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Lacandon Maya ecosystem management: sustainable design for subsistence and environmental restoration

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Abstract. Indigenous groups have designed and managed their ecosystems for generations, resulting in biodiversity protection while producing for their family's needs. Here we describe the agroecosystem of the Lacandon Maya, an indigenous group who live in Chiapas, Mexico. The Lacandon practice a form of swidden agriculture that conserves the surrounding rain forest ecosystem while cycling the majority of their land through five successional stages. These stages include an herbaceous stage, two shrub stages, and two forest stages. A portion of their land is kept in primary forest. This study presents the Lacandon traditional ecological knowledge (TEK) for agroforestry and quantitatively describes the plant community and the associated soil ecology of each successional stage. Also documented is the knowledge of the Lacandon regarding the immediate use of plant species and plant species useful for soil fertility enhancement. Woody plant diversity increases during the successional stages of the Lacandon system, and by the beginning of the first forest stage, the diversity is similar to that of the primary forest. In all stages, Lacandon use 60% of the available plant species for food, medicine, and raw materials. Approximately 45% of the woody plant species present in each fallow stage were thought by the Lacandon to enhance soil fertility. Total soil nitrogen and soil organic matter increased with successional stage and with time from intentional burn. Nutrient and soil nematode dynamics in shrub stages related to the presence of introduced and managed plants, indicating engineered soil enhancement by the Lacandon. The effects on biodiversity and soil ecology coupled with productivity for agricultural subsistence indicate that Lacandon TEK may offer tools for environmental conservation that would provide for a family's basic needs while maintaining a biodiverse rain forest ecosystem. Tools such as these may offer options for regional restoration and conservation efforts such as the Mesoamerican Biological Corridor in Mexico and Central America, where attainment of environmental goals must include methods to provide resources to local inhabitants.

Key words: ecological engineering; indigenous; Lacandon Maya; Mesoamerican Biological Corridor; plant community; soil ecology; succession; TEK; traditional ecological knowledge.

INTRODUCTION

Ecosystem degradation and poverty are linked in Mesoamerica. Environmental restoration and conservation efforts must address the subsistence needs of people if projects are to be successful. Traditional ecological knowledge (TEK) in Mesoamerica offers methods of ecosystem management that integrate human subsistence, ecological restoration, and conservation. The Lacandon Maya are one group whose ecosystem management and design may be important as we work to complete large- and small-scale conservation and restoration in the area. In this study, we consider the Lacandon system in that context and describe both the system and what appear to be key design elements. Our study suggests that studies of TEK can help to bridge the gap between humans and ecosystems for the benefit of both in Latin America.

Ecosystems are being degraded rapidly in southern Mexico and in Central America. Deforestation in the biodiverse lowlands of Chiapas State in Mexico currently stands at 2% per year, which has been estimated to lead to the extinction of 22% of the plant species in this region between 1991 and 2035 (Mendoza and Dirzo 1999). In many areas of southern Mexico, land management takes the form of short-term *milpa* (herbaceous stage; O'Brien 1998) or of cattle ranching (Mas and Puig 2001, Durand and Lazos 2004), eroding and compacting the soil over time, respectively. Both forms of management limit the diversity and productivity of woody plant species (Garciaoliva et al. 1994, Durand and Lazos 2004). Following short-term crop

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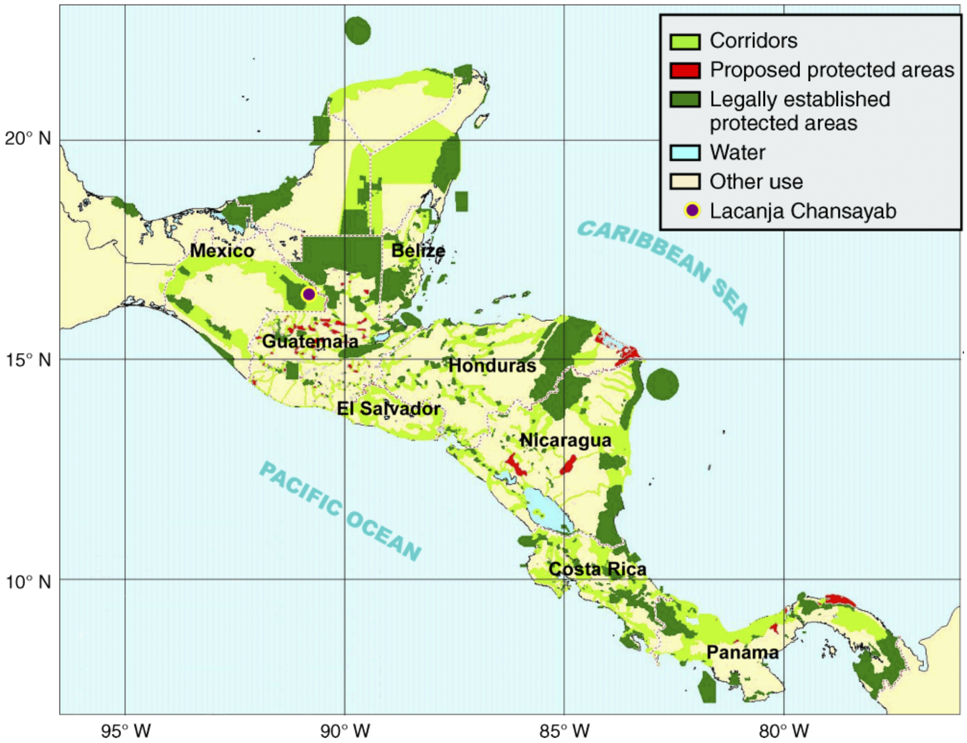

FIG. 1. The Mesoamerican Biological Corridor, showing biologically important corridors, legally established protected areas, proposed protected areas, and the study site in Lacanja Chansayab, Mexico.

and cattle production, these areas do not return to a mature, species-rich forest, but to degraded grass and brush vegetation (Ferguson et al. 2003). Such land management has severely degraded 5% and moderately degraded 10–25% of the arable land in Chiapas (Howard and Homer-Dixon 1996). Declining ecosystem health and demands on agricultural land lead to social conflict. As populations increase in size, the struggle for increasingly limited land resources will intensify future conflict (Lal 1995, Ram 1997, Álvarez and Naughton-Treves 2003).

Large-scale restoration and conservation efforts, such as the Mesoamerican Biological Corridor (MBC; Fig. 1), are complicated by the complex social and economic needs that drive ecosystem changes (Nicholson et al. 1995, Atran 1999, Mas and Puig 2001). The MBC initiative was established originally as the Paseo Pantera project in 1990, and updated to MBC in 1998, to protect 106 critically endangered species and allow for improved animal migration through Central America and southern Mexico. The MBC includes such reserves as Montes Azules Biosphere Reserve in the Lacandon rain forest of Mexico, and national parks in Belize, Guatemala, Honduras, and Costa Rica (Ray et al. 2006), but also includes extensive areas of private and community land. The complexity of the social, political, and ecological situation in Mesoamerica makes the challenges faced for completion of connections in the MBC difficult. New paradigms of conservation and restoration must be developed to move this effort toward full fruition (Rivera et al. 2002).

Research must be initiated into options that will decrease land degradation while providing for subsistence agriculture by the people who live in these areas (Nicholson et al. 1995, Foroughbakhch et al. 2001, Li 2004). Numerous researchers (Fox et al. 2000, Long and Zhou 2001, Hardwick et al. 2004) have supported TEK as a means to maintain ecosystem health and produce for agricultural subsistence. For example, indigenous swidden (periodic burn) agroforestry can be productive (Long and Nair 1999) while maintaining ecological integrity (Wang and Young 2003, Diemont and Martin 2005, Diemont et al. 2006*a*). Salafsky (1993) found when comparing agroforested to forested areas in Indonesia that >80% of mammals discovered in the forested areas used agroforested areas as well. Wang and Young (2003) saw higher migratory bird use in traditionally agroforested regions compared to nontraditionally managed areas in Yunnan, China. Harvey and González Villalobos (2007) discovered comparable bird and bat diversity in forested regions of Talamanca Reserve, Costa Rica, compared to agroforested areas surrounding the reserve. These facts support the contribution of indigenous agroforestry for better ecological management (De Clerck and Negreros-Castillo 2000, Fox et al. 2000), and it is one reason why it is important to gain a clear understanding of the sustainable traditional practices that are currently being used. This is a critical time for research into these practices in Mesoamerica because the oral traditions that preserve information related to these systems are in decline due to the increasing influence of Western culture (McGee 2002).

