# Interactions between Carbon Sequestration and Shade Tree Diversity in a Smallholder Coffee Cooperative in El Salvador

# MERYL BRETON RICHARDS\* AND V. ERNESTO MÉNDEZ†

\*CGIAR Research Program on Climate Change, Agriculture and Food Security, Gund Institute, University of Vermont, 617 Main Street, Burlington, VT 05405, U.S.A., email meryl.richards@uvm.edu

†Agroecology and Rural Livelihoods Group (ARLG), Department of Plant and Soil Science, University of Vermont, Jeffords Hall, 63 Carrigan Drive, Burlington, VT 05405, U.S.A.

**Abstract:** Agroforestry systems have substantial potential to conserve native biodiversity and provide ecosystem services. In particular, agroforestry systems have the potential to conserve native tree diversity and sequester carbon for climate change mitigation. However, little research has been conducted on the temporal stability of species diversity and aboveground carbon stocks in these systems or the relation between species diversity and aboveground carbon sequestration. We measured changes in shade-tree diversity and shade-tree carbon stocks in 14 plots of a 35-ba coffee cooperative over 9 years and analyzed relations between species diversity and carbon sequestration. Carbon sequestration was positively correlated with initial species richness of shade trees. Species diversity of shade trees did not change significantly over the study period, but carbon stocks increased due to tree growth. Our results show a potential for carbon sequestration and long-term biodiversity conservation in smallbolder coffee agroforestry systems and illustrate the opportunity for synergies between biodiversity conservation and climate change mitigation.

**Keywords:** agrobiodiversity, agroecology, biodiversity, Central America, climate change mitigation, ecosystem services

Interacciones entre el Secuestro de Carbono y la Diversidad de Árboles de Sombra en una Cooperativa de Café de Pequeños Agricultores en El Salvador

**Resumen:** Los sistemas agroforestales tienen potencial sustancial para conservar la biodiversidad nativa y proporcionar servicios ecosistémicos. En particular tienen el potencial para conservar la diversidad nativa de árboles y secuestrar carbono para la mitigación del cambio climático. Sin embargo, se ban conducido pocas investigaciones sobre la estabilidad temporal de la diversidad de especies y el capital de carbono superficial en estos sistemas o las relaciones entre la diversidad de especies y el secuestro de carbono superficial. Medimos los cambios en la diversidad de árboles de sombra y el capital de carbono de estos mismos árboles en 14 terrenos de 35 bectáreas de una cooperativa de café a lo largo de 9 años y analizamos las relaciones entre la diversidad de especies y el secuestro de carbono. El secuestro de carbono tuvo una correlación positiva con la riqueza inicial de especies de árboles de sombra. La diversidad de especies de estos árboles no cambió significativamente a lo largo del periodo de estudio, pero el capital de carbono incrementó debido al crecimiento de los árboles. Nuestros resultados muestran un potencial de secuestro de carbono y una conservación de biodiversidad a largo plazo en los sistemas agroforestales de pequeños agricultores de café; ilustran también la oportunidad de sinergias entre la conservación de la biodiversidad y la mitigación del cambio climático.

Palabras Clave: agrobiodiversidad, agroecología, biodiversidad, Centroamérica, mitigación del cambio climático, servicios ecosistémicos

# Introduction

Approximately 40% of the earth's land surface is currently in agricultural use (Chappell & LaValle 2009; Foley et al. 2011), and it is estimated that agricultural production will need to double in order to meet the food and energy needs of a projected global population of 9 billion by 2050 (Godfray et al. 2010). This will place substantial pressure on the world's land resources, particularly in the tropics, where the most significant expansions in cropland are occurring (Godfray et al. 2010; Foley et al. 2011).

Due to the projected expansion of agricultural lands, there is increasing interest in the potential for agricultural landscapes to provide and conserve ecosystem services (Nonato de Souza et al. 2011; Farley et al. 2012). Ecosystem services refer to the benefits that humans derive, directly or indirectly, from the properties and processes of ecosystems (Costanza et al. 1997).

