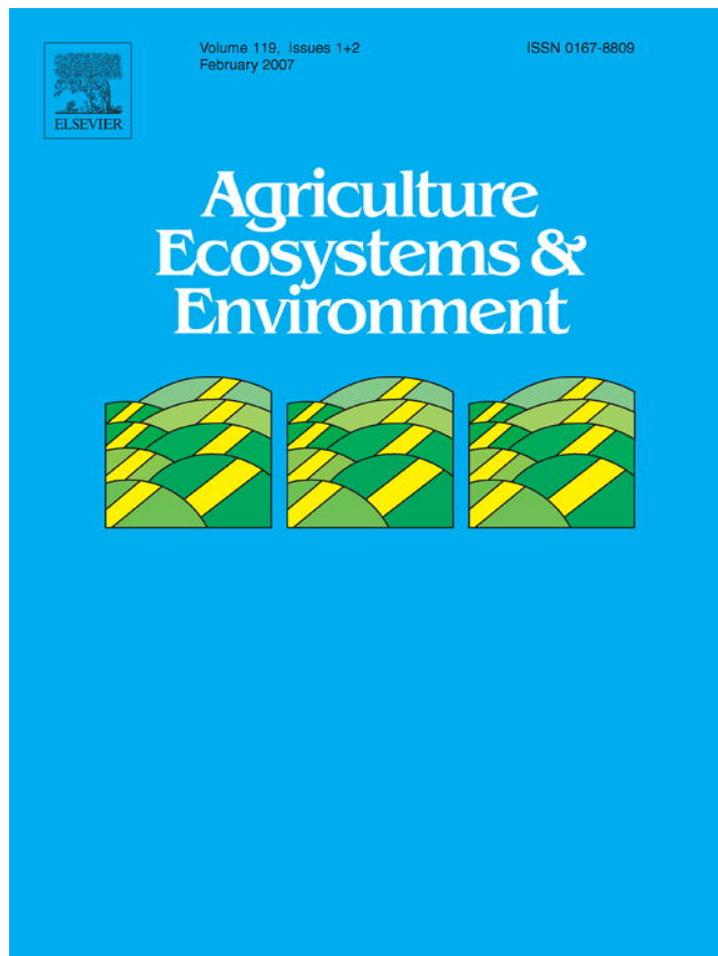


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Tree biodiversity in farmer cooperatives of a shade coffee landscape in western El Salvador

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Abstract

Conservation of tropical biodiversity in agricultural landscapes has become more important as the area covered by natural ecosystems decreases. We analyzed the effects of local livelihoods, cooperative types, and selected biophysical variables (elevation, slope, percent shade, distance to the forest, coffee density, and coffee age) on tree biodiversity in shade coffee cooperatives of El Salvador.

Tree inventories from 51 quadrats in coffee cooperatives included 2743 individuals from 46 families and 123 identified tree species. Species richness and tree diameters differed among some cooperatives, with greater richness associated with greater stem density; other biophysical variables had little impact on diversity. The amount of shade in the coffee plantations differed among cooperatives, particularly in the wet season. Of the tree species reported in a recent study of a neighboring forest and in the cooperatives ($N = 227$ species combined), 16% were present at both sites. The three coffee plantations shared 35% of total species reported from all cooperatives.

Our research shows that the number of tree species found in a coffee plantation increases with the density of shade trees included in the system. In turn, agroecological management, as influenced by farmer livelihood strategies and cooperative types, directly affects shade canopy composition. Important factors to take into account are the types of farmer organizations present, the cost of maintaining species of conservation concern, and the potential benefits that conservation could bring to the livelihood strategies of farm households.

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1. Introduction

Rural tropical landscapes that were once natural ecosystems have been transformed into mosaics containing a great variety of land uses. These include forests and other natural systems, a great diversity of agroecosystems, disturbed zones with or without tree cover, and areas of human settlement (Helming and Wiggering, 2003). The challenge to conserve biodiversity in these heterogeneous landscapes has resulted in a need to promote and manage conservation within anthropogenic ecosystems (Halladay

and Gilmour, 1995; Collins and Qualset, 1999). Vandermeer and Perfecto (1995) and Altieri (1999) discuss two main types of biodiversity associated with agroecosystems: planned biodiversity and associated or unplanned biodiversity. Planned biodiversity refers to the components of the agroecosystem purposely introduced or grown by a farmer. Unplanned or associated biodiversity comprises those organisms that colonize the agroecosystem without direct mediation from its human managers (e.g., volunteer plants, wildlife, etc.). However, farmers generally choose to either keep or remove this associated biodiversity as part of their agricultural management.

Recent work in the tropics has demonstrated that agroforestry systems are among the most promising land uses for achieving both conservation goals and supporting

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human livelihoods at the landscape scale (Buck et al., 1999; Huxley, 1999; Leakey, 1999; Harvey, 2001; Izac and Sanchez, 2001; Schroth et al., 2004). For example, cacao agroforestry systems in Cameroon, include a diversity of shade trees that provide fruit and timber for income (Sonwa et al., 2001). The highly diverse agroforests of southeast Asia, which contain many mature forest tree species, also provide rubber and a variety of agroforestry tree products to its managers (Michon and de Foresta, 1999). In the Mesoamerican tropics, several studies have documented potential conservation scenarios in different types of tree-crop systems (Lok, 1998; Steinberg, 1998; Harvey and Haber, 1999; Harvey, 2000; Méndez et al., 2001).

Given its complex biophysical structure, shade coffee systems may have exceptional potential for biodiversity conservation of tropical plant and animal species (Perfecto et al., 1996, 2003; Somarriba et al., 2004). Numerous studies on shade coffee have shown that a diversified and abundant canopy of shade trees enhances associated biodiversity of other plants and animals, including insects and birds (Perfecto et al., 1996, 2003), and herbaceous plants and epiphytes (Moguel and Toledo, 1999). However, most research on tree biodiversity in shade coffee agroecosystems has concentrated on documenting tree species richness and abundance (Somarriba et al., 2004; Moguel and Toledo, 1999; Soto-Pinto et al., 2000; Monro et al., 2001). There have been limited efforts to identify the conservation importance of the tree species found in shade coffee systems, or to explain the reasons for the presence or absence of these species in particular sites (but see Muschler, 1999). For shade coffee to contribute to the conservation of native trees, it is important that plantation management incorporates the value of conserving regionally vulnerable or threatened species, rather than focusing on exotic or domesticated species.

1.1. Advances in tropical tree conservation at the landscape scale

Recent contributions by Gordon and co-workers on conserving trees in Mesoamerican landscapes illustrate the potentials and pitfalls for tree conservation within agricultural systems (Barrance et al., 2003; Gordon et al., 2003, 2004). Their analyses in the dry tropical forest landscapes of Mexico and Honduras demonstrated that secondary forest fallows and agroecosystems can be important for the conservation of native tree species. However, tree species of priority to farmers proved to be different than the ones given global conservation importance (Gordon et al., 2003). Additionally, because farmers reported a high degree of substitutability for many of the tree species of greatest use, they would be unlikely to invest resources to conserve particular native species when they become rare. These studies point to the need to consider the priorities and needs of farmers and other actors within the landscape, as part of native tree conservation strategies.

