

The role of rustic coffee plantations in the conservation of wild tree diversity in the Chinantec region of Mexico

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Abstract. Rustic coffee plantations are characterised by the use of numerous wild and cultivated tree species for providing shade to the coffee shrubs. This paper analyses the role of these plantations in wild tree conservation through the examination of their patterns of floristic variation in southern Mexico. The studied plantations included a total of 45 plant species, most of which were wild tree species, including both mature forest and pioneer taxa. An extrapolation of the species accumulation curve among stands indicated that the whole system, composed of more than 100 coffee plantations, may harbour as many as 34 species of wild trees. The floristic structure of rustic coffee plantations was highly variable. This variation is a result of a combination of factors such as human management, original stand cover and the asynchrony in development stage of different plantations. This promotes a large β -diversity in the system. Thus, although a single plantation may have a limited potential to preserve wild tree species, it is the whole ensemble of floristically heterogeneous plantations which renders this agroforestry system valuable for plant diversity conservation, particularly in a region where native forest vegetation has almost disappeared.

Introduction

Rustic coffee plantations of the indigenous areas of Mexico are an example of complex, highly diverse and multipurpose agroforestry systems, as defined by Nair (1989). In these systems, the understorey is occupied mainly by coffee, while shade is provided by many useful wild and cultivated trees. The result is a complex 'coffee garden' (Moguel and Toledo 1999), that provides cash income, in addition to medicines, food, fuel and other plant products for the household economy (Moguel and Toledo 1999; Soto-Pinto et al. 2001). According to Moguel and Toledo (1999), by 1991 a total of 850,000 ha were devoted to coffee cultivation in Mexico, and at least 70% of the producers worked holdings less than 2 ha in size. During the 1970s and the 1980s, the originally diversified shade-tree component was eliminated or substituted by a few species of *Inga* (Mimosaceae) in one third of the total coffee producing area of Mexico

(Nestel 1995). Most of this area corresponds to large holdings whose owners have incorporated the use of agrochemicals and of sun-grown varieties. In contrast, diversified shade systems with limited or no use of agrochemicals have persisted in the majority of the small-scale holdings of the indigenous regions (Nestel 1995). This is the case for Oaxaca, one of the three most important coffee-producing states of Mexico, the other two being Chiapas and Veracruz.

Coffee growing areas in Mexico are biologically important, as most of them are located in the transitional zone between the Nearctic and the Neotropical floristic realms (Moguel and Toledo 1999). Furthermore, the forests of these areas are recognised by their large species richness (Rzedowski 1991). The landscape in these regions is generally much degraded, thus rustic coffee plantations play an important role in biodiversity conservation as they provide suitable habitats for many species (Hansen et al. 1991; Perfecto et al. 1996; Rice and Ward 1996), as has been documented for arthropods (Perfecto et al. 1996, 1997), birds (Aguilar-Ortiz 1982; Greenberg et al. 1997), small mammals (Gallina et al. 1996), vertebrates in general (Rendón-Rojas 1994), and orchids and other cloud forest epiphytes (Nir 1988; Williams-Linera et al. 1995). In the highlands of Chiapas, for example, Soto-Pinto et al. (2001) reported that 72 out of 77 plant species growing in rustic coffee plantations are wild plants typical both from the cloud forest and the tropical rain forest.

Despite its economic and biological importance, the floristic structure of coffee agroforestry systems in indigenous regions, along with its spatial and temporal variation, remains largely neglected, and except for one study (Soto-Pinto et al. 2001), plant diversity in coffee plantations has not been systematically documented. This information is required to assess their potential for plant diversity conservation. This would allow examination of questions such as: how many and which wild plant species may grow in the rustic coffee plantations? Are all of them equally important for biodiversity conservation? Are coffee plantations floristically variable? If so, what is the implication of such variability for plant diversity conservation in the coffee growing areas? Based on the examination of the floristic composition of rustic coffee plantations of a Chinantec indigenous village in Oaxaca State, this study addresses the above questions.

Study area

This study was conducted in the village of Rancho Grande, San Juan Bautista Valle Nacional Municipality (Oaxaca State, Mexico; Figure 1). This is a mountainous region with a warm and humid climate. Elevation ranges from 660 to 1150 m a.s.l. The mean annual temperature is 22 °C and mean annual precipitation is about 4000 mm (Rzedowski and Palacios-Chávez 1977). This is a transitional area between the tropical lowland forest and premontane forest in the system of Holdridge et al. (1971). Although the local landscape is highly fragmented, this region is considered a priority conservation area by the

