

## Original Articles

# Evaluating ecosystem service trade-offs and synergies from slash-and-mulch agroforestry systems in El Salvador



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## ABSTRACT

Agroforestry has been proposed as an alternative to slash-and-burn agriculture for smallholder farmers throughout the tropics in order to enhance ecosystem service (ES) supply and conserve biodiversity. Payments for ecosystem services (PES) have emerged as a promising tool to overcome socioeconomic barriers to agroforestry adoption, however PES policy remains nascent, in part due to the challenges associated with quantifying and monitoring ES provision. One key challenge stems from the need to simultaneously evaluate a suite of ES benefits and consider synergies and trade-offs among them, for example to address critiques that PES could have undesirable consequences when focused solely on an individual ES. Such evaluations are lacking, especially for smallholder systems, as are clear methods for carrying them out. Here we evaluate multiple ES in the context of the 'slash and mulch' agroforestry system (SMAS), a flexible alternative to conventional maize-bean farming currently practiced by some 11 million smallholders across Central America. We conducted on-farm trials in El Salvador comparing two variations of SMAS to conventional and organic management and forest-fallows to evaluate the adaptability of SMAS and its impact on multiple ES. We found that variability associated with SMAS made it difficult to statistically demonstrate the benefits of isolated individual ES indicators. However, when multiple indicators were evaluated simultaneously, both SMAS treatments outperformed conventional and organic management in nearly all ES categories. By developing composite indices of multiple ES we identified patterns indicating that SMAS enhances multiple ES and better capitalizes on synergies between regulating and provisioning ES compared to conventional management. Specifically, the SMAS treatments showed synergies between water regulation, pest and disease control, soil composition, belowground biodiversity and production value, while in conventional plots we found trade-offs between provisioning and regulating ES. Finally, we identified simple field proxies that correlate well with multiple ES, and discuss important management, monitoring and policy implications for adaptable agroforestry systems.

## 1. Background and introduction

### 1.1. Climate-smart agriculture and payments for ecosystem services

One of the great social and environmental challenges of the 21st century is how to support smallholder farmers on the landscape and simultaneously produce sustainable and equitable food security and environmental outcomes (FAO, 2016). Globally, smallholders make up about 20% of the world's agricultural population and manage over one billion hectares, yet they remain one of the poorest and most food insecure groups (Dixon et al., 2001; FAO, 2016; Palm et al., 2005). Furthermore, climate change is projected to have the greatest negative crop

yield impacts in less-developed regions, indicating that smallholders will be disproportionately affected (FAO, 2016). Thus, there has been a call to build resilience among smallholders through 'climate-smart' agriculture (CSA; Rioux et al., 2016), defined as management strategies that enable (1) sustainable increases in agricultural productivity and incomes; (2) increased adaptation and resilience to climate change and; (3) reduced greenhouse gases emissions (GHG), where possible (FAO, 2013).

Payments for ecosystem services (PES) have emerged as one tool to overcome socioeconomic barriers to CSA adoption (Engel and Muller, 2016) and account for the fact that many ecosystem service (ES) benefits accrue off-farm and at multiple scales. PES models are based on the

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principle that those providing services (in this case, farmers) are compensated by those receiving the benefits of those services (Hegde and Bull, 2011). It is hypothesized that even a relatively small payment to farmers, especially early on, will minimize the timeframe in which sustainable management may impose a net cost to farmers, thereby increasing adoption (Engel and Muller, 2016; Pagiola et al., 2007). However, PES policy remains nascent, in part due to the challenges associated with quantifying and monitoring ES provision (de Groot et al., 2010).

A further challenge to implementation lies in the critique that PES oversimplify the complexity of ecosystems by separating ecosystem functions into “discrete units of trade” and focusing on very specific land management strategies (Kosoy and Corbera, 2010). Promoting prescriptive production strategies for individual ES (e.g., biofuels for GHG mitigation) may reinforce systemic causes of poverty by trapping smallholders in long-term contracts for rigid management systems or restricting access to resources by local communities (Schoon et al., 2015; Wittman et al., 2015). Furthermore, PES programs singling out individual ES (e.g., carbon trading) may undermine the adoption of diversified farming systems that would better provide multiple ES, enhanced biodiversity and long-term climate resilience (Kosoy and Corbera, 2010; Palomo et al., 2016; Wittman et al., 2015).

Meeting agricultural sustainability objectives, such as Goal 2.4 of the United Nation’s Sustainable Development Goals (SDGs), will require identifying and managing for ES interactions (Hayati, 2017; Millennium Ecosystem Assessment, 2005; United Nations, 2015). Ideally, PES would encourage practices that are adaptable to farmers needs and beneficial for a suite of ES (Wendland et al., 2010), while accounting for trade-offs and synergies among them (Kremen and Miles, 2012; Naeem et al., 2015). However, accomplishing this in practice presents additional challenges to measuring ES provision (e.g. Hegde and Bull, 2011). In this paper we address these challenges within the context of agroforestry, a widely promoted example of CSA with multiple ES benefits.

## 1.2. Agroforestry and the ‘slash-and-mulch’ system

Agroforestry systems have been incorporated into discussions around CSA for their ES benefits on-farm (e.g. food, fuelwood, soil fertility, water infiltration) and off-farm (e.g. water conservation, carbon storage, biodiversity; see Mbow et al., 2014; Rioux et al., 2016; Steenwerth et al., 2014). However, a wide range of well-documented socioeconomic factors have limited widespread agroforestry adoption (e.g. Current et al., 1995a; Hellin et al., 1999; Pattanayak et al., 2003; Pollini, 2009). PES is therefore an attractive option to incentivize agroforestry adoption, and many agroforestry-related PES programs are emerging (Groom and Palmer, 2012; Kosoy et al., 2007; Pagiola et al., 2007), but there has been a call to ensure that agroforestry approaches are designed to be flexible, allowing farmers to adapt them to their preferences (Adesina et al., 1999; Pollini, 2009)

Here we consider ‘slash and mulch’ agroforestry systems (SMAS) gaining popularity in Central America. Also called the Quesungual system, named after the village in western Honduras where such systems were first documented (Hellin et al., 1999), SMAS offers an agroforestry alternative to the conventional maize-bean farming system, characterized by slash-and-burn management, and currently practiced by some 11 million smallholders (covering 65 million ha) across Mesoamerica (Dixon et al., 2001). SMAS can be considered flexible and adaptable, as it is based on three general principles (Castro et al., 2009; Hellin et al., 1999): (1) eliminating burning during field preparation; (2) maintaining a permanent vegetative soil cover or ‘mulch’ (e.g., tree prunings, crop residues); and (3) intercropping maize and beans with diverse tree species managed at varying levels of pruning.

Intercropped trees can be established by natural regeneration, planting, or left in place during conversion of secondary forest to

agriculture, and farmers choose which tree species to maintain based on their own objectives (e.g., timber, fuelwood, fodder, fruit). Tree densities can be highly variable and the majority of trees are heavily pruned to minimize competition with crops and provide a substantial mulch layer of leaves and branches to protect the soil and provide nutrients (Beer et al., 1998; Fonte et al., 2010; García, 2011). Other reported benefits, mostly from western Honduras where SMAS has been widely adopted, include: improved soil health and biodiversity (Fonte et al., 2010; Fonte and Six, 2010; Pauli et al., 2011); climate change mitigation and C storage (Castro et al., 2009; Fonte and Six, 2010); reduced erosion and improved resilience to drought and hurricanes (The World Bank, 2008; Welches and Cherrett, 2002) and improved yields (Castro et al., 2009; Welches and Cherrett, 2002)

The flexibility of SMAS could make it appropriate for a wide array of biophysical, socioeconomic and cultural contexts. Furthermore, the multiple ES benefits it provides could align well with emerging PES programs (The World Bank, 2008); however, questions remain to determine if and how SMAS can be integrated into broader sustainability strategies (e.g., the United Nation’s SDGs) and how to evaluate ES benefits associated with SMAS and other similar systems.

First, with respect to SMAS specifically, are ES benefits observed in western Honduras likely to occur in other contexts – especially the simultaneous increase in yields and other non-provisioning ES? Most SMAS research to date has been limited to western Honduras, an area where yields were below average for the region and land degradation was at crisis levels (Ayarza et al., 2010). Furthermore, research in Honduras has focused on the establishment of SMAS through conversion of forest-fallows, and it is unclear whether ES benefits would accrue if the system were implemented to restore already cleared and largely treeless fields, representative of more degraded areas of the region.

More broadly, can we quantify the multiple ES benefits expected from flexible agroforestry systems such as SMAS, and do trade-offs or synergies among services exist? Most published studies on SMAS to date have tended to focus on only one or a few ES, mostly related to soil biological health and nutrient cycling (Castro et al., 2010; Fonte et al., 2010; Fonte and Six, 2010; Pauli et al., 2011). Finally, it would be useful to identify simple field proxies that represent multiple ES to simplify monitoring efforts and support payments for a basket of ES.

To address these questions, we established on-farm trials with two variations of SMAS in El Salvador with several objectives: (1) evaluate the field-scale impact of SMAS on a suite of individual ES and biodiversity indicators as compared to other land management options; (2) develop ES indices in order to evaluate the impact of SMAS on multiple ES indicators and determine if trade-offs and synergies exist and; (3) identify simple and measurable field proxies that demonstrate the principles of SMAS and could serve as proxies for ES in a monitoring program.

## 2. Material and methods

### 2.1. Site description

This study was conducted in the municipality of Las Vueltas, El Salvador, in the northern department of Chalatenango (Fig. 1), a priority region identified by the Ministry of Environment and Natural Resources of El Salvador (MARN) for improving agricultural management due to high vulnerability associated with the steep terrain and proximity to a semi-protected forest. Elevations of experimental plots ranged from 624 to 866 m, and the region has a sub-humid tropical climate with a mean annual temperature of 22–26 °C and mean annual rainfall of about 1985 mm (MARN, 2013). Rainfall occurs mostly between the months of May and October with a pronounced dry season from late November through April, averaging less than 10 mm month<sup>-1</sup> between December and February. The landscape consists of a mountainous mosaic of mixed-pine forest, broadleaf secondary forest, forest-

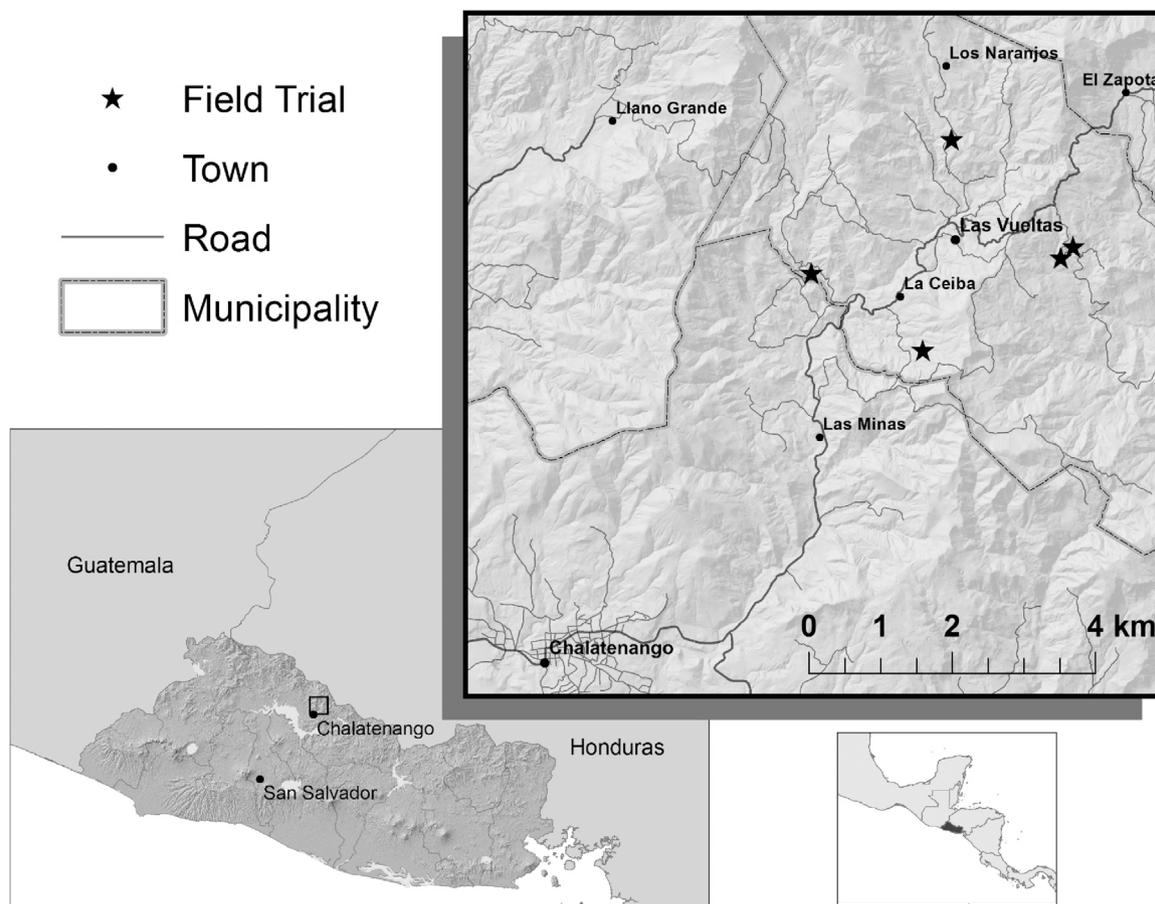


Fig. 1. Map of field trial locations in northern El Salvador.

fallow patches and widespread agricultural activity dominated by subsistence smallholder cultivation of basic grains (maize, beans and sorghum) and extensively grazed pastures.

