An increase in the cost of production from yield losses associated with a drop in natural enemy functional diversity (reported by Snyder and Wise 2001) could cause relatively large impacts on social welfare, here showing disproportionate effects on fresh market cucumber compared to squash, producers compared to consumers and how a commonly used alternative valuation model would underestimate the size of the impact on total surplus (spider photos by Maycee Hash, illustrations by DKL)

Simple-but-Sound Methods for Estimating the Value of Changes in Biodiversity for Biological
Pest Control in Agriculture

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1. Introduction

Biological pest control relies on the conservation of natural enemies of insect pests in agroecosystems and is necessary for sustainable crop production (Crowder and Jabbour, 2014; Power, 2010; Rusch et al., 2010). However, the value of marginal changes in the species richness or functional diversity of natural enemy communities in agricultural fields has not been estimated directly, in part because of data gaps linking enemy diversity to crop yields and production costs. We used published results from small-scale field experiments in Kentucky (Snyder and Wise, 2001) to generate some estimates of the values that marginal changes in biodiversity of natural enemies might represent for society in the markets for squash and cucumber in Georgia and South Carolina. In the process of generating those estimates, we demonstrate a key framework from basic microeconomics that natural scientists can apply themselves to calculate value estimates with available data, and explain the limitations of some common techniques used by non-economists in ecosystem service valuation efforts.

The overall value of natural pest control in the U.S. is very large, accounting for savings of \$4.5 billion annually, according to calculations by Losey and Vaughan (2006). Zhang and Swinton (2012) estimated that the value of biological control of a single pest in soybean production for four Midwestern states in 2005 was over \$80M. Although these studies did not focus on biodiversity, evidence suggests that a diverse assemblage of natural enemies provides better pest control services in agriculture overall (Woodcock et al., 2014), and protects against loss of these services as climate change proceeds (Crowder and Harwood, 2014) because they tend to suffer fewer functional deficits than depauperate communities with low species richness (fewer species). A functional deficit can occur when an important natural enemy species, group of functionally similar enemy species, or species that provides complementary mortality is

absent from the assemblage (Cardinale et al., 2003; Letourneau et al., 2009; Snyder et al., 2008; Tylianakis and Romo, 2010). With mounting evidence of the overuse of pesticides (Pimentel and Peshin, 2014), increasing demand for alternative agricultural production methods (Dimitri and Greene, 2002), and legislation that encourages sustainable management practices (Roubos et al., 2014), it is increasingly important to understand the value of biodiversity or functional diversity conservation for biological control. Yet, the issue of how natural enemy diversity relates to biological control is still under intensive investigation (Crowder and Jabbour, 2014), since some natural enemies of pests feed on or otherwise interfere with each other (Duffy et al., 2007; Finke and Denno, 2005; Holt and Polis, 1997; Ives et al., 2005; Rosenheim, 2007). Predation of one natural enemy species by another usually hampers biological control but can stabilize a pest population or improve biological control under certain conditions (Ong and Vandermeer, 2014). Also, ecological studies on natural enemy diversity often lack critical information needed for economic analyses, such as benefits measured in terms of yield advantages or changes in on-farm revenue (as noted by Cardinale et al., 2012; Chaplin-Kramer et al., 2011). Therefore, to our knowledge, this is the first economic valuation of changes in natural enemy diversity for biological control in agricultural systems.

Using meta-analysis to combine a wide array of studies showing positive, neutral, and negative effects of an increase in enemy species richness on prey suppression, Letourneau et al. (2009) showed that, on average, doubling enemy species richness resulted in a large, statistically significant, negative effect on the abundance of herbivores, including pest species. In addition, the magnitude of the change in enemy species richness predicted the strength of its effect on herbivores (Letourneau et al., 2009). Furthermore, Griffin et al. (2013) found that enemy species richness had positive effects on the suppression of an herbivore species compared with the effect

of an average predator species alone. Predator richness did not have effects above and beyond that of the most effective single predator – stressing the importance of superior enemy species. Nevertheless, both meta-analyses indicated that there is a positive impact of natural enemy richness on the strength of biological control of prey. However, meta-analyses of the ecology literature cannot measure how much an additional natural enemy species is worth for biological control services. Such value estimates would reveal and quantify the hidden costs to society associated with agricultural practices that cause beneficial species to become locally absent or present in such low abundances that they are unable to carry out their role in agroecosystems.

In this paper, we demonstrate how changes in producer and consumer surplus in agricultural markets could result from changes in natural enemy species richness associated with commercial crops by using data from manipulative field experiments (Snyder and Wise, 2001). In their experiments, Snyder and Wise (2001) compared crop yields in plots that were accessible to all enemy species (high enemy species richness and functional diversity) to plots manipulated to have either medium or low enemy species richness and functional diversity. Their data imply that naturally occurring enemy species associated with crop pests provide valuable ecosystem services, even just in the markets for two specialty crops. However, their results showed that the values are not a simple increasing function of the number of species of natural enemies, but rather depend on how the enemy species functioned in different assemblages of the crop-pest-enemy community. Their case study called into question a common practice in ecology and resource economics of measuring biodiversity in terms of numbers of species with little attention to how species may interact under different conditions.

Our approach estimates the values, positive or negative, of non-marginal changes in diversity of natural enemies, filling a gap between generalized attempts to quantify the total

value of natural pest control nationwide (Losey and Vaughan, 2006) and structural bioeconomic models of crop-production decision making and outcomes used in small scale studies of the value of natural biocontrol (Zhang and Swinton, 2012), optimal spatial configuration of habitat for natural enemies in agricultural landscapes (Zhang et al., 2010), and how landscape-level crop mix affects natural enemy habitat and thereby pest control costs in cellulosic biomass production (Skevas et al., 2014). The latter approach makes fewer simplifying assumptions and accounts for optimal changes in farmer behavior in response to hypothetical changes in the environment; however, it has significant data demands and is a large modeling project in its own right. Many researchers in ecology and entomology do not have easy access to economists with whom they can collaborate, have limited data, and would like to be able to at least generate approximate ecosystem service values from the limited data that are at hand. The approach presented here is useful for generating approximate economic value estimates that avoid some huge pitfalls, and can identify whether or not to pursue further efforts to generate the data needed for a more complex analysis.

