Highlights

- We assess how tree species used by Lacandon Maya affect soil fertility
- *P. armata*, *C. odorata,* and *L. guatemalensis* seem to augment available phosphorus
- *L. guatemalensis* may increase soil organic matter and nitrogen
- Lacandon Maya TEK ecosystem management could be applied to restoration in degraded forests

1. Abstract

The swidden agroforestry system of the Lacandon Maya has allowed them to sustainably manage their land for hundreds of years without observed soil degradation. Lacandon land managers plant and care for many particular tree species during the fallow period of their multi-successional system to facilitate the restoration of soil fertility. Soil samples were taken around six of these species (*Poulsenia armata*, *Cedrela odorata*, *Enterolobium cyclocarpum*, *Swietenia macrophylla*, *Lonchocarpus guatemalensis*, and *Heliocarpus appendiculatus*) to evaluate their effect on soil fertility. Soil nutrient levels increased in the later successional stages of the Lacandon agroforestry system. Available phosphorus was elevated in soils beneath *P. armata*, *C. odorata,* and *L. guatemalensis* trees, and decreased with distance away from the trunk. L. guatemalensis appears to have the same effects on total nitrogen and soil organic matter content. These results demonstrate that Lacandon Maya agroforestry management choices relate positively to soil restoration. This TEK could lend guidance to countering the ecological degradation of the surrounding Montes Azules Biosphere Reserve region and for other areas of the neotropics.

Keywords: succession, nutrient cycling, sustainability, biogeochemistry, ecosystem management, soil properties

2. Introduction

2.1 Traditional Ecological Knowledge

Traditional ecological knowledge, or TEK, has been defined as a cumulative body of knowledge, practices, and beliefs about the relationship between humans, local ecosystems, and culture (Berkes, 2008). TEK does not merely consist of an understanding of local ecosystem function and natural history, although these are basic components of this knowledge system (Usher, 2000; White, 2006). TEK includes indigenous land and resource management systems, social structures, and belief systems. These nested levels of understanding interact to contribute to the body of TEK as a whole, which has been described as a knowledge-practice-belief complex (Berkes, 2008). Agroecosystems based upon TEK have been shown to be ecologically and socio-economically sustainable because, in part, they incorporate multiple land-uses, management strategies, and resource production practices (Toledo and Barrera-Bassols, 2009). Thus, these systems are able to provide subsistence for local people while preserving natural resources for future generations (Rubio and Ordóñez, 2008).

Many scientific studies have demonstrated that TEK informs ecological management to affect biogeochemical cycling and restore soil fertility. Dhanya et al. (2013) demonstrated that Mandya farmers planted *Ficus benhalensis L.* in their agroforestry systems to enrich soil nutrient levels in their agroecosystems to obviate chemical fertilizers. The high nutrient content and slow decomposition of senesced leaves of this tree species enhanced the productivity of their agroforests. Numerous indigenous groups throughout the Amazon Basin used low-intensity burns to produce biochar residues, which were mixed with pottery shards, manure, bones, and organic debris to augment levels of nitrogen, phosphorus, and several other essential nutrients in nutrient-poor, leaching-prone tropical soils (Glaser et al., 2002, 2000; Lehmann et al., 2003; Mao et al., 2012; Steiner et al., 2008). Traditional knowledge of ecosystem management and its effects on biogeochemistry cycling is so extensive that the study of this body of knowledge has become a field of its own (ethnopedology) (Barrera-Bassols and Zinck, 2003).

2.2 Lacandon Maya Agroforestry

The Lacandon Maya are one of several indigenous groups which reside in the Montes Azules region of Chiapas, Mexico. Lacandon TEK is expressed in their multi-stage swidden agroforestry system, which allows them to conserve the surrounding tropical moist forest while still obtaining the food and other goods and services they need. Small patches of land that were previously cultivated, but since left to regenerate soil fertility, are cut near the end of the dry season, which can last from January through April (Servicio Meteorológico Nacional). They are then burned. The fire is kept at low intensity to prevent it from spreading into adjacent areas and to promote the production of black carbon, which Lacandon farmers use as a soil amendment (Diemont et al., 2011; Diemont and Martin, 2009; Nigh and Diemont, 2013).

The first stage is a *milpa*, or *kor* in Lacandon. Lacandon farmers plant a diverse polyculture of as many as 58 species and many more cultivars in their *milpas* at the onset of the rainy season around May (Diemont and Martin, 2009; Diemont et al., 2006; Martin et al., 2010; McGee, 2002). Many of the crops are planted in specific pairings to increase yields (Diemont and Martin, 2009). Crops are harvested continually throughout the year.

Lacandon farmers actively plant particular early successional (e.g., *Ochroma pyramidale*) and late successional (e.g., *Swietenia macrophylla*) tree species or allow naturally dispersed seedlings to sprout in their agroforestry plots. This is most commonly done at the end of the *milpa*, but also during later shrub and forest stages. Many of these trees provide not only provisioning ecosystem services, including food, fuel, and medicine, but regulating and supporting services, including carbon sequestration, pest control, maintenance of soil fertility after depletion due to milpa cultivation, nutrient cycling, soil stabilization, habitat, and seed dispersal. For example, Diemont et al. (2006) indicated that *Ochroma pyramidale*, which was identified as a tree Lacandon land managers utilize to accelerate restoration of soil fertility, may suppress nematode populations, which in turn may expedite soil organic matter accumulation in nearby soils. This property would be of particular benefit to highly-weathered tropical soils, which are often low in organic matter due to rapid nutrient cycling (Brown and Prance, 1987). Diemont et al. (2006) also observed elevated phosphorus in soil under *Sapium lateriflorum*¸ another tree preferentially selected by Lacandon farmers, relative to surrounding soils.

After about five years, production begins to decline and the *milpa* is either burned to increase productivity and replanted or left to continue to the *acahual*, or fallow shrub stages. These include the *robir*, which lasts for two years, and the *jurup che*, which lasts approximately another two years (Falkowski et al., 2014). Lacandon land managers will continue to manage the plots through selective trimming, planting of desirable timber species, and extraction of resources like medicinal plants, food, and firewood (Nations and Nigh, 1980). After the *jurup che* the plot of land can again either be burned and replanted as *milpa*, or allowed to progress to the early secondary forest stages *pak che kor* (which might contain more direct consumables than later stages) and *mehen che.* They may allow the system to progress to advanced secondary forest, *nu kux che*, which is often older than 40 years, or burn and replant it as *milpa* again if they believe the soil has recovered from the previous cultivation period. Lacandon land managers still take an active management role in forest plots. For example, they clear areas around desirable tree species to reduce competition for resources. Lacandon extract resources from all stages by gathering medicinal and edible plants, cutting timber for building and firewood, fishing and harvesting snails in rivers and streams, and hunting for peccary, agouti, and monkeys. Some of the land is never disturbed and maintained as primary forest, called *kax* in Lacandon, to act as seed sources, regulate water cycles, and provide wildlife habitat (Nations and Nigh, 1980). Please refer to Table 1, Diemont and Martin (2009) and Nations and Nigh (1980) for a more detailed description of Lacandon agroforestry management stages.

