Shade tree diversity, carbon sequestration, and epiphyte presence in coffee agroecosystems: A decade of smallholder management in San Ramón, Nicaragua

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ABSTRACT

Coffee smallholder management practices have received attention for their potential to conserve biodiversity and sequester carbon by maintaining structural complexity, high canopy diversity, and minimal external inputs. We conducted shade tree surveys on 95 1000 m^2 research plots over a 10-year period to identify patterns of shade tree density and diversity, epiphyte presence, and carbon stocks within smallholder shade coffee systems of northern Nicaragua. We also analyzed each of these parameters with respect to management by comparing collectively- and individually-managed farms. Our results indicate that the overall shade tree density has decreased over time ($F = 42.597$, $p < 0.001$), but that diversity remained constant. Carbon stocks in coffee systems also showed a decreasing trend over time ($F = 2.981$, $p = 0.056$), most likely due to the decreasing tree densities. Epiphytic plant presence increased over time despite decreased host tree densities, suggesting either a change in management or improved habitat conditions for epiphytes. Research plots on individually-managed coffee farms generally had higher shade tree densities than those on collectively managed farms ($t = 2.141$, $p = 0.037$), but we found no differences in shade tree species richness or carbon stocks ($t = 0.573$, $p = 0.568$). We conclude that smallholder coffee farmers continue to conserve both shade tree diversity and epiphyte communities.

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1. Introduction

Since the 1990s, coffee agroecosystems have received attention for their potential as refuges of planned and associated biodiversity (Harvey and Villalobos, 2007; Perfecto et al., 1996; Somarriba et al., 2004; Vandermeer and Perfecto, 2007). By maintaining a diversity of shade trees above a coffee crop, farmers contribute to *in situ* biodiversity conservation (Dawson et al., 2013). Shade trees, in turn, provide a number of ecosystem services—the goods and services from ecosystems that directly or indirectly benefit humans (Carpenter et al., 2006). Shaded coffee systems generate provisioning ecosystem services such as food, fuel and building materials, and regulating services such as water conservation, erosion control, nutrient maintenance and carbon storage (Nair et al., 2009). Shade trees within farms and forest fragments near agroecosystems also provide ecosystem services such as pollination (Priess et al., 2007; Ricketts, 2004; Tscharntke et al., 2008) and biological pest control (Wilby and Thomas, 2002). At the landscape scale, shade trees facilitate the movement of organisms through the agroecological matrix (Perfecto and Vandermeer, 2002; Vandermeer and Carvajal, 2001; Vandermeer et al., 2010), providing connectivity between forest fragments (Chazdon et al., 2011; Dawson et al., 2013; Harvey et al., 2008).

Biodiversity increases with structural diversity within coffee agroecosystems (Moguel and Toledo, 1999). For example, trees increase structural diversity by providing habitat for birds, ants and epiphytes. Epiphytic plants, in turn, create microhabitats and increase plant biomass and surface area on trees (Nadkarni et al., 2001; Sillett, 1994). Epiphytes—orchids, ferns and vines—and bryophytes, such as moss species, often create habitat for invertebrates and provide resources such as nesting materials, nectar, fruit and water reserves for larger tropical species (Benzing, 1990; Cruz-Angon and Greenberg, 2005; Hylander and

Nemomissa, 2008). It has also been suggested that because of this they may act as keystone species (Moorhead et al., 2010).

Up to half of plant species richness in tropical forests may be composed of epiphytes (Benzing, 1990) and they have the potential to naturally colonize coffee systems because most are wind-dispersed (Solis, 2002). Many farmers believe most epiphytes are harmful to coffee yields and commonly remove them from shade trees and coffee bushes in both Latin America (Cruz-Angon and Greenberg, 2005). Indeed, a recent study on a large coffee farm in Veracruz, Mexico found that coffee productivity (in terms of fruits and flowers) was significantly higher under shade trees from which epiphytes had been removed (Toledo-Aceves et al., 2013). Still, many certification programs require that farmers allow epiphytic plants to grow in the shade canopy to support local biodiversity (Mas and Dietsch, 2003; Mas, 1999). Despite certification stipulations, pressure to intensify coffee production and increase yields could result in farmers removing epiphytes and thus decreasing biodiversity.

Research in Mesoamerica shows that some smallholder production methods can serve both ecological and social functions by simultaneously conserving biodiversity (Daily et al., 2003; Estrada and Coates-Estrada, 2002) and increasing food security and rural incomes (Pretty et al., 2003). In general smallholder farmers are more likely to have an intimate knowledge of land, produce diverse crops, conserve traditional varieties and prioritize labor and knowledge inputs instead of chemical inputs (Nazarea, 2006; Netting, 1993).

These factors point to the importance of supporting rural livelihoods in conjunction with conserving biodiversity and ecosystem services. Tools to identify important habitats for biological conservation are abundant (Myers et al., 2000; Richards and Mendez, 2014). However, fewer strategies exist that simultaneously prioritize conservation of ecological habitat, cultural traditions, and agricultural practice in rural areas (Harvey et al., 2008). For this reason, Harvey et al. (2008) suggest the use of "rural hotspots", which are areas where "traditional smallholder livelihoods are most vulnerable and where agroecological systems and knowledge are being rapidly lost" (10). In many cases, landscapes composed of smallholdings are more likely to sustain biodiversity conservation than those containing large plantations involved in export agriculture (Rosset, 2000). Thus, policies that support smallholder farmers are also likely to support flora and fauna that depend on these same landscapes (Castillo and Toledo, 2000; Harvey et al., 2008).

