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Conservation of tree species of late succession and conservation concern in coffee agroforestry systems

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ABSTRACT

Shade-grown, montane coffee agroforestry systems have the potential to conserve native tree species of conservation concern (CC) and typical of old growth or late succession (LS) forests in montane cloud forests. However, it remains unclear how preferential selection by farmers for or against certain tree species and diameter sizes affects CC and LS trees distribution and abundance. To address this issue, we investigated how management practices may inadvertently compromise the potential of agroforestry systems to serve as reservoirs for CC and LS trees. We sampled tree diversity in 31 coffee farms and 10 forest sites in La Sepultura Biosphere Reserve in Chiapas, Mexico and assessed the relative importance of shade tree density, basal area, proportion of *Inga* spp. trees, previous land use, and age of fallow (for farms established on land with an agricultural history) on the proportions of CC and LS trees. We then examined if tree size distributions differed between farms and forests, and whether land use legacies mediated the impact of the explanatory variables of interest. These analyses found that management practices that sought to increase the proportion of *Inga* spp. trees had the largest negative impact on the proportions of trees of LS and CC, but the magnitude of the effects were dependent on land-use legacy. We also found that tree size distributions differed between farms and forests among smaller trees (5–20 cm diameter at breast height, (DBH)), but not among larger trees (>30 cm DBH). These findings suggest that in order to increase the conservation potential of coffee agroforestry systems, particularly for farms established on land with an agricultural history, it is important to promote farmers' tolerance of tree species other than *Inga* spp. and preferred tree species.

1. Introduction

Montane cloud forests (MCFs) are considered a conservation priority worldwide due to their high levels of biodiversity with exceptional concentrations of endemic species (Hamilton et al., 1995; Bubb et al., 2004; Toledo-Aceves et al., 2011). MCFs make up less than 2.5% of the world's tropical forests, but harbor a disproportionately high species richness (Bubb et al., 2004). In Mexico, MCFs are recognized as the terrestrial ecosystem with the highest concentration of diversity, harboring approximately 10% of the Mexican flora in less than 1% of the territory (Rzedowski, 1996; Pineda and Halffter, 2004). This ecosystem is severely threatened by climate change (Pounds et al., 1999; Ponce-Reyes et al., 2012) and anthropogenic disturbances, mainly land use conversion to agriculture (Ramírez-Marcial et al., 2001; Muñoz-Villers and López-Blanco, 2008; Martínez et al., 2009). As a result, up to 60% of trees in MCFs in Mexico are threatened by extinction to some degree (Gonzalez-Espinosa et al., 2011).

In coffee agroforestry systems, coffee is cultivated under the canopy of shade trees. Coffee agroforestry systems, which overlap in range with MCFs, may play an important role in providing a habitat for tree species of conservation concern and for old-growth or late succession tree species. However, research has challenged this assertion by showing lower proportions of tree species of conservation concern (CC) and late succession (LS) in coffee agroforests relative to surrounding forests (Méndez et al., 2007; Aerts et al., 2011; Valencia et al., 2014). It remains unclear what

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processes may be undermining the potential of coffee agroforestry to support higher proportions of CC and LS trees.

In this study, we focus on factors associated with coffee agroforestry management that affect structural complexity and tree composition. Additionally, we explore how land use legacies may affect the potential of coffee agroforestry systems to conserve CC and LS trees. Management practices for optimizing coffee production may inadvertently compromise the potential of agroforestry systems to serve as habitat for CC and LS tree species by altering tree structure and composition of the agroforest by preferentially selecting for or against trees of certain species (Soto-Pinto et al., 2001; Anglaaere et al., 2011; Sambuichi et al., 2012; Valencia et al., 2015) and sizes (Soto-Pinto et al., 2001; Rolim and Chiarello, 2004; López-Gómez et al., 2008; Asase et al., 2010; Valencia et al., 2014), and by modifying shade tree abundance (López-Gómez et al., 2008; Correia et al., 2010; Valencia et al., 2014).

Research in Mexico and Central America has described management strategies that seek the gradual replacement of canopy trees by *Inga* spp. and other preferred trees for the benefits associated with coffee production and for the provisioning of secondary goods, such as timber and firewood (Soto-Pinto et al., 2001; Peeters et al., 2003; Albertin and Nair, 2004; Bandeira et al., 2005; Valencia et al., 2015). Farmers' decisions to keep or remove trees from the system may also be influenced by tree size (i.e., diameter). For example, farmers often refrain from removing relatively large trees (Sambuichi, 2002; Asase et al., 2010; Anglaaere et al., 2011) both because of logistical difficulties in removal and to avoid potential damages on their crops and surrounding vegetation when the tree and its branches fall. On the other hand, small trees are subject to removal. For example, sapling and seedlings are routinely removed during weeding practices. Therefore, decisions to remove or keep trees based on their size can result in tree size distributions that are atypical of natural forests (Rolim and Chiarello, 2004; Senbeta and Denich, 2006) and after continuous practice, coffee agroforestry systems can begin to resemble secondary forest (Soto-Pinto et al., 2001). This outcome, in which management inadvertently leads to agroforestry systems that resemble secondary rather than primary forest, however, does not always occur (Asase et al., 2010).