## 2.2. Experimental design

Experimental trials were established in April 2012 on 12 m x 20 m plots on five farms (replicate blocks) and managed for three growing seasons, ending in 2015. Farms were chosen based on farmers' willingness to participate as well as farm location, size and land-use composition. Each farm consisted of five treatments (5 treatments x 5 farms; n = 25), developed in coordination with MARN, local officials and farmers, and included: conventional management (CONV); organic management (ORG); SMAS established from a plot previously under conventional management (SMAS-1); SMAS established from a forest-fallow, similar to the Quesungual approach (SMAS-2) and; a forest-fallow reference plot (FOR). The treatments CONV, SMAS-1 and ORG were randomly allocated to previously deforested plots of land under agricultural production, while SMAS-2 and FOR plots were selected from adjacent areas of secondary forest on each farm.

The CONV treatment was managed according to prevailing farmer practices in the region, similar to those observed elsewhere in El Salvador (e.g., Morris et al., 2013). Maize (*Zea mays*, variety "H5-G") was planted each year in May in rows spaced 90 cm apart, with two seeds sown every 45 cm. Beans (*Phaseolus vulgaris*, variety "Curaneteño") were inter-planted between maize rows (30-cm plant spacing, 45-cm row spacing) each year in early September, once the maize had matured and been 'doubled over' in the field to dry. Herbicides, pesticides and fertilizer were applied to both crops according to common practice for the area. A mixture of ammonium sulfate (21-0-0-24S) and formula (16-20-0) was applied to maize at 10 and 40 days

after planting, equivalent to 164 kg N ha<sup>-1</sup>, 39 kg P ha<sup>-1</sup> and 100 kg S ha<sup>-1</sup>. While these application rates are relatively high (about 1.5 times the reported national average in 2008), they are similar to rates used in other hillslope maize-bean farming regions of El Salvador (Morris et al., 2013; Olson et al., 2012). The formula fertilizer was also applied to beans at a rate equivalent to 60 kg N ha<sup>-1</sup> and 28 kg P ha<sup>-1</sup>, nearly double the national recommendations for N but slightly lower than the recommended P application rate (CENTA, 2008).

One notable departure of the CONV treatment from conventional farmer practice is that plots were not burned prior to planting at the behest of local officials since burning is technically outlawed, although rarely enforced. However, manual weeding with machetes prior to planting largely eliminated tree saplings and crop residues were removed with the harvest to simulate the loss of soil mulch cover that occurs with burning or with feeding of residues to livestock.

The SMAS-1 treatment was designed to test the adaptability of SMAS to situations where land access is limited and forest loss, degradation or laws prohibiting forest clearing may constrain farmers' ability to implement the Quesungual (SMAS-2) system. Trees were planted from seedlings and from cuttings to achieve a final density of roughly 1000–1400 trees ha<sup>-1</sup> (accounting for anticipated mortality rates of up to 50%), the approximate density of trees observed in the Quesungual system in Honduras (García, 2011; Ordonez Barragan, 2004; Pauli et al., 2011). Twenty-one tree species were chosen through participatory workshops with farmers to identify useful species of interest to them. Planted trees included native leguminous and timber species, and a mix of native and localized fruit-bearing species, namely *jocote* (*Spondias mombin*). All crop residues were left in the field and natural regeneration of saplings was managed to encourage the re-growth of priority tree species. Apart from that, SMAS-1 plots were managed in the same manner as CONV plots.

The SMAS-2 treatment was managed similar to SMAS-1, with the main difference being that it was established directly from a forest-fallow (FOR), following the Quesungual approach (Castro et al., 2009; Hellin et al., 1999). As a result, SMAS-2 tended to have a higher proportion of mature trees and slightly different species composition, reflecting the previous forest-fallow for that site and the preferences of each farmer. The FOR treatment was an unmanaged reference plot of secondary forest-fallow, approximately 10–20 years old. It was located adjacent to SMAS-2 at each farm and was the land-use from which SMAS-2 was converted.

The ORG treatment was included to explore the potential benefits and trade-offs associated with chemical-free management associated with proposed legislation in many parts of Central America. Management was similar to SMAS-1 except no trees were planted and no agrochemicals used. Instead, “bokashi” (a composted chicken manure rich in microorganisms) was added in split applications at a rate of 7.4 Mg ha<sup>-1</sup> (128 kg N and 66 kg P ha<sup>-1</sup>) for maize and 3.7 Mg ha<sup>-1</sup> (64 kg N and 33 kg P ha<sup>-1</sup>) for beans. Two organic foliar sprays, known locally as *FOREFUN* and *Sulfocalcio*, were prepared on-farm and applied 3 times during the growing season to manage for pests and diseases.

### 2.3. Framework for measuring multiple ES

We measured a suite of indicators of ES supply and biodiversity in each of the 25 plots between July 2015 and February 2016 (during and following the third year of production). Ecosystem services were classified into groups (Table 1), largely based on the Common International Classification of Ecosystem Services (CICES) developed by the European Environmental Agency (Haines-Young and Potschin, 2013). For this study, we limited our focus to two CICES sections: Provisioning services and Regulation and Maintenance services. We also include indicators of biodiversity as it is a major focal point for conservation at the local, national and international scale across Latin America (Balvanera et al., 2012) and has been linked to the supply of ES in multiple contexts (Kremen and Miles, 2012; Richards and Méndez, 2014). We present our methods for developing and measuring individual ES indicators in Sections 2.4–2.6 (see Table 2 for a complete list of indicators), and discuss our approach to statistically analyze indicators and develop and evaluate composite indices in Section 2.7.

**Table 1**

Ecosystem service (ES) groups used for index development. Final ES groups were defined by the authors, but categorized by CICES Section and Division. A list of individual ES indicators can be found in Table 3.

CICES Section	CICES Division	ES Groups
Provisioning	Nutrition	Crop production
	Energy	Fuelwood production
Regulation and Maintenance	Mediation of flows	Erosion control
		Water regulation
	Maintenance of physical, chemical, and biological conditions	Pest & disease control
		Soil composition Carbon storage
Biodiversity <sup>a</sup>	Aboveground biodiversity <sup>a</sup>	Biodiversity of woody vegetation
	Belowground biodiversity <sup>a</sup>	Biodiversity of soil macrofauna

<sup>a</sup> Note that biodiversity is not specifically defined as a section by CICES. For more information see Haines-Young and Potschin (2013).

### 2.4. Provisioning services

We estimated the quantity and value of cultivated crops and fuelwood produced in each of the managed plots as indicators of provisioning services. Timber production was excluded since participating farmers stated that wood extraction is primarily for fuelwood, not timber, and estimates of standing timber would overlap with estimates of biomass C, leading to double counting.

#### 2.4.1. Crop production

Maize and beans were harvested in November 2015 after being left in the field to dry as per farmer practice. Maize was harvested from 5 equidistant rows, leaving a 1 m buffer to avoid edge-effects, while beans were harvested from a 5 m x 10 m subplot in the center of each plot. Grain was oven dried and final yields corrected to 11% moisture content. The value of maize and bean production was based on the average annual consumer price, as reported by the Ministry of Agriculture and Livestock of El Salvador (MAG, 2016a).

#### 2.4.2. Fuelwood provision

Fuelwood yields were estimated in May 2015 during field preparation and tree pruning, prior to planting. All deadwood and tree prunings were collected as fuelwood following common local practice and yields were calculated in *cargas* – the visually estimated merchantable unit used in the region for selling fuelwood (approximately 25–35 kg). Fuelwood was harvested from each of the cultivated treatments (excluding FOR) and separated into piles equal to one *carga*, as estimated by local staff and farmers. The total number of *cargas* harvested from each treatment was then counted to the nearest one-third *carga*. Even though many farmers harvest some fuelwood from forests and forest-fallows, no fuelwood was harvested from the FOR plots monitored in this study in order to leave these plots as an unmanaged reference treatment. Fuelwood value was set at \$4.00 per *carga* based on local prices.

### 2.5. Regulation and maintenance services

#### 2.5.1. Erosion control

Comparative erosion rates were estimated using pins (0.6 cm diameter, 40 cm length) installed in late May 2012 before maize planting. Pin placement was laid out in a grid pattern of 3 columns and 6 rows at 3 m x 3 m spacing for a total of 18 pins per plot. Pins were hammered into the soil perpendicular to the slope, leaving approximately 10 cm protruding from the soil surface. Pin protrusion was measured 5 times during the 2015 rainy season using a digital depth gauge (0.02 mm precision) and checked for damage or disturbance. Pins that remained undisturbed for the entire season were used to calculate the absolute value of the change in pin height as an indicator of soil movement and erosive activity (Kearney et al., 2017b, in review; Luffman et al., 2015).

Soil mulch cover (non-living vegetative biomass) was also measured as an indicator of soil conservation in February 2016. All mulch was collected in five 1-m<sup>2</sup> quadrats randomly located in each plot, dried in an oven at 65° C for 48 h, weighed and converted to kg ha<sup>-1</sup>.

#### 2.5.2. Water regulation

We chose four indicators to estimate the effects of management on water flows: water infiltration rate, runoff, deep percolation and water stress during the 2015 rainy season. We measured infiltration as unsaturated hydraulic conductivity using a mini-disk infiltrometer from Decagon Devices (Pullman, WA, USA). The infiltration rate provides an indication of how quickly water can move into dry soil and is calculated in mm h<sup>-1</sup>.

Runoff during the 2015 rainy season was estimated using hourly precipitation data, canopy cover and the measured infiltration rate for each plot. Precipitation data was collected at each farm using an automatic tipping bucket rain gauge from Davis Instruments (Hayward,

**Table 2**  
Field proxies expected to correlate with multiple ecosystem services.

Category	Proxy	Description	Units
Trees	Stem Count (All)	The total number of boles	trees ha <sup>-1</sup>
	Stem Count (DBH < 10)	The number of boles with a DBH < 10 cm	trees ha <sup>-1</sup>
	Stem Count (DBH 10 +)	The number of boles with a DBH of 10 cm or more	trees ha <sup>-1</sup>
Mulch	Canopy Cover	Binary visual assessment of canopy cover at 60 points along 3 transects using a periscope densiometer	Percent (%)
	Soil Mulch Cover (Visible)	Binary visual assessment of non-living vegetative soil cover at 60 points along 3 transects	Percent (%)
Soil	Soil Mulch Cover (Biomass)	Oven-dry biomass of non-living vegetation collected from five 1-m <sup>2</sup> quadrats	kg ha <sup>-1</sup>
	Infiltration	Unsaturated hydraulic conductivity measured with a Decagon mini-disk infiltrometer	mm hr <sup>-1</sup>
	Soil Organic Matter	Soil organic matter content (Walkley and Black, 1934)	%
	Bulk Density	Soil bulk density measured using ring (7.25 × 7.65 cm)	g cm <sup>-3</sup>

CA, USA; Model No. 7857) set up to measure rainfall at 10-min intervals. Hourly precipitation intensity was calculated for each rain gauge location and then discounted by the canopy cover (% closure, see Table 2) to account for canopy interception. Hourly *Hortonian* runoff (Horton, 1933) was then estimated in mm as the difference between the discounted rainfall intensity and plot-measured infiltration rates when rainfall intensity exceeded infiltration rates. The sum of all runoff over the growing season was taken for each plot to estimate expected runoff. Deep percolation and water stress were estimated with crop water models developed by the FAO using the Penman-Monteith method (Allen et al., 1998), calibrated with biweekly soil moisture readings. A detailed explanation of daily water balance and deep percolation calculation methods can be found in the Supplementary Information (SI).

### 2.5.3. Pest and disease control

Weed presence and indicators of the effects of pests and diseases were measured in each of the cultivated plots. Damage from pests and disease incidence was monitored in beans approximately 6 weeks after planting in late September, when pest pressures tend to be highest. Forty plants were randomly selected and visually inspected for pests and diseases in each plot and the severity of impact was ranked as none (0), low (1), medium (2) or high (3). Pest damage and disease incidence were ranked separately and the average value for each plot was taken to give two separate continuous scores (0–3) for each plot. Weed presence was measured in February 2016 using the same quadrats and methods used to measure soil mulch cover. Pest and disease incidence and weed presence were not evaluated in FOR plots, since we were only interested in the impact of these on crops. Therefore, within FOR plots, zero values were assigned for each of these indicators for the purpose of developing the Pest and Disease Control composite index (see Section 2.7.2).

### 2.5.4. Soil composition

Soil samples were collected in February 2016, taken from the 0–20 cm depth at four points in each of two subplots established within each experimental plot. Sub-samples from each subplot were composited for analysis and the results averaged to give a single value for each plot. Soils were air-dried and passed through a 2 mm sieve prior to analysis of texture, pH (in H<sub>2</sub>O), total soil organic matter (SOM; Walkley and Black, 1934) and total nitrogen (N), available phosphorus, potassium (K), calcium (Ca) and magnesium (Mg) using the Mehlich-3 method (Mehlich, 1984) at the CENTA (Centro Nacional de Tecnología Agropecuaria y Forestal) laboratory in El Salvador. We used soil cores (7.25 cm diameter × 7.65 cm length) to calculate bulk density at 0–10 and 10–20 cm in four of the sub-sample points and an average value (0–20 cm) was taken for each plot.