In this study, we examine the swidden agroforestry of the Lacandon Maya, an indigenous group who live in Chiapas Mexico, who have produced for their families' needs while conserving primary and secondary forest for centuries (Nations and Nigh 1980, Levy Tacher 2000). The Lacandon are descendents of the ancient Maya civilization, which was considered to have reached its cultural apex in Mesoamerica circa AD 800 (Nations and Nigh 1980, Sharer 1994). Our prior research indicates that the Lacandon design their system to accelerate soil fertility restoration following the first stage of their cyclical system (Diemont and Martin 2005, Diemont et al. 2006*b*). An overall assessment of the Lacandon agroforestry plant community was conducted by Nations and Nigh (1980), but the plant community was not linked to soil ecology. This study bridges that knowledge gap, and it documents changes in the system in that 25-year period.

The Lacandon swidden agroecosystem has been presented as a multistage successional system (Nations and Nigh 1980, McGee 2002, Diemont and Martin 2005) that begins with an herbaceous stage, or *milpa*, progresses to shrub, *acahual*, and then to secondary forest. Primary forest is conserved in a portion of the land. Each stage is productive for food, raw materials, or medicines. The milpa is a polyculture of as many as 20 plants, and the shrub, secondary forest, and primary forest contain over 400 species used by the Lacandon. The Lacandon plant or maintain numerous species during the shrub and forest stages that they believe accelerate forest restoration; they selectively remove species that do not meet their criteria for ecosystem health in the fallow (Diemont et al. 2006*b*). For example, one planted species, *Ochroma pyramidale*, produces unusually large quantities of leaf litter (Levy Tacher 2004, Levy Tacher and Golicher 2004) and inhibits soil biological activity (Diemont et al. 2006*b*). The Lacandon will often plant many *O. pyramidale*, even though it is of low value for immediate use, because they recognize the positive effect of *O. pyramidale* on the ecosystem. Other species protected by the Lacandon during the fallow, such as two species of Piperacae (Anaya-Lang 1979, Gupta et al. 1996, Xuan et al. 2004) and *Cecropia obtusifolia* (Perez-Guerrero et al. 2001) have cytotoxic or allelopathic properties. These findings indicate that the Lacandon may be managing for a mosaic of species to slow soil degradation during early successional stages to preserve soil organic matter (OM) for degradation in later successional stages (Diemont et al. 2006*b*). This practice would provide OM and nutrients to agricultural species and woody species production. Another species protected in the fallow, *Sapium lateriflorum*, appears to provide phosphorus to the surface soil in the form of leaf litter by root-mediated movement from the subsoil to leaves (Diemont et al. 2006*b*). It is clear that Lacandon TEK offers tools that could help restore and maintain OM in the soil.

The Lacandon Maya agroforestry system is sustainable ecological design as described by Odum et al. (1963), where the forces available from natural systems are dominant, and human design is supplementary rather than primary. Because the Lacandon rely on the regenerative capacity of nature with few outside inputs, their techniques represent a sustainable management option for restoration of tropical forests in this region (Diemont et al. 2006*a*). They seed certain plants during the fallow and eliminate others, but in general allow the system to develop without intervention, permitting forcing functions such as sun, wind, and rain to drive the system (Diemont et al. 2006*a*). Furthermore, the Lacandon system is, as Mitsch and Jorgensen (1989) described, "ecological engineering," as being designed for the benefit of both humans and the environment. At all stages of successional development, the Lacandon recover harvestable foods, medicines, and raw materials (Nations and Nigh 1980). This production does not come at the cost of ecosystem health. The Lacandon are careful and selective in their planting and harvesting to allow the system to largely self design and develop in biodiversity and complexity (Nations and Nigh 1980, Levy Tacher 2000), as evidenced by the numerous animals drawn to the richness of this ecosystem (Nations and Nigh 1980). Although the forest stages of the system have been shown to include numerous larger animals (Nations and Nigh 1980), the designed inclusion of conserved primary forest in the Lacandon system insures high biodiversity and maintains seed storage for forest regeneration (Quintana-Ascencio et al. 1996).

In this study we identified the successional stages of the Lacandon agroecosystem with the stage distinctions used in the TEK of Lacandon Maya of Lacanja Chansayab, Mexico. Although the literature to date has presented the shrub and secondary forest as two individual stages (Nations and Nigh 1980, McGee 2002, Diemont and Martin 2005), the Lacandon subdivide each of those stages into two separate stages, or a total of four stages (A. Chan K'in, M. Chan, K'in Castellanos, and Lacanja-Chansayab, *personal communication*).

Lacandon descriptions of plant community succession are comparable to the understanding of succession that is current among neotropical forest ecologists (Guariguata and Ostertag 2001); however, the Lacandon successional classifications likely predated Western science. In this study, Lacandon names for stages are used, and the design of the system as understood by the Lacandon is described. The stages are as follows: *kor*, *robir*, *jurup che*, *mehen che*, *nu kux che*, and *taman che*. Kor is the herbaceous stage, previously identified by the local Spanish term milpa. The duration of kor depends upon the intensity of management, which can vary from daily to monthly maintenance. More intensive management will maintain the land in kor for up to five years.

Robir is the first fallow shrub stage and lasts for two years. Jurup che is the second fallow shrub stage and lasts for two to three years. Together robir and jurup che were previously identified by the local Spanish term acahual. Mehen che and nu kux che are the first and second secondary forest stages, respectively. Mehen che lasts for 10 years, and nu kux che can last from five to 20 years. An intentional burn will cycle later successional stages (i.e., mehen che, nu kux che, and in some cases jurup che) back to kor.

The objectives of this study were to (1) describe the plant community in each successional stage of the Lacandon agroecosytem using traditional Lacandon Maya stage distinctions; (2) quantify differences in plant community in terms of diversity among successional stages of the Lacandon agroecosystem; (3) evaluate the soil ecology in each successional stage of the Lacandon agroecosystem; and (4) consider how Lacandon TEK could be applied toward large-scale ecological conservation efforts such as the Mesoamerican Biological Corridor (MBC).

METHODS

Soil and plant community sampling was conducted during August 2005 in Lacandon Maya agroforestry systems in Lacanja Chansayab, Mexico. Lacanja Chansayab is located at 16°56′60″ N and 91°16′60″ W and at an elevation of 500 m (Fig. 1). The soil type is Luvisol (INEGI 1982), texture is clayey, and soil pH is neutral. The surrounding ecosystem is tall moist forest, and the annual rainfall is 2500 cm (Guillen Trujillo 1998). Distinct wet and dry seasons are present; the wet season begins in June and lasts until January. Four plots each in kor, robir, mehen che, and nu kux che field stages, and two plots each in jurup che and taman che field stages were sampled based on availability in six Lacandon systems; only one complete system as described through Lacandon TEK and in the *Introduction* to this article was available. Field stages were classified by Lacandon Maya farmers.

Sampling locations in each field-stage plot were determined using a transect method, with 10 samples collected at intersections of a 20-m grid. Two nested sampling quadrats of different sizes, 1 m^2 and 20 m^2, were assessed for plant community at each sampling point. In the kor, all plants in the 1 m^2 quadrats were identified, distinguished as cultivated or non-cultivated, and percent cover was estimated. All useful species in the 20-m^2 area of the kor were counted and identified. Because the Lacandon kor is a polyculture with up to three meters distance between maize plantings, Lacandon typically plant maize seeds so that four to seven plants grow together for effective cross pollination. Maize was therefore counted as groupings rather than individual plants. In the 1-m^2 quadrats within the robir, jurup che, mehen che, nu kux che, and taman che, all plants with a basal diameter >1 cm were identified and counted. In the 20-m^2 quadrats all plants with basal diameter >5 cm were identified and counted. In the robir, jurup che, mehen che, nu kux che, and taman che, the traditional immediate use of each plant was determined from interviews with Lacandon farmers. Immediately useful species were those plants that the Lacandon use for food, medicine, firewood, construction, or raw materials. Lacandon farmers identified plant species that were useful to enhance soil fertility. Plant species biodiversity was calculated using the Shannon-Weaver technique, $H = -\sum p_i \ln(p_i)$, where p_i is the proportion of species i relative to the total number of species. Species dominance for each successional stage was calculated as the total number of stems of a species in a successional stage counted at sampling quadrats divided by the total number of stems in a successional stage counted at sampling quadrats. Species were identified by Lacandon or Spanish name and cross referenced with species lists in Nations and Nigh (1980) and Levy Tacher et al. (2002). Voucher specimens for all plants not previously collected and identified in Nations and Nigh (1980) or Levy Tacher et al. (2002) were collected and deposited in the herbarium at El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Mexico.