Over time, gradual felling and replacement of trees in which certain species are systematically favored or eliminated has been found to lead toward homogenization (i.e., convergence) in species composition in farms (Bandeira et al., 2005). However, because generally there is a lack of synchrony in the development stage of each farm, the ensemble of coffee farms may still conserve a higher number of species at the landscape level than at the farm level (Bandeira et al., 2005; Valencia et al., 2014). High levels of beta diversity (e.g., between farm differences in diversity) have been found important to attenuate diversity loss at the landscape level (Solar et al., 2015). However, as the process of biotic homogenization continues over time, spatial diversity will be reduced (McKinney and Lockwood 1999) undermining the potential for diversity conservation at all spatial levels.

Management practices that disturb tree structure and composition may drive coffee agroforestry systems to resemble early successional states in terms of community composition, such as a high proportion of pioneer trees (Peña-Claros, 2003; Muñiz-Castro et al., 2011); and structurally, such as lower stand basal area, higher tree densities, lower variation in the distribution of stem diameters, and absence of large trees compared to mature forest (Clark, 1996; Aide et al., 1996; Guariguata and Ostertag 2001; van Breugel et al., 2006). Some studies have found decreasing (Goodall et al., 2015) or no changes (Richards and Méndez, 2014) in tree density at least in the short term (e.g., 10 years). Early successional systems, such as secondary forests, may still harbor significant levels of diversity (Peh et al., 2006; Barlow et al., 2007; Chazdon et al., 2009; Dent and Joseph Wright, 2009), but may not necessarily be a safe haven for the tree species of CC and LS that are at risk of disappearing from MCFs. Although it is understood that biological impoverishment can alter biogeochemical and dynamic properties of ecosystems (Naeem et al., 2012) and that rare species support distinct and vulnerable functions (Mouillot et al., 2013), it is difficult to anticipate the ecological consequences of losing CC and LS tree species. However, given the biodiversity loss crisis that we are facing (Barnosky et al., 2011), lack of concrete understanding of repercussions of the loss of CC and LS tree species is no reason to overlook the threat these species are facing.

The objective of this study is to uncover the management processes that may explain variability in the proportion of trees of CC and LS in coffee agroforests. We hypothesize that farmers' tree selection criteria that favors certain tree species, in particular *Inga* . spp., to the detriment of other trees, is the most important factor in driving reductions in the proportions of trees of CC and LS. The consequences of farmers' modification of shade tree density on the proportion of LS and CC trees are more difficult to predict. Intuitively, because higher shade tree density often results in higher richness (Méndez et al., 2007), one may think that higher shade tree density leads to a higher probability that a tree may be either of CC or LS. However, we hypothesize that agroforestry stands with high shade tree densities do not necessarily result in higher proportions of CC or LS trees. We additionally propose that farmers' selection and elimination of trees based on tree size (i.e., diameter) inadvertently leads to a reduction in a stand's basal area and to anomalous size distribution, which may be detrimental to the conservation of trees of CC and LS. By "anomalous," we mean that the size distribution is atypical of what one would expect from an old-growth or late succession forest. Finally, we expect that farms established on forests are more likely to hold a higher proportion of CC and LS trees than farms established on fallow land. "Fallow land," in this study, was clear-cut and is therefore more likely to resemble an early successional system. We expect that older fallows will be more likely to hold higher proportions of LS trees than younger fallows because a longer time period for forest recovery is needed for LS species to establish after early colonization by pioneer species (Chazdon, 2003). This study aims to contribute to the development of certification guidelines, government regulations, and conservation strategies that may incentivize practices that support the conservation of CC and LS trees in coffee agroforestry systems.

2. Data & methods

2.1. Study site

This study was conducted in La Sepultura Biosphere Reserve (LSBR) located in the Sierra Madre mountain range in Chiapas, Mexico (16°00′18″–16°29′01″N and 93°24′34″–94°07′35″W; 167,309 ha). LSBR is characterized by a rugged terrain with elevation ranging between 60 m.a.s.l. and 2550 m.a.s.l. (CONANP, 2013). Mean temperature ranges between 24 °C and 38 °C; at high elevation points, temperature ranges between 15 °C and 18 °C. The dominant soil type is eutric regosol and characteristics, such as texture and soil material, are homogenous in the study area (Valdivieso-Perez et al., 2012; CONANP, 2013). Annual rainfall varies between 2000 and 2500 mm and rainy season extends from May to October. LSBR encompasses a diversity of ecosystems, including short tree savanna, tropical deciduous forest, evergreen seasonal forest, pine forest, pine-oak forest, oak forest, montane rainforest, evergreen cloud forest, and evergreen cloud shrub (CONANP, 2013). The study site encompasses primarily montane rainforest and evergreen cloud forest.

In the Biosphere Reserve's buffer zone (92% of total area), human activities must be compatible with what the conservation authority considers sound ecological practices, such as agroforestry, integrated management of fire, and no new forest clearing. The core area (8% of total area) is destined for the protection of biodiversity and educational and research activities (INE, 1999). Approximately 24,500 people live in the reserve's buffer zone whose livelihoods depend primarily on small-scale agriculture, such as corn and bean cultivation, cattle raising, and coffee agroforestry (CONANP, 2013). Biosphere Reserve guidelines prevent further clear-cutting of forested areas for the expansion of agriculture and pastureland; however, the expansion of coffee agroforestry is permitted.

Fieldwork was conducted in two communities, where the oldest one was founded in the 1960 and the second one a few years later. Prior to colonization starting in 1960, there is no evidence of human settlements in this area (Cruz-Morales, 2014). In these communities (*é jidos*), farmers are currently in private possession of their land but the general assembly must approve certain decisions, such as selling land, agricultural burning or the management of riparian areas.

