Biodiversity and Ecosystem Services in Agroecosystems

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Glossary

Agroecology The application of ecological concepts and principles to the design and management of sustainable agroecosystems.
Agroecosystems Agricultural ecosystems including biophysical and human components and their interactions.
Biodiversity The variation of life in all forms from genes, to species, to communities, to whole ecosystems.
Ecosystem service providers Organisms, guilds, and ecological communities that are biological mediators of ecosystem services, providing services through their functions and interactions.
Ecosystem services Functions of ecosystems – including agroecosystems – that are useful to humans or support human well-being: (1) provisioning services include the production of food, fuel, fiber, and other harvestable goods; (2) regulating services include climate regulation, flood control, disease control, waste decomposition, and water quality regulation; (3) supporting services include the foundational processes necessary for production of other services, including soil formation, nutrient cycling, and photosynthesis (primary production); and (4) cultural services provide recreational, esthetic, spiritual, and other nonmaterial benefits.
Human well-being A context- and situation-dependent state that comprises basic material for a good life, freedom and choice, health, good social relations, and security.
Millennium Ecosystem Assessment An international synthesis released in 2005, created by more than 1000 of the world's leading scientists, that analyzed the state of the Earth's ecosystems.
Payment for ecosystem services Market-based instruments used to channel investment in ecosystem services.
Resilience The capacity of a system to absorb disturbance and retain structure and function; this includes the human capacity to anticipate and plan for the future (e.g., in managing agricultural systems).
Scale Geographical extent; relevant scales for agroecosystems often include units commonly used in management and decision making, such as field (local and on-farm cultivated area), farm (including cultivated and noncultivated areas), landscape, regional, and global.

Introduction

Historically, agricultural systems have been managed, above all, for the production of food and fiber; however, agricultural landscapes can provide a wide range of goods and services to society. 'Ecosystem services' are those functions of ecosystems – including agroecosystems – that are useful to humans or support human well-being (Daily, 1997; Kremen, 2005). The ecosystem services concept is remarkably longstanding. Mooney and Ehrlich (1997) noted that in approximately 400 BC, Plato observed how forests provided important services to Attica and forest loss resulted in drying springs and soil erosion. Plato's work highlights that people have been aware of these critical services long before the dawn of industrial agriculture (Rapidel *et al.*, 2011).

In the past two decades, work at the interface of ecology and economics to characterize, value, and manage ecosystem services has supported a paradigm shift in how society thinks about ecosystems and human relationships to them. As both major providers and major beneficiaries of ecosystem services, agricultural landscapes and the people within them are at the center of this shift. Growing calls for agriculture landscapes to be managed as 'multifunctional' systems create new mandates, as well as opportunities, to maintain and enhance ecosystem services as part of productive agroecosystems.

Work on multifunctional ecosystems draws on the Millennium Ecosystem Assessment (2005) and other recent evaluations of ecosystem services (e.g., The Economics of Ecosystems and Biodiversity and The Common International Classification of Ecosystem Services). The Millennium Ecosystem Assessment provides a globally recognized classification that emphasizes relationships between ecosystem services and human well-being and describes four types of services (The authors draw on the classification of ecosystems services used in Millennium Ecosystem Assessment throughout the article (MEA, 2005), recognizing that more recent classifications have minimized or eliminated supporting services in favor of specific, operational descriptions designed for environmental accounting (Haines-Young and Potschin, 2012) and economic valuation (TEEB, 2010)). Provisioning services include the production of food, fuel, fiber, and other harvestable goods. Regulating services include climate regulation, flood control, disease control, waste decomposition, and water quality regulation. Supporting services include the foundational processes necessary for production of other services, including soil formation, nutrient cycling, and photosynthesis (primary production). Cultural services provide recreational, esthetic, spiritual, and other nonmaterial benefits. Most classifications, despite their variations, consider interdependence between ecosystem services and human well-being as well as variation in ecosystem

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services across spatial scales ranging from local to global (**Figure 1**).

Biodiversity – the variation of life in all forms from genes, to species, to communities, to whole ecosystems – is a significant determinant of ecosystem function and provision of ecosystem services. Although relationships between biodiversity and ecosystem services are complex and vary widely across different types of ecosystems, at the broadest level, increased native biodiversity is generally associated with higher levels of ecosystem services within a given system (Balvanera *et al.*, 2006; Cardinale *et al.*, 2012). Plant diversity, for example, has been found to enhance belowground plant and microbial biomass, which is associated with the ecosystem service of erosion control through the effects of large root and mycorrhizal networks holding soil in place (Balvanera *et al.*, 2006). It is also important to note that some ecosystem services are provided in part by the abiotic (nonliving) components of ecosystems, such as aquifers and inorganic portions of soils. Biodiversity can be considered a form of 'biological insurance' that helps to assure ecosystem performance, including providing ecosystem services, as diversity increases the chances that one or more species will be able to perform critical functions, even in the event of disturbance or species loss (e.g., natural disaster and human-induced land use change) (Naeem and Li, 1997).

Agroecosystems both provide and rely on ecosystem services to sustain production of food, fiber, and other

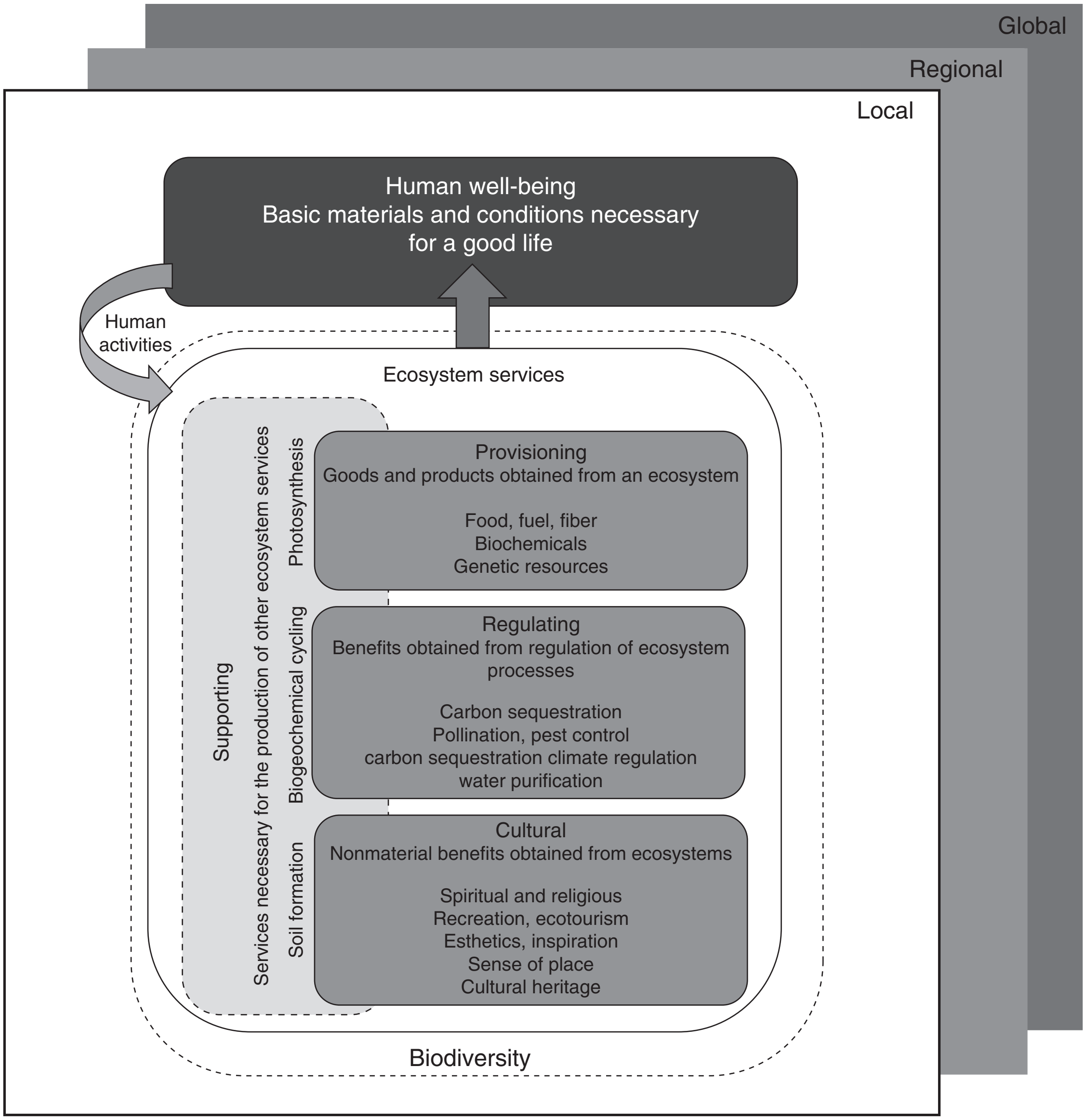

Figure 1 Typology of ecosystem services. This ecosystem service typology, adapted from the Millennium Ecosystem Assessment (MEA, 2005), considers biodiversity as a foundation for all ecosystem services (represented with a dotted line framing ecosystem services). Ecosystem services include provisioning, regulating, and cultural services (dark gray boxes, solid outline), as well as supporting services (light gray box, dashed outline). Ecosystem services support human well-being (charcoal gray box, white text), and, in turn, are influenced by human activities and land-use management decisions. Both ecosystem services and human well-being can be considered at nested spatial scales from local, to regional, to global.

harvestable goods. Many services have on-farm benefits (e.g., for farmers, plantation managers, and other people on-site), whereas others have broader public benefits to off-farm users; some benefit both groups (Table 1).