2.3 Objectives

We conducted this research to quantitatively assess the effects of several tree species Lacandon farmers deem important for restoring soil fertility. Nitrogen and phosphorus can be limiting in tropical soils (Bautista-Cruz and del Castillo, 2005), so we quantified these nutrients. Soil nutrient availability is based not only on the quantity of nutrients, but is also a function of several interrelated soil properties, including texture, structure, and organic matter content, all of which collectively determine a soil's fertility (Karltun et al., 2013). Therefore, we also quantified soil organic matter due to its importance in determining soils' texture and nutrient retention ability (Chantigny, 2003). Our objectives were to determine whether:

1. available phosphorus (AvP), organic matter (OM), and soil nitrogen (N) in Lacandon agroforests change along a successional stage gradient;
2. particular key trees incorporated into the Lacandon agroforestry system affect AvP, OM, and N and whether this effect diminishes with distance away from the trees' stems;
3. AvP, OM, and N will be positively correlated with tree DBH.

3. Methods

3.1 Site Description

The Lacandon rainforest is primarily located in the Mexican state of Chiapas near the Mexico-Guatemala border and extends into northern Guatemala. Most of the intact rainforest is within the boundaries of the Montes Azules Biosphere Reserve (Hernández-Ruedas et al, 2014). Rainfall is approximately 2,300 to 2,600 mm per year; mean temperature is 24.7ºC—a tropical moist forest according to the Holdridge life zone system. A short dry season lasts from January through April (Servicio Meteorológico Nacional). Most of the soils in the area are clayey luvisols with low phosphorus contents (INEGI, 1982). The dominant vegetation type is perennial broadleaf rainforest with an average canopy height of 30 m. Typical dominant tree species include *Ceiba* *pentandra, Swietenia macrophylla, Astronium graveolens, Cedrela odorata,* and *Enterolobium cyclocarpum* (Miranda, 1952). Soil sampling was conducted in agroforests managed by members of the Lacandon Maya community of Lacanja Chansayab, Chiapas, Mexico (16.6026° N, 90.9149° W, 500 m above sea level).

3.2 Species Description

The study species were suggested by A. Chankin, a traditional Lacandon Maya farmer, because they maintain these trees in *acahual* and *milpa* plots. They are allowed to grow because they, "increase the vitamins [*sic*] in the soil," so the Lacandon, "can make *milpa* again." Diemont (2006) conducted interviews and field studies in Lacanja Chansayab that revealed that *C. odorata, S. macrophylla, L. guatemalensis, and H. appendiculatus* were dominant trees in various stages of the Lacandon agroforestry system and were either actively planted or maintained because they provide resources and/or enhance soil fertility. Nations and Nigh (1980) listed *E. cyclocarpum* and *P. armata* in their list of plants used by the Lacandon.

Poulsenia armata (Moraceae) (Lacandon: Akun) is a shade-tolerant, long-lived tree species native to tropical moist and wet forests from Mexico to Bolivia. It frequently grows in fertile soils and near streams. (Aide and Rivera, 1998).

Cedrela odorata (Lacandon: Ku'ch) is a valuable tropical timber species that ranges from Mexico to northern Argentina. It typically grows in well-drained soils (Jesús et al., 2014).

Enterolobium cyclocarpum (Lacandon: Petz-kin) is native from central Mexico south to northern South America. *E. cyclocarpum* is either evergreen or briefly deciduous in Mexico, as its leaves can senesce at the onset of the dry season and regrow at the onset of the rainy season. It tends to delay fruit development so that the phenology of seed maturation corresponds with the onset of the rainy season (Zuchowski, 2007).

Swietenia macrophylla (Lacandon: Puuna) is native to tropical forests from Mexico and throughout much of South America. It was the first widely-traded valuable timber species to be listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) (Free et al., 2014).

Lonchocarpus guatemalensis (Lacandon: Yax-bache) is a canopy tree species native throughout Central America. Its seeds germinate quickly, but grow slowly in shaded conditions (Popma and Bongers, 1991).

Heliocarpus appendiculatus (Lacandon: Jaror) is a large pioneer tree native throughout Central America that generally grows rapidly in early successional stages of forest gaps. (Nunez-Farfan and Dirzo, 1991).

The trees identified in this report are used by the Lacandon for utilitarian purposes in addition to helping reestablish soil fertility and restore forest cover. *P. armata* produces edible seeds and the bark is used to make fibers for bags and baskets. *C. odorata* yields strong, lightweight wood used widely for construction. The wood from *E. cyclocarpum* is used for lumber and dugout canoe construction. Its seeds are used to make beads for artisanal crafts, and the leaves have medicinal uses. *S. macrophylla*'s wood is used for lumber for construction. Its bark can be used as a red paint-like pigment and be pulverized to treat insect bites. *L. guatemalensis* is used for lumber and firewood. The bark of *H. appendiculatus* can be used to make hammocks and bags.

3.3 Field Sampling

Soil sampling was performed as per Diemont and Martin (2009) for the above 6 tree species. Trees were identified by a Lacandon Maya farmer with a detailed knowledge of local plant species. Three small, medium, and large (total of 9) individuals of each species were sampled in order to account for a range of potential tree sizes. Only 5 *H. appendiculatus* were sampled because they were more prevalent in earlier successional stages and few large individuals were encountered. The study plot successional stage was identified for each tree by Adolfo Chankin, who managed the sample site. He also identified the successional stage of the plot in which each tree was located. The stage was based on the time elapsed since the last *milpa* cultivation. Trees used for sampling were located in secondary and primary forest stages. Each tree's diameter at breast height (DBH) was measured. North-south transects centered on each sampled tree were established (unless topographic barriers intersected the transect, in which case an east-west transect was used) (Figure 1). Subsamples collected from within the tree's canopy were considered to be the "treatment" group, while those located outside of the canopy were the "control," as the potential effect of the tree on soil fertility was not expected to extend beyond the litter fall boundary demarcated by the tree canopy circumference.

Three soil samples were obtained to a depth of 20 cm below the soil surface from random points within a 1 m^2 sampling quadrat centered on each sample point using a 2.5 cm diameter soil core. Individual samples collected within a given quadrat were pooled for soil analysis. Three soil moisture and pH measurements were taken using a Kelway pH/moisture probe at random points within the 1 m^2 sampling quadrats and averaged.

3.4 Soil Analysis

Soil samples were air dried, and the available phosphorus (AvP) (mg/kg), organic matter (OM) (%), and total nitrogen (N) (%), content of each dried soil sample were determined. Available phosphorus was measured as per Olsen et al. (1954). Percent organic matter was quantified as per Walkley and Black (1934). Percent total nitrogen content was measured using the semi-microkjeldhal digestion method (Bremmer, 1960; Kjeldahl, 1883).