2.2. Description of coffee agroforestry systems and management

According to Moguel and Toledo (1999)'s typology, coffee farms in LSBR are representative of traditional polyculture systems, where farmers manipulate the natural forest system. In study communities, farmers establish coffee farms by decreasing the forest's tree density and weeding the understory to create space for the introduction of coffee saplings, and by thinning the canopy to increase amount of light reaching the understory. Farmers do not apply synthetic pesticides or fertilizers and labor is done manually. During weeding, farmers usually remove all saplings and seedlings; infrequently, farmers permit preferred tree species to establish.

Farmers' tree selection criteria were documented in detail via interviews in Valencia et al. (2015). These interviews revealed that farmers strongly favor the recruitment (e.g., by planting, transplanting and sparing saplings during weeding) and survival of *Inga* spp. (e.g., by not removing adult *Inga* spp. trees during shade management) to the detriment of other species. Farmers favor *Inga* spp. above all tree species because it a fast growing tree believed to provide the best shade for coffee and benefit the soil fertility.

Coffee farms in study site are on average 2.6 ha (range: 1–6 ha) and about 90% are certified organic. Farms are on average 11 years old (range: 2–40 years old) and most are between 2 and 15 years old. The majority of farmers are members of a coffee cooperative that includes coffee farmers from the surrounding communities; the cooperative is still at an early stage in terms of organization and negotiation capabilities with potential buyers. Most farmers have received training on organic coffee management practices in workshops organized by a local nongovernmental organization and the government agency responsible for managing the Biosphere Reserve. Farmers also report sharing knowledge on management practices among each other. Although farmers are exposed to similar information on management practices, its actual application across farms is highly variable.

2.3. Sampling design

We randomly selected a sample of 31 shade coffee farms out of approximately 60 in the study area by speaking with coffee farmer representatives. We use the term "shade coffee farm" or simply "farm" to refer to the coffee agroforestry plots that belong to individual farmers. At each plot, we collected data on shade tree abundance (stem density), shade tree diameter at breast height (DBH), and identified tree species with the assistance of a taxonomist from El Colegio de la Frontera Sur (ECOSUR). At the center of each farm site, identified by the farm owner, we established a circular plot consisting of three concentric circles of 5 m, 12 m, and 17 m radii; the site's total area equals 907.5 m^2. In the entire circular plot we counted, identified, and measured DBH of shade trees (DBH >10 cm) and counted coffee shrubs. In the 12 m circle, we included shade trees of DBH >5 cm. In the smallest circle, we counted and identified seedlings (DBH <5 cm; height >50 cm; data not used in this study). We interviewed farm owners to determine management practices (described in detail in Valencia et al., 2015). We gathered data on elevation and farm location with a global positioning system (GPS) device (Garmin GPSMAP 60CSx Handheld GPS Navigator). We collected voucher specimens from sampled species and deposited them at the Herbarium at ECOSUR in San Cristobal, Chiapas. We repeated this sampling protocol in 10 forest sites, as near as possible to coffee farms, and selected to match characteristics of the sampled coffee farms, such as elevation, slope, and exposure. We also selected forest sites that were most similar to primary forests in terms of vegetative characteristics, such as tree height and girth, and which displayed no or minimal signs of grazing, or other anthropogenic disturbances.

2.4. Land use legacies

We interviewed coffee farm owners (n = 31) to gather information about the land use history of their coffee farms and, for the relevant cases, on the amount of time that land was fallow before coffee cultivation. Previous land use was categorized as "forest" or "fallow." "Forest" signified that agricultural activities had not taken place in that land before the establishment of the coffee farm. "Forest" category did not necessarily exclude other human disturbance events, such as occasional extraction of secondary products (e.g., timber or firewood) or seasonal cattle grazing, or natural disturbance events, such as fires or hurricanes. However, it did exclude clear-cutting events necessary for the establishment of crop fields or pastureland. The category "fallow" captured an agricultural history that involved complete or near complete removal of vegetation. In other words, coffee farms established on fallow land were established on vegetated land that had previously been used for cultivating corn or other crops or as pastureland, which required near or complete clear-cutting of vegetation. Among the farmers that reported establishing their farms on fallow land, we asked how many years the land remained fallow before the establishment of the coffee farm. In cases where current farm owners were not certain of how many years the land remained fallow, older family members (in most cases the former farm owner) were consulted.

3. Data analysis

3.1. Classification of conservation concern status and successional stage

A tree was considered to be of conservation concern (CC) if it was listed as critically endangered, endangered, or vulnerable in the IUCN Red List or in the Red List of Mexican Cloud Forest Trees (Gonzalez-Espinosa et al., 2011; IUCN, 2013). Tree species were classified as pioneer, intermediate, and late-successional stage based on expert opinion drawn from regional studies (González-Espinosa et al., 1991; Ramírez-Marcial et al., 1998; Galindo-Jaimes et al., 2002; Ramirez-Marcial et al., 2006).

3.2. Binomial logistic regression

We used separate binomial logistic regressions to assess the associations between managerial and land use legacy factors on the proportions of LS and CC trees. To facilitate the interpretation of effect magnitudes, we standardized continuous explanatory

Table 1
List of tree species sampled in coffee farms in La Sepultura Biosphere Reserve in Chiapas, Mexico. For successional stage: P = pioneer, I = intermediate, L = late-successional; for conservation status: CR = critically endangered, EN = endangered, or VU = vulnerable.