1.2. Looking beyond the trees

Social, economic, and political factors influence the success or failure of tree conservation in coffee agroecosystems (Somarriba et al., 2004). Research in the Dominican Republic showed the importance of examining both social and ecological issues in order to explain the composition and distribution of native trees within agricultural landscapes of the Zambrana-Chacuey region (Rocheleau et al., 2001). Gender, household livelihood strategies, and the actions of a peasant and an international non-government organization, each played direct roles in defining the types and levels of tree biodiversity in this territory (Rocheleau et al., 2001). Similarly, work in the agroecosystems of the South American Andes found that farmer livelihoods, local organizations, and local and external farmer networks greatly influence the way in which biophysical landscapes are shaped (Bebbington, 1996a,b, 1997). Kindt et al. (2004) found significant relationships between household variables such as wealth, gender of the head of household, education, and farm and family size on tree diversity in farms of Western Kenya. These and other contributions (Scoones, 1999; Rocheleau, 1999; Ewel, 2001; Bebbington and Batterbury, 2001; Walker et al., 2002; Holland and Campbell, 2005) argue for the use of interdisciplinary analysis (including biophysical and social factors) to adequately understand specific ecological outcomes such as the tree composition of a particular managed landscape.

Here we examine the native tree conservation potential of three shade-grown coffee farmer cooperatives in western El Salvador. The study explored the effects that local livelihoods, cooperative types, and selected biophysical variables of the landscape have on the levels of tree biodiversity in coffee plantations. We use these results to recommend strategies toward the successful integration of farmer livelihoods and tree conservation goals.

2. Study site

Research was carried out between October 2000 and December 2003 in the municipality of Tacuba in western El Salvador. This region has an area of approximately 130 km², and is located 188 km northwest of San Salvador, the capital city, and 18 km from Ahuachapán, the nearest urban center (Fig. 1). Altitudes range between 600 and 1400 m a.s.l., and annual precipitation ranges between 1650 and 2100 mm, on average (CNR, 1990; Cienfuegos, 1999). Soils at the site are predominantly Andisols, from volcanic origin (MARN, 2003). The farms are adjacent to Parque Nacional El Imposible (PNEI), one of the most important protected conservation reserves in the country, which was established in 1979 and has an area of 5000 ha. The park is considered a pre-montane subtropical moist forest, using the Holdridge Classification System, with elevation ranges between 300 and 1400 m.a.s.l. (Holdridge, 1987; Ramírez-Sosa, 2001).

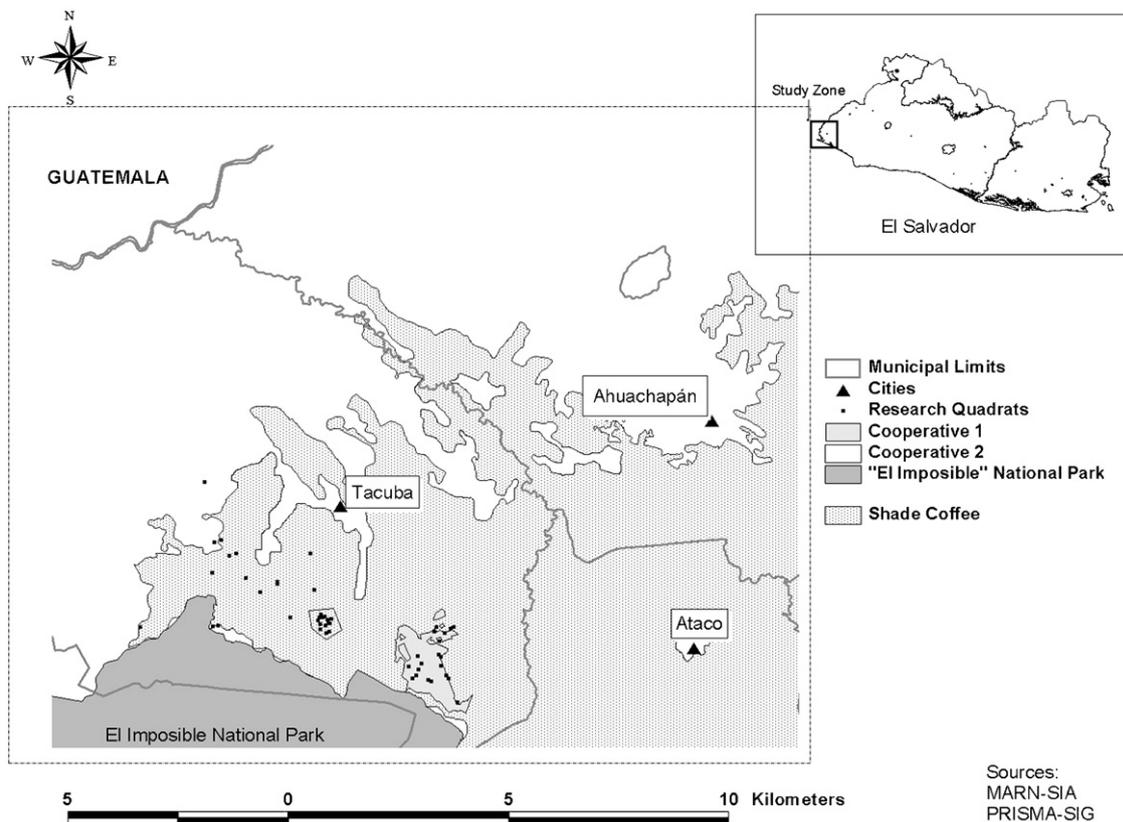


Fig. 1. Location of Tacuba in western El Salvador, showing nearby cities, cooperatives, research quadrats, and El Imposible National Park (PNEI).

Park vegetation includes areas with different disturbance histories, including abandoned cattle pasture, abandoned coffee plantations, previously selectively logged forests, and mature forests. The PNEI has had a historically conflictive relationship with the coffee farmers of Tacuba (including cooperatives and private farms). This was mostly due to the park's efforts to expand in 1994, and which farmers saw as a threat to their land tenure. Since then this relationship has improved as both farmers and park managers see that they could benefit from joint activities, such as improved buffer zones, certified shade coffee, and ecotourism (Méndez, 2004).

Biophysical characteristics (soils, elevation, rainfall, etc.) of the locations of the three cooperatives are very similar, as well as land uses (MARN, 2003; Méndez, 2004; Shapiro and Méndez, unpublished data). The main differences between the cooperatives were the size of their holdings and membership, as well as their management strategies, which were either collective or independent (Table 1).

3. Data collection on trees and biophysical characteristics of the landscape

3.1. Sampling design

Fifty-one 1000-m², rectangular quadrats (20 m × 50 m) were used to measure biophysical variables in the three

cooperatives. Quadrat positioning varied across cooperatives in an attempt to ensure a representative sample of the different types of shade present at each cooperative.

In cooperative 1, a stratified systematic sampling design was used in order to include the four shade types that were identified. Shade types were defined using the typology proposed by Moguel and Toledo (1999), and were identified through interviews with farm managers and surveys of the entire coffee plantation. The shade types included rustic shade near the border with the forest, which contains many older forest trees; traditional polyculture, which includes a diversity of tree species; commercial polyculture dominated by trees from the genus *Inga*; and a shaded monoculture with *Inga vera*. Points were selected along two random transects, for a total of 20 quadrats that were at least 50 m apart from each other and from any farm border, and with at least two quadrats in each shade type.

