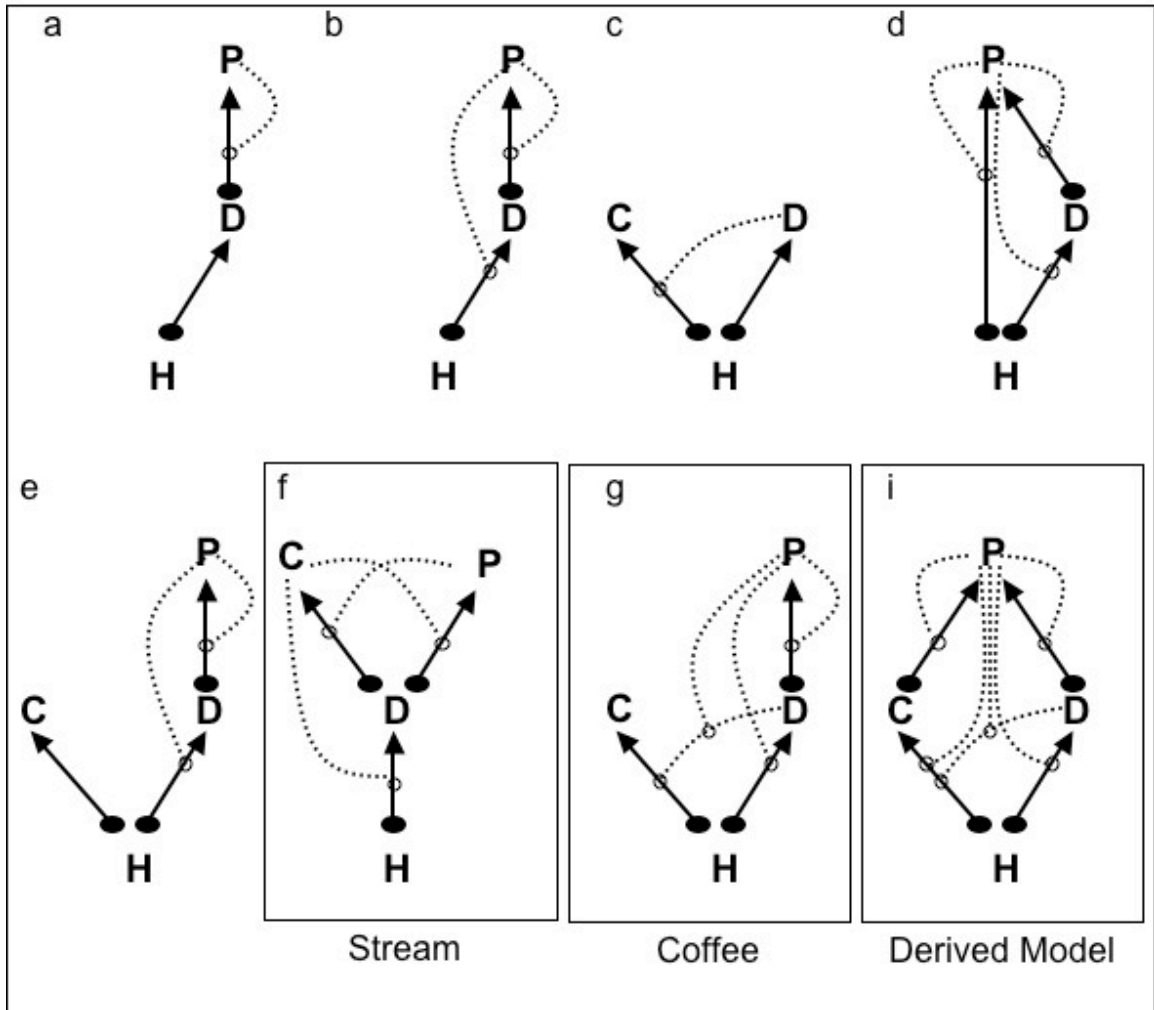