Genus species	Successional stage	Conservation status
Aiouea inconspicua	L	
Allophylus camptostachys	P	
Amphitecna montana	L	EN
Andira galeottiana	L	VU
Annona reticulata	I	
Aphananthe monoica	L	
Boraginaceae	P	
Bursera simaruba	I	
Casearia corimbosa	I	
Casearia sylvestris	P	
Casimiroa tetrameria	I	
Cecropia obtusifolia	P	
Cedrela odorata	I	VU
Chamaedorea tepejilote	L	
Chrysophyllum mexicanum	I	
Clethra purpusii	I	EN
Clethra suaveolens	I	
Cojoba arborea	I	
Cordia alliodora	P	
Cornus disciflora	I	VU
Cornutia grandifolia	P	
Critonia morifolia	P	
Crossopetalum standleyi	L	
Cupania dentata	I	
Cyrtocymura scorpioides	I	
Dendropanax arboreus	I	
Dipholis minutiflora	I	VU
Diphysa americana	P	
Ehretia luxiana	P	
Erythrina chiapesana	P	
Eugenia capuli	I	
Eugenia capuliodes	I	
Ficus aurea	I	
Ficus sp.	P	
Gyrocarpus mocinoi	I	
Hauya elegans	I	VU
Heliocarpus donnellesmithii	P	
Inga oerstediana	P	
Inga punctata	P	
Inga vera	P	
Koanophyllon pittieri	P	VU
Liquidambar styraciflua	P	
Malvaviscus arboreus	P	
Montanoa leucantha	P	
Morus celtidifolia	I	
Myriocarpa longipes	I	
Nectandra sp.	I	
Nectandra glabrescens	I	
Ocotea botrantha	L	EN
Ocotea sinuata	L	VU
Ocotea sp.	L	
Oreopanax peltatus	P	
Oreopanax xalapensis	I	
Pinus maximinoi	P	
Piper yucatanense	L	
Prunus brachybotrya	L	VU
Prunus salicifolia	I	
Quercus peduncularis	I	
Quercus skinnerii	I	CR
Rhacoma parviflora	L	
Salacia megistophylla	I	
Sapindus saponaria	I	
Sapium lateriflorum	I	
Solanum umbellatum	I	
Spondias purpurea	P	
Stemmadenia donnell-smithii	I	
Styrax argenteus	L	EN
Symplocos breedlovei	I	EN
Tapirira macrophylla	I	
Tapirira mexicana	L	VU
Ternstroemia tepezapote	I	
Tonduzia longifolia	I	
Trema micrantha	P	
Trichilia havanensis	I	
Trichospermum mexicanum	P	

Table 1 (*Continued*)

Genus species	Successional stage	Conservation status
Trophis mexicana	L	
Turpinia paniculata	L	
Ulmus mexicana	L	EN
Viburnum hartwegii	I	
Ximenia americana	I	
Xylosma flexuosa	I	
Zanthoxylum kellermanii	I	
Unidentified 1		
Unidentified 2		
Unidentified 3		
Unidentified 4		

variables to their respective z-scores. After testing for correlations we found that tree structure variables (i.e., shade trees density and basal area) were weakly correlated (0.30); however, tree species composition variables (i.e., richness, Shannon diversity, and proportion of *Inga* spp. trees) were highly correlated (at least 0.80). Due to the high correlation among tree species composition variables, we decided to only include proportion of *Inga* spp. trees as an explanatory variable indicative of changes in tree species composition. This is a suitable indicator because it is most tightly linked to farmers' tree selection strategies in the study region (see Valencia et al., 2015) and other coffee growing areas in Latin America.

In order to understand how the relative importance and magnitude of effect of explanatory variables was mediated by the farm's land use history, we repeated the above described binomial logistic regressions separately for coffee sites established in forest ($n = 18$) and land that was once fallow ($n = 13$). In analyses for coffee farms established on fallow land, we assessed the importance of the age of the fallow land as a predictor for the proportion of CC and LS tree species.

We also compared the proportions of CC and LS trees in forests and in farms established on forest to determine the measure in which farms without a prior agricultural history resembled forests in their capacity to sustain CC and LS trees. We analyzed whether these differences were statistically significant by using a two-sample *t*-test. Statistical significance was determined by alpha = 0.05. Statistical analyses were carried out using the statistical program R; Shannon diversity was calculated using Vegan package (R Core Team, 2005).

3.3. Size distribution of trees

We investigated how management is associated with tree size distribution by comparing the DBH distribution of all trees, CC, and LS trees in agroforests and reference forests. We assigned each tree to a diameter class (bin width = 5 cm) and averaged the number of trees within each diameter class across sites. This analysis was repeated to contrast the size distribution of trees in farms and forests for all tree species combined and, separately, for LS and CC species. We analyzed whether differences were statistically significant for each diameter class by using a two-sample t-test.

4. Results

4.1. Coffee farm characteristics

From the 31 sampled coffee agroforests, 18 were established on forest and 13 on fallow. We sampled 86 tree species in total, among which 24 were pioneers, 41 intermediate succession, 17 LS, and 16CC. Among the CC tree species, 1 was a pioneer, 7 were intermediate succession, and 8 were LS species (Table 1). For a summary of characteristics of agroforests see Table 2. Diversity in forest sites was higher than in coffee farms (average Shannon diversity on farms = 1.52 and in forests = 2.43, p-value < 0.001); the same trend is true for tree richness (average species richness on farms = 7.7 and in forests = 18, p-value < 0.001). Shannon diversity was a positive predictor for the proportions of CC and LS trees in farms, also when disaggregated by previous land use (see Table S1).