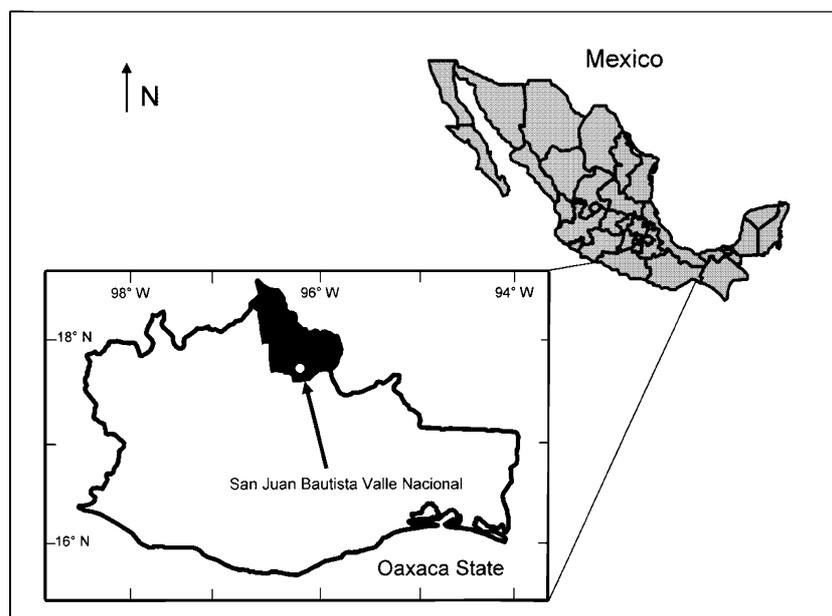


Figure 1. Location map of study area showing the Oaxaca State and Valle Nacional municipality.

Table 1. Land use and cover types at Rancho Grande, Oaxaca, Mexico.

| Land use and land cover categories | MP/p | MS (ha) | Total surface | |
|------------------------------------|------|------------|---------------|------|
| | | | (ha) | (%) |
| Rustic coffee plantations | 3 | 2.1 | 229.77 | 56.9 |
| Corn fields (milpas) | – | 0.3 | 11.30 | 2.8 |
| Early and late vegetation growth | 0.8 | 2.3 | 102.54 | 25.4 |
| Protected areas of mature forest* | – | – | 60.00 | 14.8 |

MP/p – mean number of parcels per producer; MS – mean surface.

* In this category are included the communal reserve and other areas protected because of their high risk.

National Commission for Biodiversity Conservation of Mexico (Arriaga et al. 2000).

Rancho Grande has 181 inhabitants, all Chinantec speakers, belonging to 38 households (INEGI 1991), most of which are involved in coffee production. This activity is their major source of cash income. The total coffee growing area is about 230 ha (Table 1), with each household maintaining on average three plantations. Most coffee plantations are located near the village and readily accessible by local roads and paths. Besides growing coffee, corn, beans and squash are cultivated for subsistence through slash and burn procedures. Some households cultivate vanilla (*Vanilla* spp.) intercropped with coffee shrubs, and

ixtle (*Aechmea magdalenae*) under the canopy of secondary growth. These two crops are grown for commercial purposes. Another relevant activity is the extraction of timber species such as *Cedrela odorata* and *Cordia alliodora*. These species are managed in the rustic coffee systems. Cattle raising was an important economic activity in the 1980s, but it has since been almost replaced by coffee cultivation. The combination of these land use forms by the Chinantec of Rancho Grande has produced a heterogeneous landscape composed of small patches of corn fields, coffee plantations, home gardens, fallow fields, secondary and mature forests.

Coffee plantations in Rancho Grande are dynamic systems with an effective life of around 20–40 years. Three stages may be distinguished during a plantation life cycle: establishment, development, and decline. Initially, the plantation is established in a mature or secondary forest patch, although occasionally, an abandoned former coffee plantation may be used to establish the new one. Before introducing the coffee plants, most shrubs, small trees and herbs are eliminated; in contrast, the majority of trees and useful plants, such as *C. alliodora*, *Inga latibracteata*, and *Chamaedorea tepejilote*, are spared. During the development stage of the plantation, which lasts up to 20 years, farmers continue to eliminate wild shade trees, and gradually replace them by cultivated useful species. Although many incoming pioneer species are constantly eliminated from the plantation, some are allowed to establish or are even promoted. The two most notorious examples of wild trees managed in coffee plantations are *I. latibracteata* and *C. alliodora*. The declining stage is characterised by a significant decrease in coffee production, although coffee may still be harvested for a few more years. Once harvesting is no longer profitable and depending on market value for coffee, cultivators may either abandon the plantation, renew the plantation by replacing old coffee shrubs with new ones and eliminating some shade trees, or convert the plantation into a corn field, grassland or fruit tree plantation.