### 2.5.5. Carbon (C) storage

We calculated C stored in aboveground woody biomass (AGWB) and topsoil (0–20 cm) as indicators of climate regulation services. In order to estimate AGWB we measured all trees and shrubs with a diameter at breast height (DBH, approximately 1.3 m) of at least 1 cm. All trees and shrubs were identified to the genus and species (when possible) and

height and DBH measured in order to estimate AGWB from allometric equations (see Supplementary Materials within Kearney et al., 2017a). We estimated C content as 49% of AGWB based on studies conducted in similar regions in Central America (Gómez-Castro et al., 2010; Hughes et al., 1999; Suárez, 2002) and converted all values to Mg ha<sup>-1</sup>. SOM was converted to total organic C using a factor of 0.5 based on calculated ratios from a subset of the data and following recommendations made by Pribyl (2010). We then calculated topsoil C density by multiplying percent organic C by soil bulk density and converting values to Mg ha<sup>-1</sup>.

## 2.6. Biodiversity

### 2.6.1. Aboveground biodiversity

We calculated species richness and the Shannon index (Shannon, 1948) for all trees with DBH ≥ 1 cm as indicators of aboveground biodiversity. Species richness was calculated as the total number of uniquely identifiable species found in each plot in February 2016. The Shannon index was used as a measure of biodiversity to take into account the proportions of species found in a plot using the equation:

$$H = - \sum_{i=1}^S (p_i \ln p_i) \quad (1)$$

where H is the Shannon index, S is the total number of unique species observed within a plot and  $p_i$  is the proportion of S made up by the  $i$ th species (Magurran, 1988).

### 2.6.2. Belowground biodiversity

Macrofauna present in the soil were measured in July 2015 to develop four indicators of belowground biodiversity. Following the Tropical Soil Biology and Fertility (TSFB) method (Anderson and Ingram, 1993), soil pits (25 × 25 cm) were excavated to a depth of 30 cm and soil invertebrates (> 2 mm) were hand sorted and stored in alcohol for subsequent identification of individuals to the level of species (when possible) in the laboratory at the National University of El Salvador. Two indicators of abundance were calculated as the number of individuals per m<sup>2</sup> based on the number of arthropods and earthworms, respectively, found in each pit. We also calculated macrofauna species richness and the Shannon index (see Eq. (1)) at the 'order' level of taxonomic rank.

## 2.7. Statistical analysis

### 2.7.1. Individual ES indicator variables

We first compared treatment effects on each of the individual ES and biodiversity indicators described in Sections 2.4–2.6. We used a linear mixed effects model from the *nlme* package (Pinheiro et al., 2013) in R (R Core Team, 2016) with each indicator used, in turn, as the response variable, treatment as the fixed effect and farm location as a random effect. Distributional assumptions for each model were evaluated following Pinheiro and Bates (2000). When necessary, the response variable was transformed to achieve normality of within-group

**Table 3**

Results of statistical analysis of individual ecosystem service indicators by treatment. Mean value for ecosystem service (ES) indicators by treatment. P-value denotes the significance of the fixed-effect (i.e., treatment) in the linear mixed effects model. Different letters denote significant differences ( $p < 0.05$ ) between treatments based on Tukey pairwise comparisons. N/A signifies data was not collected for that treatment and it was not included in statistical analysis. CONV = conventional management; ORG = organic (conventional management without chemical inputs); SMAS-1 = the slash-and-mulch agroforestry system, converted from CONV; SMAS-2 = the same as SMAS-1, but converted from FOR and; FOR = forest-fallow.

ES Group	ES Indicator	Unit	p-value	CONV	ORG	SMAS-1	SMAS-2	FOR					
<b>Provisioning</b>													
Crop production	Maize yield †	kg ha <sup>-1</sup>	0.002	2392	b	1033	b	1937	b	457	a	N/A	
	Bean yield	kg ha <sup>-1</sup>	0.088	978		891		793		503		N/A	
	Jocote yield	# ha <sup>-1</sup>	0.022	0.0	a	0	a	1133	b	0	a	N/A	
Fuelwood production	Fuelwood harvest	cargas ha <sup>-1</sup>	0.029	5.50	a	6.05	a	8.25	ab	16.50	b	N/A	
<b>Regulation and Maintenance</b>													
Erosion control	Erosion	mm of change	0.487	11.7		12.2		9.7		10.2		9.3	
	Soil mulch cover §	kg ha <sup>-1</sup>	< 0.001	4628	a	4312	a	6191	b	7288	c	6848	c
Water regulation	Drought stress	prop. of days	0.149	0.42		0.40		0.39		0.36		N/A	
	Runoff †	mm	< 0.001	257	b	159	b	173	b	5	a	0	a
	Deep percolation	mm	< 0.001	193	a	234	a	235	a	367	b	420	b
	Infiltration †	mm h <sup>-1</sup>	0.128	5.52		11.31		8.99		16.02		18.98	
Pest & disease control	Weed cover	kg ha <sup>-1</sup>	0.012	2337	b	1770	ab	1094	a	872	a	N/A	
	Pest presence	score (0–3)	0.024	1.24	ab	1.34	b	1.04	ab	0.99	a	N/A	
	Disease presence †	score (0–3)	0.035	1.24	ab	1.57	b	1.24	ab	0.81	a	N/A	
Soil composition	pH	pH units	0.846	5.59		5.56		5.41		5.59		5.64	
	Phosphorus (P) †	mg kg <sup>-1</sup>	0.992	22.63		15.29		22.65		29.97		44.87	
	Potassium (K)	mg kg <sup>-1</sup>	0.996	235		225		227		221		226	
	Calcium (Ca)	cmolc kg <sup>-1</sup>	0.863	12.42		11.29		13.08		11.83		11.49	
	Magnesium (Mg)	cmolc kg <sup>-1</sup>	0.930	4.52		3.87		4.31		4.12		4.05	
	SOM	%	0.709	4.29		4.10		4.35		4.54		4.76	
	Bulk Density	g cm <sup>-3</sup>	0.423	0.94		0.93		0.89		0.99		0.89	
Carbon storage	AGWB carbon †	Mg ha <sup>-1</sup>	0.001	3.9	a	9.6	ab	8.2	ab	16.9	bc	34.3	c
	Soil carbon	Mg ha <sup>-1</sup>	0.715	28.8		24.9		28.1		30.5		31.4	
<b>Biodiversity</b>													
Aboveground biodiversity	Tree/shrub richness	# of species	< 0.001	6	a	7	ab	13	bc	14	cd	20	d
	Tree/shrub diversity †	Shannon index	0.001	1.36	a	1.61	ab	2.12	bc	2.19	c	2.36	c
Belowground biodiversity	Arthropod presence †	# of individuals	0.713	1903		1188		2823		1664		1449	
	Earthworm presence §	# of individuals	< 0.001	86	a	138	bc	153	c	142	c	96	ab
	Macrofauna richness	# of species	0.329	13		13		14		12		16	
	Macrofauna diversity	Shannon index	0.393	1.80		1.77		1.42		1.47		1.85	

† Denotes that the ES indicator variable was transformed to meet model assumptions.

§ Denotes that non-constant variance among farms was detected and incorporated into the model.

errors and random effects, and the *varIdent()* variance function used to allow for non-constant variance among farm locations, following the approach utilized by Davis et al. (2012). Tukey's pairwise comparisons were made on models with a statistically significant treatment effect. Treatment effects and pairwise comparisons were considered statistically significant at  $p < 0.05$ .

### 2.7.2. Composite indices

In order to better compare and visualize the impacts of management on multiple ES, we developed composite indices of ES groups following an approach similar to those utilized to assess soil quality and soil-related ES (Lavelle et al., 2014; Mukherjee and Lal, 2014; Velasquez et al., 2007). First, we converted the values of individual ES indicators to a common scoring unit ranging from 0.1–1 using the homothetic transformation

$$Y_i = 0.1 + \left( \frac{x_i - b_i}{a_i - b_i} \right) \times 0.9 \quad (2)$$

where  $Y$  is transformed value of the variable  $i$ ,  $x$  is the original variable value, and  $a$  and  $b$  are the maximum and minimum observed values of variable  $i$ , respectively. In order to set all variables on a 'more-is-better' scale, variables originally on a 'more-is-worse' scale (e.g., pest presence and runoff) were converted using the reverse transformation

$$Y_i = 1.1 - \left( 0.1 + \left( \frac{x_i - b_i}{a_i - b_i} \right) \times 0.9 \right) \quad (3)$$

These transformations were performed on all individual variables except the provisioning and C storage services, which could already be combined using standardized units. In the case of provisioning services, we first calculated the total production value in USD as the sum of the quantity of each product multiplied by its average unit price. For C storage, above- and below-ground C stocks were summed to give total C stocks in Mg ha<sup>-1</sup>. Eq. (2) was then applied directly to these two ES groups to develop their respective composite indices.

For all other ES groups, composite indices were calculated as the weighted sum of all transformed variables within each group. Weights were applied based on each variable's relative contribution to the variance within an ES group based on principle component analysis (PCA). The respective factor scores for each variable in the first two axes were used as weights, such that the final index was calculated as

$$CI = \sum_{i=1}^n (Y_i w_{i,PC1} + Y_i w_{i,PC2}) \quad (4)$$

where  $CI$  is the composite index,  $Y_i$  is the transformed value from Eqs. (2) or (3) for each variable  $i$  (of  $n$  variables), and  $w$  is the factor score from the first and second principal component axes, respectively. Finally, each composite index was again reduced to the range 0.1–1 using

**Table 4**

Ecosystem service composite index values by treatment. Mean index value by treatment. P-value denotes ANOVA of the LME model and letters denote significant differences ( $p < 0.05$ ) between treatments based on Tukey pairwise comparisons. CONV = conventional management; ORG = organic (conventional management without chemical inputs); SMAS-1 = the slash-and-mulch agroforestry system, converted from CONV and; SMAS-2 = the same as SMAS-1, but converted from FOR and; FOR = forest-fallow.

ES Composite Index	p-value	CONV	ORG	SMAS-1	SMAS-2	FOR					
<b>Provisioning</b>											
Production Value	0.105	0.56	0.41	0.53	0.32						
Pest & Disease Control	< 0.001	0.34	a	0.35	a	0.53	ab	0.64	b	1.00	c
<b>Regulation and Maintenance</b>											
Erosion Control	0.006	0.36	a	0.31	a	0.59	ab	0.60	ab	0.71	b
Water Regulation	0.007	0.23	a	0.25	a	0.25	a	0.31	ab	0.53	b
Soil Composition	0.832	0.55		0.48		0.54		0.51		0.61	
Carbon Storage	0.003	0.25	a	0.26	a	0.28	a	0.42	ab	0.66	b
<b>Biodiversity</b>											
Aboveground Biodiversity	< 0.001	0.45	a	0.53	ab	0.73	bc	0.76	c	0.89	c
Belowground Biodiversity	0.520	0.54		0.55		0.54		0.34		0.65	

Eq. (2).

### 2.7.3. PCA of ES composite indices and correlation with field proxies

For the four cultivated treatments (non-FOR), we assessed potential trade-offs and synergies between ES composite indices using PCA. This analysis was limited to cultivated plots since we were primarily interested in evaluating synergies and trade-offs between provisioning and regulating services within production management systems.

In an effort to identify simple and measurable field proxies for multiple ES, we also explored relationships between proxies that can easily be measured in the field (Table 2) and the ES composite indices using Pearson's correlation analysis, again limiting analysis to cultivated plots. Proxies were chosen to correspond with relatively simple measurements commonly collected during rapid field surveys to evaluate land health and the benefits of CSA (Rioux et al., 2016; Shepherd et al., 2015; Vågen et al., 2010).

## 3. Results

### 3.1. Individual ES indicator variables

#### 3.1.1. Provisioning services

Maize yields for all plots were slightly lower than the 2015/16 national average ( $\sim 2500 \text{ kg ha}^{-1}$ ), while bean yields were slightly above the national average ( $\sim 850 \text{ kg}^{-1}$ ) for CONV and ORG, and below for the two SMAS treatments (MAG, 2016b). Both maize and bean yields tended to be highest under CONV and SMAS-1 management. Significant differences were only found between CONV and SMAS-2 for maize (Table 3), but maize yields in the ORG treatment averaged about half that for CONV and SMAS-1. Fuelwood production was about 300% and 50% higher in the SMAS-2 and SMAS-1 treatments, respectively, compared to CONV and ORG. While fuelwood production increases were substantial, their value relative to crop production was low. Based on current prices (see Section 2.4.2), the value of increased fuelwood production in the SMAS-2 is  $\$44.00 \text{ ha}^{-1} \text{ yr}^{-1}$ , or about 8% of average farm revenue under CONV management.

#### 3.1.2. Regulation and maintenance services

Soil mulch biomass was highest in FOR and significantly higher under agroforestry management (SMAS-1 and SMAS-2) compared to management with fewer trees (CONV and ORG). Change in erosion pin height was inversely correlated with soil mulch cover, suggesting that increased soil mulch cover contributed to reduced erosion (Kearney et al., 2017b, in review). However, statistically significant differences in erosion pin height could not be detected between any treatments.

FOR tended to have higher rates of water infiltration, although no significant differences were found between any treatments (Table 3). The SMAS-2 and FOR treatments had the best values of the modeled indicators of water flows (increased deep percolation and reduced

runoff and drought stress). Weed biomass was significantly reduced in the SMAS treatments compared to CONV (Table 3) and was negatively correlated with soil mulch cover across all treatments (Fig. S1). Pest and disease presence also tended to be lower in the two agroforestry treatments, although significant differences were only detected for pest presence between SMAS-2 and ORG (Table 3).