4.2. Binomial logistic regression

Shade tree abundance and the proportion of *Inga* spp. trees were found to be negatively associated with the presence of CC trees; while basal area and forest as a previous land use were positively associated. Forest as a previous land use was the strongest positive driver, while proportion of *Inga* spp. trees was the strongest negative driver of CC trees. All explanatory variables for CC trees were found to be statistically significant (p-value < 0.05; see Fig. 1 for standardized parameter coefficients and 95% and 68% confidence intervals).

The most important positive driver of trees of LS was forest as previous land use; the most important negative driver was the proportion of *Inga* spp. trees, followed by shade tree abundance. All explanatory variables for LS trees are statistically significant (p-value < 0.05), except basal area (p-value > 0.05; see Fig. 1 for standardized parameter coefficients and 95% and 68% confidence intervals).

For farms established on lands that were once fallow, all variables were statistically significant (p-value < 0.05), except basal area as an explanatory variable for the proportion of LS trees ($p = 0.07$) and fallow age as explanatory variable for the proportion of CC trees ($p = 0.06$). For both the proportion of CC and LS trees, shade tree abundance and the proportion of *Inga* spp. trees were negative drivers, while basal area was a positive driver for the proportion of trees of CC. The magnitude of the effect of the proportion of *Inga* spp. trees as an explanatory variable was much larger among farms established on fallow than those established on forest. Fallow age was a positive predictor for the proportion of LS trees ($p = 0.02$). For coffee farms established in forests, the proportion of *Inga* spp. trees had statistically significant a negative impact on both the proportion of CC and LS trees; the other variables did not have statistically significant effects (see Fig. 1 for standardized parameter coefficients and 95% and 68% confidence intervals).

We found that the proportion of CC trees in forests (mean = 25.3%, range: 10–44%) is higher than in farms established on forest (mean = 10.7%, range: 0-33%; p-value < 0.01). The difference between the proportions of LS trees in forests (mean = 18.2% range

Table 2
Summary of characteristics of agroforest sites (n = 31; site area = 907.5 m^2).

Variable (units)	Mean (standard deviation)	Min. value	Max. value
Proportion of trees threatened by extinction (%)	9.74 (10.25)	0	33
Proportion of late-successional trees (%)	9.98 (11.67)	0	40
Elevation (m.a.s.l.)	1267 (84.1)	1119	1490
Tree species composition			
Richness (species per site)	7.74 (4.20)	1	18
Shannon Diversity	1.52 (0.659)	0	2.81
Proportion of Inga spp. trees (%)	49.3 (28.1)	0	100
Tree structure			
Shade tree density (stems/site)	20.0 (9.57)	7	46
Basal area (m^2 per site)	1.58 (0.6)	0.27	3.2
Land use legacies			
Previous land use (categorical variable: forest or fallow)	Forest, *n* = 18 Fallow, *n* = 13		
Age of fallow (yrs.; *n* = 13)	10.7 (6.2)	3	20

0–54%) and in farms established on forest (mean = 11.3%; range 0–27.8%) was not statistically significant (p-value > 0.05).

4.3. Tree size distribution

Comparison of size distributions of trees revealed that there is a higher average number of trees in forests than farms among trees between 5 and 20 cm (p-value < 0.001) and 25 and 30 cm (p-value < 0.05) DBH (Fig. 2). This trend also held true for trees of CC between 5 and 10 cm (p-value < 0.01), 10 and 15 cm (p-value < 0.05), 15 and 20 cm (p-value < 0.01), 30 and 35 cm DBH (p-value < 0.05), and 45 and 50 (p-value < 0.05) (Fig. 3). For LS trees, there was no statistically significant difference in the size distribution of trees in any diameter class (Fig. 3). On average, CC trees had a larger DBH than non-CC trees (34.5 vs. 27.2 cm, p-value = 0.01). However, the difference in DBH between LS and non-LS trees was not statistically significant (29.0 and 27.8 cm respectively, p = value > 0.05).

5. Discussion

5.1. Farmers' selection of *Inga* spp. trees

In this study, we showed that the management outcome with the strongest negative effect on CC and LS trees was the proportion of *Inga* trees in a farm. Farmers' marked preference for *Inga* spp.