Methods

Data collection

A census of all coffee plantations in use at Rancho Grande was carried out. They were numbered for selecting 22 of them at random in order to assess their species composition and the relative abundances of shrub and tree species. The selected sample included a wide range of elevations, sizes and ages of development (Table 2). Each coffee plantation was sampled by means of parallel transects following the method used by Gentry (1982), as modified by Romero-Romero et al. (2000) for the study of small patches of secondary montane forests. A total of ten 25 × 4 m transects were established in each coffee plantation, with a minimum distance of 5 m between them. In addition to the 22 coffee plantations, one patch of natural vegetation, representing a

Table 2. Characteristics of the rustic coffee systems sampled at Rancho Grande.

| Coffee plantation | Elevation (m a.s.l.) | Area (ha) | Age (years) | Previous land cover ^a | No. of individuals per 0.1 ha | Number of species per 0.1 ha |
|-------------------|----------------------|-----------|-------------|----------------------------------|-------------------------------|------------------------------|
| 1 | 681 | 2 | 22 | Early | 61 | 15 |
| 2 | 660 | 1.75 | 16 | Early | 13 | 4 |
| 3 | 703 | 3 | 30 | Late | 55 | 9 |
| 4 | 706 | 2 | 25 | Late | 42 | 19 |
| 5 | 668 | 2 | 15 | Early | 15 | 4 |
| 6 | 724 | 1.5 | 17 | Early | 40 | 13 |
| 7 | 726 | 5 | 34 | Late | 50 | 6 |
| 8 | 740 | 3 | 9 | Early | 49 | 16 |
| 9 | 681 | 1.7 | 20 | Early | 24 | 4 |
| 10 | 766 | 5 | 7 | Early | 27 | 10 |
| 11 | 750 | 1.7 | 35 | Late | 36 | 10 |
| 12 | 843 | 1.25 | 20 | Late | 52 | 9 |
| 13 | 875 | 1 | 4 | Early | 52 | 9 |
| 14 | 900 | 2 | 19 | Late | 58 | 14 |
| 15 | 906 | 1 | 20 | Late | 23 | 6 |
| 16 | 901 | 1 | 8 | Late | 31 | 11 |
| 17 | 905 | 3 | 10 | Early | 24 | 5 |
| 18 | 917 | 1 | 20 | Early | 28 | 5 |
| 19 | 928 | 2 | 25 | Late | 57 | 11 |
| 20 | 922 | 2 | 25 | Late | 32 | 9 |
| 21 | 922 | 1.5 | 10 | Early | 31 | 11 |
| 22 | 943 | 1 | 18 | Early | 15 | 5 |

^aEarly – early secondary growth; Late – late secondary growth.

100-year-old forest, was also sampled with a 0.1 ha plot (40 × 25 m) located at its center.

All trees with a diameter at breast height ≥ 2.5 cm, along with useful shrubs and herbs indicated by the plantation owner were recorded. Ferns, epiphytes and cacti were excluded. Botanical specimens were collected for each species encountered. They were taxonomically identified using local checklists (Martin 1996; Romero-Romero et al. 2000) and reference herbarium material deposited at the National Herbarium of the Universidad Nacional Autónoma de México (MEXU); vouchers under Fábio Bandeira's collection number were also deposited at MEXU.

The owners of the 22 sampled coffee plantations were interviewed in order to obtain land use history and socio-economic information for each one, as well as the use and management of the plant species found in the plantations.

Data analysis

The sampled coffee plantations were subjected to a correspondence analysis (CA) (Reyment and Jöreskoj 1996; Rohlf 1997) in order to assess their floristic variability. Two ordinations were performed, one using binary

(presence–absence) data, and the other based on the relative abundances of wild tree species present in at least two plantations. We then assessed the effects of altitude, previous land cover, parcel age, householder's characteristics, and their interactions on the plantations' species richness, and on their floristic structure, the latter expressed as the plantations' CA scores based on the relative abundances matrix. We used a log-linear regression to analyse the relationship between the above listed factors and species richness (McCullagh and Nelder 1983; Crawley 1993), and an ANOVA for the analysis of floristic structure (Sokal and Rohlf 1995). The GLIM 4.0 software was used for these analyses, and the models were simplified following Crawley's (1993) recommendations. Normality was assessed by means of a Shapiro–Wilk test in SPSS 9.0. The proportions of wild and non-native cultivated species among coffee plantations were compared with a G heterogeneity test (Sokal and Rohlf 1995).

The contribution of within and between-plantation variation to total wild tree and shrub diversity conserved in coffee plantations was evaluated by calculating Whittaker's α and β coefficients (Magurran 1988; Colwell and Coddington 1995). A high β -diversity means that individual coffee plantations host different species, so that the larger the number of plantations, the more species would be protected. To estimate the total number of wild species that the whole system of 110 coffee plantations of Rancho Grande may protect, a mean cumulative species-richness curve for different numbers of coffee plantations was obtained by generating random combinations of the 22 sampled plantations. A two-parameter hyperbole was adjusted to these data by applying the maximum likelihood method to the Eadie–Hofstee transformation (Colwell and Coddington 1995).