3.5 Statistical Analysis

All statistical analyses were conducted using R (R Core Team, 2015). Potential outliers whose high influence could be attributed to sampling error (e.g., near depressions, waterways) were eliminated. A one-way ANOVA was used to compare the aforementioned soil fertility metrics among the 4 successional stages sampled in the Lacandon Maya agroforestry system (Table 1). A post-hoc Fisher's Protected LSD comparison was conducted to determine in which stages AvP, OM, and N differed. Fisher's LSD was used because it maintains the experimentwise error rate at approximately the nominal level of significance (α) (Meier, 2006; Yandell, 1997). Significant differences were assessed at $\alpha=0.05$ for all analyses.

Samples taken outside of the canopy boundary (control) were compared to samples taken inside the canopy (treatment). For the purposes of the analysis, the samples taken at the canopy boundary were considered with those taken outside the boundary, as we expected the effect of the trees on soil quality would be greatest well within said boundary. Mixed models were fit for all of the soil quality metrics for each of the 6 species in our study both with individual trees nested within species. The (position) fixed effect was defined as the sample position relative to the canopy boundary (in/out). Mixed models were also fit with sampling distance (from stem) as the (distance) fixed effect to assess whether the soil quality constituents decreased with increasing distance away from tree stems. Finally, mixed models were fit with tree DBH as the fixed effect to assess whether soil quality metrics increased with increasing tree size. Separate models were also run for each study tree species to further investigate the effects of the study tree species on soil nutrients.

4. Results

4.1 Comparison of Soil Fertility between Successional Stages

Soils in the primary forest (*kax*) stage were the most fertile (Table 2). Soil OM and N tended to decrease from the *pak che kor* to the *mehen che,* and then rebound, increasing through the *nu kux che* and *kax* stages. Soil AvP concentrations remained fairly constant in the *pak che kor*, *mehen che,* and *nu kux che* stages, before increasing significantly in the *kax* stage. However, only the *kax* stage was significantly different from the earlier successional stages for all quantified soil fertility metrics.

4.2 Comparison of Soil Fertility between Species

Significant sampling position fixed effects were observed for *P. armata, C. odorata,* and *L. guatemalensis*. AvP was significantly higher within the canopy boundary than outside it for *P. armata*, (p=0.021), *C. odorata* (p=0.017), and *L. guatemalensis* (p=0.038). Both OM and N were higher within the canopy boundary of *L. guatemalensis* (p=0.013 and 0.017, respectively) than outside it (Figure 2). AvP decreased significantly with increasing distance away from *P. armata* (p=0.044), *C. odorata* (p=0.002), and *L. guatemalensis* (p=0.002) stems. N and OM also decreased significantly away from C. *odorata* (p=0.006 and 0.006, respectively). The same was true for *L. guatemalensis* (p=0.001 and 0.001, respectively) (Figure 3). Tree DBH had no significant effect on any of the soil quality metrics for any of the study species.

5. Discussion

5.1 Lacandon agroforestry successional trends

Soil OM and N decreased from the *pak che kor* stage to the *mehen che* stage, but then increased after that, though the levels did not differ statistically between *pak che kor* through *nu kux che* stages. This suggests that fallow periods in the Lacandon agroforestry system, and longer fallows in particular, may aid in the regeneration of certain components of soil fertility in later successional stages after disturbance. This may be because the number of tree species the

Lacandon manage for enhancing soil fertility increases along with successional stage. The decrease in OM and N in the *mehen che* stage may have been a function of different successional management and structural conditions. For example, *O. pyramidale*, which is a dominant species in *pak che kor,* are not as prevalent in *mehen che*. *O. pyramidale*, which facilitates the accrual of large quantities of organic matter, is an early successional species which cannot compete with shade-tolerant, later successional species once the canopy closes in the *mehen che*. This decrease in *O. pyramidale* populations may reduce the OM in the soil in the *mehen che* before other species begin contributing larger quantities of OM themselves. If this is the case, it underscores the importance of *O. pyramidale* for restoring soil fertility in fallow agroecosystems.

Diemont and Martin (2009) also observed that soil fertility increased with successional stage, but the specific trends for various soil fertility constituents differed. They observed that OM and N increased continuously with successional stage. While they also did not observe a continuous, statistically significant increase in AvP, its concentrations followed a pattern similar to that which we observed for N and OM (decrease from the *pak che kor* to the *mehen che* followed by an increase through the *kax*). These differences may be attributed to the fact that they sampled all Lacandon agroforestry stages, including the *milpa*, *robir*, *and jurup che*, while the youngest plots we sampled were in the *pak che kor* stage. While past studies have also demonstrated that nitrogen mineralization rates increase along a chronosequence of tropical rainforest successional stages as detritus decomposes and is incorporated into the soil (Lamb, 1980; Robertson, 1984), others demonstrate that phosphorus is a primary factor limiting productivity in tropical rainforest ecosystems, and decreases with stand age (Bautista-Cruz and del Castillo, 2005). Thus, it would appear that Lacandon agroforestry management is having some positive effect on soil AvP to overcome this limitation.

It must be noted that soil OM and N both changed in a similar fashion with successional stage, making it difficult to determine whether Lacandon management increased soil nutrient levels directly or whether soil nutrients were being retained more effectively by the soils due to elevated quantities of OM, which elevates soil cation exchange capacity (CEC) (Brady and Weil, 2007). Few studies have been conducted to assess the role of OM in nutrient cycling in tropical ecosystems, as most have focused on the dynamics of organic carbon despite the importance of OM in determining soil nutrient retention and fertility (Chantigny, 2003). Lacandon farmers hold that a significant amount of organic matter accrues as stands age, and especially during the *pak che kor* stage, due to the emerging dominance of trees shading out herbaceous cover that was prevalent in the earlier shrubby stages of the agroforestry system. They believe that root decomposition also contributes to the fertility of the soil in this stage. This position has been corroborated by Levy and Golicher (2004), who demonstrated that Lacandon manage plants to shorten the time needed to restore sites that were previously heavily managed for agricultural production (i.e., *milpa* plots) to advanced secondary forest. However, it is questionable whether soil fertility in Lacandon agroforests can be fully restored to levels equivalent to mature, intact forest soils given that soil fertility, as measured by soil AvP, OM, and N content was markedly higher in mature forest.

5.2 Species effects on soil fertility

P. armata, *C. odorata*, and *L. guatemalensis* appear to have augmented AvP in soils beneath their canopies. This effect appears to attenuate with increasing distance from the tree stems all three species. Blair and Perfecto (2004) demonstrated that the root density of *C. odorata* increased in P-rich soil patches, suggesting that the tree was able to exploit heterogeneous distribution of AvP resources in the soil matrix. *Sapium lateriflorum*, another species managed by the Lacandon, appears to augment soil AvP (Diemont et al. 2006). This species may serve as a “phosphorus pump” in which the roots of certain trees were able to reach AvP deposits in lower soil strata and then deposit the AvP in the P-depleted upper soil horizons via leaf senescence. Research by Hiremath et al. (2002), concluded that AvP has a short residence time in *C. odorata* plant tissues, indicating that it is rapidly lost through litterfall. This is a potential mechanism by which *P. armata* and *C. odorata* may increase AvP content of surface soils.