The evaluation and management of ecosystem services in agricultural landscapes has emerged as a top priority for several reasons. First, agricultural ecosystems – including croplands and pastures – are among the largest terrestrial

Table 1 Ecosystem service descriptions and related on-farm benefits and public, off-farm benefits

Ecosystem service	*Description*	*On-farm benefits*	*Public, off-farm benefits*
Provision of food, fuel, fiber, and biochemicals	Harvestable goods from agroecosystems	Food and other goods for on-farm consumption or sale	Goods for agricultural markets
Soil structure and fertility enhancement	Soil structure and processes of nutrient cycling and delivery of nutrients to plants; processing organic matter and transforming detritus and wastes	Support for crop growth; can limit need for chemical fertilizers	May limit need to mine or manufacture chemical fertilizer
Erosion protection	Soil retention; limiting soil loss through wind and water erosion	Maintain soil, and the nutrients it contains, to support production	Potential reduction of sediment transfer to downstream systems & users
Hydrologic services: Water flow regulation	Buffering and moderation of the hydrologic cycle, including water infiltration into soils and aquifers, moderation of runoff, and plants transpiration	Water in soils, aquifers, and surface bodies available to support plant growth	Stabilize stream base flow and mitigate flooding to downstream areas; recharge into aquifers and bodies of water; plant transpiration may support precipitation patterns
Hydrologic services: Water purification	Filtration and absorption of particles and contaminants by soil and living organisms in the water and soil	Clean water available for human consumption, irrigation, and other on-farm uses	Clean water available to downstream users
Pollination	Transfer of pollen grains to fertilize flowers	Necessary for seed set and fruit production in flowering plants and crops	Necessary for outcrossing in noncultivated flowering plants
Pest control	Control of animal and insect pests by their natural enemies – predators, parasites, and pathogens	Minimize crop damage and limit competition with crops	May limit need for pesticides that threaten environmental and human health
Weed control	Botanical component of pest control; suppressing weeds, fungi, and other potential competitors through physical and chemical properties of cover crops, intercrops, and other planted elements	Minimize weed competition with crops	May limit need for herbicides that threaten environmental and human health
Carbon sequestration	Atmospheric carbon dioxide is taken up by trees, grasses, and other plants through photosynthesis and stored as carbon in biomass and soils	Few demonstrable on-farm benefits[a]	Regulation of the carbon cycle; mitigation of greenhouse gas contributions to atmospheric change
Genetic resources	Pool of genetic diversity needed to support both natural and artificial selection	Distinct genotypes (cultivars) allow fruit set in orchards and hybrid seed production; trait diversity (from landraces and wild relatives) supports disease resistance, new hybrids, and climate adaptations	Prevention against large-scale crop failure
Cultural and esthetic services	Maintaining landscapes that support: esthetics and inspiration; spiritual and religious values; sense of place; cultural heritage; recreation and ecotourism	Esthetics and inspiration; spiritual and religious values; sense of place; cultural heritage; recreation and ecotourism	Esthetics and inspiration; spiritual and religious values; sense of place; cultural heritage; recreation and ecotourism

[a]On-farm carbon sequestration can be associated with on-farm benefits in closely related ecosystem services, such as increased soil organic matter and microclimate regulation (e.g., shade provided by trees).

biomes and account for approximately 40% of the Earth's surface (Foley *et al.*, 2005). Second, increases in food and fiber production have often been achieved at the cost of other critical services. The Millennium Ecosystem Assessment (2005) reported that approximately 60% (15 out of 24) of services measured in the assessment were being degraded or unsustainably used as a consequence of agricultural management and other human activities. Finally, evaluations of 'planetary boundaries,' which describe the safe operating space for human activities with respect to the planet's biophysical systems and processes, indicate that modern, industrial agriculture is among the activities that have most significantly undermined the Earth's life-support systems (Rockström *et al.*, 2009). Major negative impacts have occurred through converting natural habitat to agriculture and infrastructure, environmental pollution, and environmental change induced by shifts in nitrogen and phosphorus use.

Recent work highlights the need for better understanding the ecological processes that underpin critical ecosystem services (Kremen, 2005). Provision of ecosystem services in farmlands is directly determined by their design and management (Zhang *et al.*, 2007) and strongly influenced by the function and diversity of the surrounding landscape (Kremen and Ostfeld, 2005; Tscharntke *et al.*, 2005). Yet, there is an outstanding need for field studies that describe the mechanisms, which control how ecosystem services vary across both space and time. Building understanding of the mechanisms underlying ecosystem services is also essential to developing the ability to predict how management activities will affect the single ecosystem services, and suites of services, needed to support both productive farmlands and human well-being.

Ecosystem Services and Disservices in Agricultural Landscapes

Ecosystem Services and Disservices

Agroecosystems both provide and rely on ecosystem services. Services that help to support production of harvestable goods can be considered services to agriculture (Zhang *et al.*, 2007). These services include soil structure and fertility enhancement, nutrient cycling, water provision, erosion control, pollination, and pest control, among others (Figure 2). Ecological

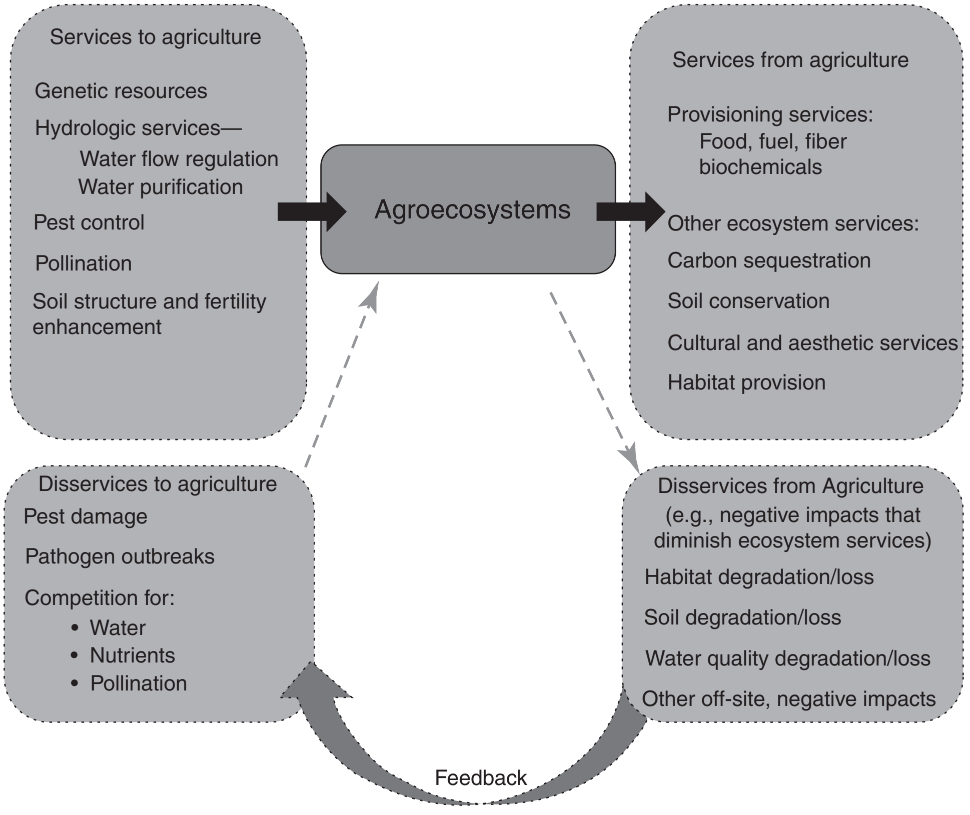

Figure 2 Ecosystem services and disservices to and from agriculture Farming systems can be both producers and beneficiaries of ecosystem services, and in many cases these relationships are deliberately managed by farmers. Such ecosystem services are represented by two gray boxes in the diagram. Production systems can also suffer from various disservices or contribute to disservices or loss of services. These negative relationships are usually the unintentional result of management action, represented by the two lower gray boxes and the dashed arrows. Disservices from agriculture can also lead to agricultural inputs and result in detrimental on-farm impacts, such as when habitat for natural enemies is removed and pest outbreaks increase, represented by the feedback arrow at the bottom of the diagram. Adapted from Zhang, W., Ricketts, T., Kremen C., *et al.*, 2007. Ecosystem services and dis-services to agriculture. Ecological Economics 64, 253–260 and Swinton, S., Lupi, F., Robertson, G., Hamilton, S., 2007. Ecosystem services and agriculture: Cultivating agricultural ecosystems for diverse benefits. Ecological Economics 64, 245–252.

processes that detract from agricultural production can be considered disservices to agriculture (Zhang *et al.*, 2007) and include pest damage, competition for water, and competition for pollination. Management of agricultural ecosystems also affects flows of ecosystem services and disservices (or diminution of naturally occurring services) from production landscape to surrounding areas. Services from agriculture include provisioning services (food, fuel, fiber, and biochemicals) as well as carbon sequestration, soil conservation, cultural and esthetic services, and habitat provision (e.g., providing habitat for endemic organisms). Disservices from agriculture can include degradation or loss of habitat, soil, water quality, and other off-site, negative impacts. Both services and disservices are typically a result of management practices within agricultural fields and landscapes. The remainder of this section describes some of the key ecosystem services that support agricultural productivity (summarized in **Table 1**) and disservices detract from it (see Swinton *et al.*, 2007 for detailed discussion of services and disservices from agriculture).

Services to Agriculture Help to Sustain Agricultural Productivity

Soil structure and fertility enhancement services include the processes of soil formation, structural development (including physical, chemical, and biological properties of soil), and nutrient cycling mediated by biotic and abiotic factors to support plant growth. These soil characteristics are important determinants of the quantity and quality of farming outputs (Zhang *et al.*, 2007). As soil organisms process dead organic matter, and their waste replenishes nutrients required for primary production, the fertility needed to support primary production is maintained (Daily *et al.*, 1997).

Soil structure is enhanced through the activities of macrofauna – such as earthworms, centipedes, millipedes, and isopods – that aerate soil by creating pores as they burrow through the soil profile, mixing organic and mineral particles, redistributing organic matter and microorganisms, and enriching soil with castings (Hendrix *et al.*, 1990; Edwards, 2004). A host of microfauna also act as biological mediators of soil fertility and structure. Their activities support soil fertility as they break down plant detritus and other organic matter, and incorporate nutrients into their biomass, which may otherwise move through the system or be lost downstream (Paul and Clark, 1996). Micro- and macrofauna (e.g., acarina and collembola) influence nutrient cycling by regulating bacterial and fungal populations, release energy by breaking down large molecules into smaller units (catabolizing organic matter), and mineralizing and immobilizing nutrients. Their activities influence soil structure by producing organic compounds that bind soil aggregates. Bacteria and fungi are also part of an important cadre of microflora that mediates nitrogen fixation from the atmosphere, transforming it into plant-available forms (Hendrix *et al.*, 1990).