First, we demonstrate a simple methodology grounded in economic theory for estimating changes in social well-being as a result of biodiversity changes associated with biological control of pests in agricultural environments. Second, we show how our methods avoid some common errors and produce more realistic estimates of economic outcomes than one of the approaches currently used in some ecological papers. Third, we challenge ecologists to include parameters in their research that link biodiversity with production outcomes and management costs to improve and expand the economic valuation of biodiversity and ecosystem services.

2. Overview of valuation methodology

A change in the diversity of natural enemies to agricultural pests could have multiple effects. It could alter the cost of producing a given amount of crop, and thus change the economic surplus in the market. It could also have effects on things like human health, populations of other animal species, and water quality by reducing the amount of pesticide that is used in farming. This paper focuses on measuring the value of the first of these changes.

To demonstrate the economic surplus approach to valuation of discrete shifts in the costs of crop production, we use a stylized graphical demonstration in a single market (Fig. 1). The vertical axis represents marginal cost and price for supply, and marginal willingness to pay and price for demand. The horizontal axis represents quantity of the crop produced and sold in the market to be studied. The marginal cost (MC) curve for the industry describes the cost of producing one more unit of output given that farmers are choosing production methods to minimize the total costs of production. MC tends to be upward sloping because as aggregate industry output increases the crop is being grown on lands that are increasingly less well suited for this kind of crop so input costs may be higher and yields may be lower in that range of production. In a competitive market, the industry supply curve is given by the industry's aggregate MC curve. If the industry supply curve is very steep we say it is inelastic, and production will not respond much to changes in price. Demand curves (showing the quantity of a good purchased for a given price) tend to be downward sloping, as the incremental benefit consumers receive from purchasing more of any one product tends to be declining. However, if the market one is studying is a regional subset of a national or international market, the demand curve is likely to be very flat; if, for example, the price of broccoli in California starts to go up, wholesale buyers can in part turn to suppliers in other states and other countries.

Profit maximization leads the competitive industry to produce at a total level of output Q_0 such that aggregate MC equals the market price P_0 of the crop. The market price settles where the quantities demanded and supplied at that price are the same. Consumer surplus is the difference between the value of the crop (captured by the demand curve) and the price of the crop over the units consumed; this is area A+B+E+F under baseline conditions. Producer surplus is the difference between the crop price and the marginal production cost over all units produced; this is area C+D+G under baseline conditions. Consumer and producer surpluses are the net benefits that flow to market participants as a result of the market existing.

Research by ecologists, entomologists, and agronomists can be used to quantify the extent to which a particular discrete (and possibly non-marginal) change in the species richness of natural enemies can affect these net benefits to society. For example, suppose that decreasing natural enemy richness from current levels to a hypothetical lower level shifts the MC curve upward on the cost axis; the incremental cost of each unit of production is higher because of some combination of the facts that yields may be lower and biological pest control services provided by natural enemies must be replaced by costly human pest-management activities.

Such a shift is modeled as follows. Note that equations 1 through 6 come from Alston et al. (1995). This method is used widely to estimate the welfare changes associated with supply shifts in agricultural markets with only simple aggregate data on those markets. By using this method, we are implicitly assuming that the agricultural products are homogeneous, their markets are competitive, and the cost changes for which we have data are applicable across the whole region of production for the market. The crops in our case study have been modeled as homogeneous competitive commodities before (Malaga et al., 2001), and we limit our study to a

small geographic area (Georgia and North Carolina), so these assumptions may not be too problematic.

If supply is linear as shown in Figure 1, then

$$Q = a + b(P + k). \quad (1)$$

The parameters a and b are constants, the status quo baseline conditions apply when $k = 0$, and if a decrease in biodiversity increases costs we have a shock to the U.S. supply curve equal to k (where k is a negative number). Such a shock is visualized in the inset graph of Figure 1. The insert shows how a yield shift $k < 0$ causes the industry supply curve to shift up. Starting with the industry producing Q_0 at a price of P_0 (the behavior dictated by S_0), the vertical shift $k < 0$ means that now the industry only produces an amount at price P_0 that it would previously have produced (with supply curve S_0) at price $P_0 + k$, which is quantity Q' . So under the new supply curve S_1 , the industry will produce Q' in response to P_0 . Thus, the proportionate supply shock is defined as $K \equiv k/P_0$, and Z is the reflection (multiplied by -1) of the relative change in price from the status quo price P_0 to a new hypothetical higher P_1

$$Z \equiv -(P_1 - P_0)/P_0. \quad (2)$$

A supply shift will cause market output to fall and market price to rise. Consumer surplus falls from area $A+B+E+F$ to A and producer surplus changes from area $C+D+G$ to $B+C$, so the total economic loss associated with decreasing natural enemy richness from its baseline level is

area D+E+F+G. Triangle F+G is lost from reduced production, and area D+E is lost social welfare associated with the increased cost of producing what was originally consumed.

Methods exist to find the areas that represent changes in surpluses using data on the baseline existing levels of crop production and price, the price elasticities of supply and demand (the percentage changes of quantity supplied and demanded in response to a percentage change in price), and the vertical shift in the MC curve associated with the change being modeled. A key part of estimating the changes in welfare or standard of living caused by changes in price (welfare effects) of a discrete change in natural enemy species richness as a mediator of biological pest control is estimating how that change in richness shifts the market supply curve. In other words, we need to estimate values for a supply shock parameter K . Changes in natural enemy richness or functional diversity can affect production costs in two ways: per-acre input costs may change if farmers alter input use in response to changes in the effectiveness of natural pest control, and yield may change, which affects marginal costs per unit by altering the output produced for a given amount of input costs.