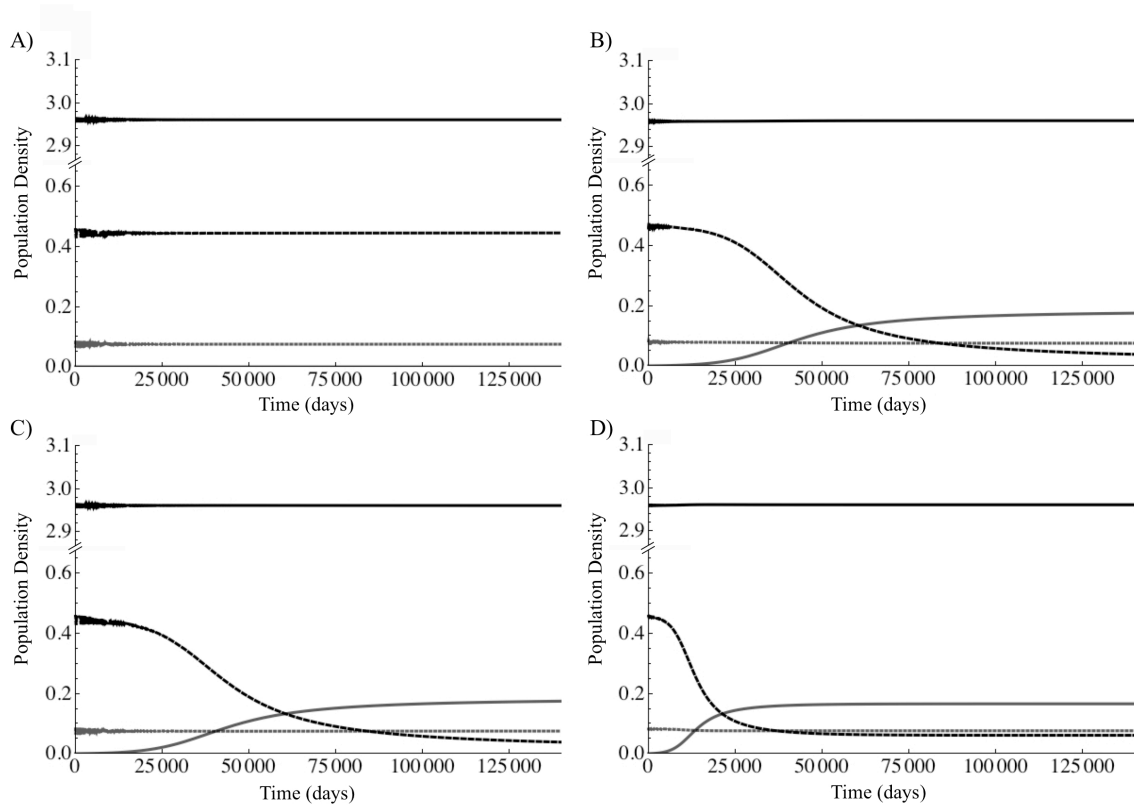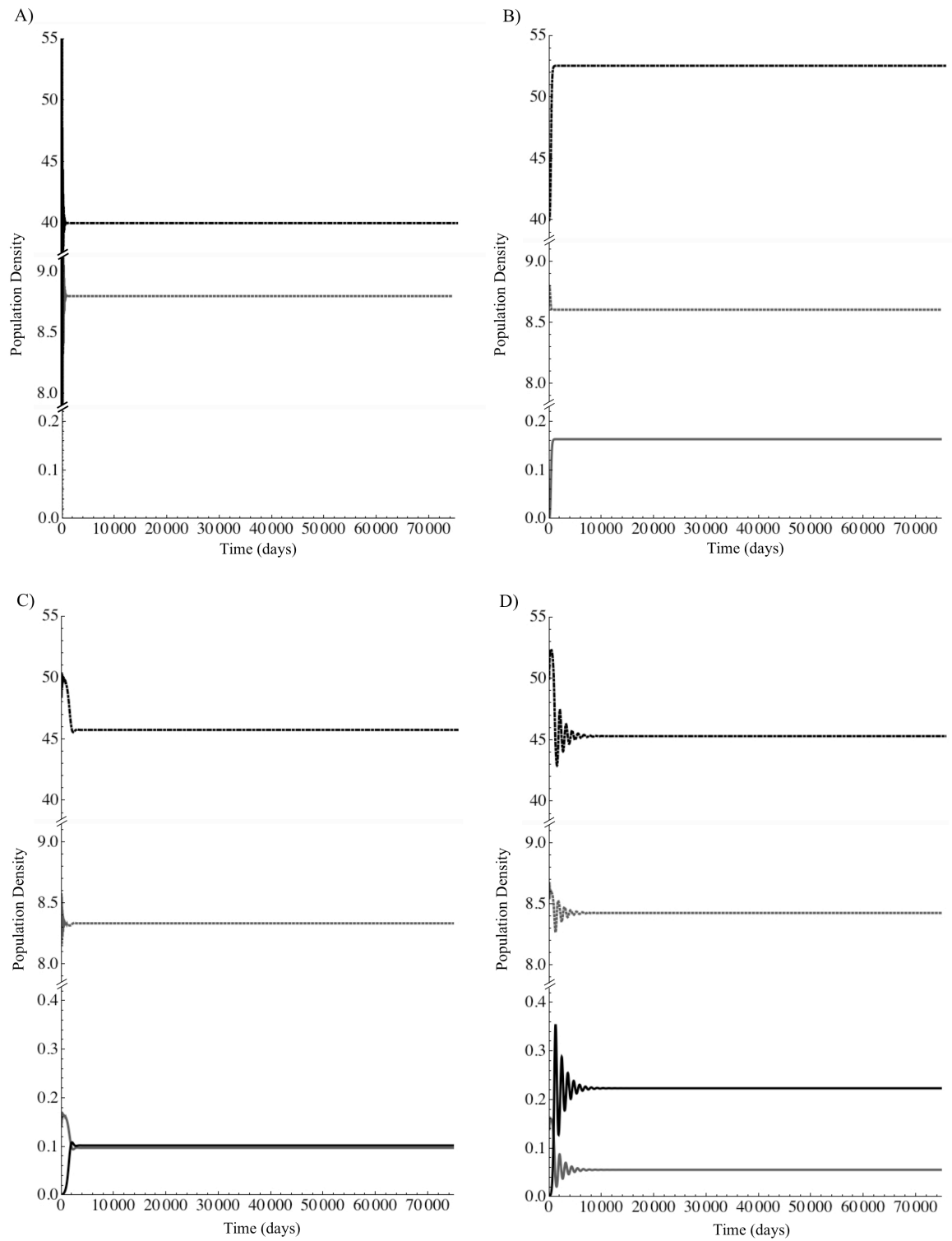