Recently, interest on agroforestry systems has shifted from production and food security benefits to include greater emphasis on climate change mitigation, carbon storage capacities (Mendez et al., 2012; Segura et al., 2006), and biodiversity conservation (Kirby and Potvin, 2007; Mendez et al., 2009; Richards and Mendez, 2014). Though much of the latter literature highlights the need to include smallholder farmers (Dawson et al., 2013; Perfecto and Vandermeer, 2008; Schroth et al., 2009; Toledo and Moguel, 2012; Tscharntke et al., 2011), the focus has largely remained at the landscape scale (Wollenberg et al., 2012; Richards and Mendez, 2014 and little is known about long-term patterns of diversity and sequestration capacity in smallholder agroecosystems (Maas et al., 2009).

Worldwide, at least 4.3 million coffee producers are smallholders, farming on less than 10 ha of land (Jha et al., 2011; Rahn et al., 2013). In Mesoamerica, over 300,000 farmers and 1,700,000 seasonal workers cultivate approximately 809,000 ha of coffee (Castro et al., 2004; Escamilla and Diaz, 2002; Flores et al., 2002), and approximately 68% of farmers are considered micro-producers, growing less than 2 ha of coffee (CEPAL, 2002; Jha et al., 2011). Though the percentage of area farmed by smallholders remains relatively low (18% in Central America according to Jha et al., 2011), the traditional farm management practices of many smallholder farmers have been shown to more closely mimic forest habitats, support wildlife populations, and maintain high levels of carbon stocks (Toledo and Moguel, 2012).

There are two different types of coffee cooperatives in Nicaragua, credit and marketing cooperatives that channel the harvests from individually managed farms into international markets, and cooperatives that provide these services and manage part or all their farms collectively. By the early 2000s, most co-ops operated in a manner closer to the former model, however, they often had common land titles and in some cases managed the coffee plots, forests, and pastures collectively.

In Nicaragua, it is common for several primary level cooperatives to unite and form a cooperative union or second level cooperative. These second level cooperatives can take advantage of economies of scale as they export coffee, manage certification systems (e.g., organic and fair trade), and seek access to lower interest pools of credit. Many smallholder farmers join cooperatives to more easily access to credit, gain better coffee prices through sales to certified markets, receive technical assistance, and to improve land tenure security (Bacon, 2010; Enriquez, 2010). There are roughly 40,000 coffee farmers in Nicaragua, more than 90% are smallholders, managing less than 10 ha of coffee production area, and more than 50% of these small-scale farmers are affiliated with a cooperative (CENAGRO, 2011). The support for and networks surrounding cooperatives and other local institutions may prove essential for decreasing vulnerability of rural livelihoods and confronting climate change (Agrawal, 2010; Bacon, 2010), as well as preserving ecosystems (Mendez et al., 2009).

This research identifies patterns of shade tree density and diversity, epiphyte presence, and carbon stocks over a 10-year period within smallholder coffee systems of northern Nicaragua. We examined how organized smallholders manage agroecosystems and how these practices either support or discourage biodiversity and carbon sequestration over time. More specifically, we focused on the following objectives:

- Analyze changes in tree and epiphyte diversity and abundance over time.
- Analyze changes in above ground tree C stocks over time.
- Assess the effects of collective vs. individual farm management on tree and epiphyte biodiversity and tree C stocks.

2. Methods

2.1. Site description

We conducted this study in five coffee cooperatives in the district of Matagalpa, Nicaragua: three in the Yasica Sur district (12°55′30″ N and 85°50′00″ W; 400–1000 m a.s.l.) and two near the small town center of San Ramon (85°50′23″ W and 12°55′25″ N, 639 m a.s.l.). Coffee in this region is grown in elevations between 400–2000 m a.s.l. (Segura et al., 2006) and the ecological landscape can be categorized as a sub-tropical humid forest, with annual precipitation between 600–2000 mm year^{-1} (Segura et al., 2006). The department of Matagalpa is the second-largest hub for coffee commerce in the country, yielding an average of 774 kg ha^{-1} (INIDE, 2009). In the 2008–2009 growing season, 33,219 ha of land in the department was dedicated to coffee, nearly 1/3 of Nicaragua's total coffee production area (INIDE, 2009).

The five primary level cooperatives are associated with a regional cooperative union that oversees administrative support, provides producers with credit, access to specialty markets and technical assistance, and exports the coffee. In San Ramon, the primary cooperatives engage in different types of coffee farm management, as determined by their origin and history. These

include properties that are managed collectively or individually. Individually managed farms are usually owned by one farmer who manages them with the help of his or her family. Collectively managed farms are co-owned by all members of the cooperative, who presumably share work and profits. Most of the coffee cooperative members that continue to collectively manage parts of their land (and many that now consist of farmers managing their land individually) accessed their land during agrarian reform periods of the 1980s (Bacon, 2010). This study includes both collectively and individually managed farms (Table 1).

Though much of the San Ramon landscape has produced coffee since the early 20th century, previous research in the area suggests considerable variation in the ages of coffee bushes and shade trees across the landscape (Bacon, 2005a,b). Select canopy trees were left standing for shade when coffee was first planted, and the farmers continue to allow natural regeneration of species they find useful. On an average, most shade cover is secondary growth, with coffee bushes that are 25–40 years old (Bacon, 2005a,b; Goodall, 2013). However, farmers renovate coffee every 5–10 years if household budgets allow for the investment (Goodall, 2013).

2.2. Data collection

Tree demography surveys were conducted in coffee farms of smallholders from February through June of 2003 (Bacon, 2005a, b), July, August and October of 2008 (Bacon et al., 2008), and March through May of 2012 (Goodall, 2013). Farmers worked with the research team to locate coffee production areas on their farms or in the collectively managed areas of the primary cooperatives, and identified the shade management type. In most cases, farmers also helped to identify coffee shade trees and conduct the inventories. The primary research assistants were from the communities and were trained in shade tree survey techniques and data collection for approximately two weeks until methods were consistent across observers.