The impact of a change in biological control effectiveness may depend heavily on the behavior of the producer. We used a generalized typology for the model, such that supply effects of categorical changes in natural enemy richness may vary among three stylized categories of farming practice: 'no-spray', integrated pest management (IPM), and prophylactic sprays. By no-spray, we refer to agricultural practices that are compatible with and rely on natural enemies for pest control rather than insecticides; thus, pests generate yield reductions in these operations that are moderated by natural enemies, and the effectiveness of that moderation can be altered by changes in the natural enemy community. At the other extreme, farmers who use prophylactic measures are those whose farming practices strongly disrupt natural enemies (especially

scheduled broad-spectrum insecticides), prevent the build-up of pests (highly resistant varieties, physical barriers to colonization), or disconnect yield loss from pest pressure (tolerant varieties). Their costs and yields are unchanged by changes in natural enemy species richness; thus, shifts in natural enemy species richness will not affect the supply functions of these farmers at all. Third, farmers who use IPM techniques theoretically avoid all yield reductions associated with insect pests by using a mixture of approaches, including insecticides when needed, so IPM supply will not be affected by yield changes from changes in natural enemy species richness; however, changes in the community of natural enemies may affect the frequency and timing of insecticide application or other interventions, and thus the marginal costs of IPM production associated with pest control measures. Organic farms, which use only approved pest control measures and tend to limit insecticide applications, can fall into any of the three categories (no-spray, IPM or prophylactic measures).

On no-spray fields the shock in the community of natural enemies results in a change in output yield per acre (Y). A calculation is needed to translate that change into a shift in the market supply curve. Assuming fixed input factor proportions, a decrease in yield shifts industry quantity supplied by dY/Y_0 ; that change is converted to a percentage shift in the supply curve in terms of price by dividing by the price elasticity of supply, so $K = (dY/Y_0)/\epsilon$ (Alston et al., 1995, p. 339). On IPM fields, spraying costs per acre (C) could hypothetically be higher with lower enemy richness than in the status quo; this can be translated into a change in the marginal cost of production by dividing the change in costs per acre by yield (assuming constant returns to scale on a given field, and upward sloping industry supply deriving from heterogeneity across fields). Thus, the supply shift, K , for the industry as a whole is calculated as a weighted average of the values of K that apply to different categories of industry supply (recall that fields with

prophylactic spray have supply functions that are unaffected by naturally occurring natural enemies). If $\sigma_{nospray}$ and σ_{IPM} are the fractions of fields that use no-spray and IPM methods, respectively, then

$$K = \sigma_{nospray}((dY/Y_0)/\varepsilon) + \sigma_{IPM}((C_0 - C_1)/Y_0 P_0). \quad (3)$$

where the price elasticity of supply is given by ε and we assume input factor proportions are fixed. This formulation allows welfare calculations carried out within the confines of a simple analysis of a single market for a crop to account for the fact that a change (here, in natural enemies) may have very different effects on costs and supply on fields managed with different protocols regarding pesticides. Note that even in cases where a change in ecological function does not alter input and labor costs per acre (this turns out to be the case in our case study), a decrease in yield will still increase the aggregate industry marginal cost of producing any given level of output, and so the supply curve shifts up.

Minus the percentage change in the price farmers receive that is induced by the supply shock, Z , is equal to

$$Z = K\varepsilon/(\varepsilon + \eta) \quad (4)$$

where ε is the supply elasticity and η is the absolute value of the demand elasticity. We can also derive expressions for the changes in consumer surplus and producer surplus:

$$\Delta CS = ZQ_0P_0[1 + .5Z\eta] \quad (5)$$

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$$\Delta PS = Q_0 P_0 (K - Z) [1 + .5Z\eta]. \quad (6)$$

231 This is referred to as the “economic surplus” approach (Alston et al., 1995).

232 This method is not a complex bioeconomic model such as those found in Zhang and
 233 Swinton (2012), Zhang et al. (2010), and Skevas et al. (2014). It may tend to underestimate the
 234 value of changes that improve biocontrol because it does not fully account for the changes
 235 farmers can make in production methods as they re-optimize their choices in response to changes
 236 in the effectiveness of natural enemies. However, this approach does avoid several
 237 oversimplifications that are commonly found in estimates of the values of changes in ecosystem
 238 services (while still requiring few data and nothing more than a spreadsheet to carry out). In one
 239 example of a common simplified method, Losey and Vaughan (2006) estimated the value of
 240 averted crop loss from native pests due to native biocontrol. They started with previous estimates
 241 of money lost due to pests and used a set of factors (the fraction of pests that are native, the
 242 percentage by which natural biocontrol lowers crop loss relative to a world with no natural
 243 biocontrol, and the fraction of natural biocontrol attributable to native natural enemies) to
 244 estimate the value of biocontrol by native natural enemies. Their calculation is a complex variant
 245 of holding the price of a crop constant, estimating a fraction of output reduction association by a
 246 reduction in yield, and multiplying price by that change in output. Gallai et al. (2008) described a
 247 similar approach in many papers in the literature that estimate the lost values associated with
 248 declines in pollinators. They calculated the total value of crops pollinated by insects, sometimes
 249 with an adjustment in the form of a “dependence ratio.” We will refer to such estimation
 250 methods as the “fixed-price changed-value” approach.

