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The Economic Value of Ecological Services Provided by Insects

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Abstract

In this article we focus on the vital ecological services provided by insects. We restrict our focus to services provided by "wild" insects; we do not include services from domesticated or mass-reared insect species. The four insect services for which we provide value estimates—dung burial, pest control, pollination, and wildlife nutrition—were chosen not because of their importance but because of the availability of data and an algorithm for their estimation. We base our estimations of the value of each service on projections of losses that would accrue if insects were not functioning at their current level. We estimate the annual value of these ecological services provided in the United States to be at least $57 billion, an amount that justifies greater investment in the conservation of these services.

Keywords: ecological services, economic value, conservation, biodiversity, environmental policy

Natural systems provide ecological services on which humans depend (Daily 1997). Countless organisms are involved in these complex interactions that put food on our tables and remove our waste. Although human life could not persist without these services, it is difficult to assign them even an approximate economic value, which can lead to their conservation being assigned a lower priority for funding or action than other needs for which values (economic or otherwise) are more readily calculated. Estimating even a minimum value for a subset of the services that functioning ecosystems provide may help establish a higher priority for their conservation.

In this article we focus on the vital ecological services provided by insects. Several authors have reviewed the economic value of ecological services in general (Daily 1997, Pimentel et al. 1997), but none of these reviews focused specifically on insects. Insects comprise the most diverse and successful group of multicellular organisms on the planet, and they contribute significantly to vital ecological functions such as pollination, pest control, decomposition, and maintenance of wildlife species (for a discussion of the biodiversity of microbes, see Nee 2004). Our twofold goal is to provide well-documented, conservative estimates for the value of these services and to establish a transparent, quantitative framework that will allow the recalculation of the estimates as new data become available. We also should clarify that by "value" we mean documented financial transactions—mostly the purchase of goods or services—that rely on these insect-mediated services.

We restrict our focus to services provided by "wild"and primarily by native insects; we do not include services from domesticated species (e.g., pollination from domesticated honey bees) or pest control from mass-reared insect biological-control agents (e.g., *Trichogramma* wasps). We also exclude the value of commercially produced insect-derived products, such as honey, wax, silk, or shellac, and any value derived from the capture and consumption of insects themselves. The main reasons for these exclusions are that domesticated insects that provide services or products have been covered in many other forums (Morse and Calderone 2000), and they generally do not require the active conservation that we believe is warranted by those undomesticated insects that provide services. Furthermore, in the case of products or food derived directly from wild insects, we simply do not have data to report and therefore wish to maintain a focus on ecological services.

The four insect services for which we provide value estimates were chosen not because of their importance, but because of the availability of data and an algorithm for their calculation. Three of these services (dung burial, pest control, and pollination) support the production of a commodity that has a quantifiable, published value. To be consistent in our analysis for all three of these commodities, we calculated an estimate for the amount of each commodity that depends on each service or on the amount saved in related expenses (e.g., the cost of fertilizer in our analysis of dung burial). We did not perform an in-depth analysis of how service-dependent changes in the quantity or quality of each commodity may have affected its per-unit price.

One way of looking at the economic implications of the removal of a service was provided by Southwick and Southwick (1992), whose study involved crop pollination by honey bees. Because per-unit cost theoretically increases as supplies decrease, thus mitigating monetary losses, the costs of the service removal in the Southwick and Southwick study were lower than those calculated using our approach (Robinson et al. 1989, Morse and Calderone 2000). However, all reported values are still within an order of magnitude of each other and, although our approach may not reflect what a consumer would pay for a commodity when these ecological services are *not* being performed, our calculations do provide a measure of the value of these crops at current estimated levels of service.

In the case of insect support of wildlife nutrition, we use a different approach to estimate costs. Instead of basing calculations on the money paid to producers for raw commodities, we use census data to find out how US consumers spent their money. By looking at the consumer end of this system, we immediately see an order-of-magnitude increase in the value reported. We believe it is important for this difference to be understood up front, because it both significantly affects our reported results and provides at least a hint of what happens when raw commodities are converted into value-added products. For example, consumers will spend potentially an order of magnitude more on jellies, pasta sauce, or hamburgers than the price paid to producers for blueberries, tomatoes, or beef.

Using the methods we describe in detail in the following sections, we estimate the annual value of four ecological services provided by primarily native insects in the United States to be more than $57 billion ($0.38 billion for dung burial, $3.07 billion for pollination, $4.49 billion for pest control of native herbivores, and $49.96 billion for recreation). We consider this estimate very conservative. If data were available to support more accurate estimates of the true value of these services (e.g., inclusion of value-added products and wages paid to those who produce such products) or to allow estimation of the value of other services, the results of our calculations would be much higher. In addition to the role of insects in the systems we analyze here, other potentially important services that insects provide could not be quantified, including suppression of weeds and exotic herbivorous species, facilitation of dead plant and animal decomposition, and improvement of the soil. Calculating the value of any of these services could add billions of dollars to our overall estimate. Nevertheless, we hope that even this minimum estimate for a subset of services provided by insects will allow these animals to be more correctly factored into land management and legislative decisions. In the following sections, we present a detailed description of how we calculated these estimates and discuss the implications of our results.