Agroforestry systems, and shade coffee agroecosystems in particular, have been recognized as having significant potential for providing ecosystem services similar to natural forests (Rapidel et al. 2011). Shade coffee agroecosystems have been noted for their ability to conserve tree, bird, bat, insect, epiphyte, and mammal species diversity, filter and regulate water sources (Lin 2010), control erosion, and regulate atmospheric CO<sub>2</sub> concentrations via C storage (Perfecto & Vandermeer 2008; Jha et al. 2011; Méndez et al. 2012). Tree conservation is particularly important to C storage because tree aboveground biomass (AGB) comprises a large fraction of C stocks in tropical forests (Chave et al. 2003).

Although natural forests remain the primary land-based C sinks (Canadell & Raupach 2008), there is increasing interest in the role that agroforestry systems could play in C sequestration (Soto-Pinto et al. 2010). Agroforestry systems can store from 12 to 228 Mg ha<sup>-1</sup> of C in AGB (median 95 Mg ha<sup>-1</sup>) (Albrecht & Kandji 2003; Soto-Pinto et al. 2010). The potential for such systems to accumulate C depends on a number of factors, including age, tree species, climate, soil conditions, land-use history, system structure, and management such as pruning or harvesting the perennial components of the system (Albrecht & Kandji 2003; Montagnini & Nair 2004; Soto-Pinto et al. 2010).

There is also some evidence that C storage and species diversity may be linked, potentially due to decreased competition for light or other resources in assemblages of polycultures relative to monocultures (Potvin & Gotelli 2008). In experimental conditions in central Panama, newly planted polycultures of up to 6 tropical tree species produced more biomass (measured as tree basal area) in 5 years than monocultures (Potvin & Gotelli 2008). Results from research in existing agroforestry systems have been murkier because competition and tree biomass production interact with land management, such as pruning and tree removal (Häger 2012). In general, the potential synergies and trade-offs between carbon sequestration and biodiversity conservation in agricultural landscapes have been understudied, and climate change and biodiversity loss are addressed as separate issues.

We examined the relationship between tree species diversity and C sequestration in AGB in 14 plots of a smallholder coffee cooperative over a 9-year period. We also examined the temporal stability of shade tree biodiversity (species richness and abundance).

# Methods

## **Study Site**

This study was conducted in a 35-ha shade coffee cooperative in the municipality of Tacuba in western El Salvador (13°52′, -90°4′). The area where the cooperative is located is of particular conservation importance because it is in the buffer zone of El Imposible National Park, one of the largest (5000 ha) and most important protected forest areas in El Salvador. Though El Salvador is, latitudinally, located within the tropics, Tacuba is bioclimatically classified as subtropical wet forest due to its elevation (Tosi & Hartshorn 1978; Holdridge 1967). The elevation of the research area ranges from 738 to 980 masl, and average rainfall of 1500 mm per year is concentrated in the months of May through October. Soils are primarily Andisols (MARN 2003).

The cooperative was formed by 19 members in 1984. The 35 hectares are managed collectively under the supervision of a board of directors, the membership of which rotates biannually. *Coffea arabica* L. is cultivated exclusively, including the Pacas, Bourbon, and Pacamara varieties. The shade type of this cooperative would be considered a traditional polyculture on the basis of Moguel and Toledo's (1999) classification system in which coffee is planted under both natural regenerated and planted trees and farmers maximize the presence of useful species. The cooperative was managed conventionally until 2003, transitioned to organic management in 2003, was certified organic in 2006, and continues to be managed under organic certification to date.

## **Data Collection**

Fourteen rectangular quadrats measuring  $20 \times 50$  m (1000 m<sup>2</sup>) were used as replicates to measure tree size and biodiversity in the cooperative. The centroids of these quadrats were established in 2001 along 5 transects, which were established using maps and GPS to avoid potential bias from surveying the terrain prior to establishing the sample locations. The first transect was randomly located, and then starting from this initial transect, 4 other transects were located 243 m from each other. Five points were then randomly located along each

transect, and points that were at least 50 m apart from each other and from the border of the cooperative were chosen for sampling, yielding a final sample of 14 points. These points were GPS referenced and were used as the centroids of the sample quadrats in both 2001 and 2010. Trees were not tagged as the initial research was not designed as a longitudinal study.

All trees of height greater than 2 m were identified to species level, and their height and diameter at breast height (dbh) were recorded. Trees that could not be identified in the field were sampled, and the samples were taken to La Laguna Botanical Garden in San Salvador for identification. Three species that could not be identified were analyzed as morphospecies groups. Tree heights were measured with telescoping poles in 2001 and with a Laser Technology Trupulse 360 laser rangefinder in 2010.