Within the 1-m^2 quadrat at each sampling location, the detrital layer was removed, and eight replicate 2.5 cm diameter cores were taken from 0–20 cm soil depth and pooled. Each soil sample was analyzed for organic matter (Walkley and Black 1934), total nitrogen (semi-microKjeldhal), and available phosphorus (Olsen et al. 1954). Nematodes were extracted from 20 g of the pooled soil from each sampling location for analysis. Soil samples for nematode extraction were kept cool and extracted over 72 hours using the Baermann wet funnel technique (McSorley and Welter 1991). Nematodes were heat fixed. Extract was stored in 2% formaldehyde, and all nematodes in the bottom 10 mL of extract were identified to trophic level at 90× magnification (Parmelee and Alston 1986, Edwards 1991, Arancon et al. 2003, Domínguez et al. 2003). Nematodes were identified as plant parasite, fungivore, bacterivore, and omnivore–predator trophic groups according to Parmelee and Alston (1986).

Differences among successional stages were evaluated using ANOVA. Data were first examined for normality and equal variance. Sampling locations were pooled to document patterns consistent with stage distinctions. Fischer's LSD post hoc test was used to determine the significance of multi-way comparisons. Pearson linear regression analysis was used to determine relations between two factors. Analyses were conducted using SYSTAT 10.2 computer software (SYSTAT, San Jose, California, USA).

RESULTS

Plant community

Twenty-six species or varieties were found in the kor in the 20-m^2 quadrats (Table 1). Of these plants, 18 were

TABLE 1. Useful species in the kor successional stage, their immediate uses, whether they were planted, whether Lacandon traditional ecological knowledge (TEK) credits them as enhancing soil fertility, and their relative dominance.

Plant name						
Latin binomial	Lacandon Maya	English	Immediate use	Planted	Soil-fertility enhancing	Dominance (%)
Zea mays	sak nar	white corn	food	yes		54.7
Canna indica	chan kara	Indian shot	beads for necklaces	yes		21.9
Zea mays	nar chak	red corn	food	yes		4.3
Arachis hypogaea	sikatelum	peanut	food	yes	yes	4.0
Phaseolus calcaratus	arrozbur	rice bean	food		yes	2.9
Heliconia librata	secre'k		leaf to wrap tamale	yes		1.4
Capsicum sp.	ik	pepper	food	yes		1.1
Spondias mombin	jujup	hog plum	food, lumber, firewood		yes	1.1
Saccharum officinarum	azucar	sugar cane	food	yes		0.7
Lycopersicon esculentum	p'ak	tomato	food	yes		0.7
Cucurbita moschata	k'um	crook neck squash	food	yes		0.7
Ananas comosus	p'ach	pineapple	food	yes		0.7
Allium porrum	sakekon	scallion	food	yes		0.7
Mentha piperita	xex		eat the leaf	yes	yes	0.7
Solanum americanum	ch'auk'	black nightshade	food		yes	0.4
	chakuckum		ornamental flower			0.4
Cyperus rotundus	guerux	cocograss	eat with eggs	yes		0.4
Serjania atrolineata	marxak		medicine			0.4
Carica papaya	put	papaya	fruit	yes	yes	0.4
Musa spp.	patan	banana	fruit	yes	yes	0.4
Allium cepa	sakibir	onion	food	yes		0.4
Baccharis trinervis	sisik'utz	assapeixe fino	food for wild animals, firewood		yes	0.4
Manihot esculenta	tz'inj	yucca	food	yes		0.4
	ujkuch		medicine for diarrhea	yes	yes	0.4
Lonchocarpus guatemalensis	yax bache'	turtle bone	firewood			0.4
	sak robir		firewood			0.4

Notes: Dominance was calculated as the number of stems of each species divided by the number of stems of all species in all fields of the kor. Kor is the herbaceous stage of Lacandon agroforestry systems. Empty cells in the Latin binomial column indicate plants with no translatable name.

planted by the Lacandon. Maize dominated the kor, 54% white maize and 4% red maize. A species used by the Lacandon to make bead necklaces, *Canna indica*, was the next most dominant species after maize, 22%. *C. indica* plantings were denser in the kor than were maize plantings. Whereas maize was evenly distributed in each kor, all stems of *C. indica* were found in two groups of 50 and 11 plants, and 4 m^2 and 16 m^2, respectively, at two separate kor sampling points.

In the fallow, all successional stages were dominated by useful species. In the robir, jurup che, mehen che, and nu kux che, of the most dominant species ($>3\%$ dominance), only three species were not useful to the Lacandon (Table 2). Two of these three species were discovered in the first successional stage, robir. All but one of the nine most dominant species in the taman che, primary forest, were useful. Of these species, uses included lumber for construction, medicine, flowers, food, tobacco, and food for birds. In every fallow stage, at least one species was planted.

In every fallow stage, the Lacandon believed that the majority of dominant species enhanced soil fertility. Three of the most dominant species in the robir and jurup che were identical and were believed to enhance soil fertility: *Cecropia obtusifolia*, *Piper aduncum*, and *Piper auritum*. In the mehen che and the nu kux che, the most dominant species was *Spondias mombin*, which was planted and believed to enhance soil fertility. Two of the three most dominant species were identical in the final fallow stage, nu kux che, and the primary forest, taman che. Both of these species, *Tetrorchidium rotundatum* and *Eupatorium nubigenum*, had $\sim$9% dominance in both the nu kux che and the taman che. *T. rotundatum* is used by the Lacandon for lumber and was believed to enhance soil fertility. *E. nubigenum* does not have a use and was not believed by the Lacandon to enhance soil fertility. Neither *T. rotundatum* nor *E. nubigenum* is planted.

Quantitative plant community indicators were correlated with successional stage. Plant biodiversity and richness stabilized by the second fallow stage to $\sim$0.4 (Fig. 2a) and 1.75 (Fig. 2b) species in the 20-m^2 quadrats, an increase from 0.1 ($P < 0.05$) and 0.5 ($P < 0.001$), respectively, in the robir. The percentage of species that were useful to the Lacandon was lowest in the robir ($<60\%$), increased to 80% in the jurup che, and then decreased to 65% in the nu kux che and taman che (Fig. 3a). Richness of useful species was statistically less in the robir than the jurup che, mehen che, and nu kux che ($P < 0.01$). Percentage of soil fertility enhancing species increased from 20% in the kor to between 45% and 75% in the fallow and primary forest stages ($P < 0.01$; Fig. 3b).

TABLE 2. Dominant species in the fallow (successional stages robir, jurup che, mehen che, nu kux che, and taman che), their immediate uses, whether they were planted, whether Lacandon TEK credits them as enhancing soil fertility, and their relative dominance.