Dung burial

Confining large mammals in small areas creates challenging waste-management problems. Cattle production in the United States provides a particularly pertinent example, because nearly 100 million head of cattle are in production (NASS 2004a, 2004b), and each animal can produce over 9000 kilograms (kg) (Fincher 1981), or about 21 cubic meters (BCMAF 1990), of solid waste per year. Fortunately, insects—especially beetles in the family Scarabaeidae (Ratcliffe 1970)—are very efficient at decomposing this waste. In doing so, they enhance forage palatability, recycle nitrogen, and reduce pest habitat (Fincher 1981), resulting in significant economic value for the cattle industry (table 1).

Dung beetles process a substantial amount of the cattle dung accumulated annually in the United States. Of the nearly 100 million head of beef and dairy cattle raised annually in the United States (C_t), approximately three-quarters (P_r; 74 million) spend most of their lives in pasture or rangeland, where dung beetles can play a role in dung decomposition (NASS 2004a). Other cattle, such as those in dairy or feedlot operations, spend the majority of their lives on artificial surfaces, such as cement, where dung beetles do not occur. In addition, certain pesticides—such as the avermectins used to treat internal parasites in cattle—leave a residue in the dung that is toxic to dung beetles (Anderson et al. 1984, Floate et al. 2005). Fifty-six percent of cattle in the United States are reportedly treated with some form of avermectin (NSF–CIPM 2001). Some of these cattle may be treated only in winter months, and thus the residue may be cleared before the dung beetles are active, but this proportion could not be calculated; we therefore assumed that dung from only the untreated 44% could be processed by dung beetles (P_{nt}). By multiplying the number of cattle that are raised on range or pasture by the proportion of those cattle that are treated with avermectins, we estimate that 32 million head of cattle (C_p)—or about one-third of the cattle in the United States—produce dung that can be processed by dung beetles (box 1).

The importance of this service is illustrated by the success of dung beetles introduced into Australia to deal with the dung of nonnative cattle brought to that continent in 1788 (Australian Bureau of Statistics 2005). Before the introduction of dung beetle species that were adapted to feed on cattle dung, Australia had no insect fauna to process cattle feces.

Consequently, rangeland across the country was fouled by slowly decomposing dung (Bornemissza 1976). In addition, this dung provided fodder for pest species. Recent research in western Australia has revealed that populations of the pestiferous bush fly (*Musca vetustissima*) have been reduced by 80% following dung beetle introductions (Dadour and Allen 2001).

Lack of data on dung decomposition rates in the presence and absence of dung beetles constrained the ability of a previous study (Fincher 1981) to estimate the value of dung beetle activity in reducing range fouling. Subsequent studies (see Floate et al. 2005 for a review), however, which compare the decomposition rates of dung treated with avermectins with the rates of untreated dung, provide excellent data on the contribution of insects to cattle dung decomposition. It is clear from these studies that a large majority of the untreated dung that is dropped on open ground is processed by dung beetles. We estimated this increase in the rate of decomposition due to dung beetles and used that figure to calculate its estimated economic value.

Using data from Anderson and colleagues (1984), we calculate (using the Lifetest procedure; SAS Institute 1996) that the average persistence—or time until complete decomposition—of an untreated dung pat on rangeland in California is 22.74 ± 0.64 months, while the average persistence of a pat treated with insecticides is 28.14 ± 0.71 months. This indicates that dung beetle activity results in a 19% decrease in the amount of time the average pat of dung makes forage unpalatable, which translates into substantial monetary savings. Note that, for the sake of this analysis, we must assume that the 19% decrease applies broadly across the United States, even though the rate of dung burial by beetles probably varies greatly depending upon the location.

Forage fouling

Fincher (1981) estimated a potential value for enhanced palatability based on the concept that cattle will not consume plant material that is fouled with dung (Marten and Donker 1964). If dung beetles were totally absent, forage fouling by dung would cause estimated annual losses of 7.63 kg of beef per head of cattle (L_{nb}; Anderson et al. 1984). This level of loss is in comparison with the theoretical zero loss of production if no forage were ever fouled by dung. Fortunately, the cattle industry is not saddled with the full force of this potential loss because range fouling is reduced by the current action of dung beetles.

If we assume that the 19% decrease in dung persistence translates into a 19% decrease in lost beef, then, for cattle whose dung is processed by dung beetles, the per-animal loss would be 6.18 kg (L_b) each year as a result of forage fouling. This assumption seems justified, since for each increment of time a given patch of forage remains fouled, it also remains unavailable for grazing. By applying these estimated losses to the 32 million head that are untreated and on pasture or rangeland, we estimate that in the absence of dung beetles, beef losses due to forage fouling would be 244 million kg of beef per year (C_p x L_{nb}), whereas losses at current levels of dung beetle function would be 198 million kg (C_p x L_b). With an average price over 34 years (1970–2003, corrected for inflation) of live beef cattle at $2.65 per kg ($V_c$; ERS 2004), losses would be $647 million ([$V_c$ x C_p x L_{nb}]) in the absence of dung beetles and $525 million ([$V_c$ x C_p x L_b]) in the presence of dung beetles. Subtracting the estimated value at current levels of dung beetle activity from the theoretical value if no dung beetles were active, we estimate the value of the reduced forage fouling (V_{rf}) to be approximately $122 million (table 1; see the equation in box 1).

Nitrogen volatilization

Another important service provided by dung beetles is promoting decomposition of dung into labile forms of nitrogen that can be assimilated by plants and thus function as fertilizer when the dung is buried. In the absence of dung beetles, cattle feces that remain on the pasture surface until they are dry lose a large proportion of their inorganic nitrogen to the atmosphere (Gillard 1967). Experiments in South Africa and the United States have shown that approximately 2% of cattle dung is composed of nitrogen, and that 80% of this nitrogen is lost if the pats dry in the sun before they are buried (Petersen et al. 1956, Gillard 1967).