Soil processes in agroecosystems are subject to removal of nutrient-rich biomass during harvest, plus elevated decomposition rates that increase with frequency of tillage and irrigation. In some systems, organic matter is also lost when fields are burned (e.g., to clear biomass for the next planting). Nutrient losses in agroecosystems contrast with unmanaged, undisturbed ecosystems in which nutrient cycles tend to be more nearly closed, with inputs approximately matching outputs (Daily *et al.*, 1997). Many high-intensity farming systems do not retain soil structure and fertility through biological processes, they are rather maintained through tillage and additions of chemical and organic fertilizers (Daily *et al.*, 1997; Matson *et al.*, 1997).

Pollination

Animal pollinators are essential for approximately 35% of global crop production, and 60–90% of all plant species are pollinator-dependent (Klein *et al.*, 2007). Bees are recognized as the taxon providing most pollination services, yet other taxa – including birds, bats, thrips, butterflies and moths, flies, wasps, and beetles – also pollinate some of the world's most important food crops (Nabhan and Buchmann, 1997). Pollination is necessary for sexual reproduction in many crops, including fruits, vegetables, nuts, and seeds (Klein *et al.*, 2007) as well as many wild plants known to contribute calories and micronutrients to human diets (Sundriyal and Sundriyal, 2004). There are also many globally important crops that are pollinated passively or by wind, including cereals, sugarcane, and grasses (Klein *et al.*, 2007).

Overall, pollinators play a significant role in the world's food systems and agricultural economies. The estimated value of insect-pollinated crops in the United States ranged from US $18–27 billion in 2003. If calculations include secondary products, such as beef and milk from cattle fed alfalfa, the estimated value more than doubles (Mader *et al.*, 2011). Although honey bees (*Apis* spp.) are the most important commercially managed pollinator, native and wild bee species also make significant contributions. Approximately 15% of the value associated with pollination services comes from native bees and other animals living in farmlands and adjacent natural habitat (Mader *et al.*, 2011). Both agricultural management and landscape configuration are important in determining availability and distribution of pollination services. Some wild (native) pollinators nest within fields, including ground-nesting bees, or disperse from nearby unmanaged habitats to pollinate crops (Ricketts *et al.*, 2004). Conserving wild pollinators in unmanaged or restored natural habitats adjacent to agricultural fields can improve pollination levels and stability, which can support increases in agricultural yields (Klein *et al.*, 2003).

The potential contributions of native pollinators have received a great deal of recent attention due to global declines in managed honey bee colonies (National Academies, 2006). Declines in honey bee abundance, driven by establishment of parasitic mites (e.g., *Varroa destructor*), hive pests, and social factors such as aging beekeeper populations, have resulted in pollination shortages in some areas (Klein *et al.*, 2007). This has caused increased prices for honey bee rental and created concern about pollination shortfalls, such as those seen in California almonds (National Academies, 2006). These factors have heightened interest in the role of native pollinators to help assure availability and stability of crop pollination services. Recommendations for managing pollinator-friendly landscapes include maintaining areas of natural and semi-natural perennial habitat (e.g., grass and woodlands, forests, old fields, and hedgerows) to provide ample floral and nesting resources available throughout the year (Kremen *et al.*, 2007; Mader *et al.*, 2011).

Pest control

Pest damage is a major limiting factor for global food production. Animal pests destroy 8–15% of global wheat, rice, maize, potato, soybean, and cotton production (Oerke, 2005) and cause more than US$30 billion in damage in the United States each year (Pimentel *et al.*, 2005). However, despite dramatic increases in pesticide application, damage levels remained roughly unchanged during the four decades following the escalation of pesticide use after World War II (Pimentel *et al.*, 1992; Oerke, 2005). Pesticides have even precipitated pest outbreaks. For instance, Southeast Asian rice fields were devastated by the brown planthopper (*Nilaparvata lugens*) after excessive pesticide application caused the pest to evolve resistance while its predators continued to suffer high mortality (Kenmore *et al.*, 1984). In Indonesia, planthopper outbreaks abated once many pesticides were banned (Naylor and Ehrlich, 1997). Instead, farmers adopted an integrated pest management approach in which natural pest predators were fostered, and pesticides were used only after damage exceeded critical economic thresholds.

The idea that farmers can harness nature to provide pest control benefits is not new. As early as AD 304, Chinese farmers created and maintained citrus ant (*Oecophylla smaragdina*) nests in their orchards to control pest outbreaks (Huang and Pei, 1987). Centuries later, in 1888, the modern concept of classic biological control emerged, again in citrus orchards, when introduced vedalia beetles (*Rodolia cardinalis*) caused the near complete collapse of cottony-cushion scale (*Icerya purchasi*) pests in California (Caltagirone and Doutt, 1989). Since then it has become widely recognized that adjusting agricultural practices to benefit pest predators can provide a valuable pest control strategy with significant benefit to farmers.

Strategies for enhancing pest control services to agriculture may require understanding predator ecology to ensure that pest predators have suitable food and habitat resources throughout their life cycles (Landis *et al.*, 2000). Plants that provide floral or nectar resources can be used to sustain predators and parasitoids. Sweet alyssum (*Lobularia maritima*) has proven especially effective for bolstering syrphid fly abundances in California (Tillman *et al.*, 2012). Predator populations can also be enhanced indirectly through agricultural practices that increase nonpest prey, for example, by applying mulch or intercropping (Riechert and Bishop, 1990; Bugg *et al.*, 1991). Small patches of native vegetation on and around farms can provide these species with food resources and overwintering habitat (Landis *et al.*, 2000; Tillman *et al.*, 2012). Emerging evidence suggests that conservation activities at a landscape scale can also benefit farmers. For example, conserving natural habitat surrounding farms increases predators and often enhances pest control services (Thies and Tscharntke, 1999; Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011b; Karp *et al.*, 2013). These examples represent but a few of many techniques that have emerged for controlling crop pests with native predators, many of which are readily accessible to farmers through government, university, and agency extension programs.

Hydrologic services – water flow regulation and water purification

Agricultural production relies on a host of water-related ecosystem services, ranging from water supply (quantity), to purification (quality), and flood protection (Brauman *et al.*, 2007). Globally, agroecosystems are a major consumer of groundwater and surface water, accounting for approximately 70% of freshwater use worldwide (UN Water, 2013). Agricultural water use may be as high as 90% of total withdraws in fast-growing economies (UN Water, 2013) or arid environments (USDA ERS, 2013). Irrigation is considered a consumptive water use, in that water is not directly returned to rivers and streams. Much of this water eventually returns to the atmosphere through evaporation and plant transpiration (e.g., the process of water moving through plant tissues and evaporating through leaves, stems, and flowers), particularly in thirsty crops, such as alfalfa and cotton.

The majority of prime land for rainfed cultivation is already in use and development of irrigated land has contributed substantially to production gains. A prime example is in India, where the growth of irrigated rice and wheat on the semiarid plains of Punjab has substantially boosted food production over the past several decades (Matson *et al.*, 1997). Globally, approximately 40% of crop production is supported by irrigated agricultural lands, which account for 20% of all agricultural areas (UN Water, 2013). Scientists project that continued increases in agricultural production would require sustained or increased supply of irrigation water (Matson *et al.*, 1997).

Ecosystems do not create water; however, they can modify the amount of water moving through the landscape. These modifications result from ecosystem influence on the hydrologic cycle, including local climate, water use by plants, and modification of ground surfaces that alter infiltration and flow patterns (Brauman *et al.*, 2007). The amount of water stored in watersheds, or discharged above and below ground, influences water supply and availability to downstream users. The understanding of how water availability changes with land use and land cover change is elementary (Brauman *et al.*, 2007). Planting of forests and trees – native or introduced – can either increase or decrease evapotranspiration and downstream water availability, depending on the context. In one study, analysis of paired catchment experiments found that stream flows were reduced 45% on an average when grasslands were converted to forests (Farley *et al.*, 2005). Other studies from the Amazon basin illustrate that evapotranspiration from a pasture can be up to 24% less than a nearby forest (Von Randow *et al.*, 2004). Vegetation can also be selected to support management goals based on water requirements. For example, Australian studies describe use of plants such as lucerne (*Medicago sativa*), eucalyptus trees (*Eucalyptus* spp.), and saltbush (*Atriplex* spp.), which are thought to mitigate potential crop damages in areas where rising water tables bring saline water into root zones by lowering water tables through high transpiration rates (Heuperman *et al.*, 2002).

Water purification depends on filtration and absorption of particles and contaminants by clay, silt, and sand particles in soil as well as living organisms in soil and water. Agricultural production depends on water quality to maintain productive capacity, but there are a number of threats and challenges the continued provision of clean water. Irrigated farmlands in arid and semiarid regions are experiencing degradation due to salinization and waterlogging (Matson *et al.*, 1997).

Maintaining water quality for agriculture and other uses is increasingly thought to require maintaining buffers of vegetation with intact groundcover and root systems throughout the watershed. Vegetation, microbes, and stabilized soils can remove pollutants from overland flow and from groundwater by physically trapping water and sediments, by adhering to contaminants, by reducing water speed to enhance infiltration, by biochemical transformation of nutrients and contaminants, and by absorbing water and nutrients from the root zone (Naiman and Décamps, 1997). Vegetated riparian buffer zones in particular perform critical functions to support water quality.

Genetic resources provide a pool of raw material necessary to support the process of natural selection and produce evolutionary adaptations in unmanaged ecosystems. In agroecosystems, crop and animal breeders draw on genetic diversity using traditional breeding and biotechnology to artificially select and perpetuate desirable traits (Zhang *et al.*, 2007). A broad portfolio of genetic resources increases the likelihood of maintaining production, particularly as environmental pressures such as climate, pests, and disease fluctuate. Production stability comes through an array of genotypes, each with different characteristics of disease resistance, tolerance for environmental extremes, and nutrient use (Esquinas-Alcázar, 2005). Different genotypes, or cultivars, are required for plants in orchard systems and hybrid seed production to set fruit or seed (Free, 1993; Delaplane and Mayer, 2000). The benefits of genetic variation at the species level include enhanced biomass production, reduced loss to pests and diseases, and more efficient use of available nutrients (Tilman, 1999).