Cooperative 2 only contained the traditional polyculture shade type. The first transect was randomly located, and starting from this initial point the other transects were located 243 m from each other, reaching a total of five transects evenly distributed through the plantation. Five points were then randomly located in each of the transects; 14 out of these 25 points were selected for sampling, based on the restriction that they were at least 50 m apart from each other and the farm border. To avoid biases resulting from surveying the terrain a priori, quadrat locations were

Sources:
MARN-SIA
PRISMA-SIG

Table 1
 Characteristics and sample sizes for data collection in three coffee cooperatives of Tacuba, El Salvador

Cooperative type	Sample size per stratum	Total population	Total area (ha)	Management
Cooperative 1—Las Colinas-Agrarian reform cooperative	25 household interviews; 20 agroecological plots	99 members and households	195	Shade coffee is managed collectively, under the supervision of the board of directors. Sales to fair trade markets and second year transition to organic management
Cooperative 2—La Concordia-Traditional cooperative (formed through decree 207)	10 household interviews; 14 agroecological plots	22 members and households	31.5 ha under collective management. Individual plots range between 0.7 and 3.5 ha	The shade coffee area is managed collectively under the supervision of the board of directors. Individual plots are managed independently. First year transition to organic management
Cooperative 3—El Sincuyo-Farmer Association	17 household interviews and plots	28 members and households	Individual farms range between 0.7 and 3.5 ha	Farms are managed independently. First year transition to organic management
Total	52 household interviews; 51 plots for agroecological research and	149 members and households		

Source: Méndez (2004).

determined using maps and global positioning systems (GPS) at reference points. In cooperative 3, which was made up of 29 individual farms, the 17 farms sampled were randomly selected from a list (see Fig. 1 for location of quadrats within cooperatives). Recent soils research in the 51 quadrats of the study area showed them to have similar nutrient and physical characteristics (Shapiro and Méndez, unpublished data).

3.2. Shade tree management by farmers

Farmers manage the shade tree canopy to balance obtaining optimum coffee production and tree products. This includes a regime used by the three cooperatives and that involves a yearly pruning of the shade tree canopy, aiming to leave 40–50% shade cover (visual estimate). During this yearly activity tree heights are also controlled to remain at about 5 m. However, farmers will selectively leave larger trees that they foresee using for timber, or simply because they like having a shady place. Trees are both planted and from natural regeneration. Cooperative 3 members plant a diversity of trees, most commonly fruit trees. Cooperatives 1 and 2 do not regularly plant trees, but tend to manage what is already there, and what grows from natural regeneration. Farmers leave naturally regenerating tree seedlings to grow when they weed (weeding is done manually with machetes at least twice per year). Trees are left to grow to provide additional shade in a particular area (regardless of the species), or until they can be identified. Uprooting and transplanting of desirable naturally regenerating species is common, but has high mortality rates (personal observation).

3.3. Shade tree biodiversity and size

Shade tree composition and abundance were evaluated through species inventories, and measurement of height and diameter at breast height (DBH). In each quadrat, all trees with a height ≥ 2 m were measured and sampled for identification. Samples were collected, catalogued, pressed on-site, and taken to the La Laguna Botanical Garden for identification and curation. Diameter data were taken with a measuring tape, and tree heights were estimated using poles 4 m long.

3.4. Shade measurements

Photosynthetically active radiation (PAR) was measured using an AccuPAR[®] 8.0 ceptometer or light meter (Decagon, Inc.), in $\mu\text{mol m}^{-2} \text{s}^{-1}$. Measurements were taken below the shade tree canopy (above coffee bushes), and at full sunlight outside the canopy, between 11 a.m. and 1 p.m. A total of 40 PAR readings were taken at each of two points, 25 m apart (12.5 and 37.5 m, respectively, from the beginning of the quadrat). At each point, four measures were taken at each of the cardinal directions. The ceptometer

contains 80 sensors that can be segmented to better represent a canopy. In this case, the probe was divided into 10 segments, which yielded averages of readings from 8 sensors per segment. Outside canopy measures were taken with an external Licor[®] sensor. Shade measurements were taken during both the wet (May–September) and dry seasons (October–April) to account for differences due to specific shade tree phenology and cloudiness.

3.5. Coffee stands

Coffee densities were estimated by counting coffee bushes in a rectangle located in the middle of the quadrat (Escalante, 2000). Bushes were counted in three rows for a distance of 10 m lengthwise (distance *a*). Then the width occupied by the three rows was documented (distance *b*), and these two lengths would be multiplied (distance $a \times b$) to calculate a rectangular unit of area in m², which contained a certain number of coffee bushes. This measure was then extrapolated to coffee bush density per ha.

3.6. Other biophysical variables

Biophysical variables measured in each quadrat included elevation, with a Barigo[®] barometric altimeter; slope using a clinometer; estimated coffee age, documented through interviews with cooperative members and farm managers; and distance to the PNEI. To analyze the effect of distances between the research quadrats and the forest of the PNEI, we measured distances between quadrats and the border of the PNEI. Quadrat coordinates were taken with a handheld Garmin II global positioning system (GPS), and were inserted into digital maps of the region and forest (Fig. 1). Integration of digital maps and GPS coordinates, as well as distance measures, were carried out using the software ArcView version 3.1.

3.7. Native tree conservation importance

In order to discuss the role that coffee farms could play in conserving tree biodiversity, we compared species composition with that of the nearby PNEI forest. To do this, we used data from a recent study at three sites in the PNEI (Ramírez-Sosa, 2001). Ramírez-Sosa's research utilized similar methods as our study, including the same quadrat size (1000 m²), complete tree inventories of individuals of diameter at breast height (DBH) >5 cm, with DBH and height measurements of all trees. The inventories were carried out at three sites of the park with different disturbance histories: (1) an abandoned coffee plantation; (2) a forest tract that had been selectively logged; (3) a site which was used for selective logging and grazing. All sites have been protected and undisturbed for at least 21 years.

To assign international conservation status to the species found in the cooperatives and the forest, we used international listings such as the World Conservation

Union's (IUCN) Red List of Threatened Species, the Convention on International Trade in Endangered Species of Flora and Fauna (CITES), and the United Nations Environment Program World Conservation Monitoring Center (UNEP-WCMC) (IUCN, 2003; UNEP-WCMC, 2003). Species were considered of international conservation concern if they were listed as of 'conservation concern', 'vulnerable', 'endangered', or were endemic to the site.

4. Household livelihoods and cooperative types

Fifty-two household interviews were undertaken to document socioeconomic information on members, which represented 35% of the total membership of the three cooperatives. In addition to data on family livelihood strategies and organizations, farmers were asked to name and rank tree species and use in order of importance (for tree ranking techniques see Franzel et al., 1996; Höft et al., 1999). These data were used to compare farmer's perception of which trees are important with those species that are given some degree of global conservation importance by international institutions, such as the IUCN and UNEP. Information from the interviews was complemented and triangulated with data from 15 focus groups with farmers, which included discussions on shade tree knowledge and management. In addition, in another focus group, which included members of the three cooperatives, we discussed the reasons that could motivate farmers to purposely maintain (or not) trees of conservation importance.

5. Data analysis

5.1. Species richness distributions

Species richness (individual-based), and species richness per stem accumulation curves were calculated to compare tree diversity across cooperatives (Gotelli and Colwell, 2001; Hubbell et al., 1999). These were done using sample-based rarefaction (randomized by quadrat 100 times) and Coleman, individual-based rarefaction curves. Both were calculated using the software EstimateS, version 6.0b1 (Colwell, 2002). Curves were compared for statistical differences through Kolmogorov–Smirnov tests, using the software SPSS, version 10.

5.2. Species, tree size and biophysical variable comparisons between cooperatives

Comparisons of total species richness, abundance, percent shade, coffee density, and age between the three cooperatives, were analyzed through a one-way analysis of variance (ANOVA), and post hoc Fisher's least significant difference (LSD) tests. Wet- and dry-season percent shade measurements for the entire sample were compared through

a Student's paired, two tailed *t*-test. Comparisons of tree size (DBH and height) were analyzed through nested ANOVA, with trees nested in quadrats and quadrats nested in cooperatives. Sample or quadrat-based rarefaction was used to transform total species richness for the comparative analysis of the cooperatives, as described in Gotelli and Colwell (2001), and using EstimateS version 6.0b1.