Using Gillard's (1967) estimate of 27 kg of nitrogen produced annually per animal and assuming that 80% of this nitrogen is lost in the absence of dung beetle activity, we estimate that 21.6 kg would be lost per animal each year if dung beetles were not functioning (L_{nb}). On the basis of our interpretation of decomposition rates, we assume that these losses will be reduced 19% by the current level of dung beetle activity, compared with the estimate for no beetle activity. Thus, we estimate a loss of 17.5 kg per year (L_b) at current activity levels. Multiplying these per-animal values by the total number of cattle whose dung can potentially be buried by dung beetles (C_p, or 32 million), 691 million kg of nitrogen would be lost annually in the United States in the absence of dung beetle activity, compared with the 560 million kg lost at current levels of activity. With nitrogen valued at $0.44 per kg ($V_n$; McEwan 2002), we estimate the value of nitrogen lost in the absence of dung beetles to be $304 million and the value of nitrogen lost at current levels of dung beetle activity to be $246 million. Subtracting the estimated value at current levels of dung beetle activity from the theoretical value if no dung beetles were active, the value of the reduction in nitrogen loss is approximately $58 million (table 1). This assumes that the value of nitrogen in terms of increased forage—and therefore increased beef production—is the same whether the nitrogen is applied as fertilizer or made available as buried dung. Note that the formula used to calculate this value is the same as that used to estimate the value of beef saved because of reduced range fouling (box 1), except that we substitute the value for nitrogen per kilogram (V_n) for V_c, and substitute losses of nitrogen in the presence and absence of beetle activity for

L_b and L_{nb}, respectively. With nitrogen constantly being lost from rangeland systems through denitrification, volatilization, leaching, runoff, and incorporation into plant and animal biomass or feces, this benefit would be realized year after year (Gillard 1967, Smil 1999).

Parasites

Many cattle parasites and pest flies require a moist environment such as dung to complete their development. Burying dung and removing this habitat can reduce the density of these pests (Fincher 1981). From field observations that reflected current levels of removal, Fincher (1981) estimated the annual losses due to mortality, morbidity, and medication of beef cattle, dairy cattle, and other livestock with internal parasites. To estimate the value of dung burial for reducing these losses, we will use only the losses associated with beef cattle, because we do not have a good estimate for the proportion of dairy cattle or other livestock that live on open pasture or rangeland. Fincher (1981) reported that beef cattle ranchers lost $428 million annually because of parasites and pests. Corrected for inflation, this is equal to $912 million in 2003 dollars. Given that 85% of beef cattle are on range or pasture (NASS 2004a) and 44% of these cattle are not treated with insecticides (NSF–CIPM 2001), we calculate that 37% of the beef cattle in the United States have fewer parasites because of the facilitation of dung decomposition by dung beetles.

We go on to assume that cattle whose dung is processed by dung beetles suffer 19% fewer losses because of parasites, on the basis of our previous calculation that dung beetles accelerate decomposition by 19%. We also assume that cattle on rangeland, pasture, and feedlots all face the same level of loss from parasites in the absence of dung beetles. Following this logic, we estimate that damage from parasites is only 93% (100% – [37% x 19%]) of what it would be if dung beetles were not providing this service. In the absence of dung beetle activity, estimated losses would be $981 million instead of the current $912 million, and thus this service saves the cattle industry an estimated $70 million per year.

Pest flies

Using a similar algorithm, we can calculate a value for the reduction in losses due to pest flies. Fincher (1981) estimated that losses due to horn flies and face flies cost ranchers $365 million and $150 million, respectively, for a total of $515 million. Corrected for inflation, this is the equivalent of $1.7 billion in 2003. Using the calculation described above for parasites, we assume that, as a result of the processing of dung by insects, damage from parasites is only 93% of what it would have been if the service were not being provided. We estimate that losses in the absence of dung beetle activity would be $1.83 billion instead of the current $1.7 billion, and thus this service is saving the cattle industry an estimated $130 million per year.

Adding the individual values of increased forage, nitrogen recycling, and reduced parasite and fly densities due to dung processing by beetles, we arrive at a combined annual total of $380 million (table 1). This is certainly an underestimate, since these same services are being provided to an unknown proportion of pasture-raised dairy cows, horses, sheep, goats, and pigs. Furthermore, what is said for dung recycling can also be said for burying beetles and flies that decompose carcasses. While the density of carcasses is much lower than the density of dung pats, their removal is important in rangeland, natural areas, and other public areas for returning nutrients to the soil, reducing potential spread of diseases, and increasing site utility.

Pollination by native insects

Pollination, especially crop pollination, is perhaps the best-known ecosystem service performed by insects. McGregor (1976) estimates that 15% to 30% of the US diet is a result, either directly or indirectly, of animal-mediated pollination. These products include many fruits, nuts, vegetables, and oils, as well as meat and dairy products produced by animals raised on insect-pollinated forage. While this estimate is probably high, it presents one of the best published measures of pollinator-dependant food in the US diet (see also Townsend 1974, Crane 1990).