## **Data Analyses**

Comparisons of tree size (basal area and height), species density, stem density, and species per stem were analyzed through paired tests of differences in means per quadrat; each pair was composed of the 2001 and 2010 quadrats corresponding to the same centroid.

Because stem density decreased from 2001 to 2010, we used Mao-Tau sample-based species rarefaction curves (rescaled by individuals as recommended by Gotelli and Colwell (2001)) to compare species richness between the 2 years. We also used the nonparametric estimator Chao2*P* (Chao 1987; Colwell & Coddington 1994) to estimate true species richness. Chao2*P* is the Chao2 estimator calculated by Chao (1987) with Lopez et al.'s (2012) adjustment to reduce bias due to undersampling, which we chose due to the high presence of singletons in both 2001 and 2010 data sets. All species richness estimators were calculated in EstimateS version 8.2.0 (Colwell 2010) and Excel 2010. Species of international conservation concern were identified using the International Union for Conservation of Nature Red List of Threatened Species.

We compared species evenness between 2001 and 2010 by calculating rank-abundance distributions and using Kolmogorov-Smirnov's 2-sample test to compare the distributions, as proposed by Magurran (2006).

We estimated AGB in the shade tree canopy using an allometric model proposed by Chave et al. (2005) for AGB estimation of dry forests and applied explicitly to shade coffee by Méndez et al. (2009). The model is based on tree height (H), diameter at breast height (D), and species-specific wood density ( $\rho$ ):

AGB(kg) =  $\exp(-2.187 + 0.916 \times \ln(\rho D^2 H))$ .

Wood density data were obtained from the World Agroforestry Center (2008) database. Density estimates were available for 30 of the 72 species found in 2001 and 2010 collectively. For the remaining 42 species, we used the average of the mean wood density for the 30 species, which was 0.61 (Chave et al. 2003; Méndez et al. 2009).

We assumed a C content of 47% to convert AGB to C stocks, as proposed by Kirby and Potvin (2007). We calculated total C stocks for each of the 14 quadrats for each year and extrapolated to Mg ha<sup>-1</sup> in order to compare our C-stock results with C stocks reported in the literature. We used correlations to look for relationships between C sequestration and tree species richness. Because stem density changed between 2001 and 2010, we divided the number of species by the number of trees found in the plot and used this variable (i.e., species per stem) (Hubbell et al. 1999) to investigate relationships between biodiversity and C sequestration in order to avoid confounding of changes in number of species with stem density changes. Because the relationship between species and individuals is not necessarily linear, we also tested the relationships between biodiversity and C sequestration and C stocks with partial correlations in which tree density was the control variable.

## Results

#### Shade Tree Biodiversity and Carbon Sequestration

Carbon sequestration rate was positively correlated with 2001 species per stem (Fig. 1); an additional 0.58 Mg ha<sup>-1</sup> yr<sup>-1</sup> was sequestered for every 0.1 unit increase in species per stem (p = 0.010). This relationship between C sequestration rate and species per quadrat in 2001 was also significant when controlling for tree density (p = 0.047). Carbon sequestration rate was not significantly correlated with species per quadrat in 2010. There were no significant correlations between standing C stock and species per quadrat (controlling for tree density) in either year (Fig. 2). Nor was there any relationship between change in species per quadrat and change in C stock. In most quadrats, the number of species decreased whereas C increased; there was no consistent pattern in the magnitude of the changes.

#### **Vegetation Structure**

In 2001, we inventoried a total of 446 trees ( $\geq 2$  m in height) in the 14 sample quadrats. In 2010, the sample quadrats contained a total of 336 trees. Stem density, measured in trees per quadrat, was lower in 2010 than in 2001, though the difference was not significant. There was greater variation in stem density between quadrats in 2001 than in 2010. The mean height, maximum height, and basal area of trees  $\geq 2$  m height were significantly higher in 2010 than in 2001 (Table 1). Mean tree height (Pearson r = -0.524, p = 0.004) and dbh (Pearson r = -0.527, p = 0.004) were negatively correlated with stem density.





Figure 2. Correlations between carbon stocks and tree species per stem in each sample year in 14 shade-tree coffee quadrats in Tacuba, El Salvador (circle, 2010 observed; triangle, 2001 observed; solid line, 2010 linear best fit; dashed line, 2001 linear best fit).