Results

Structure of coffee plantations

In general coffee plantations of Rancho Grande are structurally complex. In addition to coffee, they include many other plant species that provide food, medicines, timber, firewood and other products for the household economy and for the local market (Table 3). They include both introduced, cultivated, and wild species under different degrees of management. Cultivated species are either native or introduced from the Old World and from other Neotropical regions such as orange (*Citrus sinensis*), cassava (*Manihot esculenta*), banana (*Musa acuminata* \times *balbisiana*) and avocado (*Persea americana*). Useful plants may also be encouraged in order to maximise their availability. In general, herbs are commonly eliminated from the system as they are thought to compete with coffee. Only culturally important annuals, such as *Thalia* sp. and *Calathea lutea*, are tolerated, or even promoted, in coffee plantations. Pioneer species such as *C. alliodora* or *Inga* sp. are an important element of the wild flora of coffee plantations.

Table 3. Botanical, ethnobotanical and ecological information for the species occurring in rustic coffee plantations at Rancho Grande.

| Family | Species | Growth form | Cultural status | Uses | Destiny | RF |
|---------------|--|-------------|-----------------|------------|---------|------|
| Acanthaceae | Unidentified | t | TP | 1, 3 | I | 0.14 |
| Actinidiaceae | <i>Saurauia scabrida</i> Hemsl. | t | TM | 4,7 | I | 0.09 |
| Anacardiaceae | <i>Mosquitoxylum jamaicense</i> Krug & Urb. | t | TP | 1, 3 | I | 0.05 |
| Araceae | <i>Chamaedorea tepejilote</i> Liebm. ex Mart. | p | PM | 4 | III | 0.41 |
| Asteraceae | Unidentified | s | TP | 3 | I | 0.09 |
| Boraginaceae | <i>Cordia alliodora</i> (Ruiz & Pav.) Oken | t | TP | 1, 5 | III | 0.77 |
| Bromeliaceae | <i>Ananas comosus</i> (L.) Merr. | h | CI | 3, 4 | I | 0.05 |
| Caricaceae | <i>Carica papaya</i> L. | t | TP | - | I | 0.05 |
| Cecropiaceae | <i>Cecropia obtusifolia</i> Bertol. | t | TP | 1 | I | 0.14 |
| Euphorbiaceae | <i>Croton draco</i> Schltld. | t | TP | 1, 2 | I | 0.09 |
| Euphorbiaceae | <i>Manihot esculenta</i> Crantz. | h | CI | 4 | I | 0.09 |
| Fabaceae | <i>Erythrina folkersii</i> Krukoff & Moldenke | t | CN | 7 | I | 0.09 |
| Fabaceae | <i>Lonchocarpus</i> sp. | t | TM | 1, 3, 6, 7 | I | 0.18 |
| Lauraceae | sp. 1 (Unidentified) | t | TM | 1, 5, 6 | III | 0.14 |
| Lauraceae | sp. 2 (Unidentified) | t | TM | 1, 5, 6 | III | 0.05 |
| Lauraceae | <i>Licaria capitata</i> (Schltld. & Cham.) Kosterm. | t | TM | 5, 1, 6 | III | 0.05 |
| Lauraceae | <i>Persea americana</i> Mill. | t | CN | 1, 4 | I | 0.18 |
| Lauraceae | <i>Persea schiedeana</i> Nees | t | PM | 1,4 | III | 0.23 |
| Marantaceae | <i>Calathea lutea</i> (Aubl.) Schult. | h | PP | 7 | I | 0.05 |
| Marantaceae | <i>Calathea</i> sp. | h | PPM | 4 | I | 0.45 |
| Marantaceae | <i>Thalia</i> sp. | h | PP | 4, 7 | I | 0.36 |
| Meliaceae | <i>Cedrela odorata</i> L. | t | PP | 1, 5 | III | 0.41 |
| Meliaceae | <i>Swietenia</i> sp. | t | CN | 1, 5 | II | 0.14 |
| Mimosaceae | <i>Inga jinicuil</i> Schltld. & Cham. ex G. Don | t | CN | 1, 3, 4, | I | 0.09 |
| Mimosaceae | <i>Inga latibracteata</i> Harms | t | PP | 1, 3 | I | 1 |
| Mimosaceae | <i>Inga</i> sp. | t | PP | 1, 3 | I | 0.32 |
| Mimosaceae | <i>Leucaena diversifolia</i> (Schltld.) Benth. subs. <i>stenocarpa</i> (Urban) S. Zárate | t | TP | 1, 3 | I | 0.27 |
| Moraceae | <i>Ficus</i> sp. | t | TM | 1, 3 | I | 0.09 |

Table 3. (Continued)