Here we attempt to calculate an estimate of the value of crops produced as a result of pollination by wild (i.e., unmanaged) native insects. The US government keeps records of the production of crops (NASS 2004c) and, because of their value, their insect pollinators have been given some attention, especially pollination by managed insects such as the European honey bee (*Apis mellifera* L.). From these studies and personal accounts of crop scientists and entomologists, several authors make generalizations about the proportion of pollination attributed to various insect groups, mostly honey bees (see McGregor 1976, Robinson et al. 1989). These generalizations are essentially educated guesses of the percentage of necessary pollination provided by insects, and as such, they are likely to be inaccurate. The proportions that could be attributed to native, as opposed to managed, pollinators will vary widely for each crop, depending on geographic location, availability of natural habitat, and use of pesticides (Kremen et al. 2002a). In addition, cultivars of the same species can have drastically different dependencies on insect pollinators (Free 1993), further complicating any calculation of the value of pollinator insects.

To conduct a truly accurate economic analysis of the role of native insects in crop pollination, we would need a much better accounting of current levels of pollination by different species of managed bees (e.g., honey bee [*A. mellifera*], alfalfa leaf-cutter bee [*Megachile rotundata*], blue orchard bee [*Osmia lignaria*], alkali bee [*Nomia melanderi*]), and wild bees (e.g., bumble bees [*Bombus* spp.], southeastern blueberry bee [*Habropoda laboriosa*], squash bee [*Peponapis pruinosa*]) in crop pollination (Kremen 2005). Kevan and Phillips (2001) suggested that researchers also need to collect better data on the specific pollination requirements of each crop and cultivar, including the best pollinators for the job and the costs and effects of supplying these pollinators. Although we still lack much of this information, the estimate we provide here for the value of crops produced as a result of wild native bee–mediated pollination is informative.

Several scientists have estimated the value of insect-pollinated crops that are dependent on honey bees (Robinson et al. 1989, Morse and Calderone 2000), or the financial loss to society that could be expected if managed honey bees were removed from cropping systems (Southwick and Southwick 1992). These authors make a variety of assumptions and take different approaches to calculating a value for honey bees. For example, Southwick and Southwick (1992) take into account the reduced crop output stemming from a lack of managed honey bees, adjusting their figures for the changes in value of each commodity as demand increases because of reduced supply. They also present a range of possible values based on assumptions of the pollination redundancy of managed honey bees and other bee pollinators, including feral honey bees and other native and nonnative bees. Taking all of this into account, they give a range of \$1.6 billion (\$2.1 billion when adjusted for inflation to represent 2003 dollars) to \$5.2 billion (\$6.8 billion in 2003 dollars) for the value of honey-bee pollinators. The lower estimate included effective pollination by other bees, making the managed honey bees redundant in some localities and thereby reducing their absolute value. On the high end, Southwick and Southwick (1992) estimate that honey bees are worth \$5.2 billion if few or no other bees visit insect-pollinated crops.

Robinson and colleagues (1989) and Morse and Calderone (2000) take a simpler approach, summing the value of each commodity that they estimate is dependant on honey-bee pollinators. From this they generate a portion of the overall value of each crop that they attribute to pollination by honey bees and report values of \$8.3 billion (Robinson et al. 1989) and \$14.6 billion (Morse and Calderone 2000) (\$12.3 billion and \$16.4 billion, respectively, when adjusted for inflation to represent 2003 dollars). This approach is more consistent with our other calculations of the value of ecosystem services, and so we choose to use it here to calculate the value of crop production that relies on native insect pollinators.

Using the data from Morse and Calderone (2000) on crop dependency on insect pollination and the relative contribution of honey bees, we can generate an estimate of the value of native insects as crop pollinators in the United States. To calculate this figure, we used a modified version of the equation employed by Robinson and colleagues (1989) and Morse and Calderone (2000):

$$V_{hb} = \sum (V \times D \times P),$$

where

V_{hb} = summation of the total annual value of insectpollinated crops that are pollinated by honey bees,

V = annual value of each crop as given by the US Department of Agriculture (USDA; NASS 2004c),

D = dependency of each crop on insect pollinators (Morse and Calderone 2000), and

P = estimate of the proportion of the effective insect crop pollinators that are honey bees (Morse and Calderone 2000).

We adjust this equation slightly to calculate an estimate of the value of crops in the United States that are pollinated by native insects (V_{np}). We assume, in this case, that P includes both managed and feral honey bees. (Feral honey bees most likely have been only a negligible component of crop pollination since their drastic decline in the mid-1990s because of parasitic mites and foulbrood diseases.) Thus, our new equation is

$$V_{np} = \sum [V \times D \times (1 - P)],$$

where

V_{np} = annual value of the crop attributable to native pollinators (each crop value is an average of yearly values reported from 2001 to 2003; NASS 2004c), and

$1 - P$ = proportion of the effective insect crop pollinators that are native bee species.

In working with the proportions given by Morse and Calderone (2000), we adjusted one P value to better reflect the contribution of native species. Specifically, we assumed that the primary alternative pollinators for alfalfa are managed alfalfa leafcutter bees, which were introduced to North America from Asia. Thus, we increased the P value for alfalfa to 0.95 (see table 2). In other words, we assume that native bees—primarily *N. melanderi*—are responsible for at least 5% of alfalfa pollination in the United States (James Cane, USDA Agricultural Research Service, Logan, UT, personal communication, 1 November 2005).