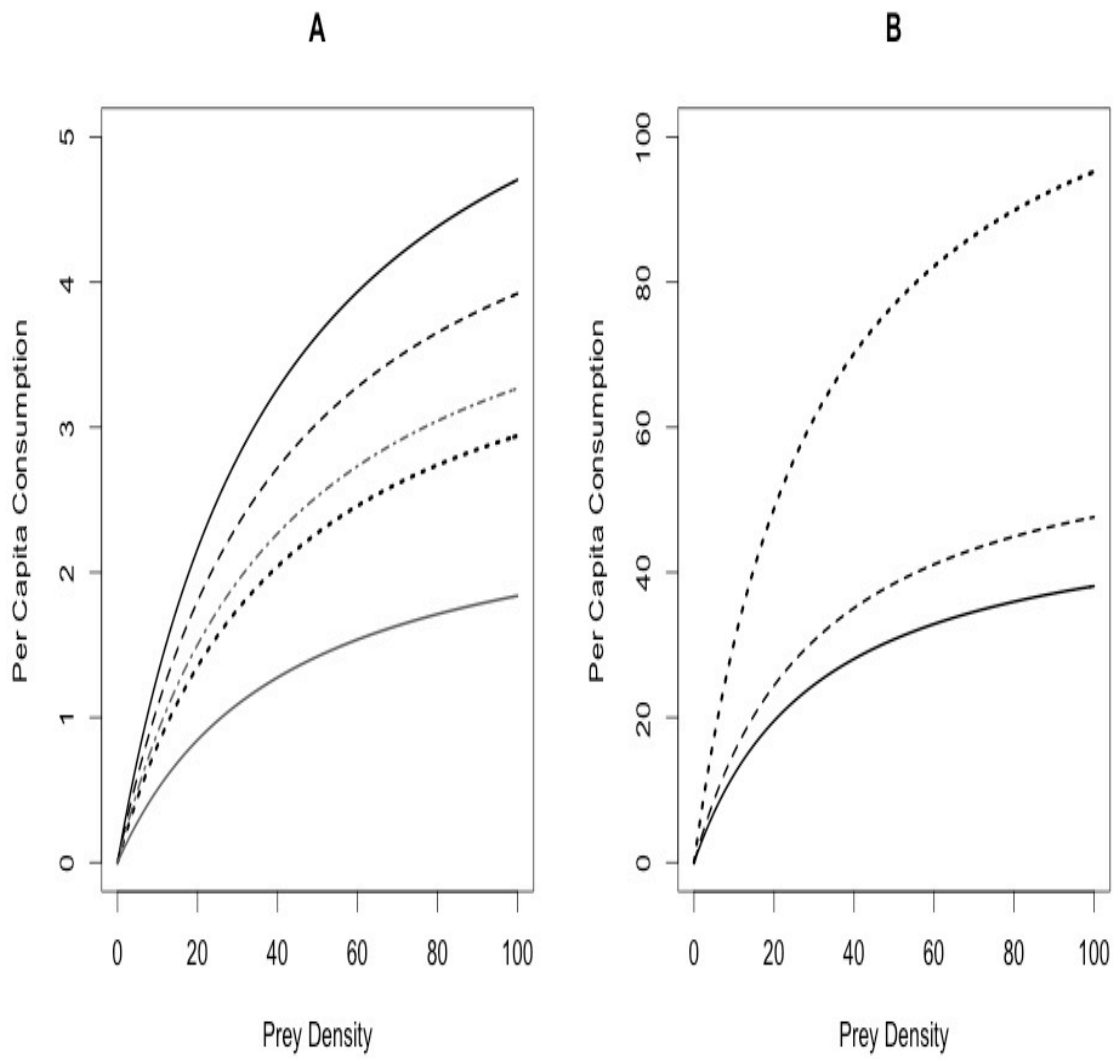
Figure 1.