The bark of *P. armata* and *C. odorata* contain cytotoxic compounds that inhibit the growth of bacteria populations (González-Coloma et al., 2011; Rushdey El-Seedi, 2005). It may be that the cytotoxic chemicals are found in greater concentrations near these trees’ stems while OM is distributed evenly around them. This would slow OM decomposition to a greater extent near the tree stems, leading to a slower release of nutrients. Retarding OM decomposition and slowing nutrient release may help prevent nutrient leaching from highly-weathered soils with low nutrient-retention capacities like those found in tropical rainforest ecosystems, which typically have rapid decomposition and nutrient cycling due to their warm and wet climate (Kiffer et al., 1981).

Increasing AvP is of particular import in luvisols and other tropical soils, as many are phosphorus-limited. This is particularly true in limestone bedrock calcareous soils, like those found in Lacanja Chansayab, where available phosphorus may be adsorbed by calcium carbonate or precipitated out of the soil solution as calcium phosphate, reducing its availability (von Wandruszka, 2006). Increasing soil AvP concentrations would enhance the productivity of these stages and reduce the time needed to fully restore ecological function and structure. It is likely, though uncertain, that recently abandoned Lacandon *milpas* are phosphorus-limited given that all soils in sampled stages contained less than 15 mg/kg of AvP, which is considered the threshold for phosphorus deficiency (Watson and Mullen, 2007). We were unable to conclusively conclude that

C. odorata, *P. armata*, *or L. guatemalensis* were actively augmenting AvP as opposed to preferentially colonizing and outcompeting other species in areas that naturally had high AvP given that it did not increase with DBH for any species. It is often difficult to conclusively prove either mechanism in isolated field studies (Ettema and Wardle, 2002). However, the fact that AvP decreased with distance away from these trees suggests that the effect is not merely a function of the patchiness of AvP in the local soil environment. AvP content of soils near these two species are still “deficient” by agricultural standards, but significantly higher than the surrounding soil.

OM and N were both significantly higher within the canopy boundary of *L. guatemalensis* trees, and decreased with increasing distance from stems. It may also be that the location of *L. guatemalensis* individuals is tied to elevated naturally-occurring OM rather than the tree affecting soil fertility, though it is also one of the most abundant pioneer trees in recently abandoned *milpas*, which are regularly cleared and weeded, and therefore unlikely to preferentially colonize areas with elevated OM. It may be that elevated OM content of soils near near *L. guagemalensis* may increase the CEC of these soils, thereby indirectly increasing AvP and N. However, *Lonchocarpus sp.* including L. guatemalensis are leguminous, allowing for nitrogen fixation (Etuk et al., 2010).

Lonchocarpus sp. resprouts in fallows, so our observations may be confounded by the effect of the same individual trees during the previous cycle, although this does not necessarily undermine the impact it has on OM. OM is particularly important in tropical agroforestry because it is the primary source of both nitrogen and phosphorus in those agroecosystems (Ewel 1986).

While a distance fixed effect was observed for OM and N with increasing distance away from *C. odorata* stems, a position fixed effect was not. This was likely due to the high variation in OM and N across all soil samples, which precluded the observation of significant differences between samples taken within and outside the canopy of this species. This variability also likely influenced the lack of observed effect of *Enterolobium cyclocarpum*, which is leguminous, on soil N (Rocha and Aguilar, 2001).

The trees in this study are not the first to have been shown to have a significant impact on soil fertility. Diemont et al. (2006) found that *Sapium lateriflorum* influenced AvP concentrations in nearby soils and that leaf litter appeared to decompose more slowly near *Ochroma pyramidale*, as measured by soil nematodes. Other trees selected by the Lacandon Maya may also have an impact on nematode populations, which have significant effect on decomposition pathways and nutrient cycling (Diemont and Martin, 2005).

5.3 Limitations

It is difficult to separate the effects individual tree species have on soil nutrient levels given the effects of local soil characteristics. For example, the presence of iron and aluminum sesquioxides tends to promote the stability of OM aggregates (Igwe et al., 2013). They also affect soil P sorption (Bortoluzzi et al., 2015). Soil texture, structure, and composition, in turn, also affect CEC, which determines the soil nutrient-holding capacity (Brady and Weil, 2007). These variables were not considered in this analysis.

Conducting these experiments in the field allowed us to study Lacandon agroforestry management as a whole. Variability of data collected in-situ may have limited ability to distinguish between the treatment effects of the various tree species studied. The presence of different trees near sample sites is an extraneous variable that was not accounted for in our analysis. It is possible that smaller conspecific trees may have been located near control sample points outside of the canopy boundary of the individual being studied. If they also imparted an effect on soil fertility outside the canopy boundary of a given study species individual, then “control” samples, which should not have been impacted by that species, would also exhibit elevated soil fertility. Thus, the treatment effect the sampled tree had on soil nutrient levels within its own canopy may have been functionally nullified, preventing the observation of a statistically significant effect. This may have been exacerbated by our inclusion of samples collected at the canopy boundary as part of the treatment group. We wanted to consider the zone of litterfall beneath each tree as the treatment area, as we suspected that as a probable cause of any potential effect. However, the effect would not be as strong near the canopy edge if the differences in fertility were caused by some other mechanism associated with the tree bark or roots rather than litterfall. This would reduce the mean values we observed for the within canopy treatment samples. Conversely, the presence of heterospecific trees near treatment sample points within the canopy of the species being studied may have suppressed or negated its effect on soil fertility. Species, distance, and DBH-related effects were observed nonetheless. Controlled plantation experiments could reduce data variability in future studies and indicate effects of other specific trees used in the Lacandon agroforestry system for soil fertility.

Another limitation of this study was that we only sampled the last four stages of the Lacandon agroforestry system. Fully quantifying changes in nutrient pools and fluxes amongst all of the successional stages of this agroforestry system was not the main goal of this study, as this was already performed by Diemont and Martin (2009). The similarity between the methods used and the distribution of trees sampled amongst Lacandon agroforestry successional stages allowed us to compare and ultimately corroborate their results.

6. Conclusions and Broader Implications

Despite the benefits potentially offered by reforestation, many projects fail in the long-term, either as a result of poor initial planning and implementation, or due to a lack of support, monitoring, and maintenance by local communities (Douterlungne and Ferguson, 2011; Dudley et al., 2005; Gonzalez-Espinosa et al., 2007). Planted tree species are often selected for their economic value, not necessarily their ecological suitability. Restoration areas are not monitored after the first two years of management and once the payments cease, many landowners clear the restored areas for cattle ranches and farmland. Disturbed land can be difficult to restore because of low rates of survival of forest vegetation in hot and dry open areas, as well as compaction by cattle, which exacerbates erosion rates and prevents root penetration of colonizing plants (Murgueitio et al., 2011). Most of the soils in the region are clayey luvisols with low phosphorus contents (Diemont et al., 2006). Many soils throughout the neotropics are highly weathered with a low nutrient holding capacity (Glaser et al., 2002).