Surveys were conducted on 95 50 m × 20 m rectangular plots (1000 m²) within coffee farms (Table 1). Tree inventories differed somewhat over the course of the 10 years, since the original study was not intended for longitudinal data collection. In 2003, 26 plots were randomly laid out in farms. The center point of each of the quadrats was recorded with a GPS handheld device (Garmin). In 2008, we used GPS centroid points to situate quadrats as similarly as possible to the original 2003 plots. However, as we did not have tree tags to guide us, the shapes of the quadrats may have differed. In addition, in 2008, we increased the number of plots to be sampled, adding four new quadrats ($n = 30$). In 2012 we consulted with farmers and field assistants from previous sample years to find as many centroids as possible around which we laid out the quadrats. Again, shapes of these quadrats may have differed form previous sampling years. In 2012, we added 11 new quadrats ($n = 40$), which were randomly selected on farms.

Within the sample plots, all canopy trees measuring at least 5 cm in diameter at breast height (DBH) were included in the survey. For each tree, data collected included species, DBH, tree height, and presence or absence of epiphytes and bryophytes including orchids, bromeliads, moss, vines, ferns, and parasitic plants. In 2003 and 2008, tree heights were measured using an adapted version of the height-matching method (Korning and Thomsen, 1994), which uses a pole of a known height and consists of one observer standing at a distance from the tree to estimate the height to the crown, a second field assistant at the base of the tree holding the pole. In 2012, tree heights were measured using a clinometer (Suunto model PM5/360 PC, Vantaa, Finland), taking the angle measurements of tree height, ground slope, and distance from the tree to the observer (Alder and Synnott, 1992).

2.3. Data analysis

2.3.1. Tree density, species density and estimated richness through time

We pooled shade tree density by year and compared among cooperatives. We normalized data for the tree density in each research plot using a square root transformation. We then compared density using one-way ANOVAs in SPSS (IBM Corp., 2011). To standardize the sampling effort and compare the number of species across the three sampling years, we created sample-based rarefaction curves and used the estimator Chao1 to estimate true species richness for each year (Chao, 1984; Magurran, 2004). Rarefaction curves express species density (as opposed to species richness) as we are interested in the number of species within a fixed area and conservation potential of those areas (Gotelli and Colwell, 2001). We performed species diversity analyses using EstimateS v.9.0 (Colwell, 2013) and Excel 2007.

Table 1
Vegetation properties, at the plot and tree level, of the shade tree canopy for 2003, 2008, and 2012 in five cooperatives of Matagalpa, Nicaragua.

	2003	2008	2012	F	p-value
Individual stems observed	878	625	433	–	–
Observed total species richness	86 (0 unknown)	77 (+11 unknown)	64 (+18 unknown)	–	–
Estimated total species richness (Chao1)	134	112	110	–	–
Plot level data					
Observed stem density (trees ha^{-1})	351 ± 158	208 ± 124	108 ± 59	35.21	<0.001
Mean observed species density (sp.1000m^{-2})	11.6 ± 5.25	9.27 ± 4.09	5.15 ± 2.34	25.21	<0.001
Mean species per stem	0.34 ± 0.11	0.50 ± 0.16	0.53 ± 0.21	9.88	<0.001
Correlation between stem density and spp. density	Pearson's $r = 0.724$ ($p < 0.001$)	Pearson's $r = 0.569$ ($p = 0.001$)	Pearson's $r = 0.667$ ($p < 0.001$)	–	–
Total basal area per ha (cm^2 ha^{-1})	16.80 ± 12.6	16.00 ± 12.4	10.40 ± 9.9	4.01	0.021
Aboveground shade tree biomass (Mg ha^{-1})	97.79 ± 94.93	104.79 ± 103.85	60.23 ± 48.85	2.981	0.056
Shade tree C stock (Mg ha^{-1})	45.96 ± 44.62	49.25 ± 48.81	28.31 ± 22.96	2.981	0.056
Correlation between species per stem and C stock (Mg ha^{-1})	$r = 0.317$ $p = 0.123$	$r = 0.041$ $p = 0.831$	$r = 0.351$ $p = 0.025$	–	–
Tree level data					
Mean basal area (cm^2)	0.05 ± 0.038	0.0782 ± 0.063	0.096 ± 0.183	56.51	<0.001
Mean dbh (cm)	16.81 ± 18.08	22.89 ± 21.73	25.59 ± 23.90	56.51	<0.001
Mean height (m)	9.27 ± 6.54	10.71 ± 7.41	11.55 ± 8.37	16.03	<0.001
Maximum height (m)	88	75	80.75	–	–

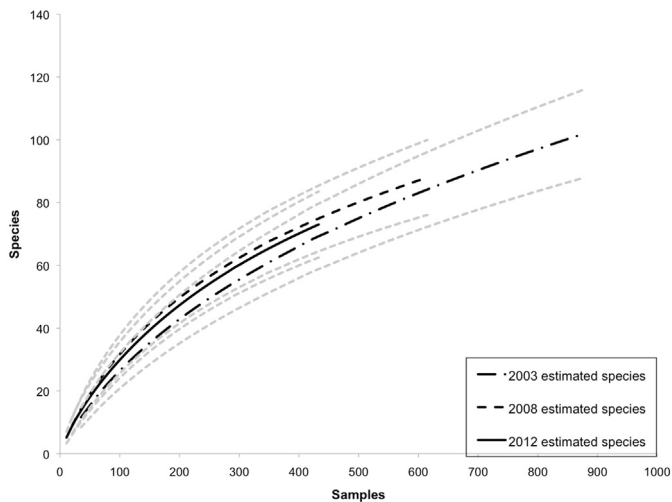All means are expressed as mean ± SD.

Fig. 1. Shade tree species rarefaction curves for 2003, 2008, and 2012 based on 95 parcels total. 95% confidence intervals are indicated by grey dashed lines.