Figure 2.

Figure 3.

Figure A1.

Table 1. Key for symbols used in derivation.

Symbol	Interpretation	Units
H	Density of resource individuals	Prey/area
D	Density of dominant consumer	Consumer/area
C	Density of competitors	Competitors/area
P	Density of predators	Predators/area
F_{ij}	Per capita predation rate of i on j	j prey/i predator/time
I_{ij}	Per capita interference rate of i due to interference with j	j prey/i predator/time
W_{ij}	Per capita interference rate of i due to interference from j	j prey/i predator/time
a_{ij}	Attack coefficient of i on j	Area/i individual/time
b_{ij}	Handling time of i consuming j	i-time/j individual captured
α_{ij}	Area searched for individuals of j by an individual of i per unit time	area/ i individual/time
β_{ij}	Units of time wasted by i on each encounter with j individual	i-time/j individual
c_{ij}	($c_{ij}=\alpha_{ij}\beta_{ij}$) Interference coefficient of i resulting from encounters with j	area/j individual
δ_{ij}	Area searched for individuals of j by an individual of i per unit time	area/ i individual/time
γ_{ij}	Units of time wasted by i per encounter from j individual	i-time/j individual
d_{ij}	($d_{ij}=\gamma_{ij}\delta_{ij}$) Interference coefficient of i from encountering j	area/ j individual

Table 2. Parameter values used to simulate example systems. Values were estimated from the literature. Where information was not available for the species in the example system, parameter values for similar species were used.