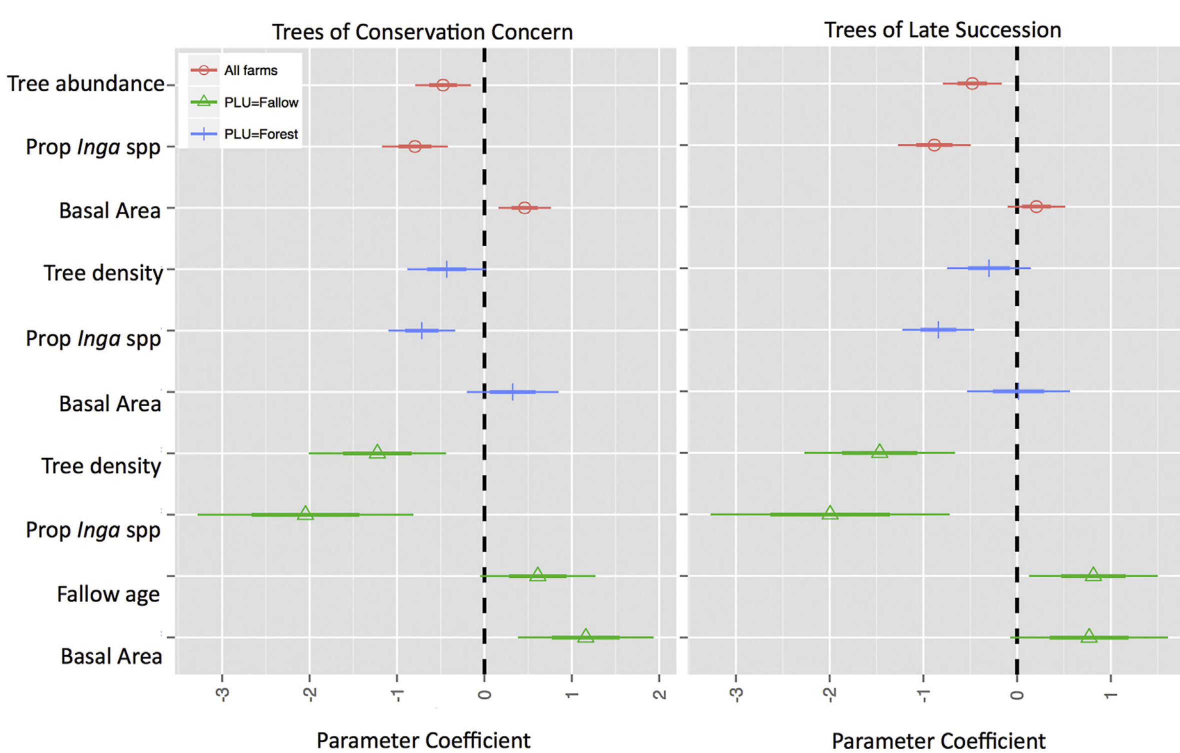

Fig. 1. Parameter estimate plots for variables considered in the models that predict proportions of trees of conservation concern (a) and late succession (b). Each plot shows regression on all farms aggregated (circles; n = 31), and then separately by previous land use (PLU) for forest (cross; n = 18) and fallow (triangle; n = 13). Outer horizontal lines correspond to 95% confidence interval (CI) and inner horizontal lines to 68% CI. If horizontal line crosses the zero line, variable is not statistically significant.

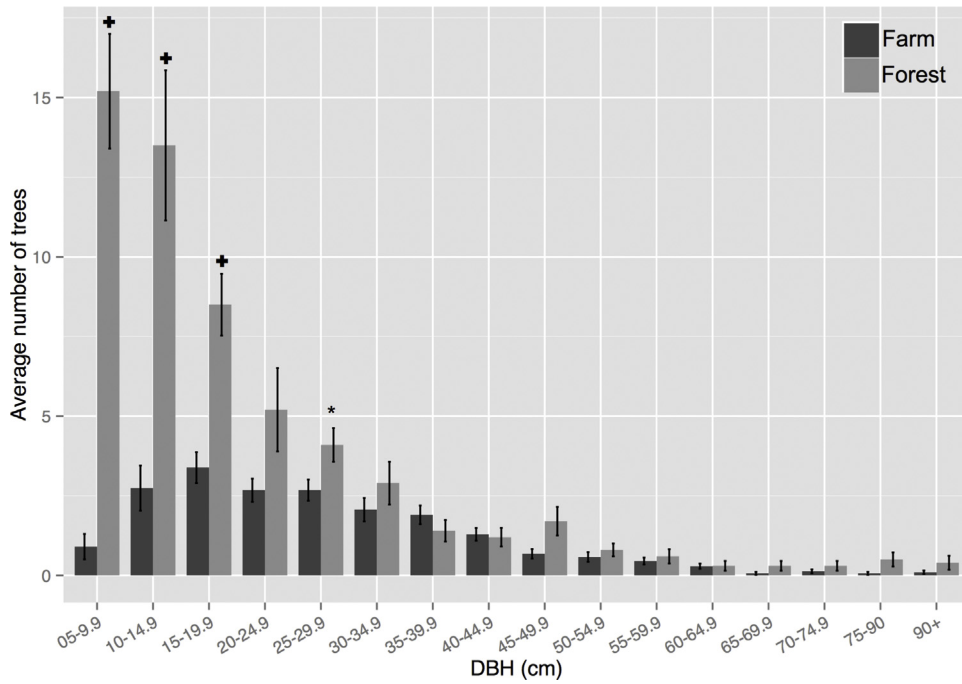

Fig. 2. Tree size distribution for trees in farms and forests. A cross denotes p-value < 0.001; an asterisk denotes p-value < 0.05. Bars represent standard error. DBH = diameter at breast height.

trees is observed not only in Mexico (Bandeira et al., 2005; Lo'pez-Go'mez et al., 2008; Soto-Pinto et al., 2007, 2002, 2001), but also throughout Central America (Albertin and Nair, 2004; Bentley et al., 2004; Me'ndez et al., 2010a; Me'ndez et al., 2010a), all the way to Venezuela (Bakermans et al., 2012), and in the cacao agroforests of the Brazilian Atlantic rainforest (Sambuichi et al., 2012; Souza et al., 2010). The use of *Inga* spp. is thought to date to pre-Columbian times when it was used for shade in cacao agroforestry systems (Gómez-Pompa et al., 1990). However, in Mexico, present day emphasis on its use dates to the 1970 and 1980s, when the Mexican Coffee Institute (INMECAFE), no longer in existence, encouraged the conversion of shade coffee polycultures