Plant name					
Latin binomial	Lacandon Maya	Immediate use	Planted	Soil-fertility enhancing	Dominance (%)
Robir					
Lonchocarpus guatemalensis	yaxbache'	firewood		yes	23.8
Cecropia obtusifolia	k'o'och	tobacco, firewood		yes	14.3
Phaseolus vulgaris	bur	food		yes	9.5
Piper auritum	jover	food		yes	9.5
	sap	no use			9.5
Cedrela odorata	k'uche'	lumber, carvings	yes	yes	4.8
Piper aduncum	makurum	corn drying hut		yes	4.8
Musa sp.	put	food	yes	yes	4.8
Carica papaya	patan	food	yes	yes	4.8
Ocimum micranthum	seyen	no use			4.8
Baccharis trinervis	sisik'uts	food for wild animals, firewood			4.8
Ceiba pentandra	yax che'	clothes decoration	yes	yes	4.8
Jurup che					
Cecropia obtusifolia	k'o'och	tobacco, firewood		yes	28.6
Tetrorchidium rotundatum	mumuche'	lumber, fruit for birds, firewood		yes	16.1
Baccharis trinervis	sisik'uts	food for wild animals, firewood			16.1
Podachaenium eminens	kibok	firewood, construction		yes	10.7
	yo'o'ch su suo	birds eat the fruits		yes	10.7
Hamelia rovirosae	cha'topche	flower	yes		3.6
Bursera simaruba	chakra	medicine for diabetes	yes	yes	3.6
Piper auritum	jover	food		yes	3.6
Piper aduncum	makurum	corn drying hut		yes	3.6
Mehen che					
Spondias mombin	jujup	food, lumber, firewood	yes	yes	12.3
Lonchocarpus guatemalensis	yaxbache'	firewood			11.1
Inga pavoniana	bitz	food, firewood		yes	8.6
Tetrorchidium rotundatum	mumuche'	lumber		yes	8.6
Quercus suber	jaror	rafts, chicken pen			4.9
Podachaenium eminens	kibok	firewood, construction		yes	4.9
Pleuranthodendron lindenii	ixim che'	fruit for birds, firewood, lumber			3.7
Solanum sp.	ujkuch	firewood			3.7
Nu kux che					
Spondias mombin	jujup	food, lumber, firewood	yes	yes	16.5
Eupatorium nubigenum	sak che'	no use			9.7
Tetrorchidium rotundatum	mumuche'	lumber		yes	8.7
Dracaena sp.	banboo	construction	yes	yes	5.8
Pleuranthodendron lindenii	iximche	seeds for birds, construction			3.9
Heliocarpus appendiculatus	jarum	to make bags	yes	yes	3.9
Piper aduncum	makurum	construct corn drying hut		yes	3.9
Taman che					
Guarea glabra	sa'bajche'	firewood and carvings		yes	14.7
Tetrorchidium rotundatum	mumuche'	lumber		yes	8.8
Eupatorium nubigenum	sak che'	no use			8.8
Hamelia rovirosae	chac topche	gum, flowers	yes		5.9
Simira salvadorensis	cha'kax	medicine for skin injury		yes	5.9
Pleuranthodendron lindenii	iximche'	seeds for birds, construction		yes	5.9
Brosinum alicastrum	ox	lumber, eat the seed		yes	5.9
Tabernaemontana amygdalifolia	ton simin	gum, firewood	yes	yes	5.9
Pseudolmedia aff. *Oxyphyllaria*	tux ambar	fruit for birds, firewood, lumber			5.9

Notes: Dominance was calculated as the number of stems of each species divided by the number of stems of all species in each fallow stage. Only species with >3% dominance are shown. Robir, jurup che, mehen che, nu kux che, and taman che are the early shrub, late shrub, early secondary forest, and late secondary forest stages and primary forest, respectively, of Lacandon agroforestry systems. Empty cells in the *Latin binomial* column indicate plants with no translatable name.

Soil ecology

Soil chemical and biological characteristics changed relative to both time-since-intentional-burn and successional stage. Soil organic matter (OM; Fig. 4a) and total soil nitrogen (TN) increased with time since the intentional burn (Fig. 4b). OM doubled from 7% the first year after intentional burn to >14% 40 years after the burn ($R = 0.4$, $P < 0.001$); TN increased from a little over 0.4% to nearly 0.8% during the same period. Available soil phosphorus (AvP) did not correlate with time since burn (Fig. 4c). Successional stage had a slightly stronger correlation with soil organic matter ($R = 0.6$, $P < 0.001$; Fig. 5a) and TN ($R = 0.6$, $P < 0.001$; Fig. 5b), compared to time since intentional burn. AvP was higher in the kor than in both the robir ($P = 0.05$) and mehen che ($P = 0.01$; Fig. 5c). The jurup che had a

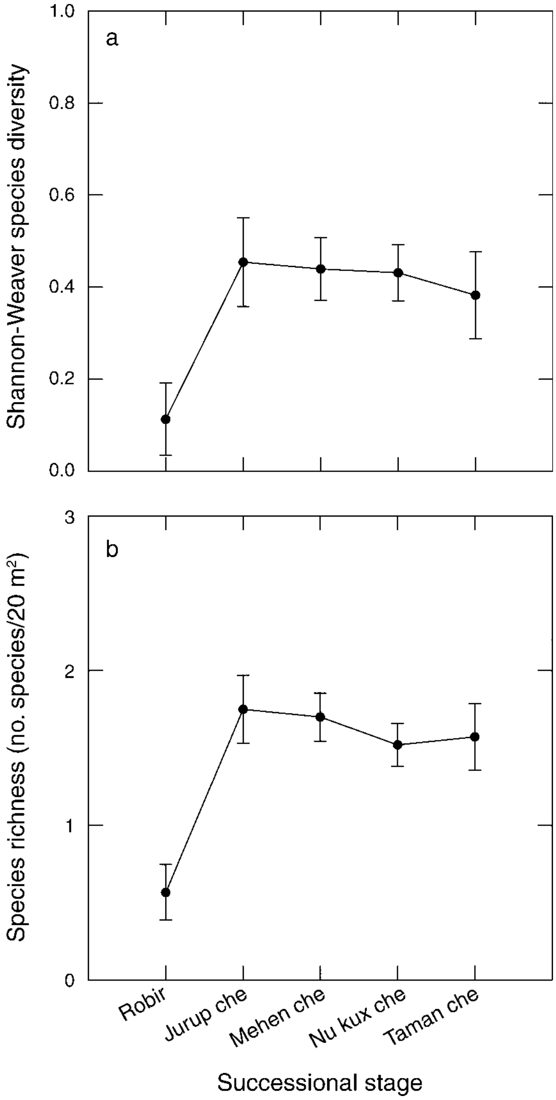

FIG. 2. (a) Shannon-Weaver plant species diversity in the 20-m^2 quadrats and (b) plant species richness in the 20-m^2 quadrats of the fallow successional stages. Error bars represent ±SE.

mean AvP >13 mg/kg, statistically equivalent to the AvP found in the primary forest and 30% higher than both the stage before, robir ($P = 0.02$), and after, mehen che ($P = 0.01$). The pattern for soil nematodes was roughly opposite to that of AvP in the first four successional stages (Fig. 6). Total soil nematode concentrations were higher in the robir and the mehen che than in the kor and the jurup che (Fig. 6a). During the fallow, bacterivore nematodes, for example, decreased by 30% from the robir to the jurup che ($P = 0.02$) and doubled between the jurup che and the mehen che ($P < 0.001$; Fig. 6b). The patterns were similar for plant parasite, fungivore, and omnivore–predator nematodes (Figs. 6c, 5d, e, respectively), which were characterized by a decrease in population concentrations during the jurup che. With the exception of the omnivore–predator nematodes, nematode community, like plant community, appeared to stabilize during later successional stages. The final fallow stages, nu kux che and taman che, were approximately equal in terms of nematode community (Fig. 6).

The presence of woody plants in the jurup che correlated with soil nematode and AvP conditions. Where plants with diameters >5 cm were present in the 20-m^2 quadrat, bacterivore nematode concentrations were found to be more than 50% lower than where woody plants were absent ($P = 0.001$; Fig. 7). Similarly,

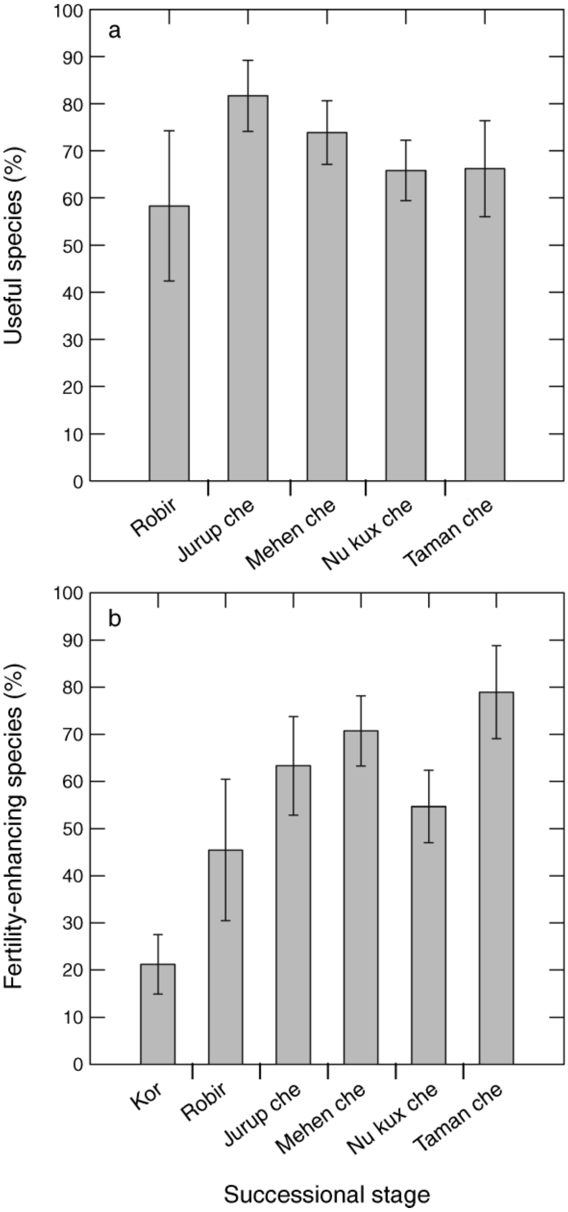

FIG. 3. Percentage of (a) useful species and (b) species considered by the Lacandon to enhance soil fertility in each successional stage. Error bars represent ±SE.