The incorporation of trees used by the Lacandon Maya to enhance soil fertility and facilitate restoration into Western science-based land management strategies in the Montes Azules Biosphere region of Chiapas and throughout the neotropics may lead to more successful restoration practices. Planting *P. armata, C. odorata,* and *L. guatemalensis* trees may help increase soil AvP in P-limited soils, which in turn will promote reestablishment of vegetation in cleared areas. The productivity of the secondary forest stages allows the Lacandon to maintain a large percentage of their land holdings in fallow. These plots would need to be felled, burned, and cultivated at shorter intervals if they were not as productive, which would further degrade soil conditions and the site's capacity to regenerate vegetation cover after repeated disturbance.

Although many regions of the neotropics are negatively impacted by human activities and bear several similarities in environmental conditions to the Montes Azules Biosphere Reserve region, including low AvP soils with high clay content, we do not advocate a one-size-fits-all approach to restoration. The application of local knowledge is one of the main benefits of incorporating trees used in the Lacandon Maya agroforestry system into restoration management of the Montes Azules Biosphere Reserve region. It may be that other indigenous groups apply similar traditional ecological knowledge of ecological functions in their agroecosystems. Further research should be conducted to understand and assess local TEK for each individual region attempting to be restored. Much of this TEK has not been studied and even less has been evaluated using scientific methods. The mechanisms proposed for the effects observed in this study are still speculative. More research needs to be done to cross-validate TEK using scientific ecological knowledge methodologies and add to the general body of ecological knowledge.

TEK is increasingly becoming accepted as valuable for many fields, including land management, resource monitoring, and ecological engineering (Berkes, 2008; Berkes et al., 2000). This research contributes to this growing realization. These results support the claim that the Lacandon Maya are actively engineering their agroecosystems to enhance soil fertility based on long-term trial-and-error experimentation and close observation of vegetation responses to different management techniques. This research demonstrates that certain tree species managed by the Lacandon Maya, in this case *P. armata*, *C. odorata*, and *L. guatemalensis* , have a significant impact on soil fertility. In particular, phosphorus appears to be related to presence of these species. Soil fertility also increases with successional stage in the Lacandon agroforestry system. However, fewer and fewer Lacandon manage their land traditionally as a result of a current socio-economic shift from agricultural production to providing ecotourism services. Many of those who maintain traditional agroecosystems have species-poorer *milpas*, shorter fallows, and may utilize modern external inputs, like chemical fertilizers, pesticides, and hired labor (McGee, 2002, Ross, 2002). By better understanding these processes, research of this nature helps preserve not only the knowledge, but also the culture of the Lacandon, which are inextricably connected and both being eroded by numerous external forces (Falkowski et al., 2014).

7. Acknowledgements

We thank the members of the Lacandon Maya community of Lacanja Chansayab for their openness and patience. Second, we thank Stephen Stehman for his assistance with the statistical analysis performed in this study. We also thank two anonymous reviewers whose comments greatly improved this article. Finally, we acknowledge the field assistance of Christopher Honess, Ken Lucas, and Ana Flores. NSF Award 1231334 awarded to PI Stewart Diemont partially funded this work.

8. Literature Cited

Aide, T.M., Rivera, E., 1998. Geographic patterns of genetic diversity in *Poulsena armata* (*Moraceae*): Implications for the theory of Pleistocene refugia and the importance of riparian forest. J. Biogeogr. 25, 695–705.

Augustine, D.J., McNaughton, S.J., 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. Ecosystems 9, 1242–1256.

Barrera-Bassols, N., Zinck, J. A., 2003. Ethnopedology: a worldwide view on the soil knowledge of local people. Geoderma 111, 171–195.

Bautista-Cruz, A., del Castillo, R.F., 2005. Soil changes during secondary succession in a tropical montane cloud forest area. Soil Science Society of America 69, 906-914.

Berkes, F., 2008. Sacred Ecology, 2nd ed. Taylor & Francis, New York, NY.

Berkes, F., Colding, J., Folke, C., 2000. Rediscovery of traditional ecological knowledge as adaptive management. Ecol. Appl. 10, 1251–1262.

Blair, B.C., Perfecto, I., 2004. Successional status and root foraging for phosphorus in seven tropical tree species. Can. J. For. Res. 34, 1128–1135.

Bortoluzzi, E.C., Pérez, C. a. S., Ardisson, J.D., Tiecher, T., Caner, L., 2015. Occurrence of iron and aluminum sesquioxides and their implications for the P sorption in subtropical soils. Appl. Clay Sci. 104, 196–204.

Brady, N.C., Weil, R., 2007. Nature and Properties of Soils, 14th ed. Pearson Education Ltd, Essex.

Bremmer, J.M., 1960. Determination of nitrogen in soil by the Kjeldahl method. The Journal of

Agricultural Science 55, 11-33.

Brown, K.S., Prance, G.T., 1987. Soils and vegetation, in: Whitmore, T.C., Prance, G.T. (Eds.), Biogeography and Quaternary History in Tropical America. Clarendon Press, Oxford, pp. 19–45.

Chantigny, M.H., 2003. Dissolved and water-extractable organic matter in soils: a review on the influence of land use and management practices. Geoderma 113, 357–380.

Dhanya, B., Viswanath, S., Purushothaman, S., 2013. Does litterfall from native trees support rainfed agriculture? Analysis of Ficus trees in agroforestry systems of southern dry agroclimatic zone of Karnataka, southern India. J. For. Res. 24, 333–338.

Diemont, S.A.W., 2006. Ecosystem management and restoration as practiced by the indigenous Lacandon Maya of Chiapas, Mexico. Doctoral Thesis. Ohio State University.

Diemont, S. A. W.., Bohn, J.L., Rayome, D.D., Kelsen, S.J., Cheng, K., 2011. Comparisons of Mayan forest management, restoration, and conservation. For. Ecol. Manage. 261, 1696–

Diemont, S.A.W., Martin, J.F., 2009. Lacandon Maya ecosystem management: sustainable design for subsistence and environmental restoration. Ecol. Appl. 19, 254–266.

Diemont, S.A.W., Martin, J.F., 2005. Management impacts on the trophic diversity of nematode communities in an indigenous agroforestry system of Chiapas, Mexico. Pedobiologia (Jena). 49, 325–334.

Diemont, S.W., Martin, J.F., Levy-Tacher, S.I., Nigh, R.B., Lopez, P.R., Golicher, J.D., 2006. Lacandon Maya forest management: Restoration of soil fertility using native tree species. Ecol. Eng. 28, 205–212.