Soil properties varied more by farm than by treatment (Fig. S3) and we found no obvious trends or significant differences between treatments for individual properties. FOR stored significantly more AGWB C than all other treatments, and nearly 10 times as much as CONV. The SMAS-2 system maintained about half the AGWB C stored in FOR and four times as much as CONV, while the SMAS-1 treatment doubled AGWB C compared to CONV. However, differences among production systems were not statistically significant for either C pool.

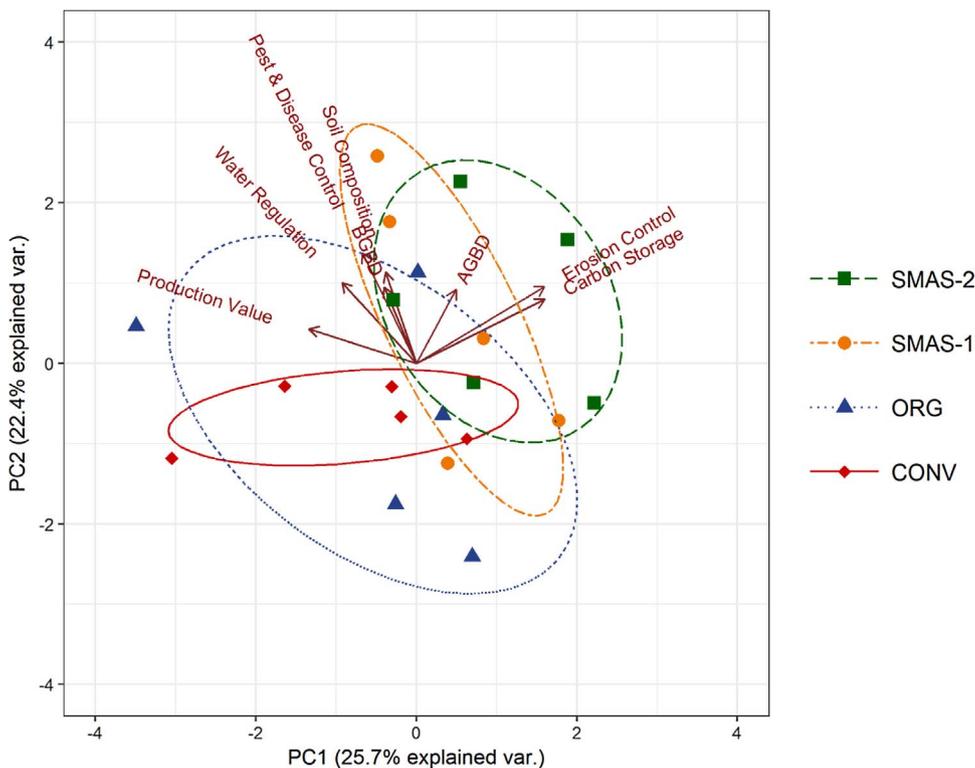
#### 3.1.3. Biodiversity

Tree species diversity (both for richness and the Shannon index) was significantly increased with agroforestry management (Table 3). The tree species diversity of the SMAS-1 and SMAS-2 systems nearly matched that of FOR and maintained twice as many species compared to CONV, but was not significantly different from ORG. Overall macrofauna abundance tended to be higher in cultivated plots than in FOR while macrofauna diversity showed the opposite trend. Earthworm abundance tended to be highest in the ORG and SMAS-1 plots; however, no statistically significant differences were found for any of the belowground biodiversity indicators measured.

### 3.2. Composite ES indices

The treatments with more trees (i.e. SMAS and FOR) tended to have higher values for most ES indices, with the exception of Production Value, Soil Composition and Belowground Biodiversity (Table 4). At the end of the three-year study period, tree densities in the SMAS treatments ranged from 1700 to 3600 trees  $\text{ha}^{-1}$ , averaging about half that of the FOR treatment (mean = 3883 trees  $\text{ha}^{-1}$ ) and more than double the densities of the CONV and ORG treatments, which averaged 517 and 867 trees  $\text{ha}^{-1}$ , respectively (Table S1). The mean Production Value index for CONV was nearly double that for SMAS-2, but results were highly variable between sites and no statistically significant differences were found (Table 4). Pest and Disease Control was significantly higher in the SMAS-2 treatment compared to CONV and ORG, with SMAS-1 falling in the middle.

Erosion Control was lowest for ORG and CONV and highest for FOR, and index values for SMAS-2 and SMAS-1 were not significantly different from FOR. Water Regulation and Aboveground Biodiversity followed similar trends and SMAS-2 was not significantly different from FOR for either index. Carbon Storage in FOR was 2–3 times higher than CONV, ORG, and SMAS-1, but again not significantly different from SMAS-2. No significant differences were found between treatments for



**Fig. 2.** Co-variation among ecosystem services indices for cultivated treatments. Distance biplot of the (scaled) first two principal components of all ecosystem service composite indices for cultivated treatments: CONV = conventional management; ORG = organic (conventional management without chemical inputs); SMAS-1 = the slash-and-mulch agroforestry system, converted from CONV and; SMAS-2 = the same as SMAS-1, but converted from forest-fallow. AGBD and BGBD are aboveground and belowground biodiversity, respectively. See Table S2 for the relative contributions of indices to each principal component.

the Soil Composition and Belowground Biodiversity indices, although FOR tended to provide higher values for these ES.

### 3.3. PCA of ES indices and correlation with field proxies

The first two principle components explain 48.1% of the variance in the composite indices, and a distance biplot shows the relationships between ES (Fig. 2). Along the x-axis (PC1), we see negative relationships between Production Value in one direction and Erosion Control and Aboveground Biodiversity in the other (see Table S2 for relative contribution of indices to each axis). We see positive relationships between Production Value, Water Regulation, Pest and Disease Control, Soil Composition and Belowground Biodiversity. Along the y-axis (PC2), however, we see positive loadings for all ES indicators, indicating potential synergies between all indicators (also see Table S2). The two SMAS treatments had comparable scores and score distributions, as represented by the overlapping and similarly shaped ellipses in Fig. 2. Scores for the CONV treatment were tightly grouped, distributed primarily along the x-axis, while scores for ORG were more variable.

In exploring potential field proxies, significant correlations were found with at least one field proxy for all ES indices in cultivated treatments, but no one field proxy was indicative of all eight indices (Fig. 3). Stem count of large trees (DBH 10+ cm) was significantly correlated with the greatest number of composite indices, with positive correlations with Pest and Disease Control, greater Erosion Control and Aboveground Biodiversity and a negative correlation with Belowground Biodiversity. The number of large trees was more highly associated with the Carbon Storage index, while measuring small trees (DBH < 10 cm) better captured Aboveground Biodiversity. Canopy cover, soil mulch cover and soil organic matter all were significantly correlated with half of the indices, with some overlap among them.

A mass-based measurement of soil mulch cover was more highly correlated with ES indices compared to a visual estimation. Infiltration was significantly correlated with Pest and Disease Control and was the only proxy associated with Water Regulation. Soil organic matter was positively correlated with increased Production Value and Pest and Disease Control.

## 4. Discussion

### 4.1. ES indicators and indices

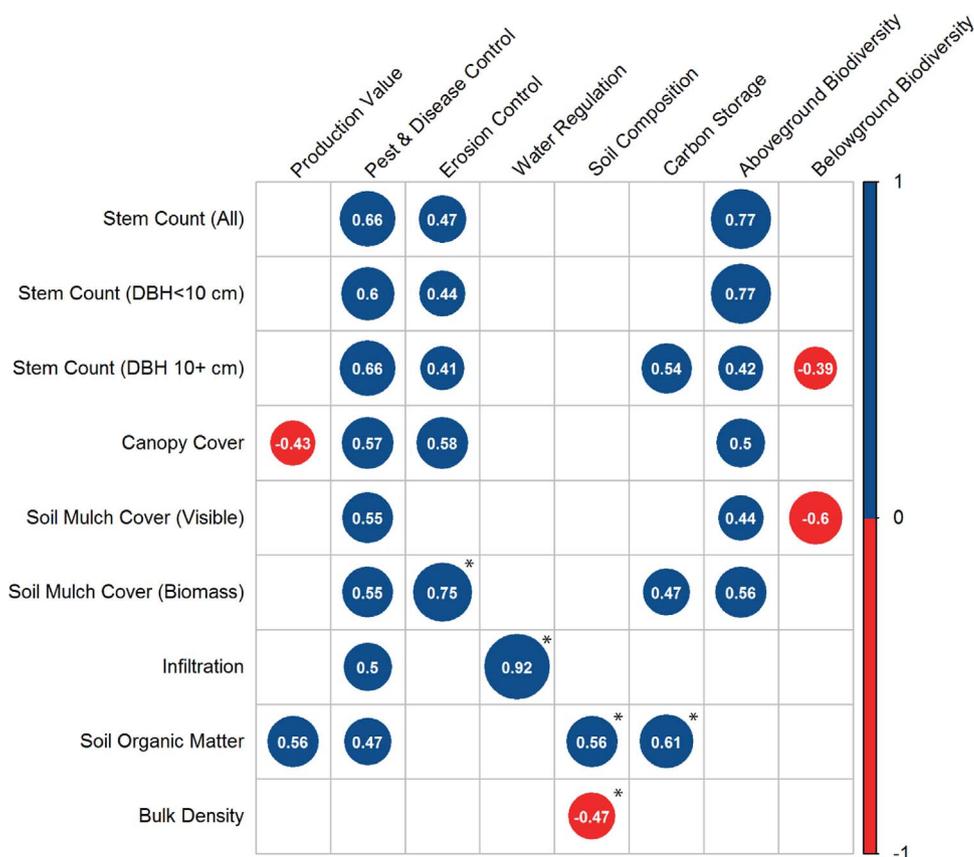
#### 4.1.1. Production of crops and fuelwood

Results of this study indicate that the SMAS can provide multiple ES, with potentially minimal reductions in farm productivity. Crop yields in the SMAS-1 were comparable to CONV and ORG while also producing fruit and fuelwood, demonstrating that strategic management of trees can diversify production without compromising overall crop production value in these systems. However, production did not increase under SMAS management, as was found in neighboring Honduras (Castro et al., 2009; FAO, 2005). There are several possible reasons for this.

First, El Salvador has the highest average maize yields in Central America, more than double that of Honduras (IICA, 2009). Low yields under conventional management in Honduras are likely the result of lower incomes that are associated with reduced use of fertilizers and improved seed. Thus, the productivity gains from the SMAS observed in Honduras may be unique to local circumstances, especially when compared to El Salvador where yields are nearer to their biophysical potential. Meanwhile, bean yields under both SMAS treatments and maize yields under SMAS-1 were similar to those achieved with the SMAS in Honduras (Castro et al., 2009).

Maize yields in the SMAS-2 were substantially lower and we suspect lateral shading from the surrounding forest may have had an impact. It was difficult to find large enough swaths of FOR in suitable sites to clear a buffer around the treatment, and SMAS-2 plots were often bordered by forest on 2 or 3 sides, resulting in substantial shading that appeared to negatively impact crop yields. We suspect this would not be an issue in the case where an entire farm field was managed as SMAS-2. However, we note that canopy cover was negatively correlated with the Production Value index in cropped treatments (Fig. 3), indicating that careful management of trees is important to minimize light competition (Beer et al., 1998).

While maize yields under ORG management were less than half that of CONV, average bean yields were comparable to CONV. The contrasting results for maize and beans highlight that N supply may be an



**Fig. 3.** Correlation matrix of field proxies and ecosystem service indices. Pearson's correlation results for field proxies (rows) and ES composite indices (columns). Dark (blue) circles represent positive correlations and light (red) circles negative correlations. Larger circles indicate a stronger correlation. Only significant correlations ( $p < 0.10$ ) are shown. \* Denotes field proxies are directly included in the development of the ES composite index. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

issue in the ORG treatment, since beans can supply a substantial portion of their N requirements through fixation. Additionally, the ORG treatment may be improving micronutrient availability and buffering pH, allowing beans to do well in this treatment despite having lower inputs of labile N and P. Beans are especially sensitive to soil acidity, which can increase with the application of ammonium sulfate. Yield impacts on beans may be especially important to producers as prices for beans in Central America generally, and in El Salvador specifically, have been rising recently and tend to be more volatile than maize prices (IICA, 2009).

Increased fuelwood and timber production is often cited as a benefit of agroforestry systems that may incentivize farmers to adopt practices such as the SMAS (e.g. Current et al., 1995b; de Sousa et al., 2016). While fuelwood production in the SMAS-2 treatment was triple that for CONV, fuelwood value was low relative to crop value (about 8% of farm revenue, see Table S3). It is unclear whether the value of fuelwood alone would be sufficient to incentivize farmers to adopt the SMAS, especially if profitability is diminished by reduced yields or increased labor costs. It is also unclear how fuelwood production in the SMAS compares to potential production in FOR. While farmers often harvest fuelwood from forest-fallows, we did not attempt to measure fuelwood production in FOR and recognize that this would increase the Production Value index for FOR. Further research on fuelwood harvesting and household consumption is needed to understand to what degree the SMAS might offset fuelwood collection in forests and fallows.