STREAM SYSTEM

Parameter	Value	Sensitive +/- 20%	Interpretation	Reference
r	1.5	N	Intrinsic growth rate of scales	Nisbet et al. 1997
K	3	N	Carrying capacity	Nisbet et al. 1997
a_{MA}	1	N	Attack coefficient of mayfly on algae	Nisbet et al. 1997
a_{SM}	0.17	Y	Attack coefficient of stonefly on mayfly	Soluk 1993
a_{FM}	0.393	Y	Attack coefficient of sculpin on mayfly	Soluk 1993
b_{MA}	1	N	Handling time of mayfly on algae	Nisbet et al. 1993
b_{SM}	0.087	N	Handling time of stonefly on mayfly	Soluk 1993
b_{FM}	0.014	N	Handling time of sculpin on mayfly	Soluk 1993
e_M	0.1386	N	Conversion efficiency of mayfly	Wallace & Gurtz 1986
e_S	0.34	Y	Conversion efficiency of stonefly	Heiman & Knight 1975
e_F	0.1	Y	Conversion efficiency of sculpin	Davis & Warren 1965
m_M	0.0277	N	Density-independent mortality of mayfly	McPeek & Peckarsky 1998
m_S	0.0044	Y	Density-independent mortality of stonefly	Kreutzweiser et al. 1999
m_F	0.003	Y	Density-independent mortality of sculpin	Eggers et al. 1978

Interference Parameters	Value	Range Explored	Interpretation	Reference
d_{MS}	0.1	0-0.8	Cost to mayfly from interference from stonefly	See text for system description
d_{MF}	0	0-0.8	Cost to mayfly from interference from sculpin	
c_{SS}	0.2	0-0.8	Cost to stonefly from intraspecifics interference	
d_{SF}	0	-0.5-0.1	Cost to stonefly from interference from sculpin	
c_{FF}	0.1	0-0.8	Cost to sculpin from intraspecifics interference	
d_{FS}	-0.1	-0.5-0.1	Cost to sculpin from interference from stonefly	

COFFEE SYSTEM

Parameter	Value	Sensitive +/- 20%	Interpretation	Reference
r	0.1	Y	Intrinsic growth rate of scales	Amarasekare & Mannion 2011
K	150	Y	Carrying capacity	Approx. max on 1 leaf

a_{AS}	0.01	Y	Attack coefficient of ant on scales	
a_{BS}	0.3	Y	Attack coefficient of beetle on scales	Liere & Larsen 2010
a_{PA}	0.12	Y	Attack coefficient of phorid on ant	Henne 2007
b_{AS}	0.5	Y	Handling time of ant on scales	
b_{BS}	0.07	Y	Handling time of beetle on scales	Liere & Larsen 2010
b_{PA}	0	Y	Handling time of phorid on ant	Henne 2007
e_A	0.3	Y	Conversion efficiency of ant	Offenberg 2010
e_B	0.1	Y	Conversion efficiency of beetle	Mishra et al. 2011
e_P	0.3	Y	Conversion efficiency of phorid	Morrison et al. 1997
m_A	0.1	Y	Density-independent mortality of ant	Kang et al. 2011
m_B	0.075	Y	Density-independent mortality of beetle	Kianpour et al. 1997
m_P	0.3	Y	Density-independent mortality of phorid	Porter 1998

Interference Parameters		Range Explored		
c_{AB}	0.1	0-0.12	Cost to ant from interfering w/beetle	See text for system description
δ_{BA}	1	0.95-1	Area 'swept out' by beetle	
γ_{AB}	1	0.95-1	Units of time wasted by beetle with ants	
c_{PA}	0.2	0.17-0.4	Cost to phorid from intraspecific interference	
d_{AP}	0.3	0.1-0.3	Cost to ant from interference from phorid	