Douterlungne, D., Ferguson, B.G., 2011. Manual de Restauración Ecologica Campesina para la Selva Lacandona, 1st ed. El Colegio de la Frontera Sur, San Cristobal de las Casas, Chiapas, Mexico.

Dudley, N., Morrison, J., Aronsoe, J., Mansourian, S., 2005. Why do we need to consider restoration in a landscape context?, in: Mansourian, S., Vallauri, D., Dudley, N. (Eds.), Forest Restoration in Landscapes: Beyond Planting Trees. New York, pp. 51–58.

Ettema, C.H., Wardle, D. A., 2002. Spatial soil ecology. Trends Ecol. Evol. 17, 177–183.

Etuk, I.M., Ndaeyo, N.U., Olajide, O., 2010. Variation in the quantities of three macro-nutrients (N : P : K) in the leaf prunings of three indigenous agroforestry tree species. Nat. Sci. 8, 148–151.

Ewel, J.J., 1986. Designing agricultural ecosystems for the humid tropics. Ann. Rev. Ecol. Syst. 17, 245-271.

Falkowski, T.B., Martinez-Bautista, I., Diemont, S.A.W., 2014. How valuable could traditional ecological knowledge education be for a resource-limited future?: An emergy evaluation in two Mexican villages. Eco. Mod. 300, 40-49.

Food and Agriculture Organization of the United Nations Land and Water Development Division, 2007. Lonchocarpus nicou [WWW Document]. Accessed: September 10, 2015. URL http://ecocrop.fao.org/ecocrop/srv/en/dataSheet?id=7396

Free, C.M., Matthew Landis, R., Grogan, J., Schulze, M.D., Lentini, M., Dünisch, O., 2014. Management implications of long-term tree growth and mortality rates: A modeling study of big-leaf mahogany (*Swietenia macrophylla*) in the Brazilian Amazon. For. Ecol. Manage. 330, 46–54.

Glaser, B., Balashov, E., Haumaier, L., Guggenberger, G., Zech, W., 2000. Black carbon in density fractions of anthropogenic soils of the Brazilian Amazon region. Org. Geochem. 31, 669–678.

Glaser, B., Lehmann, J., Zech, W., 2002. Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal - a review. Biol. Fertil. Soils 35, 219–230.

González-Coloma, A., Reina, M., Sáenz, C., Lacret, R., Ruiz-Mesia, L., Arán, V.J., Sanz, J., Martínez-Díaz, R. a, 2011. Antileishmanial, antitrypanosomal, and cytotoxic screening of ethnopharmacologically selected Peruvian plants. Parasitol. Res. 110, 1381–92.

Gonzalez-Espinosa, M., Ramirez-Marcial, N., Camacho-Cruz, A., Holz, S.C., Rey-Benayas, J.M., Parra-Vazquez, M.R., 2007. Restauración de bosques en territorios indigenas de Chiapas: Modelos ecologicos y estrategias de accion. Boletín la Soc. Botánica México 80, 11–23.

Hernández-Ruedas, M. a., Arroyo-Rodríguez, V., Meave, J. a., Martínez-Ramos, M., Ibarra-Manríquez, G., Martínez, E., Santos, B. A., 2014. Conserving tropical tree diversity and forest structure: The value of small rainforest patches in moderately-managed landscapes. *PLoS ONE*, *9*(6).

Hiremath, A.J., Ewel, J.J., Cole, T.G., 2002. Nutrient use efficiency in three fast-growing tropical trees. For. Sci. 48, 662–672.

Igwe, C. a., Zarei, M., Stahr, K., 2013. Stability of aggregates of some weathered soils in south-eastern Nigeria in relation to their geochemical properties. J. Earth Syst. Sci. 122, 1283–1294.

INEGI (Instituto Nacional de Estadistica Geografica e Informatica), 1982. Carta Edafologica, Las Margaritas, E15-12. Estados Unidos Mexicanos.

Jesús, M., Espinoza, P., Janet, G., Guillen, I., Morales, M.S., Rodríguez, R., 2014. Potencialidad de *Cedrela odorata (Meliaceae*) para estudios dendrocronológicos en la selva central del Perú. Rev. Biol. Trop. 62, 783–793.

Karltun, E., Lemenih, M., Tolera, M., 2013. Comparing farmers' perception of soil fertility change with soil properties and crop performance in Beseku, Ethiopia. L. Degrad. Dev. 24, 228–235.

Kiffer, E., Puig, H., Kilbertus, G., 1981. Biodegradation of the leaves of *Eperua falcate Aubl.* In damp tropical forests. Revue d'ecologie et de biologie du sol 18(2).

Kjeldahl, J. 1883. Neue method zur bestimmung des stickstoffs in organischen korpern, Z. Anal. Chem. 22, 366-382.

Lamb, D., 1980. Soil Nitrogen mineralisation in a secondary rainforest succession. Oecologia 47, 257–263.

Lehmann, J., Pereira, J., Steiner, C., Nehls, T., Zech, W., Glaser, B., 2003. Nutrient availability and leaching in an archaeological Anthrosol and a Ferralsol of the Central Amazon basin : fertilizer, manure and charcoal amendments. Plant Soil 249, 343–357.

Levy-Tacher, S., Golicher, J.D., 2004. How predictive is traditional ecological knowledge? The case of the Lacandon Maya fallow enrichment system. Interciencia 29(9), 496-504.

Mao, J.-D., Johnson, R.L., Lehmann, J., Olk, D.C., Neves, E.G., Thompson, M.L., Schmidt-Rohr, K., 2012. Abundant and stable char residues in soils: implications for soil fertility and carbon sequestration. Environ. Sci. Technol. 46, 9571–6.

Martin, J.F., Roy, E.D., Diemont, S. A. W., Ferguson, B.G., 2010. Traditional ecological knowledge (TEK): Ideas, inspiration, and designs for ecological engineering. Ecol. Eng. 36, 839–849.

McGee, R.J., 2002. Watching Lacandon Maya Lives. Allyn and Bacon, Boston.

Meier, U., 2006. A note on the power of Fisher's least significant difference procedure. Pharm. Stat. 5(4), 254-263.

Murgueitio, E., Calle, Z., Uribe, F., Calle, A., Solorio, B., 2011. Native trees and shrubs for the productive rehabilitation of tropical cattle ranching lands. For. Ecol. Manage. 261, 1654–1663.

Nations, J.D., Nigh, R.B., 1980. The evolutionary potential of Lacandon Maya sustained-yield tropical forest agriculture. J. Anthropol. Res. 36, 1–30.

Nigh, R., Diemont, S.A.W., 2013. The Maya milpa: fire and the legacy of living soil. Front. Ecol. Environ. 11, E45–E54.

Nunez-Farfan, J., Dirzo, R., 1991. Effects of defoliation on the saplings of a gap-colonizing neotropical tree. J. Veg. Sci. 2, 459–464.

Olsen, S.R., 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. Washingon, D.C.