5.3. Tree community similarity between the cooperatives and the PNEI forest

We compared species composition between the cooperatives and the PNEI forest sites using the Jaccard (CC_j) incidence-based coefficient (Magurran, 1988), which is calculated with the following formula:

$$CC_j = \frac{C}{S_1} + S_2 = \frac{C}{S}$$

where S_1 and S_2 are the number of species in each community (in this case each cooperative or each plot); C is the total number of species shared by the two communities; and S is the sum total of species found in both communities. Since the Jaccard index is sensitive to sample size (Wolda, 1981), species richness figures used for its calculation were transformed using sample-based rarefaction with the software EstimateS, version 6.0b1.

6. Results

6.1. Tree inventories and ecological variables

Tree samples totaled 2743 individuals representing 46 families and 169 species for the three cooperatives. A total of 123 species were identified, of which 109 were native, and 14 exotic (Appendix A). Of the remaining 46 species, some

were only identified by common name, and others were not identified due to a lack of reproductive parts.

6.2. Tree species richness and abundance

Total tree species richness was highly significantly different among the cooperatives ($F_{2,50} = 15.024$, $p \leq 0.0001$) (Table 2). Kolmogorov–Smirnov (K–S) tests performed on the individual-based, Coleman species richness curves for the three cooperatives, showed that they are significantly different from each other ($p < 0.0001$) (Fig. 2). Total species richness for cooperatives 1 and 2 was marginally significantly different (Fisher's LSD, $p = 0.053$), and cooperative 3 was significantly different from both 1 and 2 (Fisher's LSD, $p \leq 0.0001$).

Cooperative 3 contained significantly more trees than cooperatives 1 and 2 ($F_{2,50} = 14.806$, $p \leq 0.0001$; Fisher's LSD, $p \leq 0.0001$), whereas tree abundance did not differ significantly between cooperatives 1 and 2 (Fisher's LSD, $p = 0.511$). Following Hubbell et al.'s (1999) and Gotelli and Colwell's (2001) analytical approach, we found that the greater number of stems itself was largely responsible for the greater species richness observed in cooperative 3. When analyzed on a species per quadrat basis (transformed through Coleman individual-based rarefaction) (Fig. 2b), cooperative 3 shows significantly greater species richness per area than either cooperative 1 or 2 ($p < 0.0001$, K–S test) (cooperatives 1 and 2 did not differ in species richness or tree abundance; see Table 2). However, when adjusted for number of stems per quadrat, the differences among cooperatives largely collapses, showing no significant differences between cooperatives 1 and 2 ($p < 0.244$, K–S test), or cooperatives 1 and 3 ($p < 0.160$, K–S test) (Fig. 2a). Cooperatives 2 and 3 were still significantly different ($p < 0.010$, K–S test), but a large component of the differences in species richness was removed by simply

Table 2

Summary of ecological characteristics and analyses of tree communities and coffee plantations in three coffee cooperatives of Tacuba, El Salvador ($N = 51$)

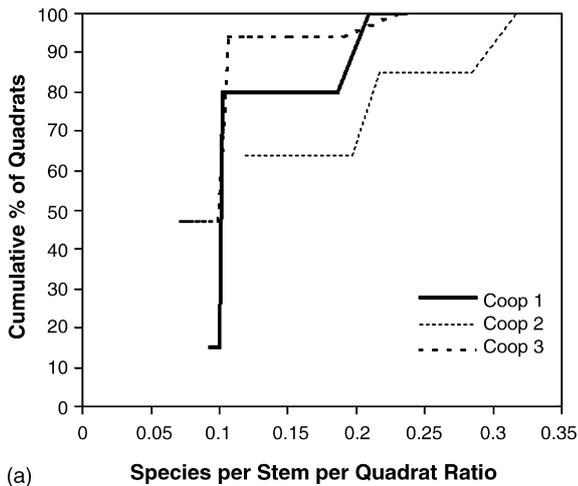
	Cooperative 1	Cooperative 2	Cooperative 3	F-statistic	p-Value
Number of quadrats	20	14	17		
Mean coffee shrub density per quadrat (# plants per ha)	6077 (± 1994)	5304 (± 889)	6768 (± 1828)	2.835	0.69
Mean coffee age (years)	31 (± 17)a	33 (± 20) a	13 (± 11) b	7.521	0.001***
Total species richness per site ^a	69 (± 16.79) a ^b	48 (± 11.16) a	93 (± 23.99) b	15.02	0.0001***
Mean richness per quadrat ^c	12 (± 4.10) a	12 (± 2.89) a	22 (± 8.33) b	15.219	0.0001***
Mean stem density (trees per quadrat) ^a	39 (± 14.92) a	35 (± 16.15) a	89 (± 52.27) b	14.81	0.0001***
Mean diameter at breast height (DBH, in cm)	14.7 (± 13) a	12.5 (± 12.51) b	8.4 (± 8.81) c	9.949	0.0001***
Mean height (m)	5.5 (± 2.4) a	5.2 (± 2.53) a	5.3 (± 3.05) a	0.019	0.981
Mean Shannon–Weiner index	2.78 (± 0.1965) a	2.94 (± 0.1453) a	3.33 (± 0.1447) b	14.072	0.0001***
Mean percent shade (1 year)	55 (± 22.21) ab	47 (± 21.15) a	63 (± 8.92) b	3.458	0.40
Mean percent shade wet season (May–September)	59 (± 20.71) a	54 (± 26.21) a	79 (± 12.00) b	7.51	0.001***
Mean percent shade dry season (October–April)	50 (± 22.21) a	40 (± 19.72) a	46 (± 15.56) a	1.112	0.337

Figures in parentheses are standard deviations.

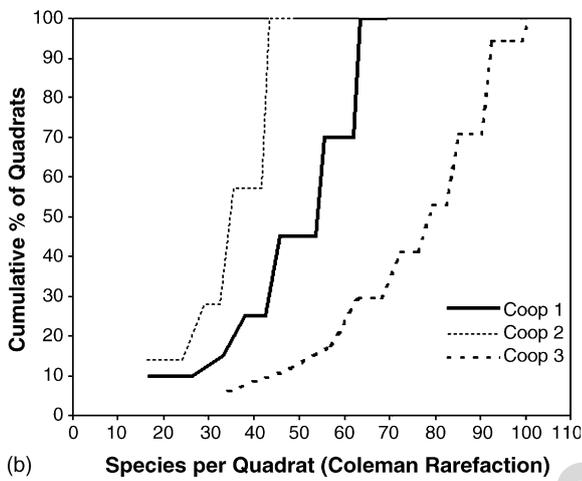
^a Because the sample sizes per cooperative (site) were different, and in order to compare them adequately, these figures were transformed through Coleman, individual-based rarefaction with the software EstimateS version 6.01.

^b Means followed by the same letter are not significantly different between cooperatives (sites), by Fisher's LSD ($p = 0.05$).

^c Quadrats were 1000 m².



(a) Species per Stem per Quadrat Ratio



(b) Species per Quadrat (Coleman Rarefaction)

Fig. 2. Species richness distributions for three coffee cooperatives in 1000 m² quadrats in Tacuba, El Salvador. (a) Distributions of species per stem per quadrat and (b) distributions of species richness per quadrat, transformed using Coleman individual-based rarefaction.

accounting for stem density. This suggests that the higher species richness was largely a function of the higher number of individual trees present in the shade coffee systems of cooperative 3.

6.3. Percent shade

Integrated across seasons, mean percent shade varied significantly among the cooperatives (Table 2, Fig. 3). Cooperative 3 had the highest mean percent shade with 63% for the year, followed by cooperative 1, with 55% and cooperative 2 with 47% ($F_{2,50} = 3.458, p = 0.04$, Table 2). However, patterns of shade varied dramatically across seasons (Fig. 3; dry season $46 \pm 19.6\%$; wet season $64 \pm 22.5\%$; paired t -test $t_{1,50} = 5.240, p < 0.0001$). During the wet season, cooperative 3 had significantly more shade than either of the other cooperatives ($F_{2,50} = 7.510, p = 0.001$, Table 2). In contrast, there were no significant differences in percent shade among any of the three cooperatives during the dry season ($F_{2,50} = 1.112, p = 0.337$, Table 2).