When we sum the average value of pollinator-dependent commodities reported in Morse and Calderone (2000), we find that native pollinators—almost exclusively bees—may be responsible for almost \$3.07 billion of fruits and vegetables produced in the United States (table 2). Here we must incorrectly assume that the proportion of honey bees to native species is constant in all settings. In some systems, such as agriculturally diverse, organic farms with nearby pockets of natural or seminatural habitat, native bees may be able to provide all of the pollination needs for certain crops (Kremen et al. 2002a, 2004). For example, Morse and Calderone (2000) assume that 90% of the insect pollinators of watermelon are honey bees. While this is probably true in most farms, some organic growers can rely on native bees for 100% of their melon pollination (Kremen et al. 2002a).

Our estimate also does not take into account the role native bees can play in crops that typically do not require insect pollinators to set fruit, or in crops that may increase their production when visited by both native bees and honey bees. For example, in the former case, tomatoes are self-fertile and only need their flowers to be jostled in the wind to release enough pollen for pollination to occur. In addition, they hold no interest for honey bees because their flowers produce no nectar and, to release pollen from the deep pores in their anthers, the flowers must be sonicated (i.e., buzz pollinated), a process in which the bee grasps the flower tightly and rapidly fires its flight muscles to vibrate the anthers. Honey bees do not perform this behavior and thus receive no reward from visiting these plants. Many native bees, such as bumble bees, do sonicate these flowers, and the resulting cross-pollination can increase fruit set by 45% and fruit weight by nearly 200% (Greenleaf and Kremen 2006).

Native bees may also interact with honey bees in such a way as to increase the honey bees' pollination efficiency. For example, in sunflower hybrid seed production, pollen from a male row of sunflowers must be moved by bees to a female (male-sterile) row. Growers typically use honey bees to accomplish this task. However, most honey-bee workers specialize as either nectar or pollen foragers. Nectar foragers tend primarily to visit female rows, while pollen foragers visit male rows. When native bees come in contact with honey bees at the flower, the honey bees are literally chased between rows and thus transfer more pollen from male to female rows, on average doubling the amount of seed set by honey bees alone (Greenleaf 2005). These two examples illustrate some of the many roles of native insects in crop pollination that researchers are just beginning to document, which will influence how we refine our calculations for the economic value of this service in the future.

Pest control

The best estimate available suggests that insect pests and their control measures cost the US economy billions of dollars every year (Yudelman et al. 1998), but this is only a fraction of the costs that would accrue if beneficial insects such as predators and parasitoids, among other forces, did not keep most pests below economically damaging levels (Hawkins et al. 1999, Turchin et al. 1999). We calculate the value (V) of these natural forces by first estimating the cost of damage caused by insect pests at current levels of control (CC) and then subtracting this value from the estimated higher cost that would be caused by the greater damage from these insect pests if no controls were functioning (NC). Finally, we calculate a value for the specific action of insect natural enemies by multiplying the value of these natural forces by an estimate of the proportion (P_i) of pests that are controlled by beneficial insects as opposed to other mechanisms (e.g., pathogens or climate).

Because of data limitations, we restrict our estimate to the value derived from the suppression of insect pests that attack crop plants. Beneficial insects certainly suppress populations of both weeds and insects that attack humans and livestock, but the data were not available to calculate the value of these services. As with the rest of our analysis, we also limit our calculations to pest and beneficial insects native to the United States (box 1).

Our first step was to calculate the cost of damage due to insect pests at current levels of control from natural enemies. Drawing on previously published estimates, Yudelman and colleagues (1998) presented monetary values for total production of eight major crops and for the losses to these crops attributable to insects. Using these values, we calculated a ratio of insect loss to actual yield that allowed estimation of losses due to insects for any period for which yield values have been published. Assuming $50.5 billion for total production and $7.5 billion for losses due to insects in North America from 1988 through 1990 (Yudelman et al. 1998), we calculated a ratio of 0.1485.

It is reasonable to question how far this ratio can be generalized. It appears fairly robust across time, as estimated crop losses changed as little as 3% in 25 years (1965–1990; Oerke et al. 1994). Applying a ratio derived from North American numbers to the United States alone also seems reasonable, since the United States is responsible for the bulk of agricultural production on the continent. In addition, Oerke and colleagues (1994) suggest that this ratio can be generalized from those eight major crops to all agricultural production. Starting with a published value of $106.1 billion for total cash receipts from US farms in 2003 (NASS 2004c), we calculated the annual US loss due to insect damage to be $15.76 billion (i.e., 106.1 x 0.1485 = 15.76). An additional $3.01 billion was lost in expenditures for insecticides (USEPA 2003), bringing the total annual loss to $18.77 billion.

Unfortunately, we could not find the necessary data to use this whole sum to calculate a value for pest control. The loss of $18.77 billion includes damage both from native pests that originated in the United States and from exotic pests that originated in other countries. To complete our estimation of the value of pest control, we needed an estimate of the cost of damage due to insects in the absence of this service. Published reports on the damage caused by invasive species provided the basis of that estimate for herbivorous insect pests native to the United States, but not for exotic pest species (Calkins 1983).

Specifically, Calkins (1983) found that only 35% of the exotic pests in the United States are pests in their home range. Extending this finding, we assume that the same relationship holds true in the United States, and thus only 35% of potential insect pest species that are native to the United States reach damaging levels. In other words, we assume that 65% of the potential damage from native pest species is being suppressed, and that 65% of the potential financial cost of this damage is being saved. We make this assumption based on (a) the abundant evidence of a strong correlation between pest density and the magnitude of loss due to pest damage, and (b) the lack of evidence of a correlation between the destructiveness of a pest and the probability that it will be suppressed.