Crop production is supported by genetic resources from two important sources. First are 'landraces,' the varieties of crops and livestock that have been cultivated and selected by farmers over many generations practicing traditional agriculture (Shand, 1997). Second are closely related species that survive in the wild, known as crop 'wild relatives.' Areas with high concentrations of landraces and wild relatives are considered centers of crop genetic diversity (Shand, 1997). These centers are critical, as many important crops could not maintain commercial production without periodic infusions of genetic resources from wild relatives (de Groot *et al.*, 2002).

The consequences of losing genetic resources in a crop system can be severe. The Irish potato famine in the 1830s is one such example. The crop failure can be attributed in part to a very limited number of genetic strains of potatoes in Ireland, which made the crop particularly susceptible to potato blight fungus (Hawtin, 2000). Reintroducing disease-resistant varieties from Latin America, where the potato originated, helped to resolve the problem. Recent reviews of crop genetic resources highlight that increases in human population size, ecological degradation in farmlands, and globalization have contributed to a dramatic reduction of crop diversity worldwide. Approximately 150 species now comprise the world's most important food crops and most human diets are dominated by no more than 12 plant species (Esquinas-Alcázar, 2005). Loss of crop genetic diversity is of great concern because it reduces the pool of genetic material available for natural selection and artificial selection by farmers and plant breeders, thereby increasing the vulnerability of crops to sudden environmental changes (Esquinas-Alcázar, 2005).

Disservices to Agriculture Detract from Agricultural Productivity

Disservices to agriculture result from the ecological processes or relationships that detract from agricultural productivity. Crop pests, including seed eaters, herbivores, frugivores, and pathogens (e.g., insects, fungi, bacteria, and viruses), can result in reduced productivity, or total crop loss in worst case scenarios (Zhang *et al.*, 2007). Weeds and other noncrop plants can reduce agricultural productivity through competition for resources. At the field scale, weeds compete with crops for sunlight, water, and soil nutrients and may limit crop growth and productivity by limiting access to these critical resources (Welbank, 1963). Within fields, plants may exhibit allelopathy (biochemical inhibition of competitors), such as the toxins exuded by some plant roots that can decrease crop growth (Weston and Duke, 2003).

Resource competition that potentially detracts from agricultural yields can also take place at larger scales. Competition for pollination from flowering weeds and other noncrop plants beyond agricultural fields can reduce crop yields (Free, 1993). Water used by other plants, such as trees that reduce aquifer recharge, can reduce water available to support agricultural production by diminishing an important source of irrigation water (Zhang *et al.*, 2007).

Food safety concerns related to pathogen outbreaks are other potential detractors from agricultural productivity. Since the 1990s these concerns have gained some prominence in highly productive regions, such as the Salinas Valley of California (the 'salad bowl of America'), which experienced *Escherichia coli* contamination of leafy greens. The unfortunate consequence has been broad-scale removal of riparian habitat to minimize wildlife intrusion into crop fields. Wildlife was posited to spread harmful bacteria, although whether it constitutes a significant food safety risk remains unclear. Nevertheless, over a 5-year period following an *E. coli* O157:H7 outbreak in spinach, 13.3% of remaining riparian habitat was removed from the Salinas Valley (Gennet *et al.*, 2013). This habitat removal may result in degradation or loss of the ecosystem services typically provided by riparian areas.

It is important to note that disservices from agriculture can also affect the productivity and environmental impacts of farming systems through multiple feedbacks. For instance, when habitat for natural enemies is removed, pest outbreaks can result in crop damage or loss, resulting in reduced productivity and potentially increased use of pesticides, which may be accompanied by further detrimental effects. Similarly, when riparian habitat is degraded or removed, the hydrologic services of water flow regulation and water purification services can be diminished or lost (**Figure 2**).

Managing Ecosystem Services in Agricultural Landscapes

Different ecosystem services are mediated and delivered at different scales, ranging from individual farm plots to entire watersheds or regions (Zhang *et al.*, 2007). Accordingly, efforts to maintain or enhance ecosystem services in farming landscapes may require deliberate management of different areas and scales, including cultivated areas within farms, noncultivated areas within farms, and broader landscapes (well beyond farm boundaries) that comprise both cultivated and noncultivated areas.

Management of cultivated fields often focuses on ecosystem services that have a direct influence on farm productivity; farmers have a direct interest in managing services, including pollination, pest control, soil fertility and nutrient cycling, soil retention, water purification, and water flow regulation. On-farm practices that target water conservation, including moisture from rainfall that is stored in the soil profile, may help to offset water shortages during dry seasons or droughts (Rost *et al.*, 2009). Mulching or modification of field tillage practices can reduce evaporation of soil water by 30–50%. In addition, farmers can harvest rainwater by installing microtopographic features in their fields (e.g., small bunds or pits) as well as ponds, dykes, or other infrastructure, enabling recovery of up to 50% of water normally lost in the system (Rost *et al.*, 2009; Power, 2010).

Management of noncultivated areas of farms may support both ecosystem services of benefit both to farmers themselves and to the broader public. Studies of smallholder farms have documented the benefits of planting trees in noncultivated areas, in both temperate and tropical regions, including Nepal (Carter and Gilmour, 1989) and Costa Rica (Casasola *et al.*, 2007). Increasing tree cover is associated with enhanced diversity and richness of mobile organisms – such as birds, bats, and butterflies (Harvey *et al.*, 2006) – soil retention (Carter and Gilmour, 1989), and carbon sequestration (Montagnini and Nair, 2004). In the case of management that supports ecosystem services, which provide public benefits but does not directly support farm productivity (e.g., carbon sequestration needed to support climate regulation), farmers may have less incentive to implement management practices. To stimulate provision of public benefits, policies and programs may be needed to offset the costs of management investments or create financial incentives for using new management practices (Garbach *et al.*, 2012).

Broader landscape management to support ecosystem services requires to understand the ways in which ecosystem processes take place across multiple parcels of land (including movement of biotic and abiotic components, such as organisms, water, and nutrients). Pollination illustrates the importance of broader landscape management, highlighting that mobile organisms respond to resources both within and beyond cultivated fields. Studies in California suggest that pollination by native bees was higher in farms near greater proportions of natural habitat (no significant relationship was found between pollination and farm type, insecticide usage, field size, or honeybee abundance) (Kremen *et al.*, 2004). There is some evidence that multiple farmers practicing diversified farming – using practices focused on maintaining and enhancing biodiversity of flora and fauna within and across fields – across a region can result in greater provision of ecosystem services than simply the sum of their individual management actions (Gabriel *et al.*, 2010).

Considerations for Managing Ecosystem Services

Managing ecosystem services requires building an in-depth understanding of the species, functional groups, and ecological processes through which services are provided (Kremen, 2005). **Table 2** highlights some of the key organisms, guilds, and communities that are the biological mediators of ecosystem services and disservices to agriculture. Their biological activities affect the provision of ecosystem services at the field, farm, landscape, and regional-to-global scales. For example, at the field scale, services of soil structure and fertility enhancement (including the processes of soil formation, development of structure, and nutrient cycling) are provided by microbes, invertebrates, and nitrogen-fixing plants. Thus, field-scale management may focus on practices such as incorporating nitrogen-fixing plants into crop rotations and planning the timing and depth of tillage to minimize impacts on beneficial invertebrates. At the farm scale, soil-related ecosystem services may also be influenced by levels and types of vegetative cover; thus, farm-scale management may focus on the total area, type, and timing of harvest (if any) of vegetation, including both cultivated and noncultivated areas (**Table 2**).

Measuring Ecosystem Services and Evaluating Service Providers

There is a great deal of interest in methods used to measure provision of ecosystem services. One method is to evaluate the presence or abundance of organisms believed to provide ecosystem services. A second method is to measure the delivery of the service themselves (Kremen and Ostfeld, 2005). For instance, in order to measure pollination in a California squash field, the first method would focus on the abundance and distribution of key pollinators, such as native squash bees (*Peponapis pruinosa*) and other insects. Alternatively, the second method would evaluate whether a squash crop was sufficiently pollinated. These two methods are complementary and may be used together to build a comprehensive understanding of ecosystem service delivery. Counting ecosystem service providers can provide insight into the likelihood of an ecosystem service being available. In contrast, measuring the outcomes (e.g., pollination metrics, such as seed set or pollination deficit) can help to verify delivery of a service but does not provide much information about the organisms providing the service. A comprehensive approach to understanding and measuring ecosystem services includes understanding key ecosystem service providers (e.g., organisms, guilds, and communities), factors influencing the ability of providers to deliver services of interest, and measuring spatial and temporal scales over which providers operate and ecosystem services are available (Kremen and Ostfeld, 2005).