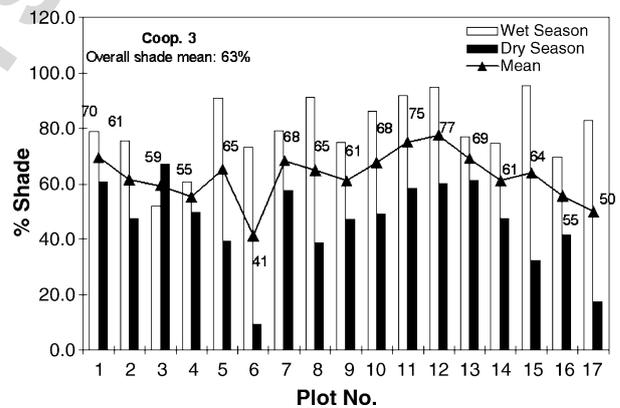
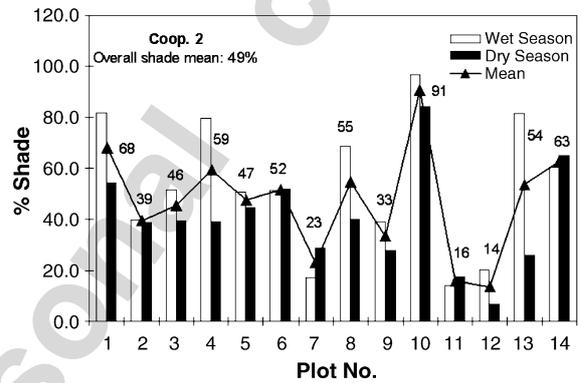
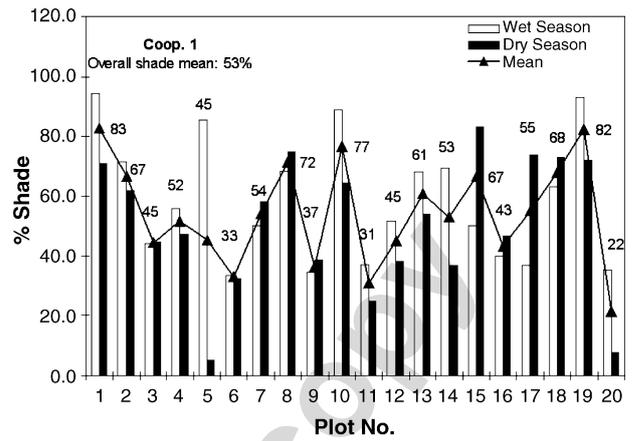


Fig. 3. Percent shade measurements for the wet (May–September) and dry (October–April) seasons (years 2001 and 2002) in three coffee cooperatives of Tacuba, El Salvador.

6.4. Tree size

The nested ANOVA showed that tree height did not differ among cooperatives ($F_{2,53} = 0.019, p = 0.98$), but was significantly different at the quadrat level ($F_{48,2691} = 8.69, p = 0.0001$) (Table 2). This corroborates the reports of similar pruning regimes by the three cooperatives, which is done once a year, and involves selective trimming of tree canopies. However, it also shows that there is great variability within cooperatives regarding the results of tree-height management. In the interviews with farm managers, they reported to try to maintain 40% shade

cover, with tree heights that are below 10 m, but direct shade measurements showed much higher cover figures for all cooperatives (see Fig. 3). There was also a significant amount of variation among trees within quadrats ($F_{1,54} = 1295.6$, $p = 0.0001$).

Tree diameters showed highly significant variances at the tree ($F_{1,54} = 529.4$, $p = 0.0001$), quadrat ($F_{48,2692} = 8.002$, $p = 0.0001$), and cooperative levels ($F_{2,53} = 9.95$, $p = 0.0001$) (Table 1). Management of trees considering their diameter was not discussed by cooperative members or farm managers. Farmers tend to focus their shade tree management practices to species selection, height and shade cover, but no explicit action seemed to be taken based on tree diameters.

6.5. Effects of biophysical factors on tree biodiversity

Regression analysis for all sites ($N = 51$) showed that tree density was a strong predictor of species richness per quadrat (adjusted $r^2 = 0.589$, $F_{1,49} = 72.701$, $p < 0.0001$). Stepwise multiple regression showed that the inclusion of elevation, percent shade in the wet and dry seasons, coffee density, coffee age, or distance to the PNEI did not contribute significantly to the model.

6.6. Comparisons of tree species richness and incidence between the cooperatives and the forest

The sum of species reported from the forest (Ramírez-Sosa, 2001) and cooperative sites included a total of 227 identified trees. Total species richness is similar for the forest

(174 species) and the shade coffee cooperatives (169 species) (141 versus 123 morphological species identified at least to the genus level in forest sites and cooperatives, respectively).

Jaccard coefficients (CC_j) of community similarity were calculated using the total 227 species identified at least to the genus level in the three cooperatives and the three forest sites (Ramírez-Sosa, 2001). Comparisons between cooperative and forest sites showed less similarity ($CC_j \leq 0.12$), than did comparisons among cooperatives ($CC_j \geq 0.38$) or among forest sites ($CC_j \geq 0.30$). In general, forest site 2, which was an abandoned coffee plantation, showed the most similarity to all cooperative sites. In total, 36 species were shared between cooperatives (pooled) and the forest (pooled) ($CC_j = 0.163$), which represents only 16% of the total of 227 species used in the analysis (123 and 141 identified species found in the cooperatives and forest, respectively).

6.7. Global conservation importance of tree species in the Tacuba landscape

Twenty-three of the species found in the cooperatives and the forest appeared in international lists of conservation concern for El Salvador and Central America (Table 3). One of these species, *Guapira witsbergeri*, does not appear in any of the lists, but is of conservation importance because of its endemism (Ramírez-Sosa, 2001). Most of the species of international concern were found in the forest, followed by cooperative 3, and in much lower numbers in cooperatives 1 and 2. These lists are by no means complete for this region of

Table 3

Tree species of international conservation importance in coffee cooperative and forest sites, Tacuba, El Salvador

Species	Family	Forest	Cooperative 1	Cooperative 2	Cooperative 3	Conservation Status	Reference
<i>Amyris elemifera</i>	Rutaceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Annona muricata</i>	Annonaceae				X	Conservation concern	UNEP-WCMC (2003)
<i>Brosimum alicastrum</i>	Moraceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Cedrela odorata</i>	Meliaceae	X				Vulnerable	IUCN (2003)
<i>Coccoloba montana</i>	Polygonaceae	X			X	Conservation concern	UNEP-WCMC (2003)
<i>Cordia garascanthus</i>	Boraginaceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Eugenia salamensis</i>	Myrtaceae		X	X	X	Conservation concern	UNEP-WCMC (2003)
<i>Eysenhardtia adenostylis</i>	Fabaceae				X	Conservation concern	UNEP-WCMC (2003)
<i>Guapira witsbergeri</i>	Nyctaginaceae	X			X	Endemic to the site	Ramírez-Sosa, 2001
<i>Hymenaea courbari</i>	Fabaceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Licania retifolia</i>	Chrysobalaceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Lonchocarpus minimiflorus</i>	Fabaceae		X	X	X	Endangered	IUCN (2003)
<i>Manilkara chicle</i>	Sapotaceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Parathesis congesta</i>	Myrsinaceae	X				Vulnerable	IUCN (2003)
<i>Psidium friedrichsthalianum</i>	Myrtaceae				X	Conservation concern	UNEP-WCMC (2003)
<i>Quercus skinneri</i>	Fagaceae		X			Vulnerable	IUCN (2003)
<i>Sideroxylon capiri</i>	Sapotaceae		X	X	X	Conservation concern	UNEP-WCMC (2003)
<i>Spondias mombin</i>	Anacardiaceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Swietenia humilis</i>	Meliaceae			X	X	Vulnerable	IUCN (2003)
<i>Swietenia macrophylla</i>	Meliaceae	X				Vulnerable	IUCN (2003)
<i>Tabebuia chrysantha</i>	Bignoniaceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Tabebuia donnell-smithii</i>	Bignoniaceae	X				Conservation concern	UNEP-WCMC (2003)
<i>Tabebuia rosea</i>	Bignoniaceae	X		X	X	Conservation concern	UNEP-WCMC (2003)
Total by site		15	4	5	10		