Papers that use the fixed-price changed-value approach to estimate the value of something less than total loss of a commodity are measuring an area such as the rectangle in panel a of Figure 2. In the calculations we do to mimic the results of this approach, we calculate the size of the grey rectangle as:

$$Area = P_0(Q_A - Q_0) \quad (7)$$

where

$$Q_A = (1 - \sigma_{nospray})Q_0 + \sigma_{nospray}Q_0(Y_1/Y_0). \quad (8)$$

The economically correct measure of lost surplus is the striped area in the same figure. Several problems with the fixed-price changed-value approach are clear. First, by ignoring the fact that a supply shock would cause price to increase from P_0 to P_1 , it overestimates the loss of output (down to Q_A) that will result: higher price will actually stimulate growers to increase planting and compensate in part for yield reductions (output will only fall to Q_I). Second, by counting the entire rectangle as lost to society, this approach neglects the fact that the solid grey area below the original supply curve was never part of social surplus – that area was the cost to society of producing those units of crop – and so its loss is not a bad thing. Third, the simplest version of this method does not include the loss to society in the form of the increased cost of producing the units that are still produced (the striped parallelogram to the left of the rectangle.) Thus, the fixed-price changed-value approach may either over- or under-estimate the correctly-defined change in consumer surplus depending on the shapes of the supply and demand curves.

A second common simplified approach is reviewed by Wenny et al. (2011). The “changed-cost” approach estimates the benefit of increased ecosystem services as the decreased

cost needed to produce the same level of output that was present in the market before the change (or estimates the losses caused by decreased ecosystem services as the increased cost needed to produce the same level of output). The well-known “replacement cost” approach (e.g., Hougner et al., 2006) is a special case of this method, in which analysts estimate the cost of having human activity actually replacing a service (like hand planting instead of seed dispersal or pollination by hand) if it is not carried out by nature. Panel b of Figure 2 shows what is estimated for the case of a decrease in ecosystem services that increases marginal costs of production. This changed-cost approach always overestimates the magnitude of the value of the deleterious change because it fails to account for the fact that the price of output would increase in response to the increase in production costs and thus output demanded would fall after the shock, so society would not have to bear the increased production costs on quite as many units of output. The magnitude of the overestimation, however, will depend on details of the situation. We do not demonstrate this approach with our case study because the changes in ecosystem services were expressed in modified production (yield), not modified cost per acre.

3. Case study methods and data: cucumbers and squash

The U.S. produced 359 million (M) kg of fresh market cucumbers (not for pickling) valued at \$248M and 284M kg of summer squash (yellow crookneck squash and zucchini) for fresh market in 2013, valued at \$237M (USDA, 2014b). Within the U.S, about a dozen states dominate commercial production of each of these crops (see Table 1). The pest-natural enemy complex associated with cucurbit crops is relatively ubiquitous, with the same or related species interacting in squash and cucumber fields from Canada to Mexico. One can estimate the value of a hypothetical change in the number of species or functional diversity of the natural enemy

community at many different spatial scales, from change in a single field to hypothetical change in all U.S. fields producing crops sold in an international market. Growing conditions vary widely across the U.S., and the prices farmers receive for vegetable crops are somewhat heterogeneous as a result of factors such as differences in transportation costs (Volpe et al., 2013). Thus, a tight regional analysis has the benefit of requiring fewer implicit assumptions about homogeneity of product, growing conditions, pest dynamics, and market conditions across the study area.

We used crop yields and pest abundances on cucumber and squash reported by Snyder and Wise (2001) in partial natural enemy exclusion experiments conducted in Kentucky in 1997 and 1998. For the purposes of our hypothetical calculations, we applied the results of their experiments to established markets in the states of Georgia and South Carolina, thus implicitly assuming that crop yield effects of the changes in natural enemy communities induced by Snyder and Wise (2001) in Kentucky would represent the percentage changes in yields in those two nearby states. We chose those two states as our region of study because of their close proximity to and larger markets than KY, and the prices of cucumbers and squash in Georgia and South Carolina are fairly similar to each other relative to prices in other states (Figure 3). Together those states produce about 25% and 10% of total U.S. production of cucumbers and squash, respectively.

Snyder and Wise (2001) measured yields of cucumber (*Cucumis sativis*, variety “Spacemaster”) and squash (*Cucumis pepo*, variety “Yellow Crookneck”) grown sequentially for two seasons, and sampled squash bugs (*Anasa tristis* (DeGeer) Hemiptera: Coreidae), striped cucumber beetles (*Acalymma vittatum* (F.) Coleoptera: Chrysomelidae), and arthropod natural enemy abundances associated with those common cucurbit crop pests. No fertilizers, pesticides

or irrigation were applied to experimental plots. To calculate the change in yields due to losses of natural enemy species and their functional diversity, we compared their crop production data from treatments with all naturally occurring enemy species (high species richness, full functional diversity), medium, and low levels of natural enemy richness. In their study, all treatments allowed plants and herbivores on plants to be accessible to all species of flying natural enemies, including insect parasitoids and predators, and spiders that ‘balloon’ in the air on webs carried by wind.¹ Their low enemy richness treatment was restricted to these aerial colonizers, and unavailable to all ground dwelling predators (approximately 13 species were excluded) because their colonization was blocked mechanically from plots. Their medium enemy richness treatment allowed access by all these aerial predators and parasitoids, plus up to 10 species of carabid beetles (+B) or up to three species of lycosid wolf spiders (+S) as ground predators. The high enemy richness treatment added both beetles and spiders (+B,+S), thus allowing all naturally occurring predators and parasitoids to access these plots (Snyder and Wise, 1999; Wise et al., 1999). We designated these treatments as high, medium and low species richness based on the number of predatory functional/taxonomic groups excluded; the actual number of enemy species occurring in each plot is unknown, but such whole plot manipulations are compatible with ordinal designations. We used mean outcomes for the two years of their experiments, which served to parsimoniously relate the range of outcomes found by Snyder and Wise (2001), including the complementary, neutral and negative effects of an increase in natural enemy biodiversity found in their study.

¹ All treatments allowed predators and parasitoids that feed on cucumber beetles, such as nabid bugs and parasitoids (Diptera: Tachinidae and Hymenoptera: Braconidae), and on squash bug eggs (Hymenoptera: Encyrtidae and Scelionidae), nymphs and adults (Diptera: Tachinidae) such as *Trichopoda pennipes* and ballooning foliage-dwelling predators such as many families of spiders: Araneidae, Lyniphiidae, Tetragnathidae, Araneidae, Thomisidae, and Salticidae to access the plants and potentially cause pest mortality.