2.4. Aboveground biomass and carbon

To calculate the aboveground biomass (AGB) of each species, we used the allometric model proposed by Chave et al. (2005) and tailored to shade coffee agroecosystems by Mendez et al. (2009):

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

in which D is the diameter at breast height, H is the tree height, and ρ is the species-specific wood density. We used wood densities from the Wood Densities Database of the World Agroforestry Center (ICRAF World Agroforestry Center, 2013) for 76 species. For the remaining 51 species, we estimated density by using the mean density from the 76 known species, which was 0.58 (Chave et al., 2005, 2003; Mendez et al., 2009; Richards and Mendez, 2014). To convert AGB to C stock estimates, we assumed a 47% C content, per the suggestion of Kirby and Potvin (2007). Next, C stocks were summed for each of the plots and extrapolated to a per hectare estimate. Mean C stocks were compared across years using a one-way ANOVA.

2.5. Management type

To investigate potential differences in coffee farms due to management type (individual vs. collective), we compared shade trees of collectively managed and individually managed farms in terms of stem density, C stocks, and species richness for the 2008 and 2012 survey years.

2.6. Epiphyte/bryophyte presence

We conducted a Chi-square (χ^2) test to compare presence of orchids, bromeliads, parasitic epiphytes, ferns, moss and vines for each of the three sampling years. We also ran a χ^2 test to compare proportional differences in epiphytic plants between collectively managed and individually managed farms in 2012.

We then predicted the overall likelihood of epiphyte/bryophyte presence in shade trees through use of binary logistic regression. All years and management types were included in the regression models, as the unit of analysis was host tree, but not the coffee farm. We generated models for each plant type. The most parsimonious regression model for all groups was the one that included the predictor variables of shade tree DBH and stem density.

3. Results

3.1. General trends

Over the 10-year period, we established research plots on 96 coffee farms. In 2003, farmers individually managed all coffee production areas included in the research ($n = 26$). In 2008 ($n = 30$) and 2012 ($n = 40$), farmers managed half of the farms for each sampling year individually, and the other half were conducted on collective coffee production areas. Of 126 species identified during the study, 29 species remained unidentified. All the years shared 31 species, though 35 species were found only in 2003, 18 species were found only in 2008, and 13 species were found only in 2012. Total basal area (cm² ha⁻¹) of shade trees decreased through time, but mean basal area (cm²) increased, as did the shade tree's DBH and height (Table 1).

Stem density significantly decreased in each successive year of sampling ($F = 42.597$, $df = 2$, $p < 0.001$). Species density correlated positively with stem density in all the 3 sampling years (Table 1), so we calculated species rarefaction curves to estimate differences in species richness (Fig. 1). The substantial overlap of the 95% confidence intervals associated with the rarefaction curves suggested that the estimated species richness did not change significantly over the 10-year period. Likewise, none of the rarefaction curves reached an asymptote, indicating further sampling is required to reach a complete inventory of these coffee-growing sites.

3.2. AGB and carbon stocks

Over the 10-year period, mean AGB changed from 97.79 Mg ha⁻¹ in 2003 to 60.23 Mg ha⁻¹ in 2012, showing a decreasing trend ($F = 2.981$, $p = 0.056$). Because C stocks were calculated as a simple percentage of AGB, means for C also showed the same trend (Table 1). In all the years, the species per stem appeared to be correlated positively with C stock but this relationship was only significant in 2012 (Pearson's $r^2 = 0.123$, $p = 0.025$).

3.3. Individual vs. collective coffee farm management

Of the 30 research plots conducted on coffee farms in 2008, the plots on individually managed farms had significantly higher shade

Table 2
Comparisons of individually- and cooperatively-managed smallholder coffee plots in 2008, 2012, and pooled 2008/2012.

	Management Type	Mean observed stem density (trees/ha)	df	t	p	Shade tree C stock (Mg/ha)	df	t	p
2008	Individual	259.33 ± 156.50	17	2.061	0.055	39.84 ± 51.28	28	1.059	0.299
	Cooperative	156.33 ± 43.99				58.66 ± 45.99			
2012	Individual	122.00 ± 66.14	38	1.389	0.173	30.85 ± 27.86	38	0.695	0.491
	Cooperative	94.50 ± 49.57				25.77 ± 17.10			
2008/2012 Combined	Individual	180.86 ± 131.47	53	2.141	0.037	34.70 ± 39.20	68	0.573	0.568
	Cooperative	121.43 ± 56.26				39.87 ± 36.15			

Table 3
Presence of epiphytes and bryophytes in coffee systems of Matagalpa, Nicaragua.

Epiphyte/bryophyte	Percent presence				
	2003	2008	2012	χ^2-statistic	p-value
Orchids	5.1	10.6	9.9	17.613	<0.001
Bromeliads	8.6	44.6	39.5	281.763	<0.001
Ferns	6.7	22.4	21.9	89.25	<0.001
Moss	9.2	71.5	60.7	674.062	<0.001
Parasitic epiphytes	2.1	9.4	12.9	63.104	<0.001
Vines	6.7	21.1	27.3	109.576	<0.001

tree densities than collectively managed farms (Table 2). In 2012, research plots on individually managed farms had higher stem density, though these differences were not significant. Combining the 2008 and 2012 data, stem densities from the research plots on the individually-managed farms were significantly higher than in the collectively-managed farms (Table 2). In 2008, 2012, and 2008–2012 pooled data, we found no difference between C stocks in research plots results on individually-managed farms vs. those from collectively managed farms (Table 2).