#### 4.1.2. Pest and disease control

Results from this study may alleviate concerns expressed by some farmers and technicians in the area that the SMAS and organic management would result in increased pest and disease pressures. The pest control methods used in the ORG treatment performed as well as CONV management and the two SMAS treatments showed reduced presence of pests, weeds and disease, suggesting the SMAS might enhance control.

Other studies have shown that diverse non-crop habitat can harbor pest predators, resulting in improved pest control (Bianchi et al., 2006; Karp et al., 2013). Weed control is likely a result of suppressed weed emergence caused by increased mulch cover in the SMAS (Schipanski et al., 2014), as demonstrated by a strong negative correlation between mulch and weed presence (Fig. S1). Disease control may be a result of multiple plant-soil interactions such as improved infiltration (Abawi and Corrales, 1990), enhanced soil biological diversity (Kremen and Miles, 2012) and better plant nutrition (e.g., Zörb et al., 2014).

#### 4.1.3. Erosion control

The two SMAS treatments increased soil mulch cover, which appears to be leading to reduced soil erosion. Soil mulch cover and absolute change in erosion pin height were significantly correlated across treatments (Kearney et al., 2017b, in review), probably resulting from both direct (e.g., raindrop interception and reduced runoff velocity) and indirect (e.g., increased SOM leading to improved soil structure and infiltration) mechanisms (Elwell and Stocking, 1976). We used absolute change in erosion pin height as an indicator of relative erosion as it was significantly correlated with slope and sediment captured in erosion pits installed on a subset of the plots (Kearney et al., 2017b, in review). Soil losses (sediment < 2 mm) in pits ranged from 300 to 1200 kg ha<sup>-1</sup> yr<sup>-1</sup>. Studies quantifying soil loss in Central America are scant, but a study from Jamaica (a slightly wetter climate) found sediment losses of 2000 to 3000 kg ha<sup>-1</sup> yr<sup>-1</sup> and also demonstrated reduced erosion with agroforestry management (McDonald et al., 2002). Our findings strengthen the link between agroforestry, soil mulch cover and erosion control, and can support erosion modeling and risk mapping for landscape planning (Delgado and Canters, 2012).

#### 4.1.4. Water regulation

Infiltration rates were similar to those found in other studies in Central America (e.g., Tully et al., 2012) and there was a strong

tendency for increased infiltration on non-CONV treatments receiving elevated inputs of organic matter from trees and composted manure. Decomposition of organic material can increase SOM, which is commonly associated with increased soil aggregation and infiltration (Craswell and Lefroy, 2001; Franzluebbers, 2002), and indeed we saw significant positive correlations between SOM and infiltration rates (Fig. S2). While we were unable to detect significant differences in infiltration rates between treatments, we did find significant results for indicators derived from water balance modeling, suggesting that the compounding effects of infiltration with other site parameters may lead to even more substantial off-site impacts for water quality and quantity. For example, increased infiltration rates combined with rainfall captured by the tree canopy and increased evapotranspiration from trees have a multiplicative effect to reduce runoff (Bruijnzeel, 2004). In our study, modeled runoff was near zero for FOR and SMAS-2, demonstrating the potentially dramatic ES benefits for downstream water quality and flood protection. As a result, forests and agroforestry systems also enhance groundwater recharge, and deep percolation was approximately doubled in FOR and SMAS-2 compared to CONV.

#### 4.1.5. Soil composition

The 3-year duration of this study likely was not sufficient to observe changes in soil properties with land management. Furthermore, we found significant spatial variability in soil properties (Fig. S3), which can complicate analysis of land-use impacts (Holmes et al., 2005). But some trends in our results do suggest that increased tree density may improve soil quality.

FOR had the highest mean index value for Soil Composition, driven by higher available P, SOM and pH, and lower bulk density. These are among the most important chemical and physical soil properties for cultivation in tropical climates (Velasquez et al., 2007), and studies from other regions show that management following the SMAS principles can mediate these properties over time (e.g., Kremen and Miles, 2012; Nziguheba et al., 2005; Thomazini et al., 2015). However, longer trials are needed to evaluate the long-term impacts of the SMAS on these soil properties in the Mesoamerican maize-bean context.

#### 4.1.6. Carbon (C) storage

Total C storage in the SMAS was similar to that found for other crop and silvopasture agroforestry systems (e.g., Henry et al., 2009; Luedeling et al., 2011), but lower than that generally found for fruit, timber or coffee agroforestry (e.g., Kirby and Potvin, 2007). Our results indicate that adoption of the SMAS-2 could increase C stocks by an average of 14.8 Mg ha<sup>-1</sup> over CONV management. It is difficult to determine from this study whether this amount of C would be sufficient to enable participation in C markets, as this would depend heavily on C prices, transaction costs and the time over which this change in C is averaged, which would be determined by the duration of the rotation with FOR. However, our findings show that regional C storage potential is substantial. There are an estimated 6 million hectares under active maize-bean cultivation in Central America alone (Dixon et al., 2001), indicating that C storage could be increased by up to 89 million tons with widespread implementation of the SMAS.

Increased C storage is expected to come primarily from AGWB as we found no significant differences in soil C stocks between treatments, although the same issues of time and spatial variability discussed in Section 4.1.5 apply here. However, maintaining regular inputs of organic matter to the soil is especially important in the tropics due to rapid decomposition and SOM turnover, and it is possible that soil C stocks under CONV management would decrease over time, especially when slash-and-burn practices are used (Fonte et al., 2010). The ORG treatment did receive elevated inputs of organic matter in the form of composted manure, but transport of such materials in steep landscapes is challenging.

Despite the high density of small trees in the SMAS, AGWB C was principally driven by the number of large trees (DBH > 10 cm) within

a plot. Others have noted the disproportionate contribution of large trees not only to C storage (e.g., Chave et al., 2001) but also to wildlife habitat and cultural values in smallholder systems (Marinidou et al., 2013). Management of large trees is therefore requisite if C sequestration is to be a primary objective of the SMAS, and would likely enhance other ES not measured in this study.

#### 4.1.7. Biodiversity

Both SMAS approaches maintained species richness comparable to that found by other agroforestry studies in Central America using similar sized plots (Ferguson et al., 2003; Richards and Méndez, 2014). Species richness in SMAS approached levels observed in FOR, which was low relative to forests in more humid tropical climates (e.g., Chave et al., 2001; Finegan and Delgado, 2000), although differing plot sizes and species assemblages makes comparison difficult without further analysis (Gotelli and Colwell, 2001). Many of the trees in the SMAS came from natural regeneration, as observed in other agroforestry systems in Central America (e.g., de Sousa et al., 2016). However, planting trees, as was done in the SMAS-1 treatment, may help to more quickly achieve biodiversity goals, especially if converting low diversity conventional fields to SMAS. Planting also provides an opportunity for farmers to select species and diversify production (e.g., fruit trees and fodder), thereby increasing the relative value of biodiversity to farmers.

The tendency for increased macrofauna abundance in cultivated plots compared to FOR aligns with findings from studies on SMAS in neighboring Honduras (Fonte et al., 2010; Pauli et al., 2011). The Honduran studies found that secondary forest plots contained lower macrofaunal abundance than agroforestry plots, perhaps due to lower quality litter in forests, which consist primarily of senesced leaves rather than pruned mulch (Fonte et al., 2010). While cultivation appeared to increase overall macrofauna abundance, we found lower species diversity in cultivated plots, which may reflect the dominance of hardy and adaptable fauna, and the loss of more sensitive taxa that can occur with forest conversion (Pauli et al., 2011; Rousseau et al., 2013). Finally, we note that the lack of statistically significant differences for Belowground Biodiversity indicators between management practices may again reflect the high spatial variability of soil properties (Fig. S3) and the relatively short treatment period considered here.

#### 4.2. ES synergies and trade-offs

A PCA analysis of the relationships between ES by treatment showed that the SMAS better demonstrates potential ES synergies compared to CONV. The upper left quadrant of the distance biplot in Fig. 2 (positive loading along the PC-2 axis and negative loading on the PC-1 axis) represents potential synergies between Production Value, Water Regulation, Pest and Disease Control, Soil Composition and Belowground Biodiversity. The tight directional grouping of Soil Composition, Water Regulation and Pest and Disease Control suggests synergies with strong theoretical underpinnings. For example, increased SOM is associated with higher infiltration rates, which in turn can reduce the incidence of bean diseases favored by high soil moisture content (Abawi and Corrales, 1990). The parallel loading for Belowground Biodiversity may indicate additional infiltration benefits from soil aggregation by organisms, especially earthworms (Rousseau et al., 2013), or direct mediation of pests and diseases from host dilution (Kremen and Miles, 2012). The loading for Production Value runs in a similar direction, suggesting that these synergies among regulating services are translating into increased production.

All of the points lying within the synergistic portion of the biplot described above are from SMAS-1, SMAS-2 and ORG plots, showing that the plots with the highest values of multiple ES belong to these treatments. The directional spread of plots within each treatment (indicated by the ellipses in Fig. 2) demonstrates the types of trade-offs or synergies occurring within each management system. Groupings for the SMAS-1 and SMAS-2 plots are spread along the upper-left to lower-right

diagonal, suggesting that the synergistic regulating ES mentioned above are more likely to translate into higher productivity for these plots, and low productivity occurs when provision for these ES is also low.

On the other hand, CONV plots tend to be associated with a lower occurrence of synergies between multiple ES and instead we see trade-offs between Production Value and non-production ES, as indicated by negative loadings on the PC-2 axis and a directional spread along the PC-1 axis. Others have found similar trade-offs between provisioning and regulating ES in intensified agricultural landscapes (Kremen and Miles, 2012; Nelson et al., 2009; Pilgrim et al., 2010; Raudsepp-Heare et al., 2010; Schipanski et al., 2014; Smukler et al., 2010), while trade-offs among regulating services were rarely observed (Pilgrim et al., 2010; Schipanski et al., 2014). ORG plots were more variable as indicated by the wide ellipse and fell between the SMAS and CONV plots, suggesting that the best management within the conventional (non-tree-based) system may improve synergies slightly, but that the tree-based principles of the SMAS are central for the ES evaluated in this study.

#### 4.3. Field proxies for multiple ES

By measuring just three field proxies – SOM and stem counts of small and large trees – one could ostensibly estimate the provision of all ES measured in this study except Water Regulation (Fig. 3). Infiltration was the only field proxy significantly correlated with the Water Regulation index, and direct monitoring of infiltration rates may be required to ensure that water-related ES are accruing. However, given that many of the ES indicators used to develop the Water Regulation index were modeled rather than measured, it is possible that the model does not fully capture the complexity of hydrologic factors and therefore difficult to conclude that other proxies aren't associated with water-related ES. For example, SOM was significantly correlated with infiltration (Fig. S2), but not the Water Regulation index.

Based on our findings, we emphasize the importance of monitoring trees of all sizes. Small trees are an important source of mulch, contribute to biodiversity and indicate the sustainability of the SMAS, since they represent healthy regeneration required to replace larger trees that may have a shortened lifespan due to pruning. Larger trees are critical for AGWB C storage (Stephenson et al., 2014) and their abundance does not correlate with lower yields, but strategic management to minimize canopy cover is required to avoid yield reductions (Fig. 3).

While increased stem counts were correlated with several ES indices, we note that the diversity of these trees may be important, and measuring aboveground biodiversity may still be desirable. Since all of the SMAS plots in this study contained a diverse mix of tree species by design, it was impossible to compare against an agroforestry system with high stem counts and low diversity; but some studies have suggested that synergies exist between tree diversity and ES benefits (Richards and Méndez, 2014). We also note that soil mulch cover appears to be an important field proxy for multiple ES, especially erosion control, although visible estimation may be a less reliable monitoring approach than biomass sampling (Fig. 3).

#### 4.4. Implications for management, ES monitoring and PES

This study demonstrates that agroforestry can increase a number of non-production ES benefits compared to either CONV or ORG management, approaching the services provided by secondary forest-fallows in the study area (Fig. 4 and Fig. S4). In our 3-year study we see no clear impacts of management on belowground biodiversity or soil composition, however we do note that these two indices were highly correlated (Fig. 2 and Fig. S4), supporting the growing evidence that biological, biophysical and biochemical interactions influence soil health (Brussaard et al., 2007).

For illustrative purposes we quantified the overall ES provision by summing all the ES composite indices for each treatment (Fig. 4, inset).

This value is highest for FOR (4.1 out of a maximum possible of 6.0), while the SMAS-2 and SMAS-1 treatments had intermediate values (about 25% lower than FOR) and the CONV and ORG treatments had the lowest values (about 45–50% lower than FOR).