The relationships between biodiversity and ecosystem function are also important for understanding provision of ecosystem services (Altieri, 1995; Hooper *et al.*, 2005; Tscharntke *et al.*, 2005). In general, species richness – measured as the number of species in a given area – is associated with enhanced ecosystem services (Balvanera *et al.*, 2006). Similarly, biodiversity loss is associated with diminished

Table 2 Ecosystem services and disservices to agriculture, the scales over which they are typically provided, and organism, guilds, and communities that provide them

	Organisms, guilds, and communities that provide services at the following scales:			
	Field	*Farm*	*Landscape*	*Region/globe*
Services to agriculture				
Genetic resources	Diversity within a single crop; genotypes help to provide pest and disease resistance	Diversity across multiple crops; rotations help to provide pest and disease resistance	Landrace varieties, wild relatives of crops; can be used to infuse crops with genetic diversity	Landrace varieties, wild relatives of crops; can be used to infuse crops with genetic diversity
Hydrologic services: Water flow regulation, water purification	Vegetation within cultivated areas	Vegetation around water sources, drains, and ponds	Vegetation cover in watershed; riparian communities	Vegetation cover in watersheds; riparian communities
Pest control	Predators, parasites (animals and insects, including vertebrates, invertebrates, and parasitoids)	Predators, parasites (animals and insects, including vertebrates, invertebrates, and parasitoids)	Predators, parasites (animals and insects including vertebrates, invertebrates, and parasitoids)	–
Weed control	Predators, competitors (herbivores, seed predators, and other competitors that limit plants and fungi)	Predators, competitors (herbivores, seed predators, and other competitors that limit plants and fungi)	Predators, competitors (herbivores, seed predators, and other competitors that limit plants and fungi)	–
Pollination	Pollinators: primarily bees but also bats, thrips, butterflies and moths, flies, wasps, beetles, and birds (note: some crops are wind-pollinated)	Pollinators: primarily bees but also bats, thrips, butterflies, and moths, flies, wasps, beetles, and birds (note: some crops are wind-pollinated)	Pollinators: primarily bees but also bats, thrips, butterflies and moths, flies, wasps, beetles, and birds (note: some crops are wind-pollinated)	–
Soil structure and fertility (including processes of soil formation, development of structure, nutrient cycling supporting fertility)	Microbes, micro and macro invertebrates, nitrogen-fixing plants	Vegetative cover	Vegetative cover	–
Erosion protection	Cover crops and perennial crops	Cover crops and perennial crops	Riparian vegetation; vegetative cover on steep areas, thin soils; floodplains	Riparian vegetation; vegetative cover on steep areas, thin soils; floodplains
Disservices to agriculture				
Pest damage and pathogen outbreaks	Insects, snails, birds, mammals, fungi, bacteria, viruses, and weeds	Insects, snails, birds, mammals, fungi, bacteria, viruses, and weeds	Insects, snails, birds, mammals, fungi, bacteria, viruses, and rangeland weeds	–
Competition for water	Weeds	Vegetation near drainage ditches	Vegetation in watersheds	Vegetation in watersheds
Competition for pollination	Flowering weeds	Flowering weeds	Flowering plants in watershed	

Source: Adapted from Zhang, W., Ricketts, T., Kremen, C., *et al.*, 2007. Ecosystem services and dis-services to agriculture. Ecological Economics 64, 253–260.

provision of ecosystem services, often due to reduced efficiency of resource capture and use in ecological communities, diminished biomass production, and diminished rates of nutrient decomposition and recycling (Cardinale *et al.*, 2012). In addition to biodiversity, ecosystem function is influenced by the identity, density, biomass, and interactions of species within a community (Kremen and Ostfeld, 2005). These attributes can aggregate at different levels (e.g., field, farm, and landscape scales). Thus, it is important to consider how ecological attributes may vary over space and time, as this can influence when and where ecosystem services are available.

Many ecological studies aim to understand which populations, species, functional groups, guilds, food webs, and habitat types produce key services. One method to do so is a functional inventory, which includes identifying and describing the focal ecosystem service providers in a landscape and quantifying their contributions (Kremen and Ostfeld, 2005). A functional inventory is most relevant at the scale of the focal ecosystem service. Thus, evaluating disease resistance in crops may require a functional inventory at the genetic level, (Zhu *et al.*, 2000) whereas evaluating biological control of pests may require an inventory at the level of a population or food web (Kruess and Tscharntke, 1994).

Functional Differences

A second method to build understanding of ecosystem service providers is evaluating functional attribute diversity (Kremen and Ostfeld, 2005). This method describes differences within the guild, functional group, or community that provides each service. A commonly used metric is ecological distance, which describes differences in morphology, ecology, or behavior of the organisms (Laliberté and Legendre, 2010; Walker *et al.*, 1999) that provide ecosystem services. Characteristics that determine how an organism performs key functions are often used for measuring ecological distance, such as root depth of plants (potential determinant of water flow regulation), timing of emergence and senescence (primary production and nutrient cycling), or pollinator's tongue length (pollination).

Response to Disturbance

Comprehensive evaluation of the abundance of ecosystem services providers, and broader patterns of ecosystem services availability, can build a solid foundation for investigating potential influence of disturbance. For example, what happens when species that provide key services are lost? Sometimes ecosystem services are resilient to disturbance and loss. If remaining species can compensate for the species that are removed or have become extinct, ecosystem services may also be maintained rather than diminished. This compensation effect can happen in several ways.

First, compensation can occur through response diversity, described as the diversity of responses to change shown among species contributing to the same ecosystem functions and services disturbance (Elmqvist *et al.*, 2003). Second, it can occur through functional compensation, which occurs when efficiencies of individual ecosystem service providers shift in response to changing community composition. Third, compensation may also happen through the portfolio effect. Just as having a diverse investment portfolio may buffer an investor against fluctuations in individual investments, a diverse biological community is more likely to contain some species that can persist through disturbances (Tilman *et al.*, 1998).

Promoting Synergies between Yield and Ecosystem Services

Recent global estimates project the need to double world food production by 2050 (World Bank, 2008a; The Royal Society, 2009; Godfray *et al.*, 2010). At the same time, there is a growing consensus that increased food production must not come at the expense of diminishing key ecosystem services, such as carbon sequestration, water flow regulation, and water purification. Additionally, the prospect of clearing additional land for agriculture is unappealing, as most of the remaining potentially arable land on the Earth is covered by tropical rainforest; agricultural expansion in these areas would come at a steep cost to biodiversity and the delivery of services from biodiversity-rich rainforests (Ramankutty and Rhemtulla, 2012). Therefore, existing farmlands are being called on to simultaneously increase crop yields and provision of ecosystem services. This call for multifunctional agricultural landscapes can be summarized as agroecosystems in which productivity and ecological integrity are complementary outcomes, rather than opposing objectives.

Agroecology is a scientific subdiscipline and farming approach intended to do precisely this by applying ecological concepts and principles to the design and management of sustainable farming systems (Altieri, 1995). Agroecology emphasizes understanding the ecology of crop, livestock, and other species in a farming system as well as the mechanisms that govern their functions. It highlights the role of human managers in maintaining and enhancing desirable functions and related ecosystem services to optimize use of water, energy, nutrients, and genetic resources (Altieri, 1995; Gliessman *et al.*, 1998). In doing so, the practice of agroecology often seeks to intensify production systems – that is, to deliver greater yields per unit of land, water, or other inputs used – in a way that is based on and, in turn, maintains healthy systems of soil, water, and biodiversity.

There is considerable evidence that systems of agroecological intensification can increase yields relative to prevailing farmer practices in many parts of the world (e.g., Pretty *et al.*, 2006). A recent quantitative review investigated whether agroecological intensification systems tend to deliver yield and ecosystem service benefits simultaneously (Garbach *et al.*, in press). Here the authors summarize results for two illustrative systems of agroecological intensification: conservation agriculture and the system of rice intensification.

Conservation agriculture is an agroecological intensification system that aims to increase productivity and sustainability of soil resources through three main practices: (1) minimal soil disturbance, (2) permanent soil cover, and (3) crop rotations (Kassam *et al.*, 2009). Development agencies, such as the Food and Agriculture Organization of the United Nations, have promoted this system due to its potential applications in farms of diverse sizes and crop systems (FAO, 2011).

Field studies of conservation agriculture report benefits in soil structure, nutrient cycling, erosion protection, and animal biodiversity relative to conventional soil tillage (Milder *et al.*, 2012). However, inconsistent results have been reported for key services, such as pest control, which was found to be diminished in some field studies due to increased pests harbored by crop residues (Van den Putte *et al.*, 2010). Other field studies have reported increased pest control associated with maintaining soil cover (e.g., mulching and retaining plant residues on soil surfaces) and increased species richness and population density of beneficial insects, such as predatory crickets, beetles, bugs, ants, and spiders (Jaipal *et al.*, 2005).

Synergistic outcomes in conservation agriculture – enhanced yield and ecosystem services – were reported in approximately 40% of comparisons (17 of 43 total quantitative comparisons with conventional cultivation, reported in 16 studies, Garbach *et al.*, in press) (**Figure 3**). However, conservation agriculture studies have also reported trade-offs, such as enhanced yield despite diminished weed control services (Haggblade and Tembo, 2003) and diminished yield but