| Family | Species | Growth form | Cultural status | Uses | Destiny | RF |
|---------------|---|-------------|-----------------|------------|---------|------|
| Musaceae | <i>Musa acuminata</i> × <i>balbisiana</i> | h | CI | 3, 7 | III | 0.09 |
| Myrtaceae | <i>Psidium guajava</i> L. | t | TP | 1, 3 | I | 0.18 |
| Poaceae | <i>Saccharum officinarum</i> L. | h | CI | 3, 4 | I | 0.09 |
| Rutaceae | <i>Citrus aurantifolia</i> (Christm.) Swingle | t | CI | 3, 4 | I | 0.09 |
| Rutaceae | <i>Citrus reticulata</i> Blanco | t | CI | 3, 4 | I | 0.23 |
| Rutaceae | <i>Citrus sinensis</i> (L.) Osbeck | t | CI | 3 | I | 0.45 |
| Sapindaceae | <i>Cupania dentata</i> DC. | t | TMP | 1, 3 | I | 0.18 |
| Sapotaceae | <i>Chrysophyllum mexicanum</i> Brandegee ex Standl. | t | TMP | 7, 3 | I | 0.09 |
| Sapotaceae | <i>Pouteria sapota</i> (Jacq.) H.E. Moore & Stearn | t | PM | 1, 3, 4, 7 | III | 0.27 |
| Solanaceae | <i>Cestrum dumetorum</i> Schltdl. | s | TP | 1, 4 | I | 0.23 |
| Sterculiaceae | <i>Theobroma cacao</i> L. | t | CN | 3, 4 | I | 0.05 |
| Tiliaceae | <i>Heliocarpus appendiculatus</i> Turcz. | t | TP | 1, 7 | I | 0.18 |
| Tiliaceae | <i>Heliocarpus donnellsmithii</i> Rose | t | TP | 1, 7 | I | 0.27 |
| Tiliaceae | <i>Trichospermum mexicanum</i> (DC.) Baill. | t | TP | 1, 3 | I | 0.05 |
| Ulmaceae | <i>Trema micrantha</i> (L.) Blume | t | TP | 7 | I | 0.27 |
| Verbenaceae | <i>Lippia myriocephala</i> Schltdl. & Cham. | t | TP | 1, 3 | I | 0.41 |
| Unidentified | | t | TM | 5, 1, 3 | I | 0.14 |

Growth form: t = tree; p = palm; s = shrub; h = herb. Cultural status: TP = tolerated pioneer; TM = tolerated mature forest; PM = promoted mature forest; CI = cultivated introduced; CN = cultivated native; PP = promoted pioneer. Uses: 1 = coffee shade; 2 = medicinal; 3 = firewood; 4 = food; 5 = timber; 6 = construction; 7 = others. Destiny: I = household consumption only; II = trade in local and regional markets; III = both. RF = relative frequency.

A total of 45 species were found in the sampled plantations. More than two thirds of them were wild species, which account for 77% of all trees recorded in the parcels. Several of them are endemic to Mexico and at least one species (*I. latibracteata*) is endemic to the studied region. Mean plant density for all life forms (trees, shrubs, palms and useful herbs) in the coffee systems was 370.5 stems/ha (range: 130–610 stems/ha). For trees alone, mean density was 275.9 stems/ha (range: 110–510 stems/ha).

Floristic structure heterogeneity

Excluding coffee, epiphytes and those herbs periodically removed by cultivators, plantations have an average of nine species (range: 4–19, Table 2) in the sampled area of 0.1 ha. Only two species (4.4%) occurred in most plantations: *I. latibracteata* (22 plantations), and *C. alliodora* (17 plantations). In contrast, 37 species (82.2%), mostly wild trees, were found in less than one third of the plantations (Figure 2).

The CA based on the binary data matrix showed no clear pattern of floristic variation, suggesting that the shade-tree component of coffee plantations is highly heterogeneous. In contrast, the CA based on the relative abundances matrix revealed a distinct pattern. Two groups of coffee systems were distinguished along the first axis, each comprising 11 coffee plantations (Figure 3). Plantations with low CA scores have a higher relative abundance of *C. alliodora* while those having large scores have higher relative abundance of *I. latibracteata*. The other 25 species present in the parcels had low

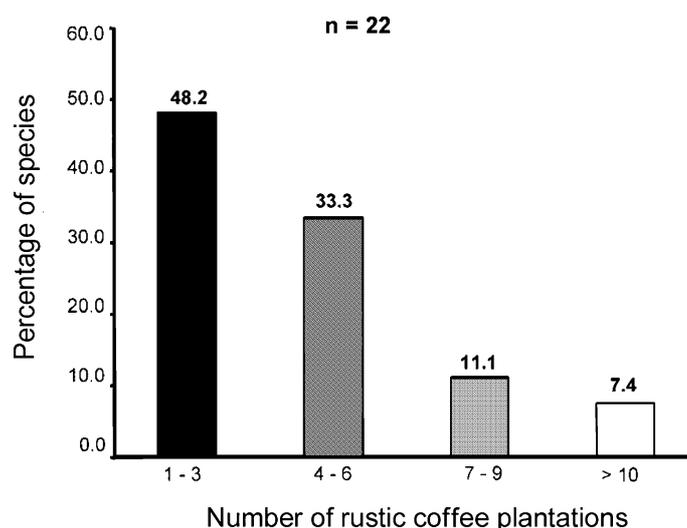


Figure 2. Relative frequency (%) of species occurring in 22 rustic coffee plantations.