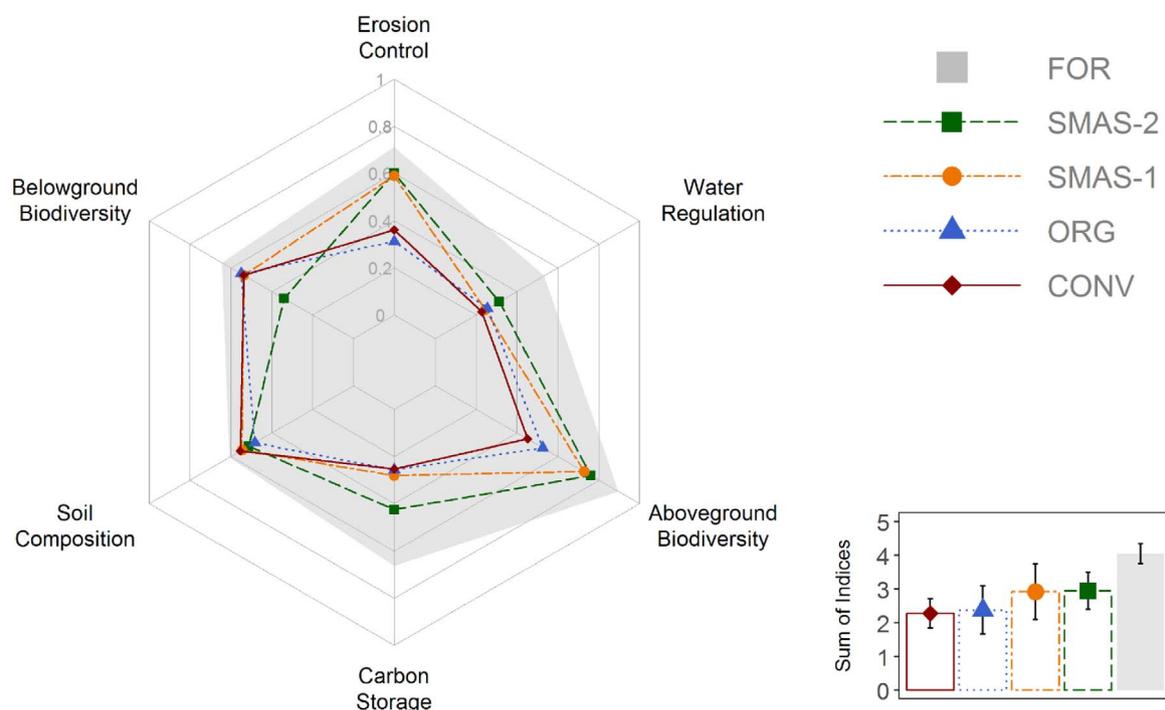
Quantifying overall service provision could be a simple way to compare land management strategies, and is indeed the goal of some ES evaluation tools (Bagstad et al., 2013). However, such a quantitative approach presents several issues. First, the selection of ES indicators and indices can never be exhaustive and is by necessity arbitrary, constrained by methods, data availability, resources and evaluation objectives. For example, in our study, comparisons to the ORG system may be limited. The ES indicators measured were chosen primarily to test the expected benefits of tree-based systems. In the ORG treatment we replaced agrochemical inputs with organic options, but did not implement the SMAS principles commonly associated with agroforestry and conservation agriculture. It is possible that ORG management provides other ES benefits not measured in the study, such as increased mycorrhizal colonization and its associated benefits (Gosling et al., 2006) or enhanced crop pollination (Kennedy et al., 2013; Kremen et al., 2002).

Second, deciding how important individual indicators are to overall ES provision is not straightforward. We used PCA in an effort to objectively determine indicator weights for construction of the composite indices, but did not weight composite indices for the overall provisioning index. Therefore, the relative weights (or importance) attributed to ES indicators determined the final ES index value, but ES indices equally contributed to the overall provisioning index. In practice, neither indicators nor indices can be weighted 'objectively', as different stakeholders have different perceptions of the relative value of services (Chan et al., 2016; Hauck et al., 2013), and demand for services varies over space and time (Chan et al., 2006). Weighting is problematic and controversial (Satterfield et al., 2013), but regional ES indices show promise as a strategy to rank ES provision and scale PES within a given context (e.g., Marinidou et al., 2013; Pagiola et al., 2007), and participatory approaches have begun to incorporate stakeholder values into relative ES weights (Satterfield et al., 2013; The Plan Vivo Foundation, 2013).

Farmer involvement in our study and varying site conditions led to a wide range of tree densities and species in the SMAS treatments, highlighting the system's adaptability. This flexibility is important for reasons outlined in Section 1, but presents challenges for quantifying the expected contribution of such systems to individual ES indicators. This quantification is increasingly desired by programs seeking to enhance the provision of individual ES (Naeem et al., 2015). Our study was able to provide empirical quantification for some indicators, but more importantly demonstrates a consistent pattern supporting the hypothesis that the principles of the SMAS do, in fact, enhance multiple ES and encourage synergies between them. Our results also suggest that diversification of farming systems and agroecological principles associated with SMAS implementation may be more important for ES supply than simply replacing chemical inputs with organic alternatives.

Finally, incentives such as PES and improved access to credit may be required for widespread adoption of the SMAS or organic management to occur. Profitability of the SMAS-1 was about the same as CONV, while SMAS-2 and ORG were lower (Table S3), demonstrating that direct incentives for farmers in the immediate term (e.g., increased fuelwood production, lower input costs and reduced labor) are low, at least in the context of our study area. Other potential benefits to farmers such as improved soil fertility and increased yields were not observed in this three-year study, suggesting they would only accrue in the long-term, and smallholder farmers without access to capital or secure land-tenure may struggle to invest in systems with long-term payoffs (Engel and Muller, 2016).

Incentives need to be combined with supporting policies and continuing collective action to address other issues. For example, Hellin et al. (1999) found that the SMAS was not adopted where available land



**Fig. 4.** Radar chart of non-production ecosystem services. Composite index values, relative to the maximum observed value for each index, for regulatory ecosystem services and biodiversity (main). Inset (bar chart) shows the sum total of all indices by treatment (error bars denote standard deviation). The shaded area represents the forest-fallow (FOR) reference treatment and lines show the four cultivated treatments: CONV = conventional management; ORG = organic (conventional management without chemical inputs); SMAS-1 = the slash-and-mulch agroforestry system, converted from CONV and; SMAS-2 = the same as SMAS-1, but converted from FOR.

area was sufficient to allow shifting slash-and-burn agriculture to continue, and the lack of family labor due to out-migration can be a barrier to adopting new practices (Ayarza et al., 2010). Ayarza and Welchez (2004) noted the importance of policies banning burning and long-term interactions among diverse stakeholders to build knowledge and technical capacity. Implementation of the SMAS combined with increased community awareness eventually led to a shift in perceptions, and land value under SMAS management in Honduras is now 30% higher than in areas without it (Ayarza et al., 2010).

In summary, we have three general recommendations for ES-related outreach, policy and incentive programs for hillside smallholder maize-bean growing regions:

- (1) Promote the *principles* of the SMAS (eliminating burning, maintaining a permanent vegetative soil cover or ‘mulch’ and intercropping with diverse tree species)
- (2) Focus on *multiple* ES groups rather than tying incentives or regulations to a single ES
- (3) Design monitoring programs to measure field proxies (e.g. tree stem counts, SOM) that relate to multiple ES and reflect the principles of the SMAS, rather than seeking out binary definitions of agroforestry

## 5. Conclusions

By using controlled on-farm experiments, we were able to empirically demonstrate that SMAS strategies improve key indicators of non-provisioning ES compared to conventional and organic management systems without trees. Results showed that substantial ES benefits accrued within just three years of conversion from conventional management (SMAS-1), comparable to those found for traditional SMAS establishment from a forest-fallow (SMAS-2). These ES increases can potentially be achieved without significant reductions to overall crop production value, although challenges with the study design (e.g., lateral shading in SMAS-2) make it difficult to determine the exact impact of mature SMAS on maize and bean yields.

The inherently flexible design of the SMAS addresses some of the critiques of previous agroforestry research, but leads to high variability, potentially limiting the ability to statistically detect ES enhancements in a study of moderate resources. By developing composite indices of multiple ES we were able to identify patterns showing that the SMAS enhances multiple ES and better capitalizes on synergies between regulating and provisioning ES compared to conventional management. Results for organic management were less clear, but we note that the study was designed primarily to evaluate the ES benefits of agroforestry.

We also identified simple field proxies that correlate well with multiple ES, with important implications for management and monitoring strategies. For example, monitoring schemes should measure both small and large trees, as small trees contribute to biodiversity and system sustainability, while large trees are critical for C storage. However, strategic management of large trees will be necessary to minimize canopy cover and potential negative yield impacts. Policies and incentives focused on multiple ES can support long-term collective action to build farmer knowledge and technical capacity, alleviate yield losses that may occur during transition and develop community awareness around the multiple ES benefits provided.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2017.08.032>.