Comparing shade tree species richness between individual and collectively managed farms reveals different trends. In 2008, the research plots on individually managed farms had a lower estimated species richness (*Chao1* (SD) = 65.52 (5.29)) than collectively-managed farms (*Chao1* (SD) = 74.89 (9.65)). In 2012, the research plots on the individually-managed coffee farms had a higher estimated shade tree species richness (*Chao1* (SD) = 80.33 (16.18)) than collectively-managed coffee (*Chao1* (SD) = 44.45 (9.19)). Pooling 2008 and 2012 data, estimated species richness on individually-managed farms was higher (*Chao1* (SD) = 116.30 (17.49)) than collectively managed farms (*Chao1* (SD) = 97.07 (10.82)). For 2008, 2012, and the combined dataset, rarefaction curves for the two management types overlap substantially, suggesting no significant difference in the species richness of different management types for the sampled periods.

3.4. Epiphyte and bryophyte presence

For all coffee shade trees included in the study, epiphytic plant groups increased dramatically from 2003 to 2008, and shifted only

slightly between 2008 and 2012 (Table 3). Chi-squared tests revealed some differences between trees in collectively managed and individually managed farms in 2012. Orchid presence was similar, with 9% of the trees in research plots on individually managed farms and 11.1% reported in collective farms ($\chi^2 = 0.522$, $p = 0.518$). Bromeliads were also similar across management types, with 37.3% presence in individual farms and 42.3% in collective farms ($\chi^2 = 1.129$, $p = 0.322$). Ferns were significantly more prevalent on individual farms (26.2%) than in collective farms (16.4%; $\chi^2 = 6.006$, $p = 0.009$). Moss followed a similar pattern with 71.3% in individual farms and 47.1% in collective farms ($\chi^2 = 26.202$, $p < 0.001$). Parasites, on the other hand, were twice as prevalent in the collective farms (18%) than in the individual farms (9.0%) ($\chi^2 = 7.615$, $p = 0.005$). Vines were present in 28.4% of individually managed trees, and 25.9% of collectively managed trees ($\chi^2 = 0.326$, $p = 0.322$).

Binary logistic regressions to determine the likelihood of epiphytic plant groups in coffee systems were most parsimonious using the predictor variables of DBH and stem density (Table 4). Overall, as DBH increases for host shade trees, likelihood of all epiphytic plants increased. In contrast, stem density had an inverse relationship with epiphytic plant presence.

4. Discussion

Though the mean stem density decreased significantly over the 10-year period, and both observed species density and estimated total species richness suggest a similar decrease, the considerable overlap of the species rarefaction curve at 95% confidence intervals (Fig. 1) suggests no major change in species richness over time. The average stem densities would be classified as a diverse polyculture based on the shade coffee classification system proposed by Moguel and Toledo (1999). A similar pattern of decreasing shade tree densities, coupled with consistent species diversity was also found in shade coffee systems of El Salvador over a similar length of time (Richards and Mendez, 2014). A recent international study found that diverse shade coffee production areas decreased significantly from 1996 to the 2010–2012, suggesting that a global pattern of intensification in shade coffee production systems (Jha et al., 2014)

The species assemblages were similar over the three sampling years, but the number of unique species decreased each successive

Table 4
Binary logistic regression models of epiphytic plant groups on host shade trees in coffee systems of Matagalpa, Nicaragua.

Epiphyte/bryophyte (% correctly predicted by model)	Predictor variable	Coeff.	S.E.	Odds ratio	p-value
Orchids	DBH	0.49	0.004	1.05	<0.001
(92.50%)	Stem density	−0.002	0.001	0.998	<0.001
	Constant	−3.337	0.243	0.036	<0.001
–					
Bromeliads	DBH	0.041	0.004	1.042	<0.001
(77.80%)	Stem density	−0.003	<0.001	0.997	<0.001
	Constant	−1.042	0.147	0.353	<0.001
–					
Ferns	DBH	0.031	0.003	1.032	<0.001
(85.20%)	Stem density	−0.002	<0.001	0.998	<0.001
	Constant	−2.007	0.167	0.134	<0.001
–					
Moss	DBH	0.019	0.003	1.019	<0.001
(67.10%)	Stem density	−0.004	<0.001	0.996	<0.001
	Constant	0.43	0.125	1.537	<0.001
–					
Parasitic epiphytes	DBH	0.025	0.003	1.025	<0.001
(93.10%)	Stem density	−0.005	0.001	0.995	<0.001
	Constant	−2.117	0.214	0.12	<0.001
–					
Vines	DBH	0.026	0.003	1.027	<0.001
(84.30%)	Stem density	−0.004	<0.001	0.996	<0.001
	Constant	−1.232	0.158	0.292	<0.001

year (Table 1). This suggests either an intensification effort on behalf of the farmers in which fewer species are supported in the coffee system, or a focus on selected species that serve multiple provisioning services (i.e., timber, food, firewood). Natural recruitment rates may have decreased through time, as farmers were less likely to practice benign neglect.

Though mean basal area increased slightly over time, the mean total basal area per hectare decreased, with a significant change from 2003 to 2012. This pattern may be attributable to farmers choosing to maintain larger shade trees, as DBH and tree height also significantly increased over time (Table 1). Stem density significantly decreased over the 10-year period overall.

Similarly, aboveground biomass and carbon stocks decreased drastically in the last half of the study, and this change was nearly significant ($p = 0.056$). These values are directly related to the sheer density of stems in the systems. Average carbon stocks over the entire study were consistent with living biomass carbon stocks found in Mexican shaded coffee polycultures (Soto-Pinto et al., 2009). As the pressure to intensify farms mounts in order to increase yields, the potential for carbon sequestration could be compromised. We found similar patterns of stem density and C stocks regardless of management type (i.e., individual vs. collective) in 2012. Such a finding suggests that the pressure to decrease densities of shade tress is indiscriminant among these communities, which differs from results found by Mendez et al. (2007), where individual farms had higher levels of species richness and stem density than collectively managed plantations.