Table 4

Most frequent species and those of international conservation importance, which were reported by farmers ($n = 52$) in three coffee cooperatives of Tacuba, El Salvador

No.	Species	Frequency			Main uses ^a	Total frequency	Global priority
		Cooperative 1	Cooperative 2	Cooperative 3			
1	<i>Mangifera indica</i>	9	2	5	Fr, F	16	
2	<i>Cordia alliodora</i>	1	5	7	T, F	13	
3	<i>Inga pavoniana</i>	11		2	S, F	13	
4	<i>Cedrela odorata</i>	1	5	5	T	11	x
5	<i>Citrus</i> spp.	2	1	6	Fr	9	
6	<i>Ficus</i> spp.	6	1	2	S, F	9	
7	<i>Inga punctata</i>	7		2	S, F	9	
8	<i>Persea americana</i>	3	1	5	F	9	
9	<i>Eugenia jambos</i>	4	2		S, W, F	6	
10	<i>Gliricidia sepium</i>		2	2	F	4	
11	<i>Inga</i> sp.	4			S, F	4	
12	<i>Ocotea sinuate</i>	1	3		T, F	4	
13	<i>Lonchocarpus minimiflorus</i>	1	2		T, F	3	x
14	<i>Enterolobium cyclocarpum</i>	2		1	S, T	3	
15	<i>Terminalia oblonga</i>			3	T, F	3	
16	<i>Tabebuia rosea</i>			2	T, F	2	x
17	<i>Inga vera</i>	2			S, F	2	
18	<i>Juglans olanchana</i>	2			T	2	
19	<i>Licania retifolia</i>	1			T	1	x
20	<i>Quercus skinerii</i>	1			T	1	x
21	<i>Sideroxylon capiri</i>	1			T	1	x
22	<i>Swietenia humilis</i>		1		T	1	x

^a F, firewood; Fr, fruit; S, shade; T, timber; W, windbreak.

El Salvador, but they provide a starting point for evaluating tree species conservation in this particular landscape.

6.8. Farmer's perceptions of important trees and management of species of conservation concern

Farmers reported a total of 58 tree species of importance for a variety of uses. Species lists by individual farmers ranged between 1 and 9 trees. Table 4 presents the most frequently cited tree species and whether they qualify in the international lists of conservation concern. Only 7 species out of the 58 trees reported by farmers were both of local importance and international conservation concern. Of these, only three species were mentioned more than once.

In a focus group directed at discussing the possibility to purposely maintain and manage tree species of conservation concern, farmer's responded they would be willing to do so for two specific reasons. The first would be to become certified by Rainforest Alliance's shade-grown seal. The organization that manages the park is also the one that provides this type of certification, and they have approached all three cooperatives to encourage them to get certified. The incentive for the farmers would be to get a premium for their coffee due to this type of certification. The second reason for maintaining trees of conservation concern was reported as an ecotourist attraction. All three cooperatives have engaged in an incipient agro-ecotourism project with visitors from international solidarity organizations (Bacon et al., 2005; Méndez and Bacon, 2005). These groups have demonstrated

interest in 'forest trees' and birds within the coffee plantations. In addition, farmers stated that 'conservation activities' could facilitate funding and support from governmental and non-governmental organizations. Their main concern related to maintaining their rights to prune or extract trees from their coffee plantations.

7. Discussion

7.1. Biophysical factors driving the present levels of tree biodiversity

A key result from this analysis is the importance of tree density as a determinant of tree species richness in the shade coffee systems (as density increased, so did richness). This pattern has also been observed in unmanaged tropical forests (Hubbell et al., 1999). However, because tree density is associated with both management and biophysical conditions, it is unclear how much of the increased diversity is a simple function of sampling effect. Our multiple regression analysis indicated that stem density alone explained nearly 60% of the variation in tree richness, with little influence from other biophysical variables. These results suggest that much of the species richness may be a primary result of management choices that affect tree density, with less influence from farmer preferences for specific species. This suggests the possibility to effectively promote the conservation of tree species through the management of shade tree densities.

However, conservation of tree richness through higher tree densities may not be adequate to capture rare species of conservation concern, or of agronomic benefit. Instead, it influences the species selections made by farmers within their desired tree densities, and may be key to improving the conservation value of tree species composition.

The similarity analysis showed that the tree communities in coffee plantations and in the PNEI forest are very different. Since tree species in tropical forests are naturally patchy, if tree diversity in the coffee plantations were primarily influenced by seed dispersal from the nearby forest, we would expect that species diversity should decline with distance from the PNEI. Our study found no influence of proximity to the PNEI on species richness. Although our research was not able to determine all the potential ecological causes (e.g., seed dispersal mechanisms), the data suggests that tree selection and farm management are very influential factors driving on-farm tree species diversity.

These results support the premise that composition of the shade tree canopy of these coffee plantations is mostly an effect of agroecological management (primarily shade tree density), and not a result of plantation biophysical characteristics. However, further research on other important biophysical characteristics is necessary to complete this analysis.

7.2. Patterns of shade provided by trees

The seasonal variation in shade provided by overstory trees puts into question the accuracy of visual shade estimations. Most farmers manage shade percentages by specifically defined areas of different sizes. In small farms, there is usually one estimate for the entire farm. However, our results show that shade percent can vary from 10 to 93% within 25 m (Fig. 3, plot 5, cooperative 1). This inaccuracy in visual shade measurements can also be transferred to variables as production, incidence of disease and others, which are related to specific shade percentages and dictate shade and crop management. This could mean that farmers are relating the behavior of some of these factors to erroneous shade levels. The percent shade differences between the wet and the dry season can be partly attributed to the presence of deciduous species that lose their leaves in the dry season. Pruning regimes in all cooperatives were very similar, and are not likely to have affected this outcome. Further analysis of species composition and abundance is necessary to shed more light on the reasons for this difference.

Another important aspect that merits attention is the effect that percent shade cover can have on naturally regenerating tree species. If higher levels of shade are propitious for the reproduction and conservation of native trees, then these parameters need to be integrated to plantation management criteria. Further analyses are needed on the reproductive and dispersal habits of selected tree species.

7.3. Effects of livelihood strategies on tree biodiversity

Méndez (2004) demonstrated that cooperative member livelihoods depend on shade tree products such as firewood, timber and fruit. For these reasons, farmers do not perceive un-shaded coffee plantations as a viable, management option. These results are in line with similar research done in other types of agroforestry systems of other tropical regions (Barrance et al., 2003; Leakey, 1999; Michon and de Foresta, 1999; Sonwa et al., 2001).

Most farmers also believe that tree diversity is beneficial to the health of the coffee agroecosystem. When asked why he maintained a diversified tree canopy, Don Pedro, an older farmer from cooperative 3 mentioned two main reasons. The first was that maintaining different trees provided different types of products and a certain variety within each of these use categories. He also expressed the following with regards to the relationship between tree diversity and soil fertility: “The leaves of different trees have different properties. The higher variety of trees that I have in my farm, the more different things that the soil gets when the leaves fall on the ground.”