# Shade Tree Biodiversity

Tree samples in 2001 totaled 446 individuals representing 27 families and 56 species. Fifty-three of these species were identified, of which 48 were native, 4 were exotic, and 1 was of unknown origin. In 2010, we found 336 individuals in quadrats of the same size (23 families and 47 species). Forty-three of these species were identified, of which 37 were native and 6 were exotic (Supporting Information). Of the 56 species found in the entire site

in 2001, 22 were rare (just 1 or 2 individuals recorded), whereas 15 of the 44 species found in 2010 were rare.

Mean observed species density per quadrat did not change significantly from 2001 to 2010 (Table 1). Species density was strongly and positively correlated with stem density in both 2001 (Pearson r = 0.784, p = 0.001) and 2010 (Pearson r = 0.694, p = 0.006), so we calculated sample-based species rarefaction (Mao-Tau) curves to test for differences in species richness (Fig. 3). There was

-				
Property	2001 (SD)	2010 (SD)	t	þ
Observed density of tree species (species/quadrat <sup><i>a</i></sup> )	14 (4)	11 (2)	2.983	0.345
Observed total species richness of trees	56	47	-	-
Estimated total species richness of trees (Chao2P)	86	71	-	-
Stem density (trees/ha)	319 (162)	239 (62)	2.119	0.054
Tree species/stem	0.50 (0.1)	0.48 (0.1)	0.372	0.716
Mean basal area of trees (cm <sup>2</sup> )	292.0 (178.5)	551.9 (366.4)	-2.560	$0.024^{a}$
Mean diameter breast height (cm)	14.0 (4.6)	20.9 (7.4)	-3.359	$0.005^{b}$
Mean tree height (m)	5.5 (0.8)	7.8 (1.8)	-5.238	$0.000^{b}$
Maximum tree height (m)	10.7 (2.1)	14.0 (2.6)	-3.541	$0.004^{b}$
Shade tree spell out (Mg/ha)	27.6 (10.6)	51.8 (27.5)	-3.751	$0.002^{b}$
Shade tree carbon stock (Mg/ha)	13.0 (5.0)	24.4 (12.9)	-3.751	$0.002^{b}$

Table 1. Properties of the shade-tree canopy and paired *t* test differences in mean per quadrat of properties (where applicable) on a 35-ha coffee cooperative in Tacuba, El Salvador in 2001 and 2010.

<sup>a</sup>Significant at 0.05.

<sup>b</sup>Significant at 0.01.



*Figure 3. Tree species rarefaction curves (Mao-Tau) and 95% confidence intervals for 2001 and 2010 in 14 shade-coffee quadrats in Tacuba, El Salvador.* 

considerable overlap in the 95% confidence intervals of the curves for 2001 and 2010, indicating no difference in species richness. The rarefaction curves did not reach an asymptote in either year, indicating that further sampling would be required to complete the inventory of tree species in this site. Because of this, we used the nonparametric estimator Chao2*P* to estimate true species richness of the study site in each study year. Based on this estimator, 30 more species were needed to complete the inventory of tree species in 2001 (Chao2*P* = 86) and 24 more species were needed to complete the inventory of tree species in 2010 (Chao2*P* = 71) (Fig. 3).

The rank-abundance curves for 2001 and 2010 both indicated moderate species evenness (Fig. 4). The Kolmogorov-Smirnov 2-sample test indicated that the species abundance distribution did not change significantly from 2001 to 2010 (K-S statistic = 1.33, p = 0.058).

Five of the tree species found in the cooperative in 2001 were threatened. Of these 5 species, 3 were also found in the cooperative in 2010 (Supporting Information). No new species of conservation concern were found in 2010. These are not complete lists of species of conservation concern for this cooperative or region, and this does not indicate that 2 species were lost altogether from the cooperative because we did not conduct a complete species inventory.

#### Shade Tree C Stocks

There was a significant increase in shade tree AGB and C stocks from 2001 to 2010 (Table 1). Above ground C in woody shade species nearly doubled (from 13.0 to 24.4 Mg ha<sup>-1</sup>) in the 9 years between sampling, a total storage of 11.4 Mg C ha<sup>-1</sup> over 9 years, or 1.3 Mg C ha<sup>-1</sup> per year. Because C stocks are a function of both tree size and tree density, it is clear that substantial increases in tree height and dbh compensated for slight decreases in tree density from 2001 to 2010. Changes in C stocks by quadrat from 2001 to 2010 were correlated with changes in mean dbh (Pearson's r = 0.567, p = 0.035) and height (Pearson's r = 0.581, p = 0.029), though not with changes in stem density.