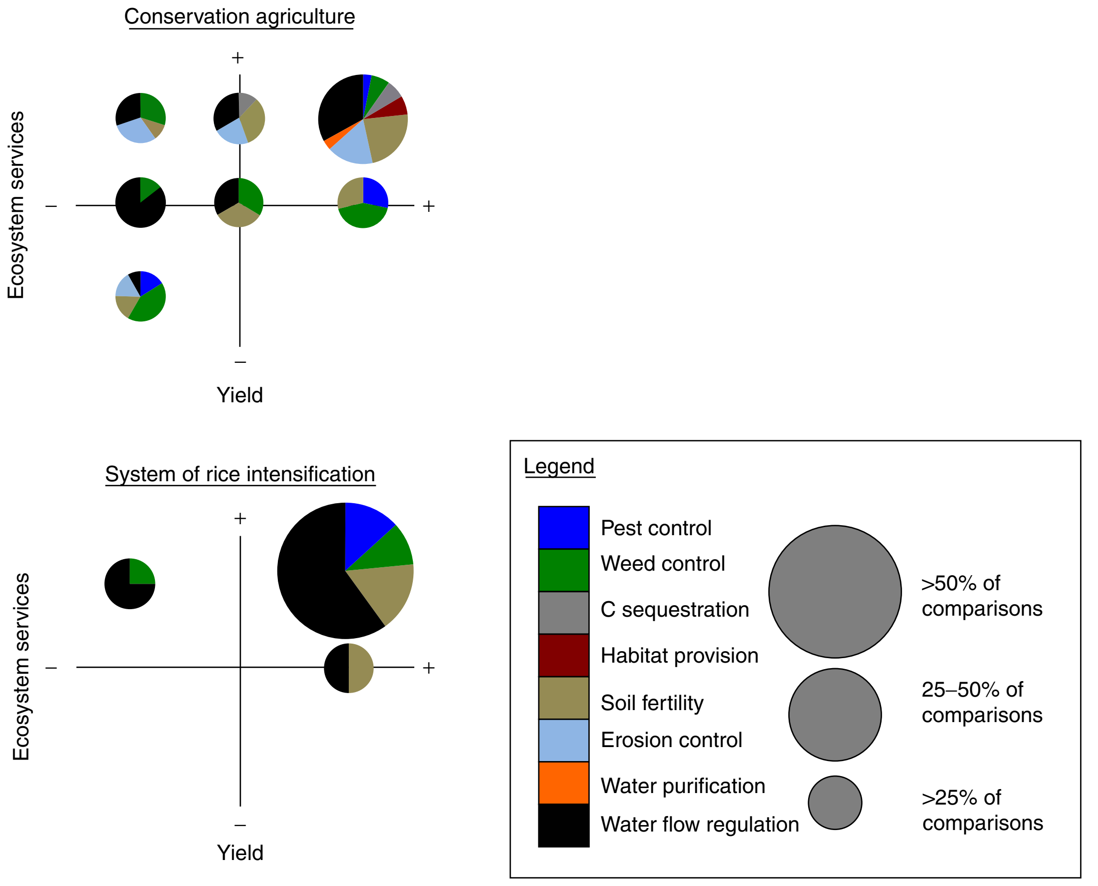

Figure 3 Synergies and trade-offs between ecosystem services and yield in conservation agriculture and system of rice intensification. Bubble location indicates the specific combination of outcomes for ecosystem services (Y-axis: enhanced, upper quadrants; diminished, lower quadrants) and yield (X-axis: enhanced, right quadrants; diminished, left quadrants) relative to comparison systems. Bubbles located on the axis indicate no significant difference from the comparison system. Bubble size indicates the percent of reviewed comparisons reporting each combination of yield and AEI outcomes: large bubbles indicate $>50\%$ of comparisons; medium bubbles indicate 25–50% of comparisons; and small bubbles indicate $<25\%$ of comparisons. The ecosystem services evaluated are represented by colored charts in each bubble and represented as the percentage of comparisons in which the ecosystem service was measured. Adapted from Garbach, K., Milder, J.C., DeClerck, F., *et al.*, in press. Closing yield gaps and nature gaps: Multi-functionality in five systems of agroecological intensification. Proceedings of the National Academy of Sciences-Plus.

enhanced soil structure and erosion control (Araya *et al.*, 2011) (7% of comparisons, **Figure 3**). A small number of studies have reported both diminished yield and ecosystem service (6% of comparisons, **Figure 3**). Diminished yield in conservation agriculture was often associated with a decrease in weed control (Narain and Kumar, 2005) and pest control services (Van den Putte *et al.*, 2010).

The system of rice intensification has received a great deal of recent attention as an agroecological intensification system developed specifically for a staple grain. This approach to irrigated rice cultivation includes six key practices: transplanting young seedlings; low seedling density with shallow root placement; wide plant spacing; intermittent application of water (vs. continuous flooding); frequent weeding; and incorporation of organic matter into the soil, possibly complemented by synthetic fertilizer (Africare, Oxfam America, WWF-ICRISAT, 2010).

Field studies report considerable evidence for synergies between yield and ecosystem services in the system of rice intensification, particularly water flow regulation. Enhancement of both yield and ecosystem services were reported in 87% of comparisons (39 of 45 quantitative comparisons reported in 15 studies, Garbach *et al.*, in press) (**Figure 3**). Most studies compared the system of rice intensification to the predominant unintensified farmer practices in the study area. Thus, the results suggest that the system of rice intensification can significantly improve productivity and ecosystem service delivery relative to current practices in many regions. However, the relative benefits of the system of rice intensification compared with regionally specific best management practices in conventional rice farming are less clear (McDonald *et al.*, 2006).

Landscape Context

From above, agricultural landscapes often resemble a patchwork of rural villages, natural and seminatural habitat, and farms cultivating a diverse array of crops. 'Natural habitat' in this context describes the full range of natural, seminatural, and weedy vegetation types that tend to be present in agricultural areas. However, over the past decades in many parts of the world, remnants of natural habitat have begun disappearing, replaced by vast fields of industrial agriculture (Perfecto *et al.*, 2009). This physical restructuring of agricultural landscapes has resulted in dramatic changes in many critical ecosystem services.

Ecological processes often occur at scales larger than individual farms, making the composition of the broader agricultural landscape an essential determinant of ecosystem service provision. Natural habitat can provide many benefits to farmers and the public (Kremen and Miles, 2012). Benefits include harvestable goods, such as fuelwood, medicinal plants, and bushmeat, as well as genetic resources provided by crop wild relatives. Natural habitat can provide recreational opportunities and has been found to support mental health in some case studies (Bratman *et al.*, 2012).

Ensuring that agricultural systems realize diverse benefits requires looking beyond on-farm practices and managing the broader landscape. Here the authors focus on examples of landscape management for two animal-mediated ecosystem services: pollination and pest control. Many other ecosystem services, including water purification, genetic resources, and soil structure and fertility enhancement, also require landscape management. Animal-mediated services, however, are among the most severely affected by landscape simplification, and landscape-level effects have been well documented.

When natural habitat is removed for agriculture, beneficial pollinators and predators of insect pests often decline in abundance, whereas pests increase, which may precipitate lower yields for farmers (Philpott *et al.*, 2008; Karp *et al.*, 2011; Melo *et al.*, 2013). The amount of natural habitat required to sustain pest control and pollination services is often a product of the home range sizes of the predator and pollinator species that provide these services, an attribute that can vary considerably among species. The relevant management scale for farmers depends on both the focal ecosystem service and on the attributes of its animal providers. Fortunately, the past decades have seen a surge of research documenting the role of landscape structure and composition in sustaining pollinators and pest control providers.

Pollination

Although managed honey bees (*Apis mellifera*) provide most pollination globally, native insects are often more effective pollinators and provide complementary pollination benefits (Garibaldi *et al.*, 2013). Further, native insects enhance pollination resilience, especially as honey bee colonies continue to collapse (Winfree and Kremen, 2009). Retaining a diverse pollinator community is thus increasingly recognized as an essential component of any sustainable food system.

Unsurprisingly, native pollinators rely on native habitat. Many species center their foraging activity around the nest, often located in patches of habitat embedded in agricultural landscapes (Lonsdorf *et al.*, 2009; Jha and Kremen, 2013). Pollinator activity matches pollinator foraging ranges, and pollination is thus consistently higher at the edges of crop fields near native habitat than in the interior of large crop monocultures (Kremen *et al.*, 2004; Ricketts *et al.*, 2004, 2008; Klein *et al.*, 2012). As large fields of a single crop variety replace more diversified farms, the total length of time during which crop species are flowering becomes shorter. As a result, pollinators may become increasingly dependent on the wild plants that flower throughout the year in noncropped areas (Mandelik *et al.*, 2012). Pollination services are thus not only higher but also more stable at field edges than in the interior (Garibaldi *et al.*, 2011).

Although pollination services may vary from crop to crop, pollinator to pollinator, and region to region, the positive influence of natural habitat on pollinator activity has proven remarkably consistent across many studies (Ricketts *et al.*, 2008). This consistency has allowed researchers to create spatial pollination models that estimate pollination provision on the farm based on the composition of the surrounding landscape (Lonsdorf *et al.*, 2009). For instance, the InVEST, the ecosystem service modeling platform operated by the Natural Capital Project, allows land managers to predict the pollination consequences of their land-use decisions and manage land assets accordingly.

Pest Control

Not all crops are animal pollinated, but every crop suffers pest damage. The shift from diversified, agricultural landscapes with patches of natural habitat to large monocultures that lack natural habitat has likely brought with it more severe pest outbreaks. High vegetation diversity ensures that specialist pests do not enjoy vast food resources (Matson *et al.*, 1997). Further, because not all crops and vegetation in natural habitat is palatable to pests, complex landscapes may inhibit pest movements and cause more localized outbreaks (Avelino *et al.*, 2012). However, natural habitat can sometimes provide pests with resources vital for completing their lifecycles and thus facilitate outbreaks (Chaplin-Kramer *et al.*, 2011b). For example, because aphids sequester chemicals in wild mustards (*Brassica nigra*) as antipredator defenses, the proximity of natural habitat with high mustard density may function to increase the density of aphids in nearby crop fields (Chaplin-Kramer *et al.*, 2011a).

Another critical consideration, however, is the predators of crop pests. Predators rely on natural habitat for essential activities, including breeding, roosting, foraging, and hibernating (Landis *et al.*, 2000; Jirinec *et al.*, 2011). Predator abundance and diversity thus regularly decline as agricultural landscapes shift from complex mosaics of natural habitat and cropland to simplified monocultures (Bianchi *et al.*, 2006; Chaplin-Kramer *et al.*, 2011b). Although diverse predator communities are not always more effective at providing pest control because predators sometimes consume each other (Vance-Chalcraft *et al.*, 2007), most studies report that more predator diversity translates to more effective pest control (Bianchi *et al.*, 2006; Letourneau *et al.*, 2009; Chaplin-Kramer *et al.*, 2011b).

An increasing number of studies have documented increased pest consumption in complex versus simple landscapes (Thies and Tscharntke, 1999; Gardiner *et al.*, 2009; Chaplin-Kramer and Kremen, 2013; Karp *et al.*, 2013). Fewer studies, however, have traced the benefit of maintaining natural habitat all the way to crop yields and profits, but some have reported positive effects (Thies and Tscharntke, 1999; Karp *et al.*, 2013). Like pollination, the relevant scale for pest management can vary from predator to predator and from pest to pest, such that distant areas may determine the abundance of highly mobile animals (Werling and Gratton, 2010). Simply focusing on local agricultural practices may be ineffective. Because predator communities often collapse after harvest, a stream of colonizers from adjacent natural habitat may be required to replenish the predator community in the following year.

Landscape Effects on Agriculture: A Costa Rican Case Study

Tropical rainforest provides an array of ecosystem services, including water purification, water flow regulation (e.g., supporting hydropower production), carbon sequestration, and cultural services such as ecotourism. Recognizing this, in the mid-1990s the Costa Rican government created the first national payment for ecosystem services (PES) scheme, in which landowners were paid to maintain rainforest on their private lands (Sánchez-Azofeifa *et al.*, 2007). For farmers, the program provided the dual benefit of monetary compensation for uncultivated lands and continued provision of critical ecosystem services.