Greater household dependence on the coffee plantations for tree products resulted in higher species richness and tree density, with the highest species richness and tree density figures found in cooperative 3. These farmers rely on the production of the farm as their main source of income and products for consumption (Table 2). Livelihood strategies of cooperatives 1 and 2 members, on the other hand, see the coffee plantations more as sources of income (through employment), and firewood (Méndez, 2004). They do not associate the collectively managed farms as reliable sources of other products for their households.

7.4. Effects of cooperative types on tree biodiversity

Our analyses demonstrated that cooperatives 1 and 2 have similar species richness and tree density, but that they differ significantly from cooperative 3. Important similarities between cooperatives 1 and 2 are that coffee plantations are collectively managed, and that both were once private, commercial estates; cooperative 3 does not share these traits. A common shade management practice of commercial farms was to simplify the shade canopy by substituting native species with trees from the genus *Inga* (both exotic and native). Cooperative members have retained, as much as possible, the type of shade management used by the previous owners, but have had to modify it in order to meet the needs of their members. This includes harvesting shade tree products, which was not of concern to the earlier landowners. The result is a shade tree canopy that is more diverse than a commercial farm, but less diverse than the individual farms of cooperative 3. Focus group discussions suggested that for cooperatives 1 and 2 collective management is in conflict with ownership issues of tree products. Some of the concerns expressed related to the allocation of responsibility for maintaining the trees, and the distribution of tree products.

Cooperative 3 members, on the other hand, maintain higher tree species richness and density in their farms than cooperatives 1 and 2. These farms also contain a higher number of species of conservation concern, which usually originate from natural regeneration. This practice has been carried out by the farmer's own initiative, and is also facilitated by a type of cooperative structure that does not include collective land management.

7.5. Developing participatory models for tree biodiversity conservation in shade coffee landscapes

The shade coffee cooperatives could play an active role in the conservation of forest species by acting as an extension of habitat to the PNEI. In the case of native trees, these farms could greatly increase the viability of some of these species in El Salvador (Monro et al., 2001). The levels of biodiversity found in the three cooperatives show great potential for conserving tree species in coffee plantations. We also observed a degree of compatibility between keeping high levels of tree biodiversity as part of livelihood strategies. However, as found elsewhere (Gordon et al., 2003, 2004), threatened species were generally of little importance to farmers, so increasing the conservation potential of coffee plantations will require considerable effort.

Farmers are interested in participating in tree conservation initiatives if these activities support their livelihood strategies. At present, cooperative members show interest in maintaining tree species of conservation concern because they perceive this might be conducive to receiving shade certifications that can result in price premiums for their coffee (e.g., Rainforest Alliance and Smithsonian); and also because these trees are attractive to ecotourists. Trees can be more easily managed than most other organisms that might be important for certification or tourists (e.g., birds). Shade certification and ecotourism are two relatively new livelihood strategies in this area, which seem compatible with conservation initiatives.

Further work needs to focus on providing farmers with the knowledge necessary to maintain and manage tree species of conservation concern. In order to do this adequately, more research needs to determine species of local and national conservation value, in addition to those of global concern. Farmers and rural communities should play

a leading role in defining these species. For example, it would be useful to develop lists of threatened species, which are appreciated for their local uses, as an alternative to substituting those species that start becoming scarce (as seen by Gordon et al., 2003). These could also be of interest to certifiers and ecotourists. If farmers and their households value these trees, it would be considerably easier to recruit them in efforts to conserve them.

The results of this research suggest that meeting goals that match species of conservation concern will require considerable effort in working with farmers to get to recognize, value, plant and maintain these trees. A first step in this direction would be to evaluate with farmers what this would represent in terms of time and financial investment, and to evaluate if this effort would enhance their livelihood strategies.

The three cooperatives studied here had different levels of tree biodiversity. Conservation initiatives with farmer cooperatives will need to take such differences into account, and develop specific strategies for each type of organization. Supporting and working with cooperatives will also allow for an integration with already existing social and marketing networks, which might support environmental initiatives.

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Appendix A. List and frequencies of identified tree species found in three coffee cooperatives of Tacuba, El Salvador (ordered alphabetically by family and species)

No.	Family	Species	Frequency	Origin ^a
1	Actinidiaceae	<i>Saurauia kegeliana</i> Schldl.	4	n
2	Amarathaceae	<i>Iresine calea</i> (Ibañez) Standley	4	?
3	Anacardiaceae	<i>Anacardium occidentale</i> (L.)	4	e
4	Anacardiaceae	<i>Mangifera indica</i>	21	e
5	Anacardiaceae	<i>Spondias</i> sp.	3	n
6	Annonaceae	<i>Annona muricata</i> L.	1	n
7	Annonaceae	<i>Rollinia rensioniana</i> Stanley	7	n

Appendix A (Continued)