To clarify, the pool of potential pest species—from which we assume 35% actually reach pest levels—is significantly smaller than the 90,000 described insect species in the United States, because many of the described species are not herbivores, and many of those that are herbivores do not feed on cultivated plants. Only 6000 (7%) of the described species in the United States and Canada cause any damage (Romoser and Stoffolano 1998). For our estimate, we assume that these 6000 species, although they make up only 7% of the total species, account for 35% of the species that would be pests if they were not controlled. Following this logic, we assume that the pool of potential pests would be about 17,000 species, 11,000 of which (65%) are being kept below damage levels by biological or climatic controls.

These native species are estimated to comprise 39% of all pest species in the United States (Flint and van den Bosch 1981). Since native pests vary greatly in the amount of damage they cause, and include some of the most damaging pests in the United States (e.g., corn rootworm, Colorado potato beetle, and potato leafhopper), we assume that they are responsible for 39% of the cost of damage from all pests in the United States. Hence, we estimate that the cost associated with native pest species at current levels of suppression by natural enemies is 39% of \$18.77 billion, or \$7.32 billion. We designate this value current control by native insects (CC_{ni}).

On the basis of these assumptions, we estimate that the \$7.32 billion lost annually to native insect pests (CC_{ni}) is 35% of what would be lost if natural controls were not functioning. If no natural forces were functioning to control native insect pests, we estimate that they would cause \$20.92 billion in damage in the United States each year (NC_{ni}). By subtraction, the value of pest control by our native ecosystems is approximately \$13.60 billion (table 3).

However, not all of this value for natural control of insect pests is attributable to beneficial insects. Some pest suppression comes from other causes, such as pathogens, climatic conditions, and host-plant resistance. One review of the factors responsible for suppression of 68 herbivore species reported that insects (e.g., predators and parasitoids) were primarily responsible for natural control in 33% of cultivated systems (P_i; Hawkins et al. 1999). On the basis of these findings, we estimate that insects are responsible for control of 33% of pests that are suppressed by natural controls, while pathogens or bottom-up forces control the rest. Using this average, we estimate the value of natural control attributable to insects to be \$4.5 billion annually (33% of \$13.6 billion).

Recreation and commercial fisheries

US citizens spend over \$60 billion a year on hunting, fishing, and observing wildlife (US Census 1996). Insects are a critical food source for much of this wildlife, including many birds, fish, and small mammals. Using 1996 US census data on the spending habits of Americans, adjusted for inflation to 2003 dollars, we estimated the amount of money spent on recreational activities that is dependent on services provided by insects. In this case, the predominant service is concentrating and moving nutrients through the food web.

Small game hunting

Since most large game are either obligate herbivores or omnivores that are not substantially dependent on insects as a source of nutrition, we restrict our estimate of the value of insects for hunting to small game species. In 1996, expenditures for small game hunting totaled \$2.5 billion (\$2.9 billion in 2003 dollars). To calculate the proportion of this expenditure that is dependent on insects, we use the proportion of days spent hunting for each insectivorous small game species (table 4) and the dependence of these birds on insects for food.

On the basis of published reports that most galliform chicks rely on insects as a source of protein and that many cannot even digest plant material (Liukkonen-Anttila 2001), we assume that quail, grouse, and pheasant could not survive without insects as a nutritional resource. Therefore, multiplying the proportion of hunting days spent on each of these small game birds (0.15, 0.13, and 0.23, respectively, for a total of 0.51) by the total value for small game (\$2.9 billion), we estimate that insects are required for \$1.48 billion in expenditures (table 4).

Migratory bird hunting

Insectivory in migratory birds—primarily waterfowl such as ducks and geese in the order Anseriformes—is not as predominant as in the primarily terrestrial galliform birds discussed above. According to Ehrlich and colleagues (1988), 19 (43%) of the 44 species in this order are primarily insectivorous (table 5). Multiplying the total money spent on migratory bird hunting (\$1.3 billion) by the 43% of species that are primarily insectivorous, we estimate the value of insects as food for hunted migratory birds at \$0.56 billion in hunter expenditures (table 4).

Sport and commercial fishing

The census also provides values for sport or recreational fishing. Since most recreational fishing is in fresh water and a majority of freshwater sport fish are insectivorous (Cliff Kraft, Cornell University, Ithaca, NY, personal communication, 3 January 2005), we assume that the entire value of recreational fishing ($27.9 billion) is dependent on insects (table 4). In contrast to recreational fishing, the target of most commercial fishing is saltwater fish. There are very few marine insect species, but many fish that are caught in marine systems spend part of their life cycle in fresh water, and insects are often critical sources of nutrition during these periods. Commercial fishing is not covered by the census, but data are available on the number and value of fish landed annually in the United States by commercial operations (NMFS 2005). Twenty-five of these fish species are primarily insectivorous during at least one life stage (Cliff Kraft, Cornell University, Ithaca, NY, personal communication, November 2004). Summing their individual values, we estimate the total value of insects for commercial fishing to be approximately $225 million (table 6). Insectivorous fish account for more than 15% of the overall value of commercial fish.