Epiphyte and bryophyte presence increased substantially and significantly from 2003 to 2008. The logistic regression models suggest that decreasing shade tree densities and increasing DBH encourage epiphytic plants. This pattern suggests that changes in shade tree management have allowed for the resurgence of epiphytic species to grow, contributing to overall biodiversity conservation (Cruz-Angon and Greenberg, 2005; Hietz, 2005; Moorhead et al., 2010; Sillett, 1994). Though some shade certification programs require that epiphytes are maintained in coffee farms (Moorhead et al., 2010), the cooperatives included in this study are not shade certified. In our case, the resurgence of some epiphytic plants in the coffee system may have been a consequence of decreased shade tree density that allowed for greater light penetration into the canopy, thereby encouraging a resurgence of some epiphytic plants. The vertical distribution of epiphytes on a host tree is determined by a number of microhabitat factors, including sunlight exposure (Krömer et al., 2007), suggesting further research should investigate species-specific distributions and life history characteristics of epiphytes in these agroecosystems. A study of epiphytes on smallholder farms in Mexico found that a substantial quantity of plants that fell to the ground could be harvested to potentially generate as much as $6857–\$11070\,USD\,ha^{-1}\,y^{-1}$ (Toledo-Aceves et al., 2013). This biodiversity-oriented livelihood diversification strategy holds potential for the farmers in this study.

Our research exemplifies how smallholder coffee farmers, despite their limited control over global coffee markets, have an impact on ecological processes occurring in the landscapes they manage. Findings show that management type (individual vs. collective) did not influence shade tree species richness or C stocks in the research plots on shade coffee farms. This contrasts with results from El Salvador, where cooperatives that collectively managed coffee farms intentionally maintained lower levels of shade tree diversity and abundance (with the goal of maximizing coffee yields), as opposed to individual farmers that chose to manage higher levels of both (Mendez et al., 2007, 2009). Until 2008, our research in Nicaragua documented similar patterns (Mendez et al., 2010), however, the most recent tree diversity inventory suggests that this did not hold over the 10-year period.

This investigation did not include sociopolitical factors and history of conflict and agrarian reforms (Bacon, 2005a,b) that influenced the formation of these cooperatives with implications for farmer livelihoods and management decisions (Mendez et al., 2009; Westphal, 2008). Future analysis could explore how farm management is influenced by historical patterns of cooperative development, current technical assistance programs, certification requirements, incentives/subsidies, and the ongoing struggle for sustainable rural livelihoods and conservation of biologically diverse landscapes in Central America's highlands.

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References

Agrawal, A., 2010. Local institutions and adaptation to climate change. In: Mearns, R., Norton, A. (Eds.), Social Dimensions of Climate Change: Equity and Vulnerability in a Warming World. World Bank Publications, Washington, D. C, pp. 319.

Alder, D., Synnott, T.J., 1992. Permanent sample plot techniques for mixed tropical forest. Tropical Forestry Papers No 25.

Bacon, C., 2005a. Confronting the coffee crisis: can fair trade, organic, and specialty coffees reduce small-scale farmer vulnerability in Northern Nicaragua? World Develop. 33, 497–511.

Bacon, C.M., 2005b. Confronting the coffee crisis: Nicaraguan farmers use of cooperative, fair trade and agroecological networks to negotiate livelihoods and sustainability. Doctoral Dissertation. University of California, Santa Cruz.

Bacon, C.M., 2010. A Spot of Coffee in Crisis: Nicaraguan smallholder cooperatives, fair trade networks, and gendered empowerment. Lat. Am. Perspect. 37, 50–71.

Bacon, C.M., Flores Gomez, M.A., Marcel, A., Diaz Flores, S.R., 2008. Cooperativas, Café, y Orquídeas en Cafetales Bajo Sombra (ACOGE) [Trees, Cooperatives, Coffee, and Orchids in Shaded Coffee Plantation]. Matagalpa, Nicaragua.

Benzing, D.H., 1990. Vascular Epiphytes. North. Cambridge University Press.

Carpenter, S.R., DeFries, R., Dietz, T., Mooney, H.A., Polasky, S., Reid, W., Scholes, V., 2006. Millenium ecosystem assessment: research needs. Science 314, 257–258.

Castillo, A., Toledo, V.M., 2000. Applying ecology in the Third World: the case of Mexico. Bioscience 50, 66–76.

Castro, F., Montes, E., Raine, M., 2004. Centroamerica la Crisis Cafetalera: Efectos y Estrategias Para Hacerle Frente. The World Bank, Latin American and Caribbean Region 23.

CENAGRO, 2011. Nicaraguan Census of Agriculture. Managua, Nicaragua.

CEPAL, 2002. Globalizacion y Desarrollo. CEPAL, Santiago.

Chao, A., 1984. Non-parametric estimation of the number of classes in a population. Scand. J. Stat. 11, 265–270.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J.-P., Nelson, B.W., Ogawa, H., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87–99.

Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B., Hubbell, S.P., 2003. Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. J. Ecol. 91, 240–252.

Chazdon, R.L., Harvey, C.A., Komar, O., Griffith, D.M., Ferguson, B.G., Mart, M., 2011. Beyond reserves: a research agenda for conserving biodiversity in human-modified tropical landscapes. Biotropica 4, 142–153.

Colwell, R.K., 2013. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, Version 9.1.0.

Cruz-Angon, A., Greenberg, R., 2005. Are epiphytes important for birds in coffee plantations? An experimental assessment. J. Appl. Ecol. 42, 150–159.

Daily, G.C., Ceballos, G., Pacheco, J., Suzan, G., Sanchez-Azofeifa, A., 2003. Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. Conserv. Biol. 17, 1814–1826.

Dawson, I., Guariguata, M., Loo, J., Weber, J., Lengkeek, A., Bush, D., Cornelius, J., Guarino, L., Kindt, R., Orwa, C., Russell, J., Jamnadass, R., 2013. What is the

relevance of smallholders' agroforestry systems for conserving tropical tree species and genetic diversity in circa situm, in situ and ex situ settings? A review. Biodiver. Conserv. 22, 301–324.

