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Secondary Succession and Indigenous Management in Semideciduous Forest Fallows of the Amazon Basin[1]

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ABSTRACT

To the discussion on secondary succession in tropical forests, we bring data on three under-addressed issues: understory as well as overstory changes, continuous as opposed to phase changes, and integration of forest succession with indigenous fallow management and plant uses. Changes in vegetation structure and species composition were analyzed in secondary forests following swidden agriculture in a semideciduous forest of Bolivian lowlands. Twenty-eight fallows, stratified by four successional stages (early = 1–5 yr, intermediate = 6–10 yr, advanced = 12–20 yr, and older = 22–36 yr), and ten stands of mature forests were sampled. The overstory (plants $\geq$5 cm diameter at breast height [DBH]) was sampled using a 20 × 50 m plot and the understory (plants <5 cm DBH) in three nested 2 × 5 m subplots. Semistructured interviews provided information on fallow management. Canopy height, basal area, and liana density of the overstory increased with secondary forest age. The early stage had the lowest species density and diversity in the overstory, but the highest diversity in the understory. Species composition and abundance differentiated mature forests and early successional stage from other successional stages; however, species showed individualistic responses across the temporal gradient. A total of 123 of 280 species were useful with edible, medicinal, and construction plants being the most abundant for both over- and understories. Most of *Los Gwarayo* preferred mature forests for making new swidden, while fallows were valuable for crops, useful species, and regenerating timber species.

RESUMEN

Presentamos datos sobre tres temas poco atendidos sobre la sucesión secundaria en los bosques tropicales: cambios en el sotobosque y el dosel, cambios continuos en vez de fases sucesionales, e integración de la sucesión con manejo indígena y usos de plantas. Se analizaron los cambios en la estructura de la vegetación y de la composición de especies en bosques secundarios, provenientes de la agricultura migratoria, de bosques semicaducifolios en las tierras bajas de Bolivia. Se muestrearon veintiocho barbechos, ordenados en cuatro estados sucesionales (temprano = 1–5 años, intermedio = 6–10, avanzado = 12–20 y tardío = 22–36), y 10 parcelas de bosque maduro. El dosel (plantas $\geq$ 5 cm dap) fue muestreado en parcelas de 20 × 50 m y el sotobosque (plantas < 5 cm diámetro) en tres subparcelas anidadas de 2 × 5 m. Entrevistas semi-estructuradas informaron sobre el manejo indígena. La altura del dosel, el área basal y la densidad de lianas incrementaron en el dosel con la edad del bosque. El estado sucesional temprano presentó la menor riqueza y diversidad de especies para el dosel, pero la más alta diversidad en el sotobosque. La composición de especies y la abundancia de individuos diferenciaron a los bosques maduros y el estado sucesional temprano de los otros estados; sin embargo, las especies tuvieron respuestas individuales en el gradiente temporal. Un total de 123 de las 280 especies fueron útiles, con plantas comestibles, medicinales y para construcción como las más abundantes en el dosel y sotobosque. La mayoría de Los Gwarayo prefirió bosques maduros para establecer nuevas chacras mientras que los barbechos fueron valiosos para cultivar, para plantas útiles, y para la regeneración de especies maderables.

Key words: Amazon basin; Bolivian lowlands; indigenous fallow management; individualistic response; Los Gwarayo; secondary succession; semideciduous forest; understory diversity.

RECENT REVIEWS OF TROPICAL FOREST SUCCESSION (*e.g.*, Finegan 1996, Guariguata & Ostertag 