340 Decreasing the species richness of natural enemies from high to medium in cucumber
 341 plots caused average yields to fall by 16% or 29% (Table 2). In this case, the exclusion of up to
 342 10 predaceous beetle species caused a steeper decline in average yield than did the exclusion of
 343 up to three wolf spider species. Average cucumber yields declined to 40% when natural enemy
 344 species richness fell from high to low levels, as functional diversity (two ground-dwelling
 345 predator taxa) was lost and potential species richness declined in the natural enemy community.
 346 Squash yield loss with the experimental removal of ground beetles was 58% on average, yet
 347 when wolf spiders were excluded in the late season crop, Snyder and Wise (2001) reasoned that
 348 intraguild predation on natural enemies, presumably nabid bugs, had been relieved, causing
 349 average yields to increase dramatically by 66% (Table 2). Consequently, the effect of lowering
 350 natural enemy species richness depended on some combination of the composition or behavior of
 351 the enemy community and their functional interactions with the kinds and abundance of prey
 352 available at the time. Excluding both wolf spiders and ground beetles caused a small decline
 353 (10%) in average squash yield as enemy richness declined from high to low levels, on average
 354 (Table 2). Thus, in four of the six cases in which Snyder and Wise (2001) excluded enemy
 355 species and reduced functional diversity, a weakening of complementary biological control
 356 resulted in lower yields. In one case, exclusion of enemy species caused little change in crop
 357 yield because biological control gains were compromised by antagonistic interactions, and in one
 358 of six cases it caused a reduction in antagonistic interactions among natural enemies, and
 359 increased yield. Relative crop yields in Table 2 provided most of the input necessary to calculate
 360 the supply shocks K using equation 3 for three simulated scenarios: changing diversity from high
 361 (that is the baseline scenario that corresponds to the real conditions underpinning observed

market equilibria) to medium including spiders (+S), from high to medium including beetles (+B), and from high to low.

The U.S. government does not track the exact acreage of crop production using no-spray approaches, but reports (USDA, 2012, 2014a) on organic acreage for fresh vegetables and insecticide usage data make it reasonable to assume that 10% of the acreage contributing to the overall national production of both crops is no-spray. We did not allow the fraction of fields that uses no-spray practices, σ_{nospray} , to change with the biodiversity of the natural enemies that would be present naturally when insecticides are eliminated. This simplifying assumption was necessary because we had insufficient information to estimate how readily farmers would change growing practices with changes in the effectiveness of biological control of pests. This simplification means that our model will tend to overestimate the economic cost of having less effective biological control (and overestimate the economic benefit of having more effective control) because the model does not allow farmers to adapt to such changes by altering the fraction of production carried out on no-spray fields. In our current case study of cucumber and squash, we treated IPM as equivalent to prophylactic spray because IPM manuals developed for squash bug and cucumber beetle in the region recommend control through insecticide application when plants first emerge from the soil in order to prevent disease transmission (<http://www.uky.edu/Ag/IPM/ipmveg/cucurbitinsect/cucurbitinsects.htm>). Thus, while experimental evidence indicated that changes in the community would affect pest populations on unsprayed fields of cucumber and squash, such changes would have no economic effect on fields managed with IPM or prophylactic spraying. An analysis that assumed the yield effects found in experimental fields would apply to all production of the crop in question would grossly overestimate the importance of the composition of the community of natural enemies.

With the supply shock parameters K in hand, we calculated the welfare change associated with a supply shift in the markets of squash and cucumbers in the combined area of Georgia and South Carolina using the economic surplus method described in Section 2. The economic parameters employed in equations (3), (4), (5) and (6) for our three scenarios of natural enemy richness change are given in Table 3. State-level data on acres harvested, quantity produced, and total revenue received by farmers were reported by the U.S. Department of Agriculture (2014c) for summer squash and non-pickling cucumbers. From those numbers we calculated average yield (cwt/acre), total production (cwt), and average price (\$/cwt) in the combined states of Georgia and South Carolina. For a given set of structural parameters, we calculated welfare change estimates for the price, quantity, and yield in each year from 2008 to 2014 and then calculated the mean and standard deviation of those annual estimates.

The price elasticity of demand would not have a large effect on the sum of consumer and producer surplus (Alston et al., 1995, p. 59). However, the price elasticity of supply may affect total welfare change estimates, and no studies (to our knowledge) have been done to quantify market price elasticities in the specific region of our case study. Thus, we ran the analysis for several different assumptions regarding the price elasticity of supply to explore the sensitivity of results to that parameter (see Table 4). Malaga et al. (2001) estimated supply and demand elasticities for squash and cucumbers in the U.S. as a whole, but supply elasticity for this small regional subset of the full market may be either higher or lower than the Malaga et al. (2001) estimate. Ornelas and Shumway (1993) estimated supply elasticities for Texas production of vegetable crops ranging from .003 for potatoes to .597 for watermelon; we used different values of the supply elasticity parameter within that range.

In summary, our analyses calculated welfare changes relative to a baseline scenario of high natural enemy species richness in which no species are excluded from the fields and show estimated welfare changes for three types of changes in natural enemy richness for both squash and cucumber pests: (1) changing from high enemy richness to medium with beetles present but not spiders; (2) changing from high richness to medium with spiders present but not beetles; and (3) changing from high to low enemy species richness. We present results using the economic surplus approach described in equations 1 through 6 using baseline national estimates of supply and demand elasticity parameters. We compared the baseline results to results obtained using the fixed-price changed-value approach and with the economic surplus approach using several different supply elasticity assumptions.