The canton of Coto Brus in Southern Costa Rica has been studied as a model system for how strategic conservation efforts influence agricultural production. Unlike many other parts of the country that now host vast expanses of pineapple, oil palm, or banana, Coto Brus still exists as a patchwork of coffee plantations, pasture, small rural villages, and tropical wet forest, perhaps a result of its hilly terrain (Mendenhall *et al.*, 2011). This complex configuration supports a remarkable concentration of biodiversity, often at par with native forest (Daily *et al.*, 2001; Mendenhall *et al.*, 2013). Coffee, the most extensively cultivated crop in the region, benefits from this biodiversity. Although coffee can self-pollinate, animal pollination increases yields, sometimes by more than 50% (Ricketts *et al.*, 2004). Because wild bees rely on rainforest habitat, coffee plants located near rainforest enjoy significantly higher pollination than sites in the middle of extensive plantations. Higher pollination translates to higher yields, better coffee quality, and increased profits. One study found that yields increased by 20% and misshaped ‘peaberries’ decreased by 27% within 1 km distance of two forest patches (Ricketts *et al.*, 2004). These benefits translated into a significant economic gain, approximately US$60 000 per year for a single coffee plantation.

Costa Rican coffee plantations also enjoy pest control benefits from forest patches. The coffee berry borer beetle (*Hypothenemus hampeii*), coffee's most damaging insect pest, arrived in Costa Rica in 2000 and the canton of Coto Brus in 2005 (Staver *et al.*, 2001). Not more than 5 years later, native birds had already expanded their diets to include the pest and began reducing infestation severity by half (Karp *et al.*, 2013). Like wild bees, many of the pest-eating birds rely on forest habitat, and pest control provision is higher on farms with more forest cover (Karp *et al.*, 2013). Small, unprotected forest patches embedded in coffee plantations provided the most benefits. Forest patches smaller than 1 ha area secured approximately 50% of the total pest control benefits across the Coto Brus valley (**Figure 4**).

Policies and Programs to Conserve and Enhance Ecosystem Services in Agricultural Landscapes

Growing interest in the management of ecosystem services has been matched, in recent years, by a proliferation of policy and programmatic strategies to promote the conservation or enhancement of these services in agricultural landscapes. Traditionally, environmental management policies were often described in terms of a dichotomy between regulatory instruments (‘command and control’ requirements put forth by governments) and market-based instruments focused on shifting incentives and price signals for farmers, businesses, and other market actors. However, this dichotomy is now understood to be too simplistic: not only have the boundaries

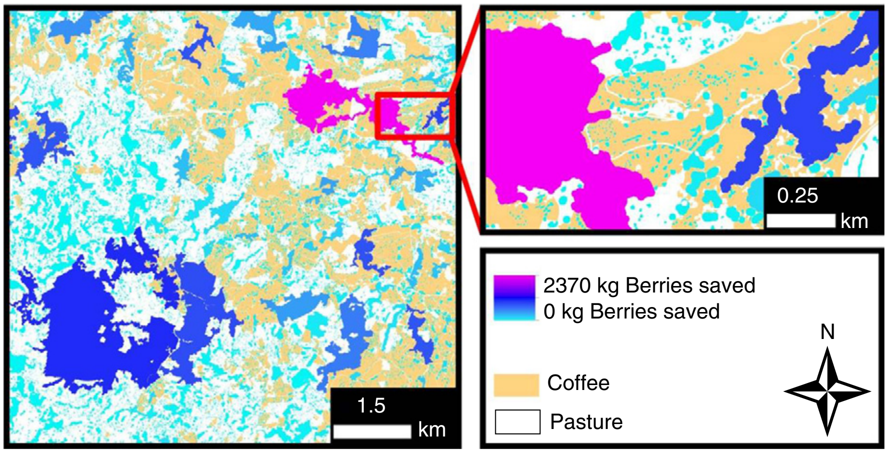

Figure 4 Pest control value of forest patches to coffee plantations in Southern Costa Rica forest provides habitat for the insectivorous birds that consume the coffee berry borer beetle (*Hypothenemus hampei*), coffee's most economically damaging insect pest. Maps show the estimated kilograms of coffee berries saved from infestation by each patch of forest across the Coto Brus Valley. Integrated together, the small, unprotected forest patches embedded within or adjacent to coffee plantations provided the majority of pest control value to coffee farmers.

between regulatory and market-based approaches blurred in many cases, but the range of market-based approaches has also proliferated to the point where further categorization is necessary (Lemos and Agrawal, 2006). This situation reflects a broader shift from the primacy of state institutions in environmental governance to the inclusion – and sometimes dominance – of other groups, including corporations, consumers, civil society organizations, and multinational organizations (Liverman, 2004).

Before describing the range of policy and programmatic strategies used to conserve and manage ecosystem services from agricultural landscapes, it is worth noting some challenges endemic to the governance of agricultural systems, which have limited the effectiveness of most if not all these strategies to varying degrees. First, in contrast to other ecosystem types that are major providers of ecosystem services (e.g., forests, wetlands, and water bodies), agricultural lands are predominately owned or managed by private individuals and companies, or in some instances collectively by rural communities. This means that government authorities generally cannot influence the use of these lands simply by adjusting management plans and policies for lands and water over which they have substantial control, as they might for a state-owned protected area or water body. Second, the historically private nature of agricultural enterprises means that there is little tradition of public sector regulation of agricultural activities, at least with regard to major agronomic decisions affecting ecosystem services, such as rural land use, tillage, planting, and soil fertility management.

Third, agricultural management systems are highly context-dependent (based on climate, soils, hydrology, and other factors), making it inappropriate to devise 'one size fits all' regulations and frequently inefficient to incentivize specific management practices, which may not be appropriate in all contexts. Fourth, most of the major ecosystem services and disservices from agriculture are 'nonpoint' in nature, meaning that they flow from the land itself, in heterogeneous patterns, and are, therefore, difficult to quantify, monitor, or regulate (Ribaudo *et al*., 2010). In contrast, point source impacts, such as water withdrawals and factory emissions from a smokestack or effluent pipe, are much easier to monitor and regulate and have been the subject of many effective environmental regulations. Fifth, monitoring and enforcement in agricultural settings is always a challenge, given the dispersed, private nature of agricultural activities and the nonpoint nature of key ecosystem service outcomes. This is particularly so on the world's approximately 350 million small farms, where the transaction and administrative costs of policies and programs can become proportionately quite high.

Table 3 provides a basic typology of policies, programs, and instruments that may be used to conserve and enhance ecosystem services from agricultural landscapes. Each of these is described further below.

Government Regulation

Agriculture in most countries is a relatively lightly regulated enterprise when compared with other land uses, such as industrial facilities, mines, urban development, and even forestry. Land-use regulations restrict or prohibit agriculture in certain locales (e.g., protected areas, watershed conservation areas, and multiuse management zones) and in some instances aim to reduce the degree to which agriculture conflicts with the provision of important ecosystem services. On a broader scale, both Brazil and Indonesia have enacted temporary moratoria on deforestation for agricultural expansion, which have been credited with reducing the loss of ecosystem services associated with soybean and oil palm expansion, respectively (Macedo *et al*., 2012). A limited number of regulation require on-farm protection of remaining natural ecosystems (e.g., remnant forest patches), or riparian buffers, recognizing their capacity to provide ecosystem services both within and beyond cultivated areas. Nonetheless, these regulations are quite limited overall, and, in many places where they exist, have been poorly enforced and widely ignored. A notable example is Brazil's Forest Code, which on paper requires farmers to establish mosaics of natural habitat within agricultural landscapes but in practice has been generally flaunted.

Regulation of certain farm inputs – particularly pesticides – is robust in many countries and may help to mitigate certain negative impacts of agriculture, including the negative off-site impacts on water quality. However, even where the most toxic pesticides are effectively regulated, use of other legal, but still toxic, pesticides may contribute to large aggregate impacts that diminish both water quality and habitat provision (Schiesari *et al*., 2013). In particular, pesticide contamination can negatively affect the ecological communities in waterways, resulting in degradation or loss of the important services these communities provide (e.g., pest control services provided by mosquito fish in small channels near populated areas; fishing and other cultural services supported by rivers and streams).

Agriculture (and the ecosystem services it provides) may also be governed by broader regulations that apply across many sectors. However, these laws are not always applied fully in the context of farms and ranches. For instance, in the United States, agricultural operations enjoy a variety of statutory or de facto exemptions from otherwise strong environmental laws including the federal Clean Water Act, federal Endangered Species Act, and certain state endangered species acts. These exemptions highlight both the privileged political status that the agriculture sector enjoys in many countries and the difficulty in enforcing these types of laws in an agricultural context. They also underscore the need for interventions focused on ecosystem services that support rather than compromise production functions.