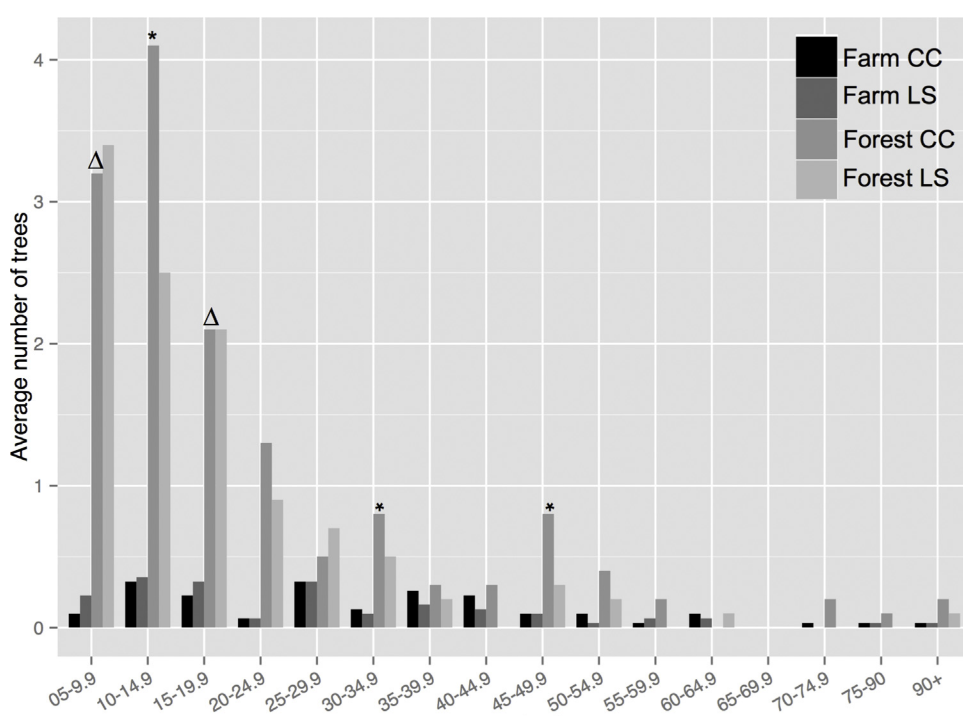

Fig. 3. Tree size distribution for conservation concern and late successional trees in farms and forests. A triangle Δ denotes p-value < 0.01; an asterisk denotes p-value < 0.05. CC = trees of conservation concern; LS = trees of late successional stage; DBH = diameter at breast height.

into monocultures (Nestel, 1995; Soto-Pinto et al., 2001). However, scientific studies have not been able to support any significant benefit of higher densities of *Inga* trees on coffee production (Romero-Alvarado et al., 2002; Peeters et al., 2003).

We also found that a major agricultural history (i.e., farms established on fallow) increases the magnitude of the negative effect of *Inga* tree density on the proportions of trees of CC and LS. This may be because the vegetation on fallow land during farm establishment was already characterized by lower LS and CC species since disturbances are expected to cause a shift to early successional species (Dietze and Clark, 2008). Furthermore, as farmers prepare fallow land for farm establishment, they may deliberately plant it with *Inga* trees or foster the regeneration of this genus thereby hindering the natural recruitment of LS trees.

Moreover, because high diversity systems harbor a higher proportion of CC and LS trees (See Table S1), if farmers relaxed their preference for *Inga* trees, coffee agroforestry systems may increase their potential to harbor CC and LS trees without compromising coffee productivity. We acknowledge that certain tree species, such as pine and oak trees, may have negative effects on coffee production due to allelopathic effects on coffee bushes and inappropriate shade levels (Beer, 1987; Soto-Pinto et al., 2000). It would be unreasonable to expect farmers to tolerate such trees in their farms. However, in the absence of scientific evidence to support that coffee agroforestry systems dominated by *Inga* trees (Romero-Alvarado et al., 2002; Peeters et al., 2003) or a few tree species result in higher coffee productivity (or other benefits such as crop disease regulation), recommendations to promote simplified systems should be discontinued. In a different study, we found that NGOs and government officials continue to promote *Inga* spp. trees in coffee farming communities (Valencia et al., 2015). More research is needed to clarify the advantages on coffee production of agroforests dominated by a few specific tree species over more diverse ones.

5.2. Farmers' selection and elimination of trees based on size

In natural systems, tree size distributions result from the demographic characteristics of individuals, such as tree growth, mortality, and recruitment as well as other processes, such as disturbance and climatic variability. Additionally, competitive thinning and disturbances also influence tree size distribution (Coomes and Allen, 2007). In managed systems, a stem's diameter is a structural characteristic that shapes how a farmer manages a particular tree. Saplings and seedlings, which are easy to manage, are periodically eliminated – whether selectively or not – during weeding practices. On the other hand, larger trees, which are more difficult to remove, are often retained in the system. These management practices are reflected in trends in size distribution in our results (Fig. 1), where the main differences between farms and forests were among smaller trees (5–20 cm DBH), while among larger trees (>30 cm in DBH) there were no differences. Changes in size distribution had more important repercussions for CC than LS trees. Among LS trees, the absence of differences among the smaller size classes may indicate that LS trees continue to regenerate in coffee agroforestry systems in spite of farm-level disturbances caused by management. On the other hand, current management practices may be undermining the establishment of CC trees.

Finally, an increase in shade tree density did not result in parallel increases in the proportion of LS and CC trees; it only resulted in increases in the proportion of intermediate succession trees (Appendix). These results should not be interpreted to imply that a reduction in tree density results in an increase in the proportion of CC and LS trees.