4. Results

Using our model for three types of reductions in natural enemy richness compared to high baseline levels produced in field manipulations by Snyder and Wise (2001), changes in economic welfare reflected the changes in crop yields they reported; however, the economic surplus method produced much larger surplus changes than those estimated with a fixed-price changed-value approach used in some standard estimates made by ecologists. Also, in this case study the welfare effects are larger for producers than for consumers and the magnitude of the results is highly sensitive to assumptions about how sensitive quantities supplied are to changes in the market price.

Figure 4 displays the results of analyses that used the economic surplus method developed in equations 1 through 6 for just one of those hypothetical changes – reduction to low richness – and explores how the price elasticity of supply affect the results. Changes in the price

elasticity of supply have large effects on the impact of this kind of supply shock on social welfare. That pattern is driven by the fact that a given yield change translates into a percentage vertical supply shift that decreases in magnitude with the price elasticity of supply (see the first element of equation 3). The actual size of the market supply shock caused by a change in yield depends on how responsive market supply is to price.

We used the parameters of the “national estimate” scenario to produce the results listed in the first four rows of Table 5 and to evaluate how the magnitude and direction of an impact from a change in natural enemies varied with the nature of that change. In the bottom row, that table lists value estimates created with the common fixed-price changed-value method so we can evaluate how close that estimate is to the estimate derived from economic theory.

The results of the economic surplus calculations indicate that the welfare effects of changes in diversity were felt disproportionately by producers. In this market, the price changes resulting from changes in growing conditions were small; consumers lost only to the extent that the price was slightly higher (and thus consumption decreases), while producer surplus fell as a result of higher production costs over all that they produce. Indeed, about 80% of the changes in surplus accrued to producers in these scenarios.

Focusing first on the top four rows of Table 5, we see that these estimated hypothetical welfare changes naturally mirrored the changes in average crop yield associated with changes in natural enemy species richness, as discovered by Snyder and Wise (2001) and reported as average values in Table 2. As explained in the development of equation (3), a decrease in yield caused the MC to be higher for a given amount of output because less output is produced for a given expenditure on inputs. The calculations indicate that agricultural practices that cause the loss of natural enemy species richness and impede biological control of cucumber beetles reduce

the total surplus for cucumber by \$6.7 to \$12 million if natural enemy richness falls from high to medium levels, and by \$16 million if the decrease is instead all the way to a low level of enemy species richness. The decrease from high to low richness consisted of the loss of more than ten enemy species representing two functional groups of ground predators, beetles and spiders. The loss of either beetles or spiders (from high to medium richness) reduced welfare because of yield loss in both medium scenarios, but the loss of spiders reduced welfare less than the loss of beetles.

The loss of enemy species richness mattered for squash as well, but the welfare effects in the market for squash depended critically on which functional enemy group was removed from the fields, and how the remaining species interacted with other enemies in the community. Consumer and producer surplus could either decrease by \$8.8 million per year or increase by \$10 million dollars per year when enemy species richness fell from high to medium; losing spiders actually increased yields, while losing beetles resulted in yield loss. If natural enemy richness fell all the way to low levels in squash fields, total surplus fell by \$1.5 million a year relative to the baseline that prevailed with high enemy richness. That outcome was not good, but would not have been as detrimental as the situation that would have prevailed if diversity were to have fallen from the full complement of species to having aerial predators and spiders without beetles.

The scenarios with welfare losses naturally have price increases and the scenarios with welfare gains have price decreases. Prices changed very little in response to these changes in natural enemy richness. Cucumber prices rose by 2%, 3.7% or 5% depending on whether species richness fell from high to medium or low. If natural enemy richness in GA and SC squash fields fell to medium, then the squash price fell or increased by 11 to 12% depending on which group

of species was lost, while that price increased by only 2% if high enemy richness fell all the way to low enemy richness.

We turn now to the bottom row of Table 5 to compare the values one would obtain from a common shortcut used by ecologists to the results of economic surplus model calculations just discussed. For this particular valuation problem, the fixed-price changed-value approach yielded estimates that are only 12-15% of the economic surplus estimates. It must be that most of the welfare loss in this case comes from the increased cost to the industry of producing the output that is still grown and sold after the yield shock, rather than the lost value associated with reduced output.

4 Discussion and Conclusions

We recognize that putting an absolute dollar value on a unit of biodiversity for biological control is hampered by biological uncertainty, and that logistical and scale limits in ecological studies may be unsurmountable in terms of making robust economic estimates. Extrapolations from small-scale ecological experiments, however, are useful for methodological comparisons and for demonstrating directional changes using field-level manipulations, as well as for demonstrating how ecologists can improve the reliability of estimates of monetary values in future. Given those caveats, and using the best ecological data currently available, we estimated that unfavorable losses in natural enemy species richness in squash and cucumber fields in Georgia and South Carolina alone could cost society between \$1.5 and \$12 million in social surplus every year, and these states produced only 10 – 25% of two crops that themselves comprise only about 4% of the value of fresh vegetable production in the U.S. (USDA 2014b). These estimates were also based on a small percentage of production operations that might

derive pest control from natural enemies rather than insecticides. At the same time, natural enemy conservation occasionally impedes effective biological control when natural enemies interfere with each other, resulting in a large cost to society. The economic effects of changes in the richness/composition of natural enemy communities were clearly important in this case; to determine if these pest-enemy-yield interactions are representative regionally or nationally, further research to estimate the values of large scale changes in natural enemy diversity with models that allow for spatial and temporal variation in the ecosystem service potential of natural enemies, their interactions with pests, the effect of those interactions on pest control cost savings, and for complex changes in farmer behavior would be worthwhile.

Promoters of biodiversity conservation in agroecosystems assume an overall (average) positive outcome of an increase in species diversity for ecosystem services, the environment and societal well-being, which is consistent with the field experiments reported by Snyder and Wise (2001) and analyzed here. Policy directed toward a reduction of insecticide applications to protect and conserve natural enemies of crop pests in combination with habitat management schemes in crop fields and surrounding landscape can restore or enhance enemy species richness (Landis et al., 2000). Pimentel and Peshin (2014) argued that as much as a 50% reduction in the amount of insecticides applied to U.S. crops is not an unrealistic goal, given that insecticide use has been curtailed by over 60% in Sweden and Indonesia. Decision-making by agricultural producers and policy-makers should take into account the social and environmental losses that could result if production changes facilitated (or at least permitted) by policy were to further injure natural enemy richness and biological control services in a broad range of fields.