Wildlife observation (bird watching)

The 1996 census reports that Americans spent $33.8 billion on wildlife observation. The census also asked respondents to note which types of wildlife they were watching (e.g., birds, mammals, reptiles, amphibians, insects). Because respondents were allowed to choose more than one category of wildlife, it was impossible to separate out observed groups of organisms that were dependent on insects from those that were not. Bird watching is the most inclusive category, with 96% of respondents indicating that they included birds in their observations. Thus, we assume that 96% of the budget for wildlife observation stems directly from birds, many of which are at least partly dependent on insects as a source of nutrition. It would not have been unreasonable to raise this proportion, since a substantial proportion (45%) of Americans who observe wildlife also indicated that they observe insects and spiders directly, while 84% and 31% report that they observe either amphibians and reptiles or small mammals, both of which are substantially insectivorous groups. Since we are unable to estimate the overlap between categories, here we use only the number for birds. Thus, we assume that bird watching accounts for 96% of $33.8 billion spent, or $32.4 billion a year, providing a conservative starting point for calculating the dependency of wildlife observation expenditures on insects.

Our next step is to estimate what proportion of this figure for bird observation was dependent on and attributable to insects. Using data from Ehrlich and colleagues (1988), we calculate that 61% of the bird species known to breed in the United States are primarily insectivorous, and another 28% are at least partially insectivorous (table 5). To be conservative, we consider only bird species that are primarily insectivorous. This probably underestimates the importance of insectivory for birds, since many passerine and galliform birds that are listed as partially insectivorous could not survive without the vital protein that insects provide young chicks (Kobal et al. 1998). This estimate is conservative also because it is based on bird species numbers rather than population numbers, and the passerines, which are overwhelmingly insectivorous, have relatively high population densities. Taking these factors into account, we estimate that insects are responsible for $19.8 billion, which is 61% of the $32.4 billion spent on bird observation annually in the United States (table 4).

Discussion

We estimate the value of those insect services we address to be almost $60 billion a year in the United States, which is only a fraction of the value for all the services insects provide. The implication of this estimate is that an annual investment of tens of billions of dollars would be justified to maintain these service-providing insects, were they threatened. And indeed, these beneficial insects are under ever increasing threat from a combination of forces, including habitat destruction, invasion of foreign species, and overuse of toxic chemicals.

Fortunately, no evidence suggests a short-term drastic decline in the insects that provide these services. What the evidence does indicate, however, is a steady decline in these beneficial insects, associated with an overall decline in bio-diversity, accompanied by localized, severe declines in environments heavily degraded by human impacts (Kremen et al. 2002a). New evidence indicates that in some situations, the most important species for providing ecosystem services are lost first (Larsen et al. 2005). The overall, gradual decline in species, coupled with nonlinear changes in service levels, makes it difficult to pinpoint an optimal level of annual investment to conserve beneficial insects and maintain the services they provide.

To make a quantitative recommendation, we need to know the marginal value of the services provided, not the total value. The marginal value of a service can be defined as the value of one unit of that service or benefit. For example, the marginal value of dung decomposition could be defined as the value of having dung buried at a rate of 5 grams (g) per day by a given number of beetles. If the marginal value of each service could be calculated and the relationship between the density of beneficial insects and the level of service determined, then it would be straightforward to calculate the optimal density of beneficial insects that should be maintained. This density then could be compared to the costs associated with providing an environment that best supports these species in order to give a true cost–benefit analysis (Dasgupta et al. 2000). Alternatively, understanding this marginal value would allow managers to factor the degradation of a service into a more accurate economic assessment of current practices (Dasgupta et al. 2000, Kremen 2005).

We can estimate current service levels and current beneficial insect densities, so it might seem that it should be simple to determine this relationship by dividing the level of service by the density of insects. We might expect that if 10 dung beetles in a square meter process 10 g of dung in a day, then each one is processing 1 g per day. Thus, if the density of beneficial insects decreased by 50%, then the level of service would be expected to decrease by 50% as well.

Unfortunately, this simple calculation is inadequate, because the relationship between the decreasing densities of beneficial insects and the services they provide is almost certainly not a simple linear one. In most systems, there is an inherent redundancy, with multiple species performing similar functions. A decrease in the density of one species performing a function may be compensated by an increase in the density of another, with no loss in ecosystem functionality. However, recent studies suggest that the capacity of systems to absorb perturbation without losing functionality is limited and may in fact drop precipitously when some—invariably unknown—threshold level is passed (Schwartz et al. 2000). In addition, as noted above, in some environments the most important providers of a service may be lost first, resulting in an early, drastic decline in the provision of a service (Larsen et al. 2005).

Thus, even though we provide an estimate of the total value of certain insect services, the complications of redundancy and nonlinearity make it impossible to quantitatively gauge the level of resources that are justified for efforts aimed at conserving the services that insects provide. However, our findings lead us to espouse three qualitative guidelines. First, cost-free or relatively inexpensive measures are almost certainly justified to maintain and increase current service levels. Examples include volunteer construction of nest boxes for wild pollinators and the inclusion of a diverse variety of native plant species in plantings for bank or soil stabilization and site restoration (Shepherd et al. 2003, Vaughan et al. 2004). Second, actions or investments that are estimated to have an economic return at or slightly below the break-even point, such as the use of less toxic pesticides, are probably justified because of their nontarget benefits. Third, actions that lead to substantial decreases in biodiversity should be avoided because of the high probability of a major disruption in essential services.