Popma, J., Bongers, F., 1991. Acclimation of seedlings of three Mexican tropical rain forest tree species to a change in light availability. J. Trop. Ecol. 7, 85.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Robertson, G.P., 1984. Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America. Oecologia1 61, 99–104.

Rocha, O.J., Aguilar, G., 2001. Reproductive biology of the dry forest tree *Enterolobium cyclocarpum* (Guanacaste) in Costa Rica: a comparison between trees left in pastures and trees in continuous forest. Am. J. Bot. 88, 1607–1614.

Ross, N., 2002. Cognitive aspects of intergenerational change: Mental models, cultural change, and environmental behavior among the Lacandon Maya of Southern Mexico. Human Org. 61, 125-138.

Rubio, J.E., Ordóñez, J., 2008. Ciencia, Tecnología y Sociedad en México. Tecnológico de Monterrey.

Rushdey El-Seedi, H., 2005. Antimicrobial triterpenes from *Poulsenia armata* miq. standl. Nat. Prod. Res. 19, 197–202.

Servicio Meterologico Nacional., 2010. Normales Climatologicas Estacion 00007017 Bonampak. CONAGUA (Comision Nacional del Agua).

Stehman, S., Meredith, M.P., 1995. Practical analysis of factorial experiments in forestry. Can. J. For. Res. 25, 446–461.

Steiner, C., Glaser, B., Geraldes Teixeira, W., Lehmann, J., Blum, W.E.H., Zech, W., 2008. Nitrogen retention and plant uptake on a highly weathered central Amazonian Ferralsol amended with compost and charcoal. J. Plant Nutr. Soil Sci. 171, 893–899.

Toledo, V.M., Barrera-Bassols, N., 2009. A etnoecologia: uma ciência pós-normal que estuda as sabedorias tradicionais Ethnoecology: A post-normal science studying the traditional knowledge and wisdom. Desenvolv. e Meio Ambient. 20, 31–45.

Usher, P.J., 2000. Traditional ecological knowledge in environmental assessment and management traditional ecological knowledge. Arctic 53, 183–193.

Von Wandruszka, R., 2006. Phosphorus retention in calcareous soils and the effect of organic matter on its mobility. Geochem. Trans. 7.

Walkley, A., Black, L.A., 1934. An examination of the Degtjareff method for determining soil organic matter, and a proposed modification of the chromic acid titration method. Soil Sci. 37, 29–38.

Watson, M., Mullen, R., 2007. Understanding Soil Tests for Plant-Available Phosphorus. Columbus, OH.

White, G., 2006. Cultures in collision: Cultures traditional and Euro-Canadian governance knowledge processes in northern boards. Arctic 59, 401–414.

Yandell, B., 1997. Practical Data Analysis for Designed Experiments. Chapman & Hall/CRC Press.

Zuchowski, W., 2007. Tropical Plants of Costa Rica. Zona Tropicala, Ithaca.

Figures

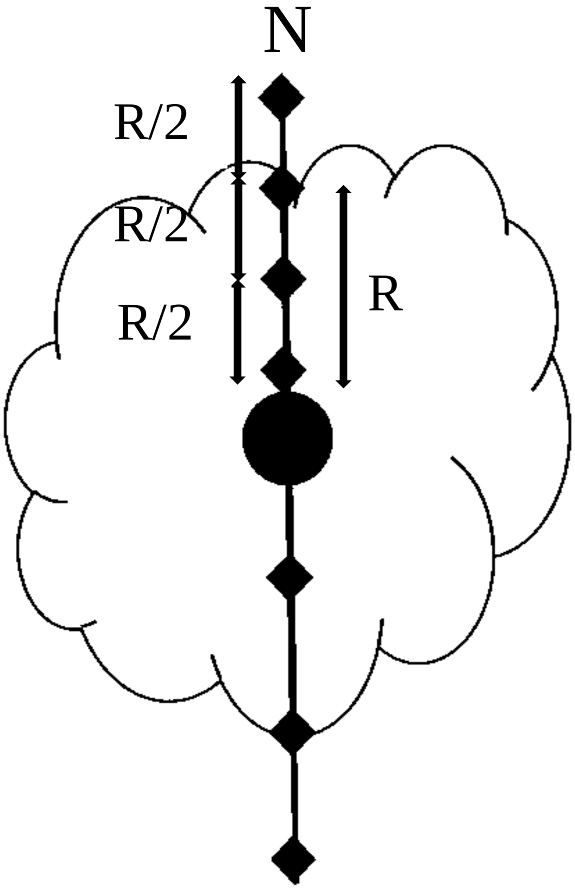

Figure 1: Diagram of sampling transect for each tree. Diamonds represent relative locations of subsample points. The black circle at the transect midpoint represents the tree trunk and the thin, curved line represents the canopy edge. Seven subsample points were spaced evenly along each transect so that the sampling location second to the end at each side of each transect was located where the canopy edge intersected the transect. The center subsample was located on the north side of the sampled tree's trunk and the end points were located outside of the canopy cover. One subsample point was located halfway between the canopy edge and the tree stem (R/2) on either side of the transect. Subsamples at the end of the transect were located at the same distance as the within-canopy subsamples (R/2), but at this distance from the canopy boundary.