Carbon sequestration differed by quadrat (Fig. 5). In most quadrats, additional C accumulated in shade trees over the study period (2001–2010). However, in 3 quadrats, C stocks decreased between 2001 and 2010. In these quadrats, the trees remaining in 2010 were either fewer or of smaller size (or both) than in 2001, indicating that several large trees had been harvested during the study period.

Removal of trees by farmers in quadrats 2, 6, 9, and 12 did not negate the C stock increases of the larger trees (Fig. 5). In quadrats 4 and 5, mean dbh and C stocks decreased from 2001 to 2010, indicating that this was an area where the farmers had harvested larger trees.

Biophysical factors such as elevation may also influence carbon sequestration. There was, however, no



Figure 4. Shade-tree rank-abundance curves for 2001 and 2010 in 14 shade-coffee quadrats in Tacuba, El Salvador. A rank of 1 indicates the most abundant species, a rank of 2 the second-most abundant, and so on. Relative abundance is the abundance of a given species relative to the abundance of the other species in the sample.

Figure 5. Carbon stocks stored in shade trees over 9 years in a coffee cooperative of Tacuba, El Salvador.

correlation between elevation and carbon sequestration or between elevation and carbon stocks in either year.

# Discussion

## **Conservation of Shade Tree Biodiversity**

None of the measures of biodiversity that we used suggested that species richness or evenness changed significantly from 2001 to 2010. Any difference in observed species richness was likely due to the marginally significant decrease in stem density from 2001 to 2010 because there was very little change in species per stem between the 2 years.

Species assemblages in 2001 and 2010 were similar but not identical, indicating that the farmers were likely selectively harvesting some species while leaving others. There were, for example, marked decreases in the

abundances of Croton reflexifolius and Ricinus communis (the 2 most abundant species in 2001) between our 2001 and 2010 samples (Supporting Information). The managers of the cooperative confirmed that they deliberately eliminated Ricinus communis, which is generally used as a fast growing species planted alongside new coffee plantings or re-plantings. Croton reflexifolius is a common windbreak species, and the managers eliminated some windbreaks between 2001 and 2010. Species that were maintained in high abundances (relative to other species) from 2001 to 2010 tended to be those that are considered important by farmers for their benefits in agroforestry systems or those that provide locally useful products. Such species included several species from the genus Inga, which are valued for their nitrogenfixing properties and are used for firewood; Machaerium arboretum, another nitrogen-fixing species, reported as useful for providing timber and firewood; and Eugenia jambos, an exotic, which produces edible fruit and is valued as a shade and windbreak species because it is an evergreen (Méndez et al. 2007).

#### **Carbon Sequestration in Coffee Agroforestry Systems**

The structure of the shade tree canopy of the coffee cooperative changed over 9 years in a way that increased AGB and, consequently, C storage. The size of the shade trees-height and dbh-increased significantly, whereas tree density remained stable. This indicates that while some thinning and pruning was occurring, the managers of the cooperative were not maintaining the shade tree canopy at a homogeneous height of 10 m, as previously stated in interviews (Méndez et al. 2007). Shade coffee farmers in this region generally prune shade trees at least once a year, with the purpose of providing more sunshine for the coffee plants and to harvest firewood. However, interviews conducted by Méndez et al. (2009) regarding the management of the cooperative in 2002 indicated that farmers were pruning only an average of 0.8 times per year. The main reason for decreasing pruning activities usually has to do with a shortage of labor or funds to hire external workers.