Enriquez, L., 2010. Reactions to the Market: Small Farmers in the Economic Reshaping of Nicaragua, Cuba, Russia, and China. Pennsylvania State University Press, University Park, PA.

Escamilla, P., Diaz, S., 2002. Sistemas de Cultivo de Cafe en Mexico. Universidad Autonoma de Chapingo, Mexico & Fundacion Produce, Huatusco, Ver. Mexico.

Estrada, A., Coates-Estrada, R., 2002. Dung beetles in continuous forest, forest fragments and in an agricultural mosaic habitat island at Los Tuxtlas. Mex. Biodivers. Conserv. 11, 1903–1918.

Flores, M., Bratescu, A., Martinez, J., 2002. Centroamerica: El impacto de la Caida de Los Precios del Cafe. CEPAL/ECLAC, Mexico.

Goodall, K., 2013. Conservation, agroecology, and livelihoods: shade trees, birds and farmer decisions in smallholder coffee cooperatives of northern Nicaragua. Doctoral Dissertation. University of Vermont.

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.

Harvey, C.A., Komar, O., Chazdon, R., Ferguson, B.G., Finegan, B., Griffith, D.M., Martínez-Ramos, M., Morales, H., Nigh, R., Soto-Pinto, L., Van Breugel, M., Wishnie, M., 2008. Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. Conserv. Biol. J. Soc. Conserv. Biol. 22, 8–15.

Harvey, C.A., Villalobos, J.A.G., 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodivers. Conserv. 16, 2257–2292.

Hietz, P., 2005. Conservation of vascular epiphyte diversity in Mexican coffee plantations. Conserv. Biol. 19, 391–399.

Hylander, K., Nemomissa, S., 2008. Home garden coffee as a repository of epiphyte biodiversity in Ethiopia. Front. Ecol. Environ. 6, 524–528.

IBM Corp., 2011. SPSS Version 20.0.

ICRAF World Agroforestry Center, 2013. Wood density database [WWW Document]. . (accessed 23.06.13) http://www.worldagroforestry.org/sea/Products/AFDbases/wd/Index.htm.

INIDE, 2009. Anuario Estadistico [WWW Document], Anuario Estadistico. . http://inide.gob.ni/bibliovirtual/Anuarios/ANUARIO09/anuario09.html.

Jha, S., Bacon, C.M., Philpott, S.M., Ernesto Mendez, V., Laderach, P., Rice, R.a., 2014. Shade coffee: update on a disappearing refuge for biodiversity. BioScience 64, 416–428.

Jha, S., Bacon, C.M., Philpott, S.M., Rice, R.A., Mendez, V.E., Läderach, P., 2011. A review of ecosystem services, farmer livelihoods, and value chains in shade coffee agroecosystems. In: Campbell, W.B., Lopez Ortiz, S. (Eds.), Issues in Agroecology Present Status and Future Prospects. Springer, Netherlands, pp. 1–75.

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.

Korning, J., Thomsen, K., 1994. A new method for measuring tree height in tropical rain forest. J. Veg. Sci. 5, 139–140.

Krömer, T., Kessler, M., Gradstein, S.R., 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecol. 189, 261–278.

Maas, B., Putra, D.D., Waltert, M., Clough, Y., Tscharntke, T., Schulze, C.H., 2009. Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species. Biol. Conserv. 142, 2665–2671.

Magurran, A., 2004. Measuring Biological Diversity. Blackwell Science Ltd., Malden, MA.

Mas, A.H., 1999. Butterflies as biodiversity indicators and shade coffee certification in Chiapas, Mexico. University of Michigan, Ann Arbor, MI.

Mas, A.H., Dietsch, T., 2003. An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. Ecol. Appl. 13, 1491–1501.

Mendez, V.E., Bacon, C., Olson, M., Morris, K., Shattuck, A., 2010. Agrobiodiversity and Shade Coffee Smallholder Livelihoods: A Review and Synthesis of Ten Years of Research in Central America. Prof. Geogr. 62, 357–376.

Mendez, V.E., Castro-Tanzi, S., Goodall, K., Morris, K., Bacon, C.M., Laderach, P., Morris, W.B., Georgeoglou-Laxalde, M.U., 2012. Livelihood and environmental trade-offs of climate mitigation in smallholder coffee agroforestry systems. In: Wollenberg, E.K., Nihart, A., Grieg-Gran, M., Tapio-Bistrom, M.L. (Eds.), Climate Change Mitigation and Agriculture. Earthscan, London, pp. 370–381.

Mendez, V.E., Gliessman, S.R., Gilbert, G.S., 2007. Tree biodiversity in farmer cooperatives of a shade coffee landscape in western El Salvador. Agric. Ecosyst. Environ. 119, 145–159.

Mendez, V.E., Shapiro, E.N., Gilbert, G.S., 2009. Cooperative management and its effects on shade tree diversity: soil properties and ecosystem services of coffee plantations in western El Salvador. Agroforest. Syst. Forum 76, 111–126.

Moguel, P., Toledo, V.M., 1999. Biodiversity conservation in traditional coffee systems of Mexico. Conser. Biol. 13, 11–21.

Moorhead, L.C., Philpott, S.M., Bichier, P., 2010. Epiphyte biodiversity in the coffee agricultural matrix: canopy stratification and distance from forest fragments. Conserv. Biol. 24, 737–746.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nadkarni, N.M., Merwin, M.C., Nieder, J., 2001. Forest canopies, plant diversity. In: Levin, S.A. (Ed.), Encyclopedia of Diversity. Academic Press, London, pp. 27–40.

Nair, P.K.R., Mohan Kumar, B., Nair, V.D., 2009. Agroforestry as a strategy for carbon sequestration. J. Plant Nutr. Soil Sci. 172, 10–23.