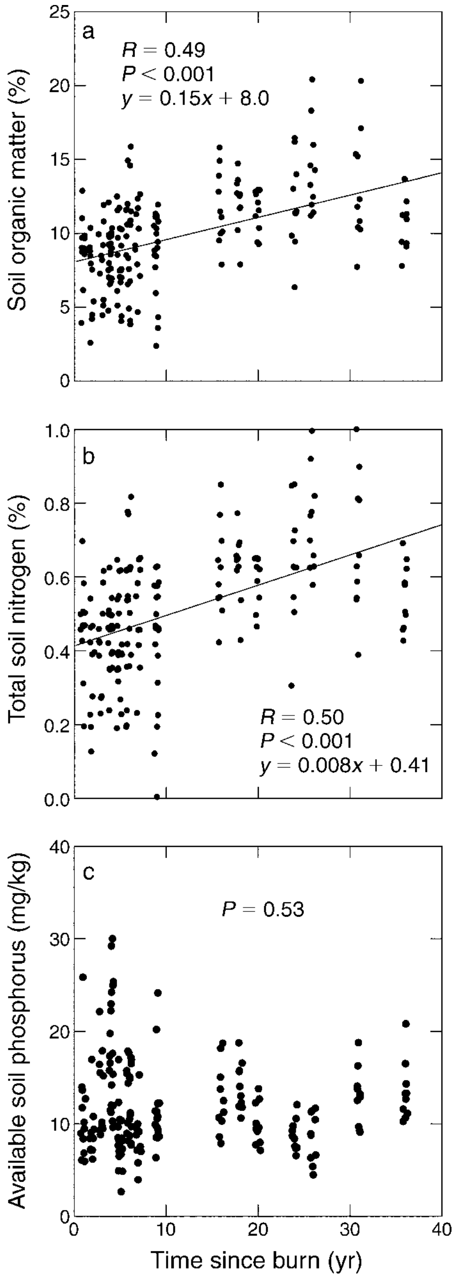

FIG. 4. (a) Soil organic matter, (b) total soil nitrogen, and (c) available soil phosphorus as a function of time since the intentional burn to prepare the fields for kor.

where woody plants were present in the 20-m^2 quadrat, AvP was found to be 50% higher than where woody plants were absent ($P < 0.001$). OM and TN did not vary with plant cover in the jurup che.

DISCUSSION

Maize was dominant in the Lacandon system, averaging over 55% of the vegetative cover of useful species in the kor (Table 1). These results are similar to findings by Nations and Nigh (1980), who discovered high species richness within maize-dominated milpas (kor). This study found fewer species than Nations and Nigh (1980), 26 compared to 56; this difference may be due in part to the transect–quadrat methodology incorporated in this study, which could have undercounted species. For example, we observed *Phaseolus vulgaris* in the kor during sampling, but this species was never within a sampling quadrat. Nonetheless, cultivat-

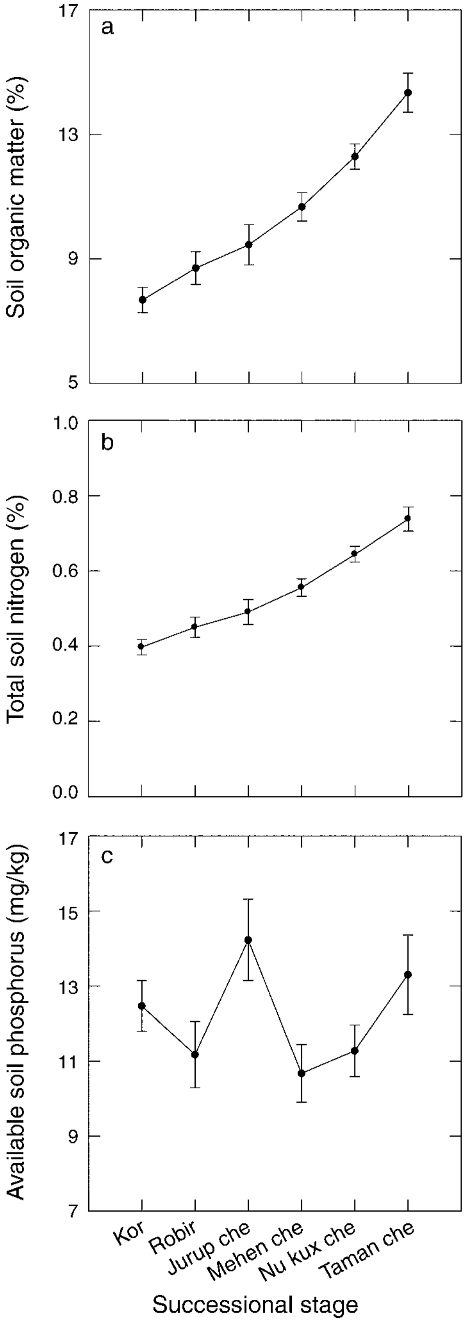

FIG. 5. (a) Soil organic matter, (b) total soil nitrogen, and (c) available soil phosphorus as a function of successional stage. Error bars represent ±SE.