No.	Family	Species	Frequency	Origin ^a
8	Annonaceae	<i>Sapranthus violaceus</i> (Dunal) Saff.	2	n
9	Apocynaceae	<i>Alstonia longifolia</i> (A.DC.) Pichon	14	n
10	Apocynaceae	<i>Plumeria rubra</i> L.	1	n
11	Apocynaceae	<i>Stemmadenia</i> sp. Donnell-Smithii (Rose) Wood	8	n
12	Asteraceae	<i>Critonia morifolia</i> (Mill.) R.M. King & H. Rob.	23	n
13	Asteraceae	<i>Montanoa guatemalensis</i> Robinson & Greenman	1	n
14	Asteraceae	<i>Sinclairia sublobata</i> (Robinson) R y db.	3	?
15	Asteraceae	<i>Vernonia patens</i> Kunth	6	n
16	Bignoniaceae	<i>Tabebuia rosea</i> (Bertol) DC.	1	n
17	Bignoniaceae	<i>Tecoma stans</i> (L.) Juss. Ex. Kunth	6	n
18	Bombacaceae	<i>Ceiba aesculifolia</i> (Kunth) Britten & Baker f.	1	n
19	Bombacaceae	<i>Ceiba pentandra</i> (L.) Gaertner	1	n
20	Boraginaceae	<i>Cordia alliodora</i>	28	n
21	Boraginaceae	<i>Cordia</i> sp.	7	n
22	Burseraea	<i>Bursera simaruba</i>	1	n
23	Caricaceae	<i>Carica papaya</i> (L.)	2	n
24	Cecropiaceae	<i>Cecropia obtusifolia</i> Bertol	8	n
25	Celastraceae	<i>Zinowiewia integerrima</i> (Turcz.)	1	n
26	Clethraceae	<i>Clethra mexicana</i> A.DC.	6	n
27	Combretaceae	<i>Terminalia oblonga</i> (Ruiz&Pavon) Steudel	6	n
28	Cupressaceae	<i>Cupressus lusitanica</i>	1	n
29	Dichapetalaceae	<i>Dichapetalum</i> sp. Donnell-smithii Engl.	2	n
30	Euphorbiaceae	<i>Acalypha schiedeana</i> Schldl.	1	?
31	Euphorbiaceae	<i>Alchornea latifolia</i> Sw.	1	n
32	Euphorbiaceae	<i>Croton reflexifolius</i> Kunth	29	n
33	Euphorbiaceae	<i>Gymnanthes riparia</i> (Schltdl.) Kotsch	3	n
34	Euphorbiaceae	<i>Jatropha curcas</i> L.	2	n
35	Euphorbiaceae	<i>Ricinus communis</i> L.	11	n
36	Fabaceae	<i>Acacia hindsii</i> Benth	1	n
37	Fabaceae	<i>Albizia adinocephala</i> (J.D. Smith) Britton & Rose	12	n
38	Fabaceae	<i>Bauhinia unguolata</i> L.	6	n
39	Fabaceae	<i>Cajanus cajan</i> (L.) Millsp.	2	e
40	Fabaceae	<i>Diphysa</i> sp.	9	n
41	Fabaceae	<i>Enterolobium cyclocarpum</i> (Jacq.) Griseb.	1	n
42	Fabaceae	<i>Erythrina berteriana</i> Urb.	1	n
43	Fabaceae	<i>Eysenhardtia adenostylis</i> Baill	2	n
44	Fabaceae	<i>Gliricidia sepium</i> (Jacq.) Kunth ex. Steudel	7	n
45	Fabaceae	<i>Inga calderonii</i> Standley	11	n
46	Fabaceae	<i>Inga hintonii</i> Sandwith	2	n
47	Fabaceae	<i>Inga oerstediana</i> Benth ex. Seemann	25	n
48	Fabaceae	<i>Inga paterno</i> Harms	5	n
49	Fabaceae	<i>Inga pavoniana</i> G. Don	13	n
50	Fabaceae	<i>Inga punctata</i> Willd	29	n
51	Fabaceae	<i>Inga vera</i> Willd.	13	n
52	Fabaceae	<i>Lonchocarpus minimiflorus</i> Donn. Sm.	15	n
53	Fabaceae	<i>Lonchocarpus rugosus</i> Benth	4	n
54	Fabaceae	<i>Lonchocarpus</i> sp.	14	n
55	Fabaceae	<i>Lysiloma divaricatum</i> (Jacq.) Macbride	2	n
56	Fabaceae	<i>Machaerium</i> sp.	7	n
57	Fabaceae	<i>Machaerium arboreum</i> (Jacq.) Vogel	15	n
58	Fabaceae	<i>Machaerium biovulatum</i> Michelli	2	n
59	Fagaceae	<i>Quercus skinneri</i> Benth	3	n
60	Flacourtiaceae	<i>Casearia arguta</i> Kunth	5	n
61	Gramineae	<i>Bambusa longispiculata</i> Gambre ex Brandis	3	?
62	Guttiferae	<i>Calophyllum</i> sp.	3	n
63	Lauraceae	<i>Ocotea sinuata</i> (Mez) Rohwer	12	n
64	Lauraceae	<i>Ocotea</i> sp.	1	n
65	Lauraceae	<i>Ocotea veraguensis</i> (Meisn.) Mez	1	n
66	Lauraceae	<i>Persea americana</i> Miller	14	n
67	Malpighiaceae	<i>Bunchosia cornifolia</i> Kunth.	9	n
68	Malpighiaceae	<i>Byrsonima crassifolia</i> (L.). Kunth	2	n
69	Malpighiaceae	<i>Malpighia glabra</i> L.	2	?
70	Malvaceae	<i>Abutilon andrieuxii</i> Hemsley	1	n
71	Meliaceae	<i>Cedrela salvadorensis</i> Standley	9	n

Appendix A (Continued)

No.	Family	Species	Frequency	Origin ^a
72	Meliaceae	<i>Melia azederach</i> L.	3	e
73	Meliaceae	<i>Swietenia humilis</i> Zucc.	5	n
74	Meliaceae	<i>Trichilia havanensis</i> Jacq.	8	n
75	Meliaceae	<i>Trichilia martiana</i> C.DC.	8	n
76	Meliaceae	<i>Trichilia</i> sp.	1	n
77	Meliaceae	<i>Trichilia</i> sp.	1	?
78	Moraceae	<i>Chlorophora tinctoria</i> (L.) Gaudich	1	n
79	Moraceae	<i>Ficus pertusa</i> L.F.	8	n
80	Moraceae	<i>Ficus</i> sp.	11	n
81	Moraceae	<i>Ficus</i> sp.	1	n
82	Myrsinaceae	<i>Rapanea myricoides</i> (Schldl.) Lundell	1	?
83	Myrtaceae	<i>Eucalyptus</i> sp.	1	e
84	Myrtaceae	<i>Eugenia jambos</i> (L.) Alston	21	e
85	Myrtaceae	<i>Eugenia salamensis</i> Var. <i>Rensoniana</i> (Standley)	16	n
86	Myrtaceae	<i>Eugenia</i> sp.	1	e
87	Myrtaceae	<i>Psidium friedrichsthalianum</i> (Berg.) Niedenzu	1	n
88	Myrtaceae	<i>Psidium guajava</i> L.	2	n
89	Nyctaginaceae	<i>Guapira witsbergeri</i> Lundell	6	n
90	Piperaceae	<i>Piper amalago</i> L.	4	?
91	Polygonaceae	<i>Coccoloba montana</i> Standley	1	n
92	Polygonaceae	<i>Triplaris melaenodendron</i> (Bertol) Standley & Steyerm	2	n
93	Polygonaceae	<i>Triplaris</i> sp.	3	n
94	Rhamnaceae	<i>Karwinskia calderonii</i> Standley	1	n
95	Rosaceae	<i>Prunus brachybotrya</i> Zucc.	6	n
96	Rubiaceae	<i>Coutarea hexandra</i> (Jacq.) Schum	1	?
97	Rubiaceae	<i>Hamelia patens</i> Jacq.	4	n
98	Rubiaceae	<i>Vanguena madagascariensis</i> Amel	1	e
99	Rutaceae	<i>Citrus aurantifolia</i>	2	e
100	Rutaceae	<i>Citrus</i> sp.	6	e
101	Rutaceae	<i>Citrus</i> sp.	16	e
102	Rutaceae	<i>Citrus</i> sp.	2	e
103	Sapindaceae	<i>Melicoccus bijugatus</i> Jacq.	1	e
104	Sapindaceae	<i>Thouinidium decandrum</i> (Bonpl.) Radlk.	6	n
105	Sapotaceae	<i>Chrysophyllum cainito</i> L.	8	e
106	Sapotaceae	<i>Pouteria sapota</i> (Jacq.) H.E. Moore & Stearn	2	n
107	Sapotaceae	<i>Sideroxylon capiri</i> ssp. <i>Tempisque</i> (Pittier) Pennington	5	n
108	Simaroubaceae	<i>Simarouba glauca</i> DC.	5	n
109	Solanaceae	<i>Cestrum lanatum</i> Martius & Galeotti	8	n
110	Solanaceae	<i>Cestrum nocturnum</i> L.	1	n
111	Solanaceae	<i>Cestrum racemosum</i> Ruiz & Pavon	3	?
112	Solanaceae	<i>Lycianther heteroclita</i> (Sendtner) Bitter	5	n
113	Solanaceae	<i>Solanum erianthum</i> D. Don	5	n
114	Staphylaceae	<i>Turpinia occidentalis</i> (Sw.) G. Don	2	n
115	Sterculiaceae	<i>Guazuma ulmifolia</i> Lam	6	n
116	Styracaceae	<i>Styrax argenteus</i> Presl	4	n
117	Tiliaceae	<i>Apeiba tiboubou</i> Aublet	1	?
118	Tiliaceae	<i>Heliocharpus mexicanus</i> (Turcz.) Sprague	2	n
119	Tiliaceae	<i>Prockia crucis</i> P.Br. Ex L.	1	?
120	Ulmaceae	<i>Trema micrantha</i> (L.) Blume	9	n
121	Urticaceae	<i>Myriocarpa longipes</i> Liebm.	11	n
122	Verbenaceae	<i>Citharexylum</i> sp. <i>Donnell-smithii</i> Greenm.	5	n
123	Verbenaceae	<i>Lantana camara</i>	1	n

^a Origin can be native (n) or exotic (e).

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