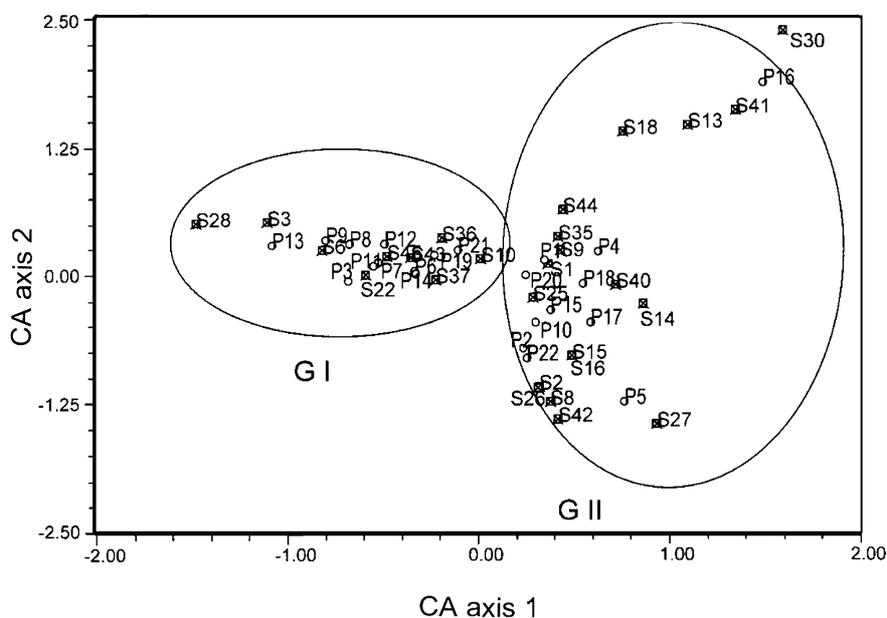


Figure 3. CA ordination of 22 coffee plantations (P) and species (S) based on a relative abundance matrix for wild tree species.

abundances and did not contribute significantly to the distinction between the two groups.

The regression analyses showed that variation in species richness and floristic structure (the latter defined as the relative abundance-based CA score for each plantation) is neither related to elevation nor to technological and socio-economic differences between coffee producers. The floristic structure of shade trees was only significantly influenced by the interaction between plantation age and the existing forest cover type before the establishment of the plantation ($F=6.224$, $p=0.022$). CA scores for plantations established in late secondary-growth decreased significantly with plantation age, whilst those of plantations established in early secondary-growth showed no significant change. The mean floristic structure of both kinds of plantations converges around the twentieth year (Figure 4). Residuals were normal (Shapiro–Wilk = 0.948, $p=0.375$).

The role of coffee plantations in biodiversity conservation

Rustic coffee plantations harbour a considerable number of wild tree species. The plantations include significantly more wild (27) than cultivated (12) plant species ($G_{\text{Goodness of fit}}=214.09$, $df=2$, $p < 0.0001$), but there were no differences in the proportions of wild and cultivated species among plantations ($G_{\text{Heterogeneity}}=40.12$, $df=42$, $p=0.553$). Thirteen wild tree species grow

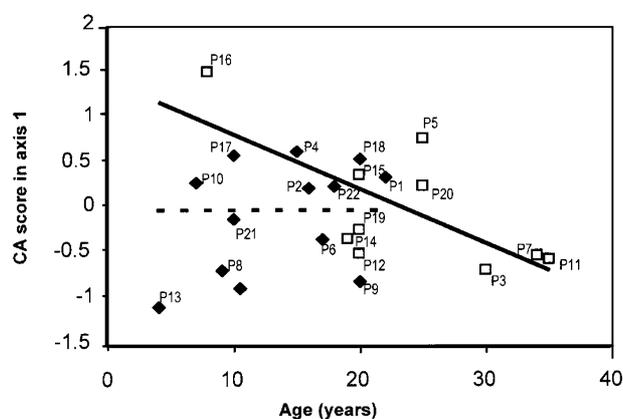


Figure 4. Effect of age on the floristic structure of plantations established on early (—◆—) and late (---□---) secondary growth. Y-axis values are the score for each coffee plantation in the first CA axis based on the relative abundance matrix for wild species.

exclusively in mature forest; the remaining are pioneer plants frequent in secondary vegetation, albeit they may also occur in mature stands.

Variability in pioneer species composition is lower, as their overall frequency is higher throughout all plantations. Thus, α -diversity is higher for pioneer species (3.5 species/plantation) and lower for mature forest trees (2.2 species). The opposite was found for β -diversity (3.3 and 4.9, respectively). The number of species predicted for the whole study area by the two-parameter hyperbole is very similar for both groups (18 pioneers; 16 mature forest species). Pioneer species richness grows more rapidly than that of mature forest species with increasing number of plantations (Figure 5), implying that more area would be required to maintain the same number of mature forest species. The potential number of wild tree species (34) in all 110 coffee plantations of Rancho Grande is virtually identical to the number recorded in the 0.1 ha plot of mature forest sampled in this study (35 species; Table 4). However, this similarity contrasts with the fact that the number of species shared by the two systems is very small, as only six species occurred in both of them: *Saurauia scabrida*, *Lonchocarpus* sp., *Licaria capitata*, *Persea schiedeana*, *Chrysophyllum mexicanum* and *Heliocarpus* sp.