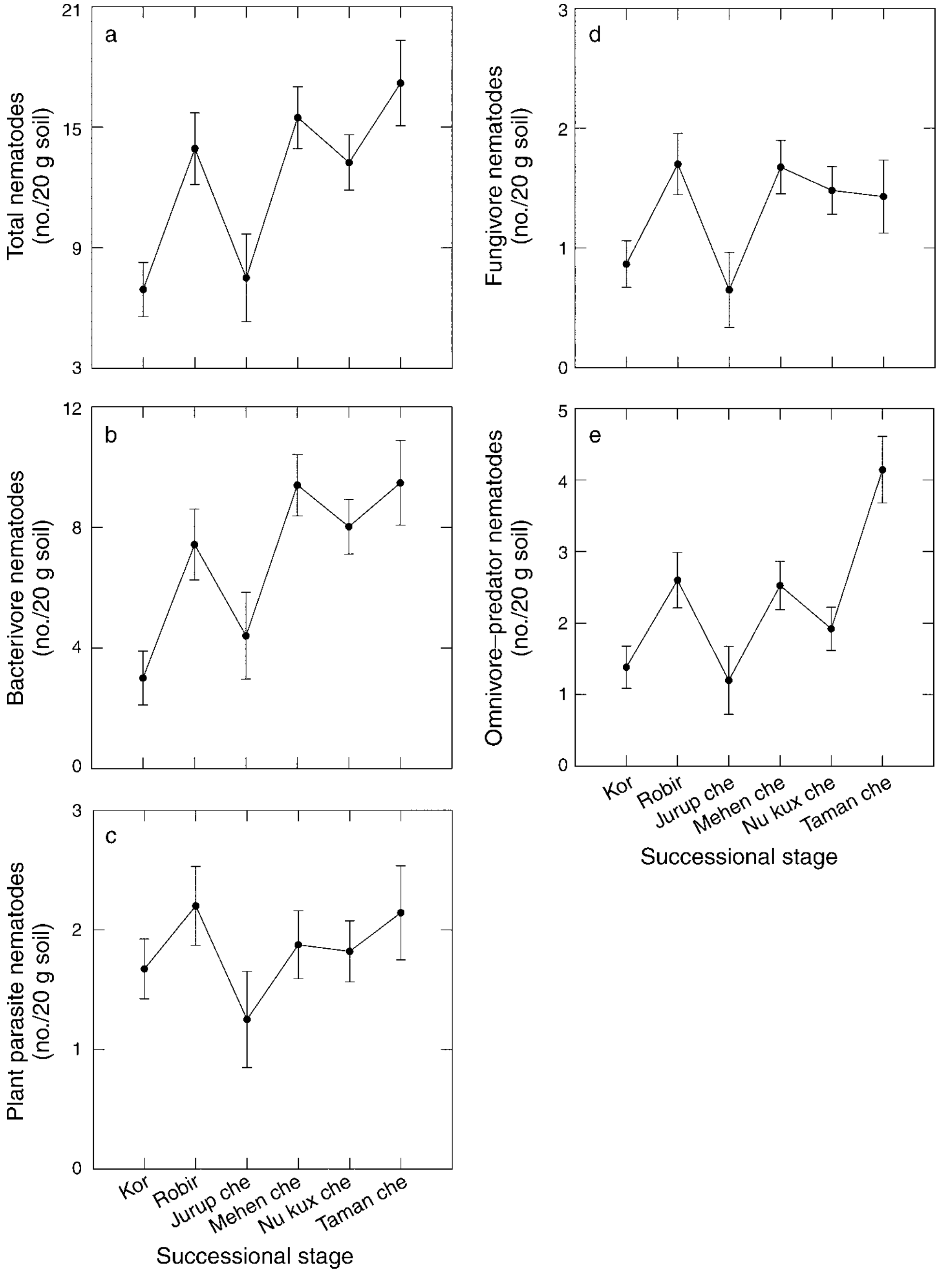

FIG. 6. (a) Total nematodes, (b) bacterivore nematodes, (c) plant parasite nematodes, (d) fungivore nematodes, and (e) omnivore–predator nematodes as a function of successional stage. Error bars represent ±SE.

ed species richness in the kor stage may be decreasing as systems change. This finding may be evidence of cultural changes that are occurring in the community, such as devoting more time to ecotourism and less time to farming (McGee 2002). The dominance of *Canna indica* is further evidence that these cultural changes could be affecting the kor. *C. indica* seeds are used to make bead necklaces, which are traditionally worn by Lacandon women, but are increasingly sold to tourists. Because maize is historically the most important crop, farmers with less time focus their efforts on its propagation at the cost of other cultivated species, but possibly have increased the production of *C. indica* to make a commercial jewelry product.

Lacandon ecological management and design results in a large number of immediately useful plants available during the fallow (Table 2). Nearly all the most dominant species, and >60% of the overall species, are

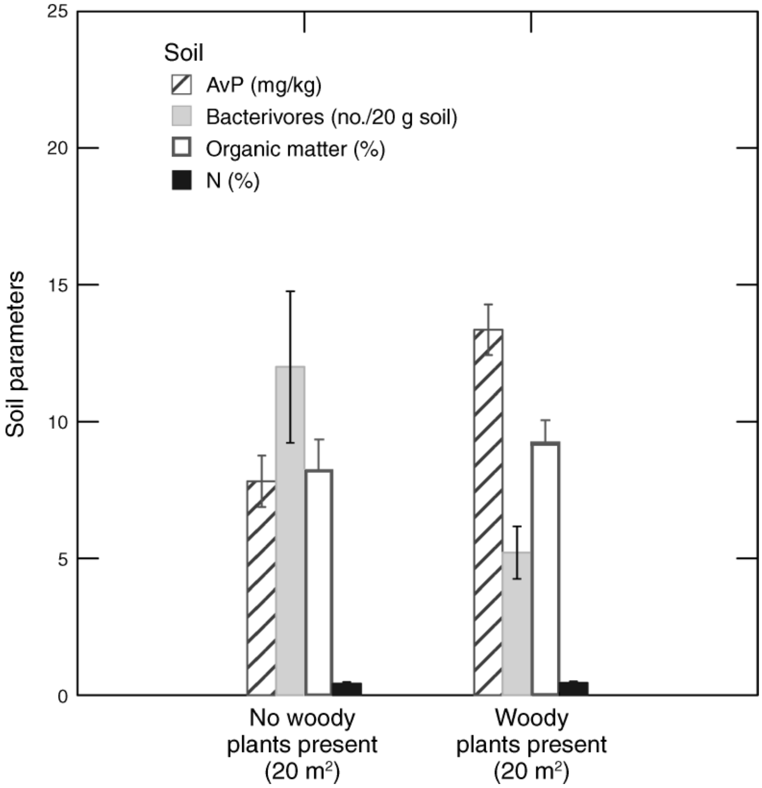

FIG. 7. Concentrations of soil available phosphorus (AvP), bacterivore nematodes, organic matter, and total nitrogen (N) in the jurup che where plants are present and not present in the 20-m^2 quadrat. Error bars represent ±SE.

useful in fallow stages. Typically the Lacandon spend one day a month in the mehen che and nu kux che, compared to almost daily activity in the kor, robir, and jurup che (Diemont et al. 2006*a*). Therefore, it is likely that the investment of work in the earlier stages, as opposed to direct work in the secondary forest, results in increased quantities of immediately useful plants in the secondary forest. In each successional stage, the most dominant species included a number of species planted by the Lacandon during the earlier successional stages. Thus, Lacandon management early in the successional process has an effect ~20 years into the future in the secondary forest. The high number of immediately useful plants in the secondary forests that provide food and raw material permit the Lacandon to maintain the system in secondary forest longer than is observed in other swidden agricultural systems (Kunstadter 1987, Speirs and Olsen 1992, Moseley 1997).

Numerous plants in each stage, including the kor, were believed by the Lacandon to enhance soil fertility (Tables 1 and 2). Previous studies have shown that the Lacandon manage fertility through selective planting and weeding (Levy Tacher 2004, Levy Tacher and Golicher 2004). That 50% or more of the most dominant species in all but the kor are thought to be useful for soil fertility enhancement is a strong indication that the Lacandon are managing for soil fertility. While the system is being maintained with present actions such as intentional plantings, it is also likely affected by historical planting and management that have modified the seed bank and forest structure. Campbell et al. (1995) and others have suggested that the makeup of the Mesoamerican forests is largely an artifact of centuries of Mayan forest engineering. It is unclear to what extent current practices affect the woody plant community, although this study gives evidence that contemporary Maya plant many dominant species (Table 2).

The increase of soil organic matter and nitrogen following the kor were positively related to both time since intentional burn (Fig. 4) and successional stage (Fig. 5), both nearly doubling in the 40 years following the burn. A greater correlation was present with successional stage than with time since intentional burn, which leads to the conclusion that soil ecology is in part affected by the management of each successional stage. The results of soil phosphorus and nematodes are further evidence of this possibility. Typically a swidden system will increase in soil phosphorus during the first 100–120 years of system recovery following the field stage (Lawrence and Schlesinger 2001), however, available soil phosphorus (AvP) in the Lacandon system did not increase linearly with age (Fig. 5c).

Plant community design may have affected soil characteristics in particular during the jurup che (Fig.

6). The presence of woody plants in the jurup che correlated with lower nematode concentrations, indicating a potential plant-mediated nematode inhibition. In other successional swidden systems, similar to the Lacandon system, fallow length appeared to increase both the abundance and diversity of nematode species (Pate et al. 2000, Villenave et al. 2001). Nematode communities have been shown to increase in number and diversity as systems develop through successional stages (Sohlenius 2002, Thornton and Matlack 2002, Hanel 2003). These changes were a function of the changing plant community that in turn affected OM and bacterial and fungal communities, nematode food sources (Thornton and Matlack 2002). Results from this study appear to partially conflict with these previous studies. Nonetheless, Diemont et al. (2006*b*) also observed soil nematode inhibition in parts of the Lacandon system related to the presence of *Ochroma pyramidale* in the fallow. Lacandon plant *O. pyramidale* in the fallow to increase soil fertility by contributing carbon through the high litter accumulation of this species. Diemont et al. (2006*b*) posited that Lacandon were intentionally slowing soil degradation with this species and with the cytotoxic and allelopathic compounds of other species (i.e., *Piper* spp.). The accumulated organic matter would then be available for later successional species. Three dominant species in the robir and jurup che are also believed by the Lacandon to enhance soil fertility: *Cecropia obtusifolia*, *Piper aduncum*, and *Piper auritum*. These species all have been shown to have potential cytotoxic and allelopathic effects (Anaya-Lang 1979, Gupta et al. 1996, Perez-Guerrero et al. 2001, Xuan et al. 2004), which may result in nematode inhibition.