Nazarea, V.D., 2006. Local knowledge and memory in biodiversity conservation. Ann. Rev. Anthropol. 35, 317–335.

Netting, R.M., 1993. Smallholders, householders: farm families and the ecology of intensive, sustainable agriculture. Sociologia Ruralis. Stanford University Press.

Perfecto, I., Rice, R.A., Greenberg, R., Voort, M.E., van der, 1996. Shade coffee: a disappearing refuge for biodiversity. Bioscience 46, 598–608.

Perfecto, I., Vandermeer, J., 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in Southern Mexico. Conserv. Biol. 16, 174–182.

Perfecto, I., Vandermeer, J., 2008. Biodiversity conservation in tropical agroecosystems: a new conservation paradigm. Ann. N.Y. Acad. Sci. 1134, 173–200.

Pretty, J.N., Morison, J.I.L., Hine, R.E., 2003. Reducing food poverty by increasing agricultural sustainability in developing countries. Agric. Ecosyst. Environ. 95, 217–234.

Priess, J.A., Mimler, M., Klein, A.M., Schwarze, S., Tscharntke, T., Steffan-Dewenter, I., 2007. Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems. Ecol. Appl. 17, 407–417.

Rahn, E., Laderach, P., Baca, M., Cressy, C., Schroth, G., Malin, D., van Rikxoort, H., Shriver, J., 2013. Climate change adaptation, mitigation and livelihood benefits in coffee production: where are the synergies? Mitig. Adapt. Strategies Global Change 2013.

Richards, M., Mendez, V.E., 2014. Interactions between carbon sequestration and shade tree species diversity in a smallholder coffee cooperative of El Salvador. Conserv. Biol.

Ricketts, T.H., 2004. Tropical forest fragments enhance pollinator activity in nearby coffee crops. Conserv. Biol. 18, 1262–1271.

Rosset, P., 2000. The multiple functions and benefits of small farm agriculture in the context of global trade negotiations. Development 43, 77–82.

Schroth, G., Laderach, P., Dempewolf, J., Philpott, S., Haggar, J., Eakin, H., Castillejos, T., Garcia Moreno, J., Soto Pinto, L., Hernandez, R., Eitzinger, A., Ramirez Villegas, J., 2009. Towards a climate change adaptation strategy for coffee communities and ecosystems in the Sierra Madre de Chiapas, Mexico. Mitig. Adapt. Strategies Global Change 14, 605–625.

Segura, M., Kanninen, M., Suárez, D., 2006. Allometric models for estimating aboveground biomass of shade trees and coffee bushes grown together. Agrofor. Syst. 68, 143–150.

Sillett, T.S., 1994. Foraging ecology of epiphyte-searching insectivorous birds in Costa Rica. Condo 96, 863–877.

Solis, M.L., 2002. Estudio Poblacional y Biologia Reproductiva de las Orquideas Silvestres de un Cafetal de la Orduña, Veracruz México. Universidad de las Americas.

Somarriba, E., Harvey, C.A., Samper, M., 2004. Biodiversity in coffee plantations. In: Schroth, G., de Fonseca, G., Harvey, C.A. (Eds.), Agroforestry and Biodiversity Conservation in Tropical Landscapes. Island Press, Washington, D.C, pp. 198–226.

Soto-Pinto, L., Anzueto, M., Mendoza, J., Ferrer, G.J., Jong, B., 2009. Carbon sequestration through agroforestry in indigenous communities of Chiapas, Mexico. Agrofor. Syst. 78, 39–51.

Toledo, V.M., Moguel, P., 2012. Coffee and sustainability: the multiple values of traditional shaded coffee. J. Sustain. Agric. 36, 353–377.

Toledo-Aceves, T., Mehltreter, K., García-Franco, J.G., Hernández-Rojas, A., Sosa, V.J., 2013. Benefits and costs of epiphyte management in shade coffee plantations. Agriculture. Ecosyst. Environ. 181, 149–156.

Tscharntke, T., Clough, Y., Bhagwat, S.A., Buchori, D., Faust, H., Hertel, D., Hölscher, D., Juhrbandt, J., Kessler, M., Perfecto, I., Scherber, C., Schroth, G., Veldkamp, E., Wanger, T.C., 2011. Multifunctional shade-tree management in tropical agroforestry landscapes – a review. J. Appl. Ecol. 48, 619–629.

Tscharntke, T., Sekercioglu, C.H., Dietsch, T., Sodhi, V., Hoehn, N.S., Tylianakis, P., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. Ecology 89, 944–951.

Vandermeer, J., Carvajal, R., 2001. Metapopulation dynamics and the quality of the matrix. Am. Natur. 158, 211–220.

Vandermeer, J., Perfecto, I., 2007. The agricultural matrix and a future paradigm for conservation. Conserv. Biol. 21, 274–277.

Vandermeer, J., Perfecto, I., Schellhorn, N., 2010. Propagating sinks, ephemeral sources and percolating mosaics: conservation in landscapes. Landscape Ecol. 25, 509–518.

Westphal, S.M., 2008. Coffee agroforestry in the aftermath of modernization: diversified production and livelihood strategies in post-reform Nicaragua. In: Bacon, C.M., Méndez, V.E., Gliessman, S.R., Goodman, D., Fox, J.A. (Eds.), Confronting the Coffee Crisis: Fair Trade, Sustainable Livelihoods and Ecosystems in Mexico and Central America. MIT Press, Cambridge, MA, pp. 179–206.

Wilby, A., Thomas, M.B., 2002. Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. Ecol. Lett. 5, 353–360.

Wollenberg, E.K., Nihart, A., Grieg-Gran, M., Tapio-Bistrom, M.L. (Eds.), 2012. Climate Change Mitigation and Agriculture. Earthscan, London.