Discussion

A comparison of our results with those derived from a study conducted in a coffee growing area in northern Chiapas, Mexico (Soto-Pinto et al. 2001) showed that the general patterns of floristic structure observed at Rancho Grande may be generalised, despite some notable differences. More than two thirds of the plant species and most trees at Rancho Grande's coffee plantations were wild

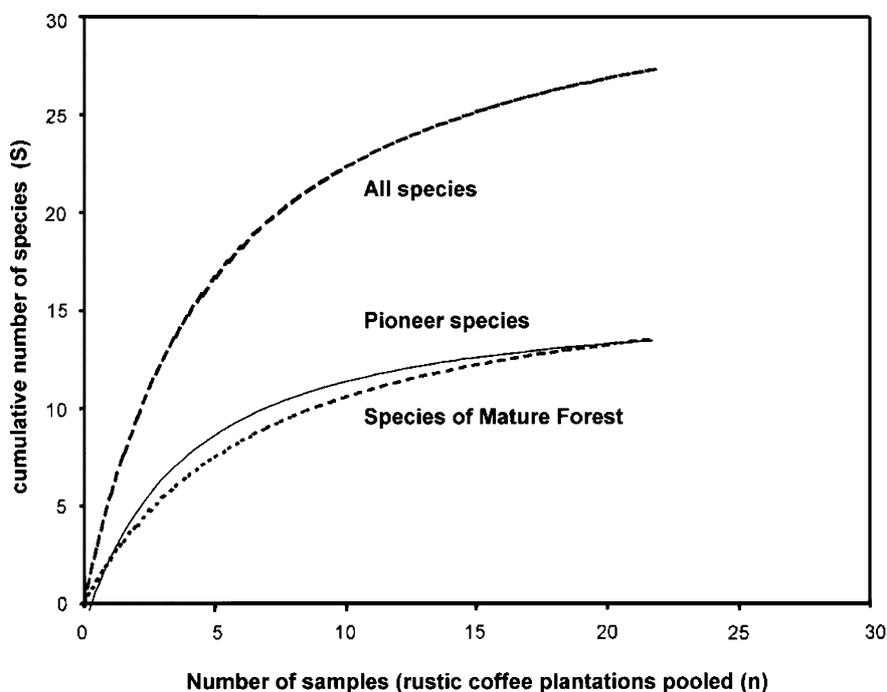


Figure 5. Species accumulation curve in rustic coffee plantations at Rancho Grande.

plants, while in Chiapas 90% of the 77 recorded woody species were native. The average tree density found in this study (275.9 trees/ha; range: 110–510) was somewhat lower than in Chiapas (371.4 trees/ha; range 100–800). Contrastingly, frequency distributions of species encountered at both locations were very similar, with less than 10% of the species being common to most plantations, and over 80% of the species occurring in only one or few plantations. This pattern is confirmed by the large heterogeneity revealed by the CA.

The floristic structure of plantations appears to be affected by cultural factors. This is well illustrated by the two most common trees in plantations, namely *I. latibracteata* and *C. alliodora*. The former has been an element of utmost importance in Mesoamerican agroforestry systems since pre-Hispanic times, when it served as a tutor tree in cocoa (*Theobroma cacao*) plantations (Gómez-Pompa 1987). At present, most indigenous coffee growers recognise *Inga* as a sort of archetypical shade tree, and promote its establishment by means of seed. In turn, *C. alliodora* is a valuable timber tree, thus it is tolerated in coffee plantations since it is viewed as a savings account that may be used to cope with economic crises or emergencies such as sickness or debt. In addition to management, ecological and historical factors determine the abundance of these trees. Both are heliophytes that colonise plantations when other trees are felled. They also invade disturbed areas such as the secondary growth where coffee plantations are established, and remain in the system from then on.

Table 4. Species list for the 0.1 ha plot of mature forest at Rancho Grande.