Estimates of the economic gain derived from a richer community of beneficial species associated with agricultural production are needed to guide policy on insecticide reduction

targets and for re-designing agroecosystems to enhance ecosystem services for crop production
 in the U.S., yet most ecological studies on biodiversity-driven benefits of biological pest control
 lack data on crop yield (Cardinale et al., 2012; Chaplin-Kramer et al., 2011), economic pest
 thresholds and insecticide costs (Letourneau and Bothwell, 2008), and therefore, the potential to
 estimate societal well-being in economic terms. We developed an approach to assess economic
 outcomes resulting from changes in natural enemy richness, and demonstrated its use with one of
 the few studies reporting changes in yield resulting from experimental changes in enemy species
 richness and functional diversity -- exclusion of ground-dwelling beetle and spider natural
 enemies associated with vegetable crops (Snyder and Wise, 2001). This case study reflects and
 reinforces the distribution of outcomes predicted by theory (e.g., Dyer and Stireman, 2003) and
 shown in synthetic reviews (Cardinale, 2006). That is, far reaching benefits of natural enemy
 diversity prevail as they strengthen ecosystem services, yet exceptions occur in which increased
 enemy species richness in the assemblage can cause costly decreases in the effectiveness of
 biological control.

Specifically, 70% of more than 250 comparisons in a meta-analysis by Letourneau et al.
 (2009) tended towards stronger suppression of herbivores with greater enemy species richness.
 Griffin et al. (2013) found that 52% of 46 experiments showed stronger herbivore suppression
 with greater diversity, 43% showed no effect, and 5% showed negative effects on suppression
 relative to the average predator's impact. The majority of yield outcomes for greater enemy
 species richness in the comparisons of squash and cucumber reported here were also favorable
 (67% of six scenarios). A favorable change in pest suppression in 67% of the cases is almost as
 large as the 77% of comparisons showing a decrease in herbivores when Halaj & Wise (2001)
 analyzed the effect of removing predators from the system *entirely*. In some cases, however, an

increase in species richness will increase the chances of antagonistic effects such as intraguild predation, decreasing the effectiveness of pest control. Indeed, beyond interactions within the predator community themselves, the same species of natural enemy can function differently in habitats that differ in herbivore pest species richness and vegetational diversity, complicating simple economic and ecological predictions of the effect of enemy richness in agricultural fields (Letourneau et al., 2009), as was illustrated in the case study by Snyder and Wise (2001) that we analyzed.

On another dimension, the reliance of biological control on species richness or functional diversity in the natural enemy community is more relevant to some production systems than others. Biological control of the soybean aphid worth an estimated \$239 million annually (Landis et al., 2008), occurs primarily through predation by a single introduced species of lady beetle. However, other pests are consumed by many predators; for example, the glassy-winged sharpshooter pest is consumed by 15 families of spiders and predatory insects in California vineyards (Fournier et al., 2008), and at least 86 natural enemy species were associated with onion fly pests (Tomlin et al., 1985). The crop pests used in our example are consumed by multiple species in a moderately complex community. The values of changes in natural enemy diversity will clearly be very case specific.

We present this economic model as a first step in measuring the potential economic value to society of benefits that agroecologists attribute to ecosystem services through biodiversity conservation. The economic surplus method we used is easily applied, but yields more accurate estimates of the values of changes in natural enemy diversity than simple methods used commonly by non-economists. The fixed-price changed-value approach produced very large underestimates of the values in our case study -- typically only about 13% as large. Further steps

to link ecological studies with economic estimation require, first, that ecologists quantify parameters such as marketable yields, management costs for pest control, and discrete losses from different pests. Of 48 research articles on enemy species richness and herbivore suppression representing all of the crop-related studies used in meta-analyses by Letourneau et al. 2009 and Cardinale et al. 2012, we found only four that measured marketable crop yields and only two that determined whether pest insect numbers or plant injury had reached economic threshold levels. Second, we need ecological studies that are conducted across production zones of economic importance using realistic production practices, and multi-year studies with results that can be demonstrated to be robust over time. Third, multi-tiered, large- and small-scale field studies can be used to both parameterize economic models (crop yield, densities of pests compared to economic threshold densities, etc.) and allow for the randomized and factorial manipulations of natural enemy richness and composition necessary for understanding the underlying biodiversity effects on pest suppression and simulating pest control outcomes. Mechanistic studies can inform changes in management practices to achieve the “right” kind of diversity for effective biological control. Griffin et al. (2013) found that when pest suppression was compared to the impact of the single best predator on its own, only 13% of high diversity communities provided better pest suppression than the best predator alone. Whether these mechanisms reflect interactions in the field is an important consideration. Future experimental research in ecology will be better able to inform studies on the value of biodiversity in agricultural settings if they compare realistic alternative scenarios of species richness and measure economically meaningful data associated with changes in biodiversity (e.g., yield, production costs) in a field setting that comes close to the conditions that prevail on actual farms.

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712

713 **Table 1:** Average Cucumber and Squash Production and Prices by State^{a, b}

	Cucumbers	Cucumbers	Squash	Squash
	Quantity	Price (\$/cwt)	Quantity	Price (\$/cwt)
	Produced		Produced	
	(100,000 cwt)		(100,000 cwt)	
California	7.0	29	12	31
Florida	26	25	9.5	54
Georgia	17	26	5.5	31
Maryland	.19	36		
Michigan	8.0	21	14	12
New Jersey	5.8	25	3.6	35
New York	3.7	39	8.2	45
Ohio			3.2	32
Oregon			4.1	15
North Carolina	8.1	19	3.1	40
South Carolina	2.8	23	1.4	34
Tennessee			.50	29
Texas	1.9	24	1.8	49
Virginia	30	26		
United States	80	25	67	32

714 ^a Source is (USDA-NASS, 2014) .