The aboveground C stock in the cooperative that was the subject of this study was in the low end of the potential range for agroforestry systems of 12 to 228 Mg ha<sup>-1</sup> (Albrecht & Kandji 2003; Soto-Pinto et al. 2010). However, lianas, nonwoody species such as *Musa*, and coffee bushes were not included in this study, which results in an underestimation of AGB C stocks. The mean shade tree C stock in 2010 was higher than the mean for coffee shade tree C stocks of 15.3 Mg ha<sup>-1</sup> cited in Méndez et al. (2012), lower than the value reported by Schmitt-Harsh et al. (2012) for coffee agroforests in Guatemala, and similar to the value reported for organic coffee farms in Costa Rica by Häger (2012). The C fixation rate in shade trees (1.3 Mg ha<sup>-1</sup> year<sup>-1)</sup> was similar to rates found in coffee agroforestry systems around the globe (Méndez et al. 2012). The actual C sequestration rate in trees may be slightly lower than calculated because the allometric equations used to estimate AGB do not account for pruning.

The farmers involved in this study did not have any external incentives for C sequestration. There was no evidence in our study that the managers of the cooperative were deliberately limiting tree harvesting in order to increase C storage, yet C stocks increased simply by allowing tree growth and natural regeneration. Similar studies (Nakakaawa et al. 2010; Soto-Pinto et al. 2010) have focused on farmers or plantations that were involved in payment for ecosystem services (PES) schemes, which compensate farmers for C sequestration on their farms, generally by planting more trees. Although the carbon sequestered in this coffee cooperative would not be eligible for compensation under most carbon market schemes because it is not additional to what would happen ordinarily, there is potential for the existing sequestration to be supported by more traditional agricultural development pathways or product certifications.

## Shade Tree Biodiversity and Carbon Sequestration

Although C sequestration was positively correlated with species diversity in our data, the relationship between shade tree C stock and species diversity was not significant. The existing literature on this relationship is mixed, with most studies failing to find a relationship between aboveground C stocks and species diversity. Kirby and Potvin (2007) found no correlation between aboveground C and species diversity in Panamanian forests or agroforests. Soto-Pinto et al. (2010) found that a technified coffee agroforest with just 2 shade species had larger tree C stocks than a diverse polyculture. Henry et al. (2009) examined a number of land uses in Kenya and did not find any clear relationship between species diversity and aboveground C storage. Likewise, Méndez et al. (2009) found no relationship between shade tree species diversity and soil C storage in El Salvador. However, 2 recent studies found a correlation when soil C storage was included. Woody plant species richness was associated with higher total C (aboveground and soil) storage in a recent study of Costa Rican coffee agroforestry systems by Häger (2012), and Saha et al. (2009) found a positive correlation between soil organic C and plant diversity in home gardens of India.

Although greater species diversity may not equate to greater standing C stock in shade trees, our data suggest that species diversity may support greater accumulation of aboveground C over time. This relationship is most relevant for C finance projects, which fund C sequestration but do not reward farmers for existing C stocks. Our study, however, was limited in geographic and temporal scope. Longer-term studies in multiple geographies would be needed to confirm the relationship between species diversity and carbon sequestration in agroforestry systems.

Ecologists have hypothesized that biodiversity enhances ecosystem function via resource partitioning and positive intraguild interactions (species complementarity) or by the presence of highly efficient, competitive species that improve functioning (sampling effects) (Tscharntke et al. 2005; Häger 2012). In this way, it is not only the diversity of species but the assemblage of species that might matter to ecosystem services such as C sequestration (Häger 2012). More diverse tree communities may be more likely to contain the fast-growing or dense species that contribute to greater carbon sequestration. Experimental studies with various tree communities could tease out these relationships.

Because agroforests are human-managed systems, this may present an opportunity for farmers to manage such systems for greater C sequestration. However, this would require a re-examination of mechanisms to support or reward shade coffee farmers; current initiatives have generally failed to include them (Davis & Méndez 2011). For example, small-scale farmers have generally been excluded from REDD, Clean Development Mechanism (CDM), and other PES schemes for C sequestration because of the expense involved in managing multiple small farms and the lower per-hectare mitigation benefits relative to afforestation and reforestation projects (Wunder & Börner 2012). Agroforestry systems have been especially complicated for C finance because it is difficult to quantify additional mitigation benefits, in the form of C sequestered as a result of the funded project, which would not have been sequestered otherwise. A better understanding of the relationship between species diversity and C sequestration could help clarify the additional mitigation benefits associated with farmer management changes and choices and uncover potential synergies between C sequestration, biodiversity conservation, and other ecosystem services.