5.3. Land use legacies and the conservation potential of coffee agroforestry systems

An important finding of this study is that land use legacies mediated the impact of management on the potential of coffee agroforestry systems to conserve CC and LS trees. In farms established on fallow, the significance and magnitude of the negative impacts of management on LS and CC tree species were higher than in farms established on forest. Age of fallow was an important predictor for trees of late succession where a longer fallow period was predictive of a higher proportion of LS trees. Factors such as past land use intensity, time since abandonment, and a complex set of interactions between local site factors and landscape history affect species composition (Guariguata and Ostertag 2001; Chazdon, 2003; Chazdon et al., 2007) at the time of farm establishment with far reaching consequences on the system's potential to conserve LS and CC trees. Research in natural systems suggests that over time, after a strong disturbance, such as clear-cutting for crop cultivation or pastureland, the natural process of forest succession increases in its potential to conserve LS species (Chazdon et al., 2009; Muñiz-Castro et al., 2011). However, the potential of recovery of LS and CC species may not be reached to the same extent in agroforestry systems than in forests because in agroforests, farmers manage succession by favoring the regeneration and establishment of preferred trees such as *Inga* spp. and other pioneer trees (Soto-Pinto et al., 2001; Bandeira et al., 2005; Valencia et al., 2015).

From an ecological perspective, the establishment of coffee farms on fallow, rather than on forests, is preferable because it would leave forests intact and not contribute to new clearings or modifications of forests. However, adjustments in management practices should occur in order for coffee farms established on fallow to enable the process of succession to increase in its potential to conserve LS and CC species. An important goal is to promote farmers' tolerance of the establishment of tree species other than *Inga* spp. and other preferred tree species. Based on interviews about farmers' tree selection criteria and their sources of knowledge (reported in detail in Valencia et al., 2015), we found that strong preferences for *Inga* spp., and the ensuing management practices to increase their abundance, are in large part acquired in workshops and through interactions with external actors (e.g., local NGO representatives, agricultural extension agents). We found that conservation of CC and LS trees may understandably not be a priority for farmers, as their primary incentive is to optimize coffee production since their livelihoods largely depend on it. Currently farmers believe that *Inga* spp. contributed to such optimization. Because to date there is no research led, experimental evidence to support that *Inga* -dominated coffee farms support higher yields (Romero-Alvarado et al., 2002; Peeters et al., 2003), discontinuing the conversion of diverse coffee agroforests to *Inga* -dominated systems could be a fundamental management change. This change would benefit tree diversity on coffee farms regardless of their land use history and without necessarily reducing coffee yields. This management change would also be particularly beneficial for the recovery and maintenance of LS and CC trees in farms established on fallow.

Certification guidelines for eco-friendly coffee (e.g., Bird Friendly, Rainforest Alliance), agricultural extension agents, NGOs, and academic and research institutions may provide the incentives and information necessary to propel the proposed management changes. Incentives may come in the form of certification guidelines that explicitly discourage high abundances of *Inga* trees in favor of more diverse farms. Although often there is only indirect evidence of positive biodiversity effects delivered by certification, there is a strong potential to deliver conservation benefits (Dietsch, 2005; Tscharntke et al., 2014), which may vary widely across certification schemes (e.g., organic, Bird Friendly, etc.) (Mas and Dietsch, 2004; Philpott et al., 2007). Research has shown that price premiums associated with certification may also support the well-being of farmers and their communities (Rueda and Lambin, 2013). Although some studies have shown that livelihood improvements are limited (Bacon et al., 2008; Méndez et al., 2010; Weber, 2011). Moreover, agricultural extension agents, NGOs, academic and research institutions in partnership with farmers, their cooperatives and local institutions may discuss the role of *Inga* spp. and a diverse canopy in coffee cultivation in order to co-create and redesign coffee management strategies that are congruent with farmers' needs and knowledge, while also addressing conversation concerns.

6. Conclusion

The loss and fragmentation of MCFs has resulted in increased extinction vulnerability for up to 60% of its trees (Gonzalez-Espinosa et al., 2011). Coffee agroforestry systems, which overlap in range with MCFs, incorporate forest trees in their systems thereby opening the possibility of serving as a refuge to vulnerable trees in MCFs. In this study, we showed that management strategies, mediated by land use legacies, resulted in coffee agroforests with varying habitat potentials for the conservation of trees of CC and LS. We suggest that the potential to safeguard these vulnerable tree species hinges primarily on the adoption of management practices that are more tolerant of tree diversity on farms. Based on the DBH distribution of trees, there is no reason to believe that CC and LS tree species are not recruiting in farms, either because there are still seeds in the soil bed, or because seeds are dispersing from trees in farms or nearby forest patches. However, there is a need for more research to assess how management and ecological factors affect forest tree regeneration in coffee agroforestry systems in order to determine the long-term potential of this system to conserve tree diversity, in particular LS and CC trees native to MCFs. Because this study area is representative of other coffee regions in Mexico and Central America, and possibly beyond this geographic range, these findings may inform conservation strategies and policies beyond our study area to find synergies between MCF conservation and coffee production in agroforestry systems.

In coffee agroforestry systems, land-use history and farmers' management practices, in particular their tendency to plant *Inga* spp., adversely affect the potential of these systems to serve as habitat suitable for the conservation of CC and LS tree species. Over time, however, if alternative practices are adopted, shade-grown, smallholder agroforestry coffee systems can serve as safe havens for the native trees. Incentives to foster farmers' tolerance for a wider range of recruiting and adult tree species may magnify the potential of coffee agroforestry systems to serve as a haven for CC and LS trees species native not just to La Sepultura Biosphere Reserve in Chiapas, Mexico, but to MCFs wherever coffee agroforestry systems co-occur.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2015.12.004.

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