The elevated AvP concentrations in the presence of woody plants in the jurup che may be due to plants pioneering nutrient-rich areas (Siemanns and Rogers 2003), or it may be due to phosphorus pumping (Perezllorens et al. 1993, Badejo 1998, Vejre and Hoppe 1998). Diemont et al. (2006*b*) reported that a Lacandon protected species, *Sapium lateriflorum*, may be providing phosphorus to the upper soil layers by root–shoot–leaf–litter transport from the lower soil layers. Although *S. lateriflorum* is not present in the jurup che, it is possible that other species protected or planted by the Lacandon to enhance soil fertility have similar functions.

By the nu kux che, 16–30 years after the intentional burn (Table 2), the plant community (Table 2, Figs. 3 and 4) and nematode community (Fig. 6) had begun to strongly resemble the primary forest, taman che. Two of the three most dominant species were found be identical between the nu kux che and taman che, an indicator that the plant community may have recovered to pre-disturbance (intentional burn) levels in, on average, 27 years. Although similarities were noted in terms of plant community, it is not clear that the nu kux che and the taman che are the same in terms of maturity. Lawrence and Schlesinger (2001) estimated that fallow recovery to achieve biomass of pre-disturbance levels would require >100 years. Saldarriaga et al. (1988) determined that species composition could not reach pre-disturbance levels in swidden systems for 200 years. Although it is possible that recovery in the Lacandon system is more rapid than other similar systems due to ecological design in the form of plant protection and plantings, it is unlikely that the Lacandon system is recovering in a quarter of the time of other similar systems. We analyzed only a few of the many parameters that would need to be evaluated to give a full assessment of similarities between stages. Other indicators such as bird and large mammal diversity and tree size were not evaluated. Nonetheless, the similarity in plant species biodiversity and richness (Fig. 2) between the later successional stages and primary forest indicates that the Lacandon systems recover rapidly, at least in species composition, if not in biomass.

Conservation and restoration efforts such as the Mesoamerican Biological Corridor (MBC) are important steps for animal and plant community preservation in Latin America and other areas with fragmented ecosystems. Nonetheless, we are far from a solution as to how to link areas that are not already parks and reserves. Depressed economic conditions exist in much of southern Mexico and Central America, the focus for the MBC. Solutions for change and for construction of the MBC need to consider those conditions as part of conservation and design.

The results of this study demonstrate that biodiversity can be maintained and restored in systems while maintaining subsistence production. In other words, farmers can grow a diverse forest that would theoretically support mammals while growing food and raw materials for their own needs. Furthermore, the Lacandon appear to be managing the plant community to accelerate soil restoration during the fallow. In particular, design for cytotoxic species inclusion in the early successional stages may maintain soil organic matter in the system for later successional species, accelerating later forest recovery or soil fertility for another farming stage. The Lacandon appear to employ these techniques to preserve soil carbon and increase soil nutrients for a future agricultural phase. The similarity between the 30-year-old secondary forest and the primary forest implies that Lacandon ecological design and management could assist restoration of degraded fields in tropical areas. Specific methods that may be useful for large-scale linkages to the MBC include (1) planting and protecting species that are useful to the farmer during the fallow, (2) planting and protecting trees in the fallow that enhance soil fertility recovery, (3) clearly distinguishing fallow developmental stages in terms of species composition for both production and fertility recovery, and (4) conserving primary forest to provide seeds and animal refuge.

This study of the Lacandon system lends credence to traditional ecological knowledge (TEK) as a tool for restoring degraded tropical forests and linking fragmented tropical forests. An urgent need exists for additional studies into animal migration in traditional swidden agroforestry and how TEK in agriculture and ecological design and management can facilitate progress in the MBC and other large-scale conservation and restoration efforts throughout the world.

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Literature Cited

Alvarez, N. L., and L. Naughton-Treves. 2003. Linking national agrarian policy to deforestation in the Peruvian Amazon: a case study of Tambopata, 1986–1997. Ambio 32: 269–274.

Anaya-Lang, A. L. 1979. Consideraciones sobre el potencial aleleopatico de la vegetacion secundaria. Pages 428–445 *in* A. Gómez-Pompa, C. Vazquez-Yanes, R. Silvia del Amo, and C. Butanda, editors. Regeneración de Selvas. México CECSA, Mexico City, Mexico.

Arancon, N., P. Galvis, C. Edwards, and E. Yardim. 2003. The trophic diversity of nematode communities in soils treated with vermicompost. Pedobiologia 47:736–740.

Atran, S. 1999. Managing the Maya commons: the value of local knowledge. Pages 190–214 *in* V. D. Nzarea, editor. Ethnoecology: situated knowledge/located lives. University of Arizona Press, Tucson, Arizona, USA.

Badejo, M. A. 1998. Agroecological restoration of savanna ecosystems. Ecological Engineering 10:209–219.

Campbell, D. G., J. Walker, V. Castillo, J. Lake, C. Ocampo-Raeder, and S. Smith. 1995. The signature of the Classic Maya Empire on Belizean tropical forests. American Association for the Advancement of Science, Atlanta, Georgia, USA.

De Clerck, F. A. J., and P. Negreros-Castillo. 2000. Plant species of traditional Mayan homegardens of Mexico as analogs for multistrata agroforests. Agroforestry Systems 48: 303–317.

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

Diemont, S. A. W, J. F. Martin, and S. I. Levy Tacher. 2006*a*. Emergy evaluation of Lacandon Maya indigenous swidden agroforestry in Chiapas, Mexico. Agroforestry Systems 66: 23–42.

Diemont, S. A. W., J. F. Martin, S. I. Levy Tacher, R. B. Nigh, P. Ramirez-Lopez, and J. D. Golicher. 2006*b*. Lacandon Maya forest management: restoration of soil fertility using native tree species. Ecological Engineering 28:205–212.

Domínguez, J., R. W. Parmelee, and C. A. Edwards. 2003. Interactions between *Eisenia andrei* (Oligochaeta) and nematode populations during vermicomposting. Pedobiologia 47:53–60.

Durand, L., and E. Lazos. 2004. Colonization and tropical deforestation in the Sierra Santa Marta, southern Mexico. Environmental Conservation 31:11–21.

Edwards, C. A. 1991. Methods for assessing populations of soil-inhabiting invertebrates. Pages 145–176 *in* D. A. Crossely, D. C. Coleman, P. F. Hendrix, W. Cheng, and C. A. Edwards, editors. Modern techniques on soil ecology. Elsevier, New York, New York, USA.

Ferguson, B. G., J. Vandermeer, H. Morales, and D. Griffith. 2003. Post-agricultural succession in the Maya lowlands. Conservation Biology 17:818–828.

Foroughbakhch, F., L. A. Hauad, A. E. Cespedes, E. E. Ponce, and N. Gonzalez. 2001. Evaluation of 15 indigenous and introduced species for reforestation and agroforestry in northeastern Mexico. Agroforestry Systems 51:213–221.

Fox, J., D. M. Truong, A. T. Rambo, N. P. Tuyen, L. T. Cuc, and S. Leisz. 2000. Shifting cultivation: a new old paradigm for managing tropical forests. Bioscience 50:521–528.

Garciaoliva, F., I. Casar, P. Morales, and J. M. Maass. 1994. Forest-to-pasture conversion influences on soil organic-carbon dynamics in a tropical deciduous forest. Oecologia 99:392–396.

Guariguata, M. R., and R. Ostertag. 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management 148:185–206.

Guillen Trujillo, H. A. 1998. Sustainability of ecotourism and traditional agricultural practices in Chiapas, Mexico. Dissertation. Environmental Engineering Sciences, University of Florida, Gainesville, Florida, USA.

Gupta, M. P., et al. 1996. Screening of Panamanian medicinal plants for brine shrimp toxicity, crown gall tumor inhibition, cytotoxicity and DNA intercalation. Pharmaceutical Biology 34:19–27.

Hanel, L. 2003. Recovery of soil nematode populations from cropping stress by natural secondary succession to meadowland. Applied Soil Ecology 22:255–270.

Hardwick, K., J. R. Healey, S. Elliott, and D. Blakesley. 2004. Research needs for restoring seasonal tropical forests in Thailand: accelerated natural regeneration. New Forests 27: 285–302.

Harvey, C., and J. González Villalobos. 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodiversity and Conservation 16: 2257–2292.