# Acknowledgments

We thank the members and families of the Associacion de Caficultores Organicos del Occidente de El Salvador (ACOES) for their collaboration in this research. J. Diaz and O. Ortiz of ASINDEC also provided valuable support. M.B.R. received funding for this research from the University of Vermont's College of Agriculture and Life Science and the Annie's Homegrown Sustainable Agriculture Scholarship.

## **Supporting Information**

Frequency, origin, and conservation status of identified tree species (Appendix S1) are available online. The

authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

## **Literature Cited**

- Albrecht, A., and S. T. Kandji. 2003. Carbon sequestration in tropical agroforestry systems. Agriculture Ecosystems & Environment 99:15-27.
- Canadell, J. G., and M. R. Raupach. 2008. Managing forests for climate change mitigation. Science 320:1456–1457.
- Chao, A. 1987. Estimating the population size for capture-recapture data with unequal catchability. Biometrics **43**:783-791.
- Chappell, M. J., and L. A. LaValle. 2009. Food security and biodiversity: Can we have both? An agroecological analysis. Agriculture and Human Values 28:3–26.
- Chave, J., R. Condit, S. Lao, J. P. Caspersen, R. B. Foster, and S. Hubbell. 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. Journal of Ecology 91:240–252.
- Chave, J., et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia **145**:87-99.
- Colwell, R. K. 2010. EstimateS: statistical estimation of species richness and shared species from samples. Available from http://viceroy.eeb. uconn.edu/estimates.
- Colwell, R. K., and J. A. Coddington. 1994. Estimating terrestrial biodiversity through extrapolation. Philosophical Transactions of the Royal Society B: Biological Sciences 345:101-118.
- Costanza, R., et al. 1997. The value of the world's ecosystem services and natural capital. Nature **387**:253-260.
- Davis, A., and V. E. Méndez. 2011. Prioritizing food security and livelihoods in climate change mitigation mechanisms: experiences and opportunities for smallholder coffee agroforestry, forest communities and REDD+. Salvadoran Research Program on Development and Environment (PRISMA), San Salvador, El Salvador.
- Farley, J., A. Schmitt, F. J. Alvez, and N. Ribeiro de Freitas Jr. 2012. How valuing nature can transform agriculture. Solutions 2:64–73.
- Foley, J. A., et al. 2011. Solutions for a cultivated planet. Nature **478**: 337-342.
- Godfray, H. C. J., J. R. Beddington, I. R. Crute, L. Haddad, D. Lawrence, J. F. Muir, J. Pretty, S. Robinson, S. M. Thomas, and C. Toulmin. 2010. Food security: the challenge of feeding 9 billion people. Science 327:812–818.
- Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379-391.
- Häger, A. 2012. The effects of management and plant diversity on carbon storage in coffee agroforestry systems in Costa Rica. Agroforestry Systems 86:159-174.
- Henry, M., P. Tittonell, R. J. Manlay, M. Bernoux, A. Albrecht, and B. Vanlauwe. 2009. Biodiversity, carbon stocks and sequestration potential in aboveground biomass in smallholder farming systems of western Kenya. Agriculture, Ecosystems & Environment 129:238– 252.
- Holdridge, L. R. 1967. Life Zone Ecology. Tropical Science Center, San Jose, Costa Rica.
- Hubbell, S. P., R. B. Foster, S. T. O' Brien, K. E. Harms, R. Condit, S. J. Wechsler, S. J. Wright and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. Science 283:554-557.
- Jha, S., C. M. Bacon, S. M. Philpott, R. A. Rice, V. E. Méndez, and P. Läderach. 2011. A review of ecosystem services, farmer livelihoods, and value chains in shade coffee agroecosystems. Pages 141–208 in B. W. Campbell and S. Lopez-Ortiz, editors. Integrating

agriculture, conservation, and ecotourism: examples from the field. Springer Academic Publishers, New York.