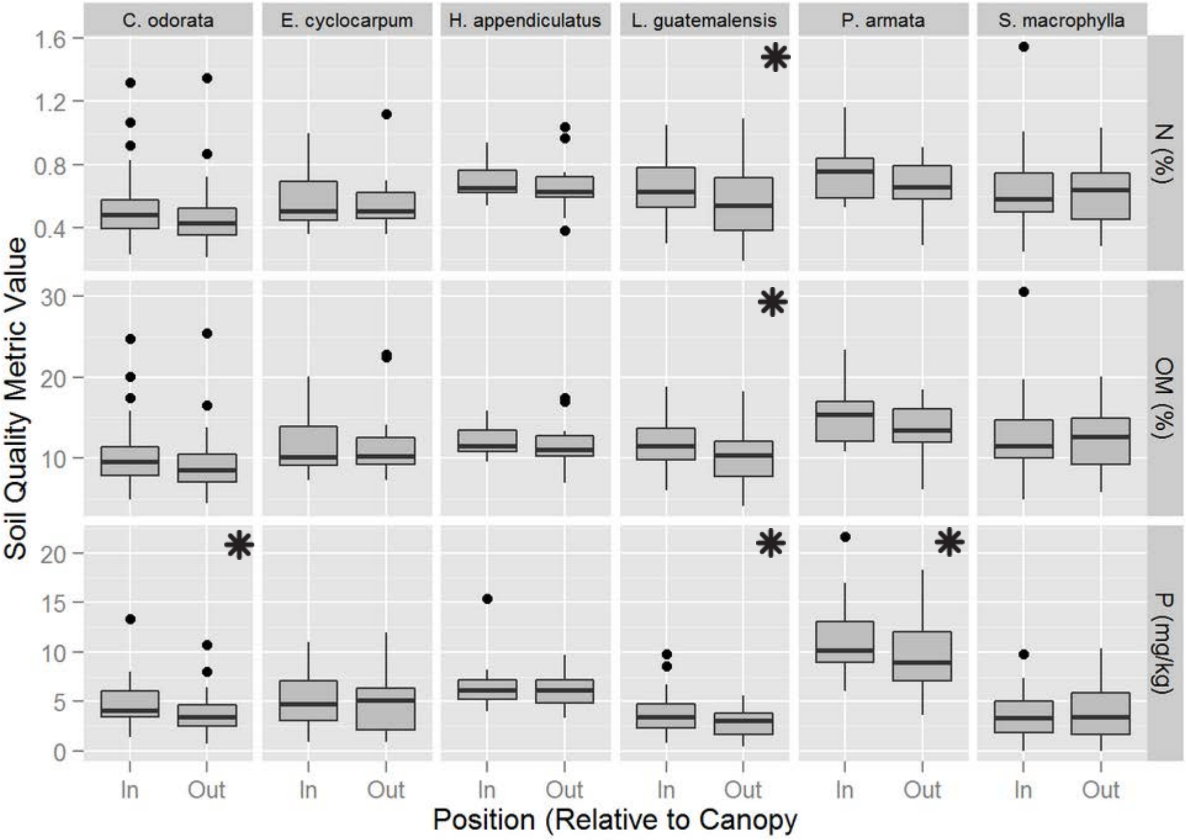

Figure 2: Comparison of AvP, N, and OM concentrations in soils sampled within and outside the tree canopies of study species. Species with significant position fixed effect are marked with an asterisk in the top right portion of the panel.

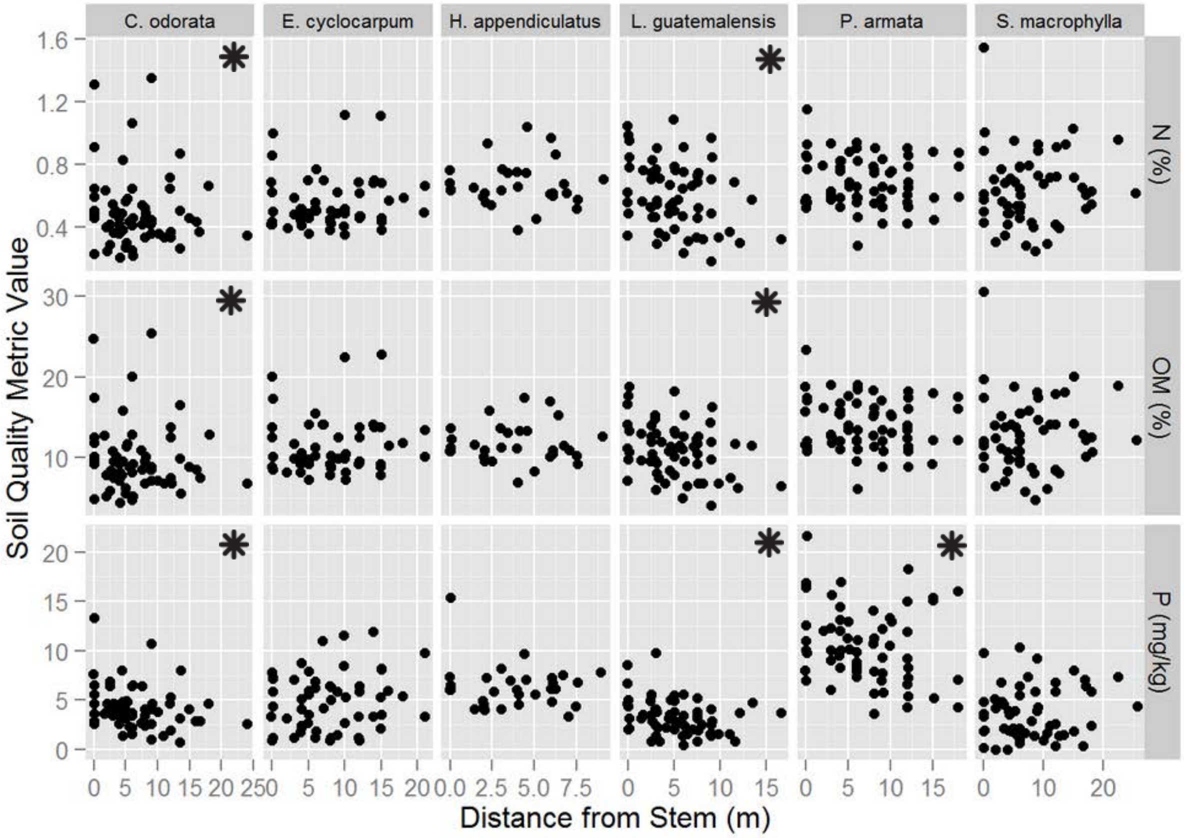

Figure 3: Graphs of AvP, N, and OM concentrations as a function of distance from study tree stems. Species with significant distance fixed effect are marked with an asterisk in the top right portion of the panel.

Tables

Table 1: Description of Lacandon successional stages sampled. The translations listed are literal. *Selva* literally translates to advanced forest; it has the colloquial connotation of being dense, species rich, and undisturbed tropical forest. The ages of sample site stages were determined from the date of the last burn. Average ages are listed in parenthesis. N is the number of trees sampled in each respective stage.

Successional stage (Lacandon)	Successional stage (Translation)	Stage age range	n
Pak che kor	Planted tree milpa	10-19 (14)	19
Mehen che	Little tree	12-30 (26)	8
Nu kux che	Big tree	32-56 (40)	10
Kax	Selva (in Spanish)	58-Primary (85)	13

Table 2: Comparison of AvP, OM, and N in the various successional stages of the Lacandon agroforestry system. P values are the results are the ANOVA by stage for each variable. The successional stages are ordered from the youngest (top) to oldest (bottom) for each variable. Letters in the Fischer comparison test column are the results of the Fischer LSD test. Stages that share a letter are not significantly different. Stages that do not have any letters in common are significantly different.

Phosphorus (mg/kg)	p<0.001	Successional stage	Mean	Standard error	Fisher comparison test
		Pak che kor	4.781	0.253	B
		Mehen che	4.661	0.4	B
		Nu kux che	4.459	0.4	B
		Kax	7.988	0.406	A
Organic matter (%)	p<0.001	Successional stage	Mean	Standard error	Fisher comparison test
		Pak che kor	10.94	0.251	C
		Mehen che	10.244	0.413	C
		Nu kux che	12.011	0.366	B
		Kax	14.196	0.483	A

		Successional stage	Mean	Standard error	Fisher comparison test
Nitrogen (%)	$p<0.01$	Pak che kor	0.58	0.016	D
		Mehen che	0.523	0.022	B
		Nu kux che	0.637	0.021	C
		Kax	0.712	0.025	A