| Family | Species | Relative abundance |
|-----------------|--|--------------------|
| Actinidiaceae | <i>Saurauia scabrida</i> Hemsl. | 0.03 |
| Annonaceae | <i>Guatteria galeottiana</i> Baill. | 0.03 |
| Arecaceae | <i>Chamaedorea pinnatifrons</i> (Jacq.) Oerst. | 0.01 |
| Asteraceae | <i>Eupatorium araliaefolium</i> Less. | 0.01 |
| Bignoniaceae | <i>Amphitecna macrophylla</i> (Seem.) Miers ex Baill. | 0.12 |
| Clusiaceae | <i>Garcinia intermedia</i> (Pittier) Hammel | 0.02 |
| Euphorbiaceae | <i>Cnidocolus multilobus</i> (Pax) I.M. Johnst. | 0.01 |
| Fabaceae | <i>Lonchocarpus</i> sp. | 0.04 |
| Flacourtiaceae | <i>Casearia corymbosa</i> Kunth | 0.02 |
| Flacourtiaceae | Unidentified sp. 1 | 0.13 |
| Flacourtiaceae | Unidentified sp. 2 | 0.01 |
| Lauraceae | <i>Beilschmiedia</i> aff. <i>mexicana</i> (Mez) Kosterm. | 0.01 |
| Lauraceae | <i>Licaria capitata</i> (Schltdl. & Cham.) Kosterm. | 0.07 |
| Lauraceae | <i>Nectandra longicaudata</i> (Lundell) C.K. Allen | 0.13 |
| Lauraceae | <i>Persea schiedeana</i> Ness | 0.04 |
| Malpighiaceae | <i>Bunchosia lanceolata</i> Turcz. | 0.01 |
| Melastomataceae | <i>Miconia argentea</i> (Sw.) DC. | 0.02 |
| Meliaceae | <i>Guarea glabra</i> Vahl | 0.03 |
| Monimiaceae | <i>Mollinedia oaxacana</i> Lorence | 0.01 |
| Moraceae | <i>Ficus</i> sp. | 0.01 |
| Piperaceae | <i>Piper marginatum</i> Jacq. | 0.01 |
| Rubiaceae | <i>Faramea schultesii</i> Standl. | 0.01 |
| Rubiaceae | <i>Hamelia calycosa</i> Donn. Sm. | 0.01 |
| Rubiaceae | <i>Hoffmania carlsoniae</i> Standl. & L. Williams | 0.01 |
| Rubiaceae | <i>Hoffmania excelsa</i> (Kunth) K. Schum | 0.01 |
| Rubiaceae | <i>Hoffmania nicotanaefolia</i> (M. Martens & Galeotti) L.O. Williams | 0.02 |
| Rubiaceae | <i>Psychotria costivenia</i> Griseb. | 0.01 |
| Rubiaceae | <i>Psychotria panamensis</i> Standl. | 0.04 |
| Rubiaceae | <i>Sommeria</i> sp. | 0.10 |
| Sapindaceae | <i>Cupania</i> sp. | 0.01 |
| Sapotaceae | <i>Chrysophyllum mexicanum</i> Brandegee ex Standl. | 0.02 |
| Tiliaceae | <i>Heliocarpus</i> sp. | 0.01 |
| Turneraceae | <i>Erblichia odorata</i> Seem. | 0.01 |
| Urticaceae | <i>Myriocarpa longipes</i> Liebm. | 0.01 |
| Verbenaceae | <i>Callicarpa</i> sp. | 0.01 |

The conservation potential of coffee plantations

According to our calculations, the 34 tree species potentially harboured in the whole coffee-growing area of Rancho Grande represent a richness similar to that found in 0.1 ha of primary vegetation. Nonetheless, the fact that more than half of the species in plantations are pioneers would lead to think that the contribution of coffee plantations to the conservation of wild trees, mainly those of the mature forest, is limited. However, such reasoning may overlook other factors relevant in assessing their conservation role.

The original stand cover affects floristic structure as a whole, especially in recently established holdings; however, a tendency towards homogenisation in composition with time was observed. Thus, after a period of around 20 years, plantations originating from old secondary forests become similar to those originally set on younger stands, whose mean floristic composition does not undergo any changes (Figure 4). This convergence indicates that coffee growers actually eliminate those species that are able to colonise stands with a more advanced successional stage. Interviews with the cultivators pointed out that, during the 20-year development stage of the plantation, shade trees are gradually felled and replaced. This may explain why various mature-forest tree species occurred only in young coffee plantations. An important conservation implication of these results is that recently established plantations on old secondary growth stands have a larger potential to conserve native tree diversity.

At this point, it must be borne in mind that there is a complete lack of synchrony in the development of coffee plantations. This is precisely why we observed such a large spatial floristic heterogeneity among plantations, despite the converging trend discussed above. Thus, it is necessary to take into account the β -diversity of the whole system in order to adequately assess the contribution of rustic coffee plantations to plant diversity conservation. In other words, the number of tree species that could be maintained in all coffee plantations of Rancho Grande depends mostly on the existing variation between plantations. This variation is particularly important in the case of mature forest trees, given that most of them occur in few plantations.

A further consideration in evaluating the conservation role of coffee plantations in a given region is the extent and integrity of the surrounding forests. In those regions where natural vegetation still covers large areas, rustic coffee plantations may only play a minor role in biodiversity conservation. In contrast, in those areas where forest cover has been drastically reduced and fragmented, as is the case of Rancho Grande, these plantations may stand out as the only viable way of conserving native tree diversity.

Conclusions

Rustic coffee plantations of Rancho Grande are complex and floristically highly heterogeneous. A single coffee plantation does not contribute significantly to plant conservation. Rather, it is the sum of the heterogeneous patches in the fragmented landscape which makes this agroforestry system valuable for wild tree diversity conservation.

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