- Kirby, K. R., and C. Potvin. 2007. Variation in carbon storage among tree species: implications for the management of a small-scale carbon sink project. Forest Ecology and Management 246:208– 221.
- Lin, B. B. 2010. The role of agroforestry in reducing water loss through soil evaporation and crop transpiration in coffee agroecosystems. Agricultural and Forest Meteorology **150:**510–518.
- Lopez, L. C. S., M. P. D. Fracasso, D. O. Mesquita, A. R. T. Palma, and P. Riul. 2012. The relationship between percentage of singletons and sampling effort: a new approach to reduce the bias of richness estimates. Ecological Indicators 14:164–169.
- Magurran, A. E. 2006. Measuring biological diversity. Blackwell Publishing, Malden, Massachusetts.
- MARN (Ministerio de Medio Ambiente y Recursos Naturales). 2003. Mapas del Sistema de Información Ambiental. MARN, San Salvador, El Salvador. Available from www.marn.gob.sv/gis/png/pedolo.htm (accessed October 2003).
- Méndez, V. E., S. Castro-Tanzi, K. Goodall, K. S. Morris, C. M. Bacon, P. Läderach, W. B. Morris, and M. U. Georgeoglou-Laxalde. 2012. Livelihood and environmental trade-offs of climate mitigation in smallholder coffee agroforestry systems. Pages 370–381 in E. K. Wollenberg, A. Nihart, M. Grieg-Gran, and M. L. Tapio-Biström, editors. Climate mitigation and agriculture. Earthscan, London.
- Méndez, V. E., S. R. Gliessman, and G. S. Gilbert. 2007. Tree biodiversity in farmer cooperatives of a shade coffee landscape in western El Salvador. Agriculture Ecosystems & Environment 119:145– 159.
- Méndez, V. E., E. N. Shapiro, and G. S. Gilbert. 2009. Differentiated cooperative management and its effects on shade tree diversity and soil properties of coffee plantations in western el salvador. Agroforestry Systems 76:111-126.
- Moguel, P., and V. M. Toledo. 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology 13:11-21.
- Montagnini, F., and P. K. R. Nair. 2004. Carbon sequestration: an underexploited environmental benefit of agroforestry systems. Agroforestry Systems 61:281-295.
- Nakakaawa, C., J. Aune, and P. Vedeld. 2010. Changes in carbon stocks and tree diversity in agro-ecosystems in south western Uganda:

What role for carbon sequestration payments? New Forests **40**: 19–44.

- Nonato de Souza, H., J. d. Graaff, and M. M. Pulleman. 2011. Strategies and economics of farming systems with coffee in the Atlantic Rainforest Biome (Online first). Agroforestry Systems. 84:227–242.
- Perfecto, I., and J. Vandermeer. 2008. Spatial pattern and ecological process in the coffee agroforestry system. Ecology 89:915–920.
- Potvin, C., and N. J. Gotelli. 2008. Biodiversity enhances individual performance but does not affect survivorship in tropical trees. Ecology Letters 11:217-223.
- Rapidel, B., F. DeClerck, J. F. L. Coq, and J. Beer, editors. 2011. Ecosystem services from agriculture and agroforestry. Earthscan, London.
- Saha, S. K., P. K. R. Nair, V. D. Nair, and B. M. Kumar. 2009. Soil carbon stock in relation to plant diversity of homegardens in Kerala, India. Agroforestry Systems 76:53–65.
- Schmitt-Harsh, M., T. P. Evans, E. Castellanos, and J. C. Randolph. 2012. Carbon stocks in coffee agroforests and mixed dry tropical forests in the western highlands of Guatemala. Agroforestry Systems 86:141– 157.
- Soto-Pinto, L., M. Anzueto, J. Mendoza, G. J. Ferrer, and B. de Jong. 2010. Carbon sequestration through agroforestry in indigenous communities of Chiapas, Mexico. Agroforestry Systems 78:39–51.
- Tosi, J. and G. Hartshorn. 1978. Mapa Ecologico de El Salvador: Sistema de Zonas de Vida del Dr. L.R. Holdridge (Ecological Map of El Salvador: Life Zone System of Dr. L.R. Holdridge). Minsterio de Agricultura y Ganaderia de El Salvador (Agriculture and Livestock Ministry of El Salvador), San Salvador.
- Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. Ecology Letters 8:857–874.
- World Agroforestry Center. 2008. Tree functional attributes and ecological database. World Agroforestry Center, Nairobi, Kenya. Available from http://db.worldagroforestry.org/wd World Agroforestry Center (accessed November 2012).
- Wunder, S., and J. Börner. 2012. Payments for environmental services to mitigate climate change: agriculture and forestry compared. Pages 170-180 in E. K. Wollenberg, A. Nihart, M. Grieg-Gran, and M. L. Tapio-Biström, editors. Climate mitigation and agriculture. Earthscan, London.