## References

- Abawi, G.S., Corrales, M.A.P., 1990. Root Rots of Beans in Latin America and Africa: Diagnosis, Research Methodologies, and Management Strategies. Centro Internacional de Agricultura Tropical (CIAT), Cali, Columbia.
- Adesina, A.A., Coulbaly, O., Manyong, V.M., Sanginga, P.C., Mbila, D., Chianu, J., Kamleu, D.G., 1999. Policy Shifts and Adoption of Alley Farming in West and Central Africa. IITA, Nigeria.
- Allen, R.G., Pereira, L.S., Raes, D., Smith, M., 1998. FAO Irrigation and Drainage Paper (No. 56). Rome.
- Anderson, J.M., Ingram, J.S.I., 1993. Tropical Soil Biology and Fertility: A Handbook of Methods, 2nd ed. CAB International, Wallingford, Oxon, UK.
- Ayarza, M.A., Welchez, L.A., 2004. Drivers effecting the development and sustainability of the Quesungual Slash and Mulch Agroforestry System (QSMAS) on hillsides of Honduras, in: Comprehensive Assessment Bright Spots Project Final Report. Cali, Colombia, p. 15.
- Ayarza, M., Huber-Sannwald, E., Herrick, J.E., Reynolds, J.F., García-Barrios, L., Welchez, L.A., Lentos, P., Pavón, J., Morales, J., Alvarado, A., Pinedo, M., Baquera, N., Zelaya, S., Pineda, R., Amézquita, E., Trejo, M., 2010. Changing human-ecological relationships and drivers using the Quesungual agroforestry system in western Honduras. *Renew. Agric. Food Syst.* 25, 219–227. <http://dx.doi.org/10.1017/S1742170510000074>.
- Bagstad, K.J., Semmens, D.J., Waage, S., Winthrop, R., 2013. A comparative assessment of decision-support tools for ecosystem services quantification and valuation. *Ecosyst. Serv.* 5, 27–39. <http://dx.doi.org/10.1016/j.ecoser.2013.07.004>.
- Balvanera, P., Uriarte, M., Almeida-Leñero, L., Altesor, A., DeClerck, F., Gardner, T., Hall, J., Lara, A., Laterra, P., Peña-Claros, M., Silva Matos, D.M., Vogl, A.L., Romero-Duque, L.P., Arreola, L.F., Caro-Borrero, A.P., Gallego, F., Jain, M., Little, C., de Oliveira Xavier, R., Paruelo, J.M., Peinado, J.E., Poorter, L., Ascarrunz, N., Correa, F., Cunha-Santino, M.B., Hernández-Sánchez, A.P., Vallejos, M., 2012. Ecosystem services research in Latin America: the state of the art. *Ecosyst. Serv.* 2, 56–70. <http://dx.doi.org/10.1016/j.ecoser.2012.09.006>.
- Beer, J., Muschler, R., Kass, D., Somarriba, E., Kass, D., Somarriba, E., 1998. Shade management in coffee and cacao plantations. *Agrofor. Syst.* 38, 139–164. <http://dx.doi.org/10.1023/A:1005956528316>.
- Bianchi, F.J.J.A., Booij, C.J.H., Tschamtké, T., 2006. Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc. Biol. Sci.* 273, 1715–1727. <http://dx.doi.org/10.1098/rspb.2006.3530>.
- Bruijnzeel, L.A., 2004. Hydrological functions of tropical forests: not seeing the soil for the trees? *Agric. Ecosyst. Environ.* <http://dx.doi.org/10.1016/j.agee.2004.01.015>.
- Brussaard, L., Pulleman, M.M., Ouedraogo, É., Mando, A., Six, J., 2007. Soil fauna and soil function in the fabric of the food web. *Pedobiologia (Jena)*. 50, 447–462. <http://dx.doi.org/10.1016/j.pedobi.2006.10.007>.
- CENTA, 2008. Guía técnica para el manejo de variedades de frijol. Programa de Granos Básicos.
- Castro, A., Rivera, M., Ferreira, O., Pavon, J., García, E., Amezquita, E., Ayarza, M., Barrios, E., Rondón, M., Pauli, N., Baltodano, M.E., Mendoza, B., Welchez, L.A., Rao, I.M., 2009. Quesungual slash and mulch agroforestry system (QSMAS): Improving crop water productivity, food security and resource quality in the sub-humid tropics Cali, Colombia.
- Castro, A., Menjivar, J.C., Barrios, E., Asakawa, N., Borrero, G., García, E., Rao, I., 2010. Dinámica del nitrógeno y el fósforo del suelo bajo tres sistemas de uso de la tierra en laderas de Honduras. *Acta Agronómica* 59, 410–419.
- Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C., Daily, G.C., 2006. Conservation planning for ecosystem services. *PLoS Biol.* 4, 2138–2152. <http://dx.doi.org/10.1371/journal.pbio.0040379>.
- Chan, K.M.A., Balvanera, P., Benessaiah, K., Chapman, M., Díaz, S., Gómez-Baggethun, E., Gould, R., Hannahs, N., Jax, K., Klain, S., Luck, G.W., Martín-López, B., Muraca, B., Norton, B., Ott, K., Pascual, U., Satterfield, T., Tadaki, M., Taggart, J., Turner, N., 2016. Opinion: why protect nature? Rethinking values and the environment. *Proc. Natl. Acad. Sci.* 113, 1462–1465. <http://dx.doi.org/10.1073/pnas.1525002113>.
- Chave, J., Réiera, B., Dubois, M., 2001. Estimation of biomass in a neotropical forest of French Guiana: spatial and temporal variability. *J. Trop. Ecol.* 17, 79–96.
- Craswell, E., Lefroy, R., 2001. The role and function of organic matter in tropical soils. *Nutr. Cycl. Agroecosyst.* 61, 7–18. <http://dx.doi.org/10.1023/A>.
- Current, D., Lutz, E., Scherr, S.J., 1995a. Costs, Benefits, and Farmer Adoption of Agroforestry: Project Experience in Central America and the Caribbean (No. 14), World Bank Environment Paper. The World Bank, Washington, DC.
- Current, D., Lutz, E., Scherr, S.J., 1995b. The costs and benefits of agroforestry to farmers. *World Bank Res. Obs.* 10, 151–180. <http://dx.doi.org/10.1093/wbro/10.2.151>.
- Davis, A.S., Hill, J.D., Chase, C.A., Johanns, A.M., Liebman, M., 2012. Increasing cropping system diversity balances productivity, profitability and environmental health. *PLoS One* 7, 1–8. <http://dx.doi.org/10.1371/journal.pone.0047149>.
- de Groot, R.S., Alkemade, R., Braat, L., Hein, L., Willemsen, L., 2010. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecol. Complex* 7, 260–272. <http://dx.doi.org/10.1016/j.ecocom.2009.10.006>.
- Delgado, M.E.M., Canters, F., 2012. Modeling the impacts of agroforestry systems on the spatial patterns of soil erosion risk in three catchments of Claveria, the Philippines. *Agrofor. Syst.* 85, 411–423. <http://dx.doi.org/10.1007/s10457-011-9442-z>.
- Dixon, J., Gulliver, A., Gibbon, D., 2001. Farming Systems and Poverty. Improving Farmers' Livelihoods in a Changing World. Food and Agriculture Organization of the United Nations, Rome, Italy.
- de Sousa, K.F.D., Detlefsen, G., de Melo, Virginio, Filho, E., Tobar, D., Casanoves, F., 2016. Timber yield from smallholder agroforestry systems in Nicaragua and Honduras. *Agrofor. Syst.* 90, 207–218. <http://dx.doi.org/10.1007/s10457-015-9846-2>.
- Elwell, H.A., Stocking, M.A., 1976. Vegetal cover to estimate soil erosion hazard in Rhodesia. *Geoderma* 15, 61–70. [http://dx.doi.org/10.1016/0016-7061\(76\)90071-9](http://dx.doi.org/10.1016/0016-7061(76)90071-9).
- Engel, S., Muller, A., 2016. Payments for environmental services to promote climate-smart agriculture? Potential and challenges. *Agric. Econ.* 47, 173–184. <http://dx.doi.org/10.1111/agec.12307>.
- FAO, 2005. El Sistema Agroforestal Quesungual. Litografía López, Rome, Italy.
- FAO, 2013. Climate-Smart Agriculture Sourcebook, Sourcebook on Climate-Smart Agriculture Forestry and Fisheries.
- FAO, 2016. The State of Food and Agriculture 2016. Rome, Italy ISBN: 978-92-5-107671-2 I.
- Ferguson, B.G., Vandermeer, J., Morales, H., Griffith, D.M., 2003. Post-agricultural succession in El Petén. Guatemala. *Conserv. Biol.* 17, 818–828. <http://dx.doi.org/10.1046/j.1523-1739.2003.01265.x>.
- Finegan, B., Delgado, D., 2000. Structural and floristic heterogeneity in a 30-year-old Costa Rican rain forest restored on pasture through natural secondary succession. *Restor. Ecol.* 8, 380–393. <http://dx.doi.org/10.1046/j.1526-100x.2000.80053.x>.
- Fonte, S.J., Six, J., 2010. Earthworms and litter management contributions to ecosystem services in a tropical agroforestry system. *Ecol. Appl.* 20, 1061–1073. <http://dx.doi.org/10.1890/09-0795.1>.
- Fonte, S.J., Barrios, E., Six, J., 2010. Earthworms, soil fertility and aggregate-associated soil organic matter dynamics in the Quesungual agroforestry system. *Geoderma* 155, 320–328. <http://dx.doi.org/10.1016/j.geoderma.2009.12.016>.
- Franzluebbers, A.J., 2002. Water infiltration and soil structure related to organic matter and its stratification with depth.pdf. *Soil Tillage Res.* 66, 197–205. [http://dx.doi.org/10.1016/S0167-1987\(02\)00027-2](http://dx.doi.org/10.1016/S0167-1987(02)00027-2).
- Gómez-Castro, H., Pinto-Ruiz, R., Guevara-Hernández, F., Gonzalez-Reyna, A., 2010. Estimaciones de biomasa aérea y carbono almacenado en *Gliricidia sepium* (lam.) y *Leucaena leucocephala* (jacq.) y su aplicación en sistemas silvopastoriles. *Inf. Técnica Económica Agrar.* 106, 256–270.
- García, E.D., 2011. Evaluación Del Impacto Del Uso Ganadero Sobre Suelo Y Vegetación En El Sistema Agroforestal Quesungual (SAQ) En El Sur De Lempira. CATIE, Honduras.
- Gosling, P., Hodge, A., Goodlass, G., Bending, G.D., 2006. Arbuscular mycorrhizal fungi and organic farming. *Agric. Ecosyst. Environ.* 113, 17–35. <http://dx.doi.org/10.1016/j.agee.2005.09.009>.
- Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391. <http://dx.doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Groom, B., Palmer, C., 2012. REDD+ and rural livelihoods. (Special Issue: REDD+ and conservation). *Biol. Conserv.* 154, 42–52. <http://dx.doi.org/10.1016/j.biocon.2012.03.002>.
- Haines-Young, R., Potschin, M., 2013. Common International Classification of Ecosystem Services (CICES): Consultation on Version 4, August–December. pp. 2012.
- Hauk, J., Görg, C., Varjopuro, R., Ratamáki, O., Jax, K., 2013. Benefits and limitations of the ecosystem services concept in environmental policy and decision making: some stakeholder perspectives. *Environ. Sci. Policy* 25, 13–21. <http://dx.doi.org/10.1016/j.envsci.2012.08.001>.
- Hayati, D., 2017. A Literature Review on Frameworks and Methods for Measuring and Monitoring Sustainable Agriculture. 98.
- Hegde, R., Bull, G.Q., 2011. Performance of an agro-forestry based payments-for-environmental-services project in Mozambique: a household level analysis. *Ecol. Econ.* 71, 122–130. <http://dx.doi.org/10.1016/j.ecolecon.2011.08.014>.
- Hellin, J., Welchez, L.A., Cherrett, I., 1999. The Quesungual system: an indigenous agroforestry system from western Honduras. *Agrofor. Syst.* 46, 229–237. <http://dx.doi.org/10.1023/A:1006217201200>.
- Henry, M., Tittonell, P., Manlay, R.J., Bernoux, M., Albrecht, A., Vanlauwe, B., 2009. Biodiversity, carbon stocks and sequestration potential in aboveground biomass in smallholder farming systems of western Kenya. *Agric. Ecosyst. Environ.* 129, 238–252. <http://dx.doi.org/10.1016/j.agee.2008.09.006>.
- Holmes, K., Kyriakidis, P., Chadwick, O., 2005. Multi-scale variability in tropical soil nutrients following land-cover change. *Biogeochemistry* 74, 173–203.
- Horton, R.E., 1933. The role of infiltration in the hydrologic cycle. *Eos Trans. Am. Geophys. Union* 14, 446–460.
- Hughes, R., Kauffman, J., Jaramillo, V., 1999. Biomass, carbon and nutrient dynamics of secondary forests in a humid tropical region of Mexico. *Ecology* 80, 1892–1907. <http://dx.doi.org/10.2307/176667>.
- IICA, 2009. Mapeo del mercado de semillas de maíz y frijol en centroamérica. Proyecto Red SICTA, Managua, Nicaragua.
- Karp, D.S., Mendenhall, C.D., Sandif, R.F., Chaumont, N., Ehrlich, P.R., Hadly, E.A., Daily, G.C., 2013. Forest bolsters bird abundance, pest control and coffee yield. *Ecol. Lett.* 16, 1339–1347. <http://dx.doi.org/10.1111/ele.12173>.
- Kearney, S.P., Coops, N.C., Chan, K.M.A., Fonte, S.J., Siles, P., Smukler, S.M., 2017a. Predicting carbon benefits from climate-smart agriculture: high-resolution carbon mapping and uncertainty assessment in El Salvador. *J. Environ. Manage.* 202, 287–298. <http://dx.doi.org/10.1016/j.jenvman.2017.07.039>.
- Kearney, S.P., Fonte, S.J., García, E.D., Siles, P., Smukler, S.M. (2017b). Improving the utility of erosion pins: absolute value of pin height change as an indicator of relative