Finally, although we cannot provide a quantitative formula to determine the optimal level of investment in the conservation of beneficial insects that provide essential services, we do feel justified, on the basis of our estimates, in making some specific recommendations. First, we recommend that conservation funding allocated via Farm Bill programs—such as the Conservation Security Program, Conservation Reserve Program,Wetlands Reserve Program, and Environmental Quality Incentives Program—pay specific attention to insects and the role they play in ecosystems. In particular, funding to provide habitat for beneficial insects such as predators, parasitoids, and pollinators in natural, seminatural, unproductive, or fallow areas in agricultural landscapes not only provides direct benefits to growers but, by focusing on the ecological needs of insects, results in habitat that supports a great diversity of wildlife (de Snoo and de Leeuw 1996, Jamison et al. 2002, Vaughan et al. 2004).

Second, we recommend that ecosystem services performed by insects be taken into account in land-management decisions. Specifically, maintaining ecosystem services should be a goal of land management. With this goal in mind, specific practices such as grazing, burning, and pesticide use should be tailored to protect insect biodiversity. For example, it may be important to treat only a small portion of an area of habitat at any one time (Schultz and Crone 1998); to ensure that a diverse forb community is included with any habitat restoration or riparian bank stabilization (Kremen et al. 2002b); or to choose the most targeted pesticides for control of invasive species.

Once the benefits of insect-provided services are realized, there may be some call for increased funding to conserve rare insects through the Endangered Species Act. Insects are certainly underrepresented and underfunded through this legislation, and increased funding could save many rare insect species from extinction. However, while increasing funds targeted for the conservation of endangered species would help those beneficial insect species that share habitat with listed species, it would not in itself be sufficient to ensure the continuation of the services provided by beneficial insects.

Most insects that provide essential services are not, at least at present, rare or endangered (though the recent dramatic decline of bumble-bee species in the subgenus *Bombus*—once abundant crop pollinators—provides an interesting and alarming counterexample; Thorp 2003, Thorp and Shepherd 2005). The optimal strategies for conserving these still common but declining beneficial insects are almost certainly very different from those that are most effective in conserving rare and endangered insects. We believe it is imperative that some federal and local funds be directed toward the study of these beneficial insects and the vital services they provide so that conservation efforts can be optimally allocated, either through the agricultural programs listed above or through other means.

These steps are just a beginning. With greater attention, research, and conservation, the valuable services that insects provide can not only be sustained but increase in capacity. As a result, growers will be able to practice a more sustainable form of agriculture while spending less on managing pest insects or acquiring managed pollinators; ranchers will get more productivity out of their land; and wildlife lovers will find that the birds and fish they hunt occur in greater abundance than in the past few decades. In less direct but no less important ways, everyone would benefit from the facilitation of the vital services that insects provide. Judging from our estimate of the value of these four services, increased investment in the conservation of these services is justified.

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Appendix

Box 1. Formulas used to estimate insect services.

Formula used to estimate the number of cattle in the United States whose dung can be processed by dung beetles:

$$C_p = (C_t \times P_r) \times P_{nt},$$

where

C_p = head of cattle producing dung that can be processed by dung beetles,

C_t = total head of cattle produced annually in the United States,

P_r = the proportion of cattle that are raised on range or pasture, and

P_{nt} = the proportion of cattle not treated with avermectins.

Formula used to estimate the value of beef saved because of reduced range fouling resulting from dung burial by dung beetles:

$$V_{rf} = [V_c \times (C_p \times L_{nb})] - [V_c \times (C_p \times L_b)],$$

where

V_{rf} = value of reduced forage fouling,

V_c = value of cattle (per kilogram),

C_p = head of cattle producing dung that can be processed by dung beetles,

L_{nb} = losses (per animal) with no dung beetle activity, and

L_b = losses (per animal) at current levels of dung beetle activity.

Formula used to estimate the value of native insects for suppressing populations of potentially pestiferous native herbivorous insects:

$$V_{ni} = (NC_{ni} - CC_{ni}) \times P_i,$$

where

V_{ni} = the value of suppression of native insect pests by other insects,

NC_{ni} = the cost of damage from native insect pests with no natural control,

CC_{ni} = the cost of damage from native insect pests at current levels of natural control, and

P_i = the proportion of herbivorous insects controlled primarily by other insects.

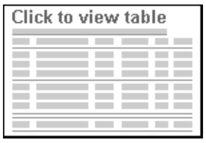


Table 1.
Total economic losses averted annually as a result of accelerated burial of livestock feces by dung beetles.

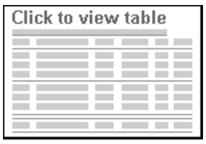


Table 2.
The value of crop production resulting from pollination by native insects, 2001–2003.

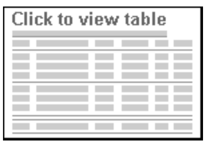
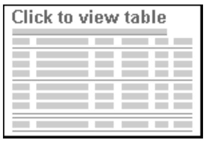


Table 3.
Value of averted crop losses as a result of predation or parasitism of native agricultural pests by native beneficial insects.

Table 4.
Expenditures for hunting, fishing, and observing wildlife that rely on insects as a critical nutritional resource.



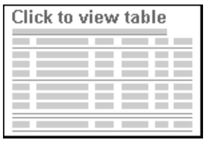


Table 5.
Insectivory in North American bird species.

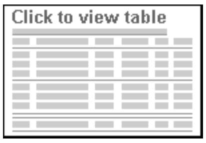


Table 6.
Value of commercially landed fish that rely upon insects as a critical nutritional resource.

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