Market-Based Instruments

In the context of policy options, the term 'market-based' is used broadly to refer to strategies that seek to influence behavior by adjusting the price signals to various market actors, including farmers, corporations, and consumers. Such instruments are often intended to remedy 'market failures' that can occur when the providers of ecosystem services do not reap the full benefit of delivering these services, or when they avoid bearing the full cost when they diminish these services. For instance, farmers usually receive little or no monetary benefit from protecting wildlife habitat, although this is an important

Table 3 Typology of policies, programs, and instruments that may be used to conserve and enhance ecosystem services from agricultural landscapes

Type of policy, program, or instrument	*Level of state involvement*	*Role of farmers*	*Examples*
Government regulation ('command and control')			
Land use regulations	High (set and enforce regulations)	Subject of regulations	Land-use zoning; temporary moratoria; riparian buffer zone requirements
Regulation of agricultural inputs			Bans and restrictions on use of certain pesticides; prohibition on planting genetically modified organisms
Regulation of other agricultural practices			Good agricultural practices regulations focused on food safety
Other regulations affecting agricultural lands			Regulations on water, wetlands, and endangered species
Market-based instruments (*influencing price signals or incentive structures*)			
Taxes and subsidies	High (establish tax and subsidy policies)	Payer of taxes or recipient of subsidies	Earning tax credits for best management practices (e.g., Resource Enhancement and Protection Program in PA, USA) subsidies for no-till planters
Markets formed through regulation (e.g., cap-and-trade), leading to PES	Moderate to high (set regulations and oversee market)	Buyers or sellers of ecosystem services, where required or eligible to participate	Water quality trading, regulated carbon markets
Public sector PES	High (deploy funds and administer PES program)	Sellers of ecosystem services	Agri-environment payments (Europe), Farm Bill environmental programs (USA)
Private and voluntary PES	None or low	Buyers or sellers of ecosystem services	Various watershed, biodiversity, and carbon PES involving farmers
Eco-standards and certification	None to moderate	Sellers of agricultural goods produced in accordance with eco-standards	IFC Performance Standards, Rainforest Alliance, and Roundtable on Sustainable Palm Oil
Rural development and farmer assistance programs			
Technical assistance and cost-share programs	None to high (some programs are funded or run by the public sector, others by private or civil society entities)	Program participants and beneficiaries	Farm Bill programs for conservation measures on US farms
Education and training programs			Conservation Farming Unit (Zambia)
Rural development projects and programs			Sustainable Land Management investments (Global Environmental Facility/World Bank)

Note: Some of these instruments also serve additional aims or are not always used to manage ecosystem services in agricultural landscapes. The abbreviation PES stands for payment for ecosystem services.

public benefit. Conversely, when fertilizer runoff from farms contributes to downstream eutrophication and its attendant environmental and economic harms, the farmers responsible for these harms usually bear no economic consequences. Market-based instruments can address such environmental 'externalities,' which would otherwise result in suboptimal delivery of or investment in the provision of ecosystem services.

The most long-standing types of market-based instruments are various forms of taxes and subsidies, which are deployed across many different economic sectors, including agriculture. Historically, agricultural subsidies (e.g., for fertilizer inputs) played a significant role in promoting both the expansion and intensification of agriculture to the significant detriment of ecosystem services. However, taxes and subsidies can also promote conservation-friendly agriculture that may deliver increased levels of ecosystem services. For instance, in Kazakhstan, the government in 2008 began subsidizing farmers to adopt conservation agriculture technologies – including continuous soil cover, direct seeding, and no-till management – that are credited with helping to increase farmer yields and profitability while reducing soil erosion.

PES are abroad set of market-based instruments that have proliferated since the mid-1990s to channel new investment in ecosystem services. Formally, PES has been defined as voluntary transactions between ecosystem service seller(s) (such as farmers or other land managers) and ecosystem service buyer (s) (such as water users or conservation organizations) that provide cash or other payment in exchange for the provision of specific defined ecosystem services (Engel *et al.*, 2008). In practice, however, many PES schemes do not conform to this definition, for instance, because they do not target specific ecosystem services or make payments contingent on actual delivery of these services (Muradian *et al.*, 2010). For instance, many publicly administered PES schemes – including those in Costa Rica, Mexico, Europe, and the United States – function more like environmentally focused farmer subsidy programs than true conditional payments targeted to deliver the largest quantity of ecosystem services for the least cost.

Ecosystem service payments that involve the creation of open markets (as opposed to government payments) are likely to more closely resemble market-based instruments in the classic sense of the term. In the United States and other countries, such markets have been established through regulations that cap total levels of pollution or degradation to a given ecosystem or ecosystem type but enable landowners to trade the limited allocated rights to pollute or degrade. Such 'cap-and-trade' mechanisms are intended to reduce the overall cost of achieving specific environmental goals and have resulted in robust markets for wetland mitigation, wildlife habitat, and agricultural runoff, among other ecosystem services and disservices. Truly voluntary private markets for ecosystem services involving farmers as ecosystem service sellers have also developed in places, although on a smaller scale. These markets have formed around carbon sequestration, watershed conservation, and biodiversity protection, with buyers ranging from private companies (e.g., water bottling businesses), to individuals and corporations wishing to offset their carbon emissions, to conservation organizations.

On a global scale, PES makes only a modest contribution to incentivizing increased ecosystem service delivery from agricultural landscapes. However, this contribution is proportionately much larger in the United States, Europe, and China, where large government PES programs – totaling perhaps US$20 billion per year – exist to support watershed protection, biodiversity conservation, and esthetic protection ('landscape beauty') services (Milder *et al.*, 2010). The future size of ecosystem service markets affecting farmers remains uncertain: although it is clear that farmers deliver critical ecosystem services to a wide range of stakeholders, it is not clear whether these beneficiaries will actually be willing to pay for such services on a large scale, or whether markets will be formed that support the cost-effective procurement and management of these services. The future regulation of greenhouse gas emissions (or lack thereof) at national or global level is a critical factor, as farmers stand to participate heavily in carbon markets if they coalesce at full scale.

Experience from a wide range of contexts suggests that PES in agricultural landscapes is likely to be most effective and scalable where management practices that sustain or increase ecosystem service delivery also support agricultural productivity or profitability. In these situations, PES can provide farmers with supplemental revenue that helps them to overcome initial investment barriers or other constraints to adopting more conservation-friendly management practices (FAO, 2007; Majanen *et al.*, 2011). However, where there is a high opportunity cost to manage agricultural landscapes for increased levels of ecosystem services, PES schemes are unlikely to be able to compete with the profitability of environmentally destructive farming and will find few willing sellers of ecosystem services. A prime example is at the agricultural frontiers of major commodity crops, such as palm oil (Southeast Asia), where levels of carbon payments supported by ecosystem service markets may provide insufficient incentive to prevent deforestation and the significant loss of ecosystem services (Fisher *et al.*, 2011).

A final market-based instrument is the adoption and use of voluntary sustainability standards – often called 'eco-standards' – and associated 'eco-certification' labels for agricultural products and investments. Agricultural sustainability standards are sets of social and environmental criteria put forth to define and encourage sustainable farming by providing market recognition for sustainable producers. These include standards developed and managed by nonprofit organizations (e.g., Fairtade, Rainforest Alliance, and UTZ Certified), multi-stakeholder 'roundtables' for various commodities (e.g., for soybeans, palm oil, sugar, beef, and cotton), individual food companies (e.g., Unilever, Nestlé, Mars, and others), and the finance sector (e.g., IFC Performance Standards and the Equator Principles). By participating in such schemes, farmers, traders, and food companies that produce and sell certified products may benefit from improved market access or market share, price premiums, or improved legitimacy and reputation in the eyes of consumers and regulators. Most, if not all, agricultural sustainability standards include provisions intended to help conserve biodiversity, including sensitive habitat that supports organisms of conservation concern, and ecosystem services (e.g., water purification and water flow regulation and soil fertility and erosion control) (UNEP-WCMC, 2011). Thus, e co-certification may provide monetary incentives for farmers to maintain or enhance ecosystem services, although such incentives are not necessarily explicit or direct with respect to specific ecosystem services.

Rural Development and Farmer Assistance Programs

Governments, international donors, civil society organizations, and others have been involved for decades in supporting agricultural development around the world. In the past 10–15 years, an increasing proportion of these efforts have begun to orient program objectives and activities toward maintaining or increasing flows of ecosystem services in concert with increased yields and farmer profitability. Some initiatives, particularly in developed countries, provide technical assistance, farmer training, or cost sharing of on-farm investments to reduce the negative environmental impacts of agriculture. For instance, a variety of programs funded under the US Farm Bill provide technical assistance and cost sharing for practices such as improved water management structures, erosion control practices, integrated pest management, and transitioning to organic practices.

In the developing world, agricultural development efforts that strongly integrate ecosystem management have been advanced under a variety of names and approaches. A 2006 review surveyed 286 such interventions covering a total of 37 million hectares and found evidence of substantial increases in crop yields together with water-use efficiency gains and potential gains for carbon sequestration and other ecosystem services (Pretty *et al.*, 2006). More recently, the World Bank and other multilateral institutions have supported 'sustainable land management' programs in dryland regions of dozens of countries to enable farmers and pastoralists to increase productivity while conserving water, forests, and other natural resources on which rural livelihoods depend (World Bank, 2008b). The recent dialog around 'climate-smart agriculture' prioritizes the conservation of ecosystem services that help to build resilience in agroecosystems (e.g., water flow regulation, flood control, water storage, and erosion protection) and allow farmers to maintain food production in changing or extreme weather conditions as well as access other livelihood resources if crops fail. In addition, climate-smart agriculture promotes climate change mitigation through carbon sequestration in farm soils and vegetation as well as reduction of greenhouse gas emissions from sources such as livestock, rice paddies, and soil denitrification.

Knowledge Gaps

Although scientific understanding of ecosystem services and their biological mediators in agricultural landscapes has grown dramatically in the past couple of decades, several critical knowledge gaps remain.

First, there is a need to develop mechanistic understanding of the organisms, guilds, and ecological communities that provide ecosystem services (Kremen and Ostfeld, 2005; Kremen, 2005). Identifying key ecosystem service providers and understanding their requirements for performing the biological functions that underpin service delivery are essential for effective management of agroecosystems that deliver both sustained crop yield and ecosystem services. However, to date, these biological requirements are known for only a small subset of key ecosystem service providers (e.g., area requirements for pollination by native bees; Kremen *et al.*, 2004). Second, there are relatively few studies that examine quantitative measures of yield and ecosystem services in the same system (Milder *et al.*, 2012). For instance, although recent metareviews have included 300 or more comparisons of yield effects relative to conventional systems (e.g., Seufert *et al.*, 2012), relatively few studies provide rigorous data on paired outcomes for yield as well as ecosystem services. A third knowledge gap is the lack of studies that link management practices to ecosystem service outcomes at multiple scales. Measuring the spatial and temporal scales over which ecosystem service providers deliver key services is imperative to addressing this gap (Kremen and Ostfeld, 2005). Specifically, building understanding of how ecosystem functions are influenced by the species and communities within an area is needed to understand how their attributes and services can aggregate at different scales from cultivated fields to broader regions, including cultivated and noncultivated areas.

Addressing these knowledge gaps is essential to designing and managing multifunctional agroecosystems. Continued work on this front is needed to answer the growing call for agricultural landscapes that can simultaneously meet production and conservation goals.

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