715 ^b Numbers are averages over all years 2008 – 2014.

716

717 **Table 2.** Effect of Natural Enemy Species Richness on Average Crop Yields^a

Crop	Natural Enemy Species Richness	1997 Yield (kg/plot)	1998 Yield (kg/plot)	Average. Yield (kg/plot)	% Change in Average Yield from High Scenario
Cucumber	Low ^b	24.7	12.9	18.8	-40%
	Medium (+B) ^c	24.3	20.2	22.3	-29%
	Medium (+S) ^c	29.3	23.1	26.2	-16%
	High (+B,+S) ^d	36.7	25.8	31.3	-
Squash	Low ^b	6.2	6.5	6.3	-10%
	Medium (+B) ^c	9.0	14.1	11.6	+66%
	Medium (+S) ^c	1.0	4.9	2.9	-58%
	High (+B,+S) ^d	7.6	6.4	7.0	-

718 ^a Source: Snyder and Wise (2001).

719 ^b Low enemy richness excluded all ground predators.

720 ^c Medium enemy richness added either predacious carabid beetles (+B) or lycosid spiders (+S)
 721 relative to the low treatment.

722 ^d High richness treatments added both taxa (so all naturally occurring predators are present).

723 **Table 3.** Economic Data for Regional (Georgia and South Carolina) Estimates^a

Year	Cucumbers			Squash		
	Production	Yield	Price	Production	Yield	Price
	(1M cwt)	(100 cwt/acre)	(\$/cwt)	(1M cwt)	(100 cwt/acre)	(\$/cwt)
2008	2.4	2.0	31	.63	1.0	30
2009	2.9	2.5	23	1.2	1.9	29
2010	2.4	2.4	24	.55	1.2	32
2011	1.4	1.7	28	.66	1.3	35
2012	1.7	2.4	22	.62	1.6	31
2013	1.7	2.1	29	.56	1.4	33
2014	1.3	1.5	24	.63	1.5	33

724

725 ^a Calculated from state numbers reported in the USDA database (USDA-NASS, 2014)

726

727 **Table 4.** Economic Parameter Scenarios for Regional (Georgia and South Carolina) Estimates

Crop	η : demand elasticity	ϵ – Supply elasticity	Scenario Name
	.41	.14	National estimate ^a
Squash	.41	.10	More inelastic supply ^b
	.41	.30	More elastic supply ^b
	.66	.12	National estimate ^a
Cucumber	.66	.10	More inelastic supply ^b
	.66	.30	More elastic supply ^b

728

729 ^a National estimates of price elasticities come from Malaga et al. (2001).

730 ^b Other price elasticity of supply values are hypothetical.

731

Table 5. Estimated Welfare Effects of Decreases in Natural Enemy Species Richness^a

	High to Medium w/Beetles		High to Medium w/Spiders		High to Low	
	Squash	Cucumbers	Squash	Cucumbers	Squash	Cucumbers
Estimates from economic surplus method ^b						
% change in price ^c	-12%	3.7%	11%	2.1%	1.8%	5.1%
	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)	(0.0)
Change of consumer surplus (\$1,000,000)	\$2.7 (0.67)	-\$1.9 (0.54)	-\$2.2 (0.56)	-\$1.0 (0.30)	-\$0.39 (0.010)	-\$2.5 (0.75)
Change of producer surplus (\$1,000,000)	\$7.8 (2.0)	-\$10 (3.0)	-\$6.6 (1.7)	-\$5.6 (1.6)	-\$1.2 (0.29)	-\$14 (4.1)
Change of total surplus (\$1,000,000)	\$10 (2.6)	-\$12 (3.5)	-\$8.8 (2.2)	-\$6.7 (2.0)	-\$1.5 (0.39)	-\$17 (4.8)
Estimated change in total value from fixed-price changed-value approach ^d (\$1,000,000)	\$1.4 (.36)	-\$1.5 (.43)	-\$1.3 (.31)	-\$0.81 (.24)	-\$0.22 (.05)	-\$2.0 (.59)

^a Welfare changes are annual gains or losses to producers and purchasers in Georgia and South Carolina in millions of dollars. Effects are calculated separately for each of seven years of price, quantity, and yield data from 2008 to 2014. The main numbers reported here are the means of those calculations and the numbers in parentheses are standard errors associated with the means.

^b These estimates use the “national estimate” set of parameters given in Table 4.

^c The percent change in price equals $-Z \times 100$.

^d Estimates of the change of total surplus in the bottom row use the fixed-price changed-value approach from equations (7) and (8).

Figure 1. Framework for Calculating Change in Welfare from Supply Shock^a

^a The marginal costs of production increase from scenario 0 to scenario 1 due to a shock of $k < 0$ (shown in the inset graph).

751 **Figure 2:** Common Incorrect Measures of Welfare Reduction from a Supply Shock

752 Panel a: Fixed-Price Changed-Value Approach to Estimating Lost Value of Marginal Change

753

754 Panel b: Changed-Cost Approach

755

756

Figure 3: Prices of Cucumbers and Squash in Study States^a

Panel (a): Price of cucumbers (\$/cwt)

Panel (a): Price of squash (\$/cwt)

^a Source is USDA (2014c).

Figure 4: Effect of Elasticity Assumptions on Estimates of Welfare Changes

Panel (a): Welfare Effects of Change to Low Richness in GA and SC Squash (\$1000)^a

Panel (b): Welfare Effects of Change to Low Richness in GA and SC Cucumbers (\$1000)

^a These results use the economic surplus method for estimating welfare changed. The parameter assumptions in each of the scenarios are listed in Table 4. Each number displayed is the average of the welfare changes calculated for each year 2008 – 2014.