Howard, P., and T. Homer-Dixon. 1996. Environmental scarcity and violent conflict: the case of Chiapas, Mexico. Project on Environment, Population and Security, American Association for the Advancement of Science and the University of Toronto, Washington, D.C., USA.

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

Kunstadter, P. 1987. Swiddeners in transition: Lua' farmers in northern Thailand. Pages 130–155 *in* B. L. Turner, II and S. Brush, editors. Comparative farming systems. Guilford Press, New York, New York, USA.

Lal, R. 1995. Erosion–crop productivity relationships for soils of Africa. Soil Science Society of America Journal 59:661–667.

Lawrence, D., and W. H. Schlesinger. 2001. Changes in soil phosphorus during 200 years of shifting cultivation in Indonesia. Ecology 82:2769–2780.

Levy Tacher, S. I. 2000. Sucesión causada por roza-tumba-quema en las selvas de Lacanhá, Chiapas. Dissertation. Institution de Ensenanza e Investigacion en Ciencias Agricolas, Instituto de Recursos Naturales. Montecillo, Texcoco, Mexico.

Levy Tacher, S. I. 2004. El papel de *Ochroma pyramidale* Cav en la agricultura tradicional Lacandona. Report to Secretaria del Medio Ambiente y Recursos Naturales (Semarnat) of Mexico, San Cristóbal de las Casas, Mexico.

Levy Tacher, S. I., J. R. Aguirre, M. M. Martínez Romero, and A. Durán Fernandez. 2002. Caracterización del uso tradicional de la flora espontánea en la comunidad Lacandona de Lacanhá, Chiapas, México. Interciencia 27:512–520.

Levy Tacher, S. I., and J. D. Golicher. 2004. How predictive is traditional ecological knowledge? The case of the Lacandon Maya fallow enrichment system. Interciencia 29:496–503.

Li, W. H. 2004. Degradation and restoration of forest ecosystems in China. Forest Ecology and Management 201: 33–41.

Long, A. J., and P. K. R. Nair. 1999. Trees outside forests: agro-, community, and urban forestry. New Forests 17:145–174.

Long, C. L., and Y. L. Zhou. 2001. Indigenous community forest management of Jinuo people's swidden agroecosystems in southwest China. Biodiversity and Conservation 10: 753–767.

Mas, J., and H. Puig. 2001. Deforestation methods in southwestern Campeche (Mexico). Canadian Journal of Forest Research 31:1280–1288.

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

McSorley, R., and E. E. Welter. 1991. Comparisons of soil extraction methods for nematodes and micro-arthropods. Pages 201–208 *in* D. A. Crossely, D. C. Coleman, P. F. Hendrix, W. Cheng, and C. A. Edwards, editors. Modern techniques on soil ecology. Elsevier, New York, New York, USA.

Mendoza, E., and R. Dirzo. 1999. Deforestation in Lacandonia (southeast Mexico): evidence for the declaration of the northernmost tropical hot-spot. Biodiversity and Conservation 8:1621–1641.

Mitsch, W. J., and S. E. Jorgensen. 1989. Ecological engineering: an introduction to ecotechnology. Wiley, New York, New York, USA.

Moseley, W. G. 1997. A foundation for coping with environmental change: indigenous agroecological knowledge among the Bambara of Djitoumou, Mali. Pages 11–130 *in* W. M. Adams and L. J. Slikkerveer, editors. Indigenous knowledge and change in African agriculture, studies in technology and social change, No. 26. Center for Indigenous Knowledge for Agriculture and Rural Development, Iowa State University, Ames, Iowa.

Nations, J. D., and R. Nigh. 1980. Evolutionary potential of Lacandon Maya sustained-yield tropical forest agriculture. Journal of Anthropological Research 36:1–30.

Nicholson, C. F., R. W. Blake, and D. R. Lee. 1995. Livestock, deforestation, and policy-making—intensification of cattle production systems in Central America revisited. Journal of Dairy Science 78:719–734.

O'Brien, K. 1998. Sacrificing the forest: environmental and social struggles in Chiapas. Westview Press, Boulder, Colorado, USA.

Odum, H. T., W. L. Siler, R. J. Beyers, and N. Armstrong. 1963. Experiments with engineering of marine ecosystems. Pages 373–403 *in* Publications of the Institute of Marine Science. Volume 9. The University of Texas Marine Science Institute, Port Aransas, Texas, USA.

Olsen, S. R., C. V. Cole, F. S. Watanabe, and L. A. Dean. 1954. Estimation of available phosphorus in soils by extraction with sodium bicarbonate. Circular 939. U.S. Department of Agriculture, Washington, D.C., USA.

Parmelee, R. W., and D. G. Alston. 1986. Nematode trophic structure in conventional and no-tillage agroecosystems. Journal of Nematology 18:403–407.

Pate, E., N. Ndiaye-Faye, J. Thioulouse, C. Villenave, T. Bongers, P. Cadet, and D. Debouzie. 2000. Successional trends in the characteristics of soil nematode communities in cropped and fallow lands in Senegal (Sonkorong). Applied Soil Ecology 14:5–15.

Perez-Guerrero, C., M. D. Herrera, R. Ortiz, M. A. de Sotomayor, and M. A. Fernandez. 2001. A pharmacological study of *Cecropia obtusifolia* Bertol aqueous extract. Journal of Ethnopharmacology 76:279–284.

Perezllorens, J. L., P. Devisscher, P. H. Nienhuis, and F. X. Niell. 1993. Light-dependent uptake, translocation and foliar release of phosphorus by the intertidal seagrass *Zostera noltii* Hornem. Journal of Experimental Marine Biology and Ecology 166:165–174.

Quintana-Ascencio, P. F., M. Gonzalez-Espinosa, N. Ramirez-Marcial, G. Dominguez-Vazquez, and M. Martinez-Ico. 1996. Soil seed bank and regeneration of tropical rain forest from milpa fields at the Selva Lacandona, Chiapas, Mexico. Biotropica 28:192–209.

Ram, R. 1997. Tropics and economic development: an empirical investigation. World Development 25:1443–1452.

Ray, D. K., R. M. Welch, R. O. Lawton, and U. S. Nair. 2006. Dry season clouds and rainfall in northern Central America: implications for the Mesoamerican Biological Corridor. Global and Planetary Change 54:150–162.

Rivera, V. S., P. M. Cordero, I. A. Cruz, and M. F. Borras. 2002. The Mesoamerican Biological Corridor and local participation. Parks 12:42–54.

Salafsky, N. 1993. Mammalian use of a buffer zone agroforestry system bording Gunung Palung National Park, West Kalimantan, Indonesia. Conservation Biology 7:928–933.

Saldarriaga, J. C., D. C. West, M. L. Tharp, and C. Uhl. 1988. Longterm chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. Journal of Ecology 76:939–958.

Sharer, R. J. 1994. The ancient Maya. Fifth edition. Stanford University Press, Stanford, California, USA.

Siemanns, E., and W. E. Rogers. 2003. Changes in light and nitrogen availability under pioneer trees may indirectly facilitate tree invasions of grasslands. Journal of Ecology 91:923–931.

Sohlenius, B. 2002. Influence of clear-cutting and forest age on the nematode fauna in a Swedish pine forest soil. Applied Soil Ecology 19:261–277.

Speirs, M., and O. Olsen. 1992. Indigenous integrated farming systems in the Sahel. World Bank Technical Paper Series Number 179, Africa Technical Department Series, Washington, D.C., USA.

Thornton, C. W., and G. R. Matlack. 2002. Long-term disturbance effects in the nematode communities of south Mississippi woodlands. Journal of Nematology 34:88–97.

Vejre, H., and C. Hoppe. 1998. Distribution of Ca, K, Mg, and P in acid forest soils in plantations of *Picea abies*—evidence of the base-pump effect. Scandinavian Journal of Forest Research 13:265–273.

Villenave, C., T. Bongers, K. Ekschmitt, D. Djigal, and J. L. Chotte. 2001. Changes in nematode communities following cultivation of soils after fallow periods of different length. Applied Soil Ecology 17:43–52.

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

Wang, Z. J., and S. S. Young. 2003. Differences in bird diversity between two swidden agricultural sites in mountainous terrain, Xishuangbanna, Yunnan, China. Biological Conservation 110:231–243.

Xuan, T. D., T. Eiji, T. Shinkichi, and T. D. Khanh. 2004. Methods to determine allelopathic potential of crop plants for weed control. Allelopathy Journal 13:149–164.