- erosion (in review).
- Kennedy, C.M., Lonsdorf, E., Neel, M.C., Williams, N.M., Ricketts, T.H., Winfree, R., Bommarco, R., Brittain, C., Burley, A.L., Cariveau, D., 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecol. Lett.* 16, 584–599.
- Kirby, K.R., Potvin, C., 2007. Variation in carbon storage among tree species: implications for the management of a small-scale carbon sink project. *For. Ecol. Manage.* 246, 208–221. <http://dx.doi.org/10.1016/j.foreco.2007.03.072>.
- Kosoy, N., Corbera, E., 2010. Payments for ecosystem services as commodity fetishism. *Ecol. Econ.* 69, 1228–1236. <http://dx.doi.org/10.1016/j.ecolecon.2009.11.002>.
- Kosoy, N., Martínez-Tuna, M., Muradian, R., Martínez-Alier, J., 2007. Payments for environmental services in watersheds: insights from a comparative study of three cases in Central America. *Ecol. Econ.* 61, 446–455. <http://dx.doi.org/10.1016/j.ecolecon.2006.03.016>.
- Kremen, C., Miles, A., 2012. Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecol. Soc.* 17. <http://dx.doi.org/10.5751/es-05035-170440>.
- Kremen, C., Williams, N.M., Thorp, R.W., 2002. Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. U. S. A.* 99, 16812–16816. <http://dx.doi.org/10.1073/pnas.262413599>.
- Lavelle, P., Rodríguez, N., Arguello, O., Bernal, J., Botero, C., Chaparro, P., Gomez, Y., Gutierrez, A., del Pilar Hurtado, M., Loaiza, S., Xiomara Pullido, S., Rodriguez, E., Sanabria, C., Velasquez, E., Fonte, S.J., 2014. Soil ecosystem services and land use in the rapidly changing Orinoco River Basin of Colombia. *Agric. Ecosyst. Environ.* 185, 106–117. <http://dx.doi.org/10.1016/j.agee.2013.12.020>.
- Luedeling, E., Silvestri, G., Beedy, T., Dietz, J., 2011. Carbon sequestration potential of agroforestry systems. *Adv. Agrofor. Adv. Agrofor.* 8, 61–83. <http://dx.doi.org/10.1007/978-94-007-1630-8>.
- Luffman, I.E., Nandi, A., Spiegel, T., 2015. Gully morphology, hillslope erosion, and precipitation characteristics in the Appalachian Valley and Ridge province, south-eastern USA. *Catena* 133, 221–232. <http://dx.doi.org/10.1016/j.catena.2015.05.015>.
- MAG, 2016. Retrospectiva de precios de granos básicos 2001 – 2016 [WWW Document]. Retresp. Mens. precios Prod. Agropecu. URL <http://www.mag.gob.sv/retrospectiva-mensual-de-precios-de-productos-agropecuarios/> (Accessed 04, August 2016).
- MAG, 2016b. Anuario de estadísticas agropecuarias. Santa Tecla, El Salvador.
- MARN, 2013. Datos históricos de precipitación: estaciones G-12 de Concepción Quezaltepeque y G-7 de Arcatao (1971 – 2012). *Pers. Commun.*
- Magurran, A.E., 1988. Ecological diversity and its measurement. *Statewide Agricultural Land Use Baseline 2015*, first. ed. Springer, Netherlands. [http://dx.doi.org/10.1007/978-94-015-7358-0\\_1](http://dx.doi.org/10.1007/978-94-015-7358-0_1).
- Marinidou, E., Finegan, B., Jiménez-Ferrer, G., Delgado, D., Casanoves, F., 2013. Concepts and a methodology for evaluating environmental services from trees of small farms in Chiapas, México. *J. Environ. Manage.* 114, 115–124. <http://dx.doi.org/10.1016/j.jenvman.2012.10.046>.
- Mbow, C., Van Noordwijk, M., Luedeling, E., Neufeldt, H., Minang, P.A., Kowero, G., 2014. Agroforestry solutions to address food security and climate change challenges in Africa. *Curr. Opin. Environ. Sustain.* 6, 61–67. <http://dx.doi.org/10.1016/j.cosust.2013.10.014>.
- McDonald, M.A., Healey, J.R., Stevens, P.A., 2002. The effects of the secondary clearance forest and subsequent land-use on erosion losses and soil properties in the Blue Mountains of Jamaica. *Agric. Ecosyst. Environ.* 92, 1–19.
- Mehlich, A., 1984. Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. *Commun. Soil Sci. Plant Anal.* 15, 1409–1416.
- Millennium Ecosystem Assessment, 2005. Ecosystems and Human Well-Being Ecosystems. Island Press, Washington, DC. <http://dx.doi.org/10.1196/annals.1439.003>.
- Morris, K.S., Mendez, V.E., Lovell, S.T., Olson, M., 2013. Conventional food plot management in an organic coffee cooperative: explaining the paradox. *Agroecol. Sustain. Food Syst.* 37, 762–787. <http://dx.doi.org/10.1080/21683565.2013.774303>.
- Mukherjee, A., Lal, R., 2014. Comparison of soil quality index using three methods. *PLoS One* 9, 1–15. <http://dx.doi.org/10.1371/journal.pone.0105981>.
- Naeem, B.S., Ingram, J.C., Varga, A., Agardy, T., Barten, P., Bennett, G., Bloomgarden, E., Bremer, L.L., Burkill, P., Cattau, M., Ching, C., Colby, M., Cook, D.C., Costanza, R., Declerck, F., Freund, C., Gartner, T., Gunderson, J., Jarrett, D., Kinzig, A.P., Kiss, A., Koontz, A., Kumar, P., Lasky, J.R., Masozera, M., Meyers, D., Milano, F., Nichols, E., Olander, L., Olmsted, P., Perge, E., Perrings, C., Polasky, S., Potent, J., Prager, C., Quétiér, F., Redford, K., Saterson, K., Thoumi, G., Vargas, M.T., Vickerman, S., Weisser, W., Wilkie, D., Wunder, S., 2015. Get the science right when paying for nature's services. *Science* (80-) 347, 1206–1207. <http://dx.doi.org/10.1126/science.aaa1403>.
- Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D.R., Chan, K.M.A., Daily, G.C., Goldstein, J., Kareiva, P.M., Lonsdorf, E., Naidoo, R., Ricketts, T.H., Shaw, M.R., 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Front. Ecol. Environ.* 7, 4–11. <http://dx.doi.org/10.1890/080023>.
- Nziguheba, G., Merckx, R., Palm, C. a., 2005. Carbon and nitrogen dynamics in a phosphorus-deficient soil amended with organic residues and fertilizers in western Kenya. *Biol. Fertil. Soils* 41, 240–248. <http://dx.doi.org/10.1007/s00374-005-0832-0>.
- Olson, M.B., Morris, K.S., Méndez, V.E., 2012. Cultivation of maize landraces by small-scale shade coffee farmers in western El Salvador. *Agric. Syst.* 111, 63–74. <http://dx.doi.org/10.1016/j.agsy.2012.05.005>.
- Ordóñez Barragan, J., 2004. Main Factors Influencing Maize Production in the Quesungual Agroforestry System in Southern Honduras: An Exploratory Study. Wageningen University <http://dx.doi.org/10.1017/CBO9781107415324.004>.
- Pagiola, S., Ramírez, E., Gobbi, J., de Haan, C., Ibrahim, M., Murgueitio, E., Ruiz, J.P., 2007. Paying for the environmental services of silvopastoral practices in Nicaragua. *Ecol. Econ.* 64, 374–385. <http://dx.doi.org/10.1016/j.ecolecon.2007.04.014>.
- Palm, C.A., van Noordwijk, M., Woomer, P., Alegre, J.C., Arévalo, L., Castilla, C.E., Cordeiro, D.G., Hairiah, K., Kotto-Same, J., Moukam, A., Parton, W.J., Risce, A., Rodrigues, V., Sitompul, S.M., 2005. Carbon losses and sequestration after land use change in the humid tropics. In: Palm, C.A., Vosti, S.A., Sanchez, P.A., Erickson, P.J. (Eds.), *Slash-and-Burn Agriculture: The Search for Alternatives*. Columbia University Press, New York New York USA, pp. 41–63.
- Palomo, I., Felipe-Lucia, M.R., Bennett, E.M., Martín-López, B., Pascual, U., 2016. Disentangling the pathways and effects of ecosystem service Co-Production. *Advances in Ecological Research*. Elsevier Ltd. pp. 245–283. <http://dx.doi.org/10.1016/bs.aecr.2015.09.003>.
- Pattanayak, S.K., Mercer, D.E., Sills, E., Yang, J.C., 2003. Taking stock of agroforestry adoption studies. *Agrofor. Syst.* 57, 173–186. <http://dx.doi.org/10.1023/A:1024809108210>.
- Pauli, N., Barrios, E., Conacher, A.J., Oberthür, T., 2011. Soil macrofauna in agricultural landscapes dominated by the Quesungual Slash-and-Mulch Agroforestry System, western Honduras. *Appl. Soil Ecol.* 47, 119–132. <http://dx.doi.org/10.1016/j.apsoil.2010.11.005>.
- Pilgrim, E.S., Macleod, C.J.A., Blackwell, M.S.A., Bol, R., Hogan, D.V., Chadwick, D.R., Cardenas, L., Misselbrook, T.H., Haygarth, P.M., Brazier, R.E., Hobbs, P., Hodgson, C., Jarvis, S., Dungait, J., Murray, P.J., Firbank, L.G., 2010. Interactions Among Agricultural Production and Other Ecosystem Services Delivered from European Temperate Grassland Systems, *Advances in Agronomy*. Elsevier Ltd. <http://dx.doi.org/10.1016/B978-0-12-385040-9.00004-9>.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-Effects Models in S and S-Plus*. Springer-Verlag, New York.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Development Core Team, 2013. *nlme: Linear and Nonlinear Mixed Effects Models*.
- Pollini, J., 2009. Agroforestry and the search for alternatives to slash-and-burn cultivation: from technological optimism to a political economy of deforestation. *Agric. Ecosyst. Environ.* 133, 48–60. <http://dx.doi.org/10.1016/j.agee.2009.05.002>.
- Pribyl, D.W., 2010. A critical review of the conventional SOC to SOM conversion factor. *Geoderma* 156, 75–83. <http://dx.doi.org/10.1016/j.geoderma.2010.02.003>.
- R Core Team, 2016. *R: A Language and Environment for Statistical Computing*.
- Raudsepp-earne, C., Peterson, G.D., Bennett, E.M., 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proc. Natl. Acad. Sci.* 107, 5242–5247. <http://dx.doi.org/10.1073/pnas.0907284107>.
- Richards, M.B., Méndez, V.E., 2014. Interactions between carbon sequestration and shade tree diversity in a smallholder coffee cooperative in El Salvador. *Conserv. Biol.* 28, 489–497. <http://dx.doi.org/10.1111/cobi.12181>.
- Rioux, J., Juan, M.G.S., Neely, C., Seeberg-Elverfeldt, C., Karttunen, K., Rosenstock, T., Kirui, J., Massoro, E., Mpanda, M., Kimaro, A., Masoud, T., Mutoko, M., Mutabazi, K., Kuehne, G., Poulouchidou, A., Avagyan, A., Tapio-Bistrom, M.-L., Bernoux, M., 2016. Planning, implementing and evaluating Climate-Smart Agriculture in Smallholder Farming Systems (No. 11), *Mitigation of Climate Change in Agriculture Series*. Rome.
- Rousseau, L., Fonte, S.J., Téllez, O., Van Der Hoek, R., Lavelle, P., 2013. Soil macrofauna as indicators of soil quality and land use impacts in smallholder agroecosystems of western Nicaragua. *Ecol. Indic.* 27, 71–82. <http://dx.doi.org/10.1016/j.ecolind.2012.11.020>.
- Satterfield, T., Gregory, R., Klain, S., Roberts, M., Chan, K.M., 2013. Culture, Intangibles and metrics in environmental management. *J. Environ. Manage.* 117, 103–114. <http://dx.doi.org/10.1016/j.jenvman.2012.11.033>.
- Schipanski, M.E., Barbercheck, M., Douglas, M.R., Finney, D.M., Haider, K., Kaye, J.P., Kemanian, A.R., Mortensen, D.A., Ryan, M.R., Tooker, J., White, C., 2014. A framework for evaluating ecosystem services provided by cover crops in agroecosystems. *Agric. Syst.* 125, 12–22. <http://dx.doi.org/10.1016/j.agsy.2013.11.004>.
- Schoon, M.L., Robards, M.D., Brown, K., Engle, N., Meek, C.L., Biggs, R., 2015. Politics and the resilience of ecosystem services. *Principles for Building Resilience: Sustaining Ecosystem Services in Social-Ecological Systems*. pp. 32–49. <http://dx.doi.org/10.1017/CBO9781316014240.003>.
- Shannon, C.E., 1948. The Shannon information entropy of protein sequences. *Bell Syst. Tech. J.* 27, 379–423. [http://dx.doi.org/10.1016/S0006-3495\(96\)79210-X](http://dx.doi.org/10.1016/S0006-3495(96)79210-X). (NaN-656).
- Shepherd, K.D., Shepherd, G., Walsh, M.G., 2015. Land health surveillance and response: a framework for evidence-informed land management. *Agric. Syst.* 132, 93–106. <http://dx.doi.org/10.1016/j.agsy.2014.09.002>.
- Smukler, S.M., Sánchez-Moreno, S., Fonte, S.J., Ferris, H., Klonsky, K., O'Gen, A.T., Scow, K.M., Steenwerth, K.L., Jackson, L.E., 2010. Biodiversity and multiple ecosystem functions in an organic farmscape. *Agric. Ecosyst. Environ.* 139, 80–97. <http://dx.doi.org/10.1016/j.agee.2010.07.004>.
- Steenwerth, K.L., Hodson, A.K., Bloom, A.J., Carter, M.R., Cattaneo, A., Chartres, C.J., Hatfield, J.L., Henry, K., Hopmans, J.W., Horwath, W.R., Jenkins, B.M., Kearey, E., Leemans, R., Lipper, L., Lubell, M.N., Msangi, S., Prabhu, R., Reynolds, M.P., Sandoval Solis, S., Sisco, W.M., Springborn, M., Tittonell, P., Wheeler, S.M., Vermeulen, S.J., Wollenberg, E.K., Jarvis, L.S., Jackson, L.E., 2014. Climate-smart agriculture global research agenda: scientific basis for action. *Agric. Food Secur.* 3, 11. <http://dx.doi.org/10.1186/2048-7010-3-11>.
- Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D., Lines, a, Morris, E.R., Rüger, W.K., Alvarez, N., Blundo, E., Bunyavechewin, C., Chuyong, S., Davies, G., Duque, S.J., Ewango, A., Flores, C.N., Franklin, O., Grau, J.F., Hao, H.R., Harmon, Z., Hubbell, M.E., Kenfack, S.P., Lin, D., Makana, Y., Malizia, J.-R., Malizia, A., Pabst, L.R., Pongpattananurak, R.J., Su, N., Sun, S.-H., Tan, I.-F., Thomas, S., vanMantgem, D., Wang, P.J., Wiser, X., Zvala, S.K., 2014. Rate of tree carbon accumulation increases continuously with tree size. *Nature* 507, 90–93. <http://dx.doi.org/10.1038/nature12914>.

- Suárez, D., 2002. Cuantificación y valoración económica del servicio ambiental almacenamiento de carbono en sistemas agroforestales de café en la Comarca Yassica Sur. CATIE, Matagalpa Nicaragua.
- The Plan Vivo Foundation, 2013. The Plan Vivo Standard 2013 The Plan Vivo Standard for Community Payments for Ecosystem Services Programmes. <http://dx.doi.org/10.1017/CBO9781107415324.004>.
- The World Bank, 2008. Sustainable Land Management Sourcebook, Agriculture and Rural Development. The World Bank, Washington, DC. <http://dx.doi.org/10.1596/978-0-8213-7432-0>.
- Thomazini, A., Mendonça, E.S., Cardoso, I.M., Garbin, M.L., 2015. SOC dynamics and soil quality index of agroforestry systems in the Atlantic rainforest of Brazil. *Geoderma Reg.* 5, 15–24. <http://dx.doi.org/10.1016/j.geodrs.2015.02.003>.
- Tully, K.L., Lawrence, D., Scanlon, T.M., 2012. More trees less loss: nitrogen leaching losses decrease with increasing biomass in coffee agroforests. *Agric. Ecosyst. Environ.* 161, 137–144. <http://dx.doi.org/10.1016/j.agee.2012.08.002>.
- United Nations, 2015. Transforming our world: the 2030 agenda for sustainable development. General Assembly 70th Session.
- Vågen, T.-G., Shepherd, K.D., Walsh, M.G., Winowiecki, L., Desta, L.T., Tondoh, J.E., 2010. AfSIS Technical Specifications. *Soil Health Surveillance*.
- Velasquez, E., Lavelle, P., Andrade, M., 2007. GISQ, a multifunctional indicator of soil quality. *Soil Biol. Biochem.* 39, 3066–3080. <http://dx.doi.org/10.1016/j.soilbio.2007.06.013>.
- Walkley, A., Black, I.A., 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. *Soil Sci.* 37, 29–38.
- Welches, L.A., Cherrett, I., 2002. The Quesungual system in Honduras – an alternative to slash-and-burn. *LEISA Mag.* 10–11.
- Wendland, K.J., Honzák, M., Portela, R., Vitale, B., Rubinoff, S., Randrianarisoa, J., 2010. Targeting and implementing payments for ecosystem services: opportunities for bundling biodiversity conservation with carbon and water services in Madagascar. *Ecol. Econ.* 69, 2093–2107. <http://dx.doi.org/10.1016/j.ecolecon.2009.01.002>.
- Wittman, H., Powell, L.J., Corbera, E., 2015. Financing the agrarian transition? the clean development mechanism and agricultural change in latin america. *Environ. Plan. A* 47, 2031–2046. <http://dx.doi.org/10.1068/a130218p>.
- Zörb, C., Senbayram, M., Peiter, E., 2014. Potassium in agriculture-status and perspectives. *J. Plant Physiol.* 171, 656–669. <http://dx.doi.org/10.1016/j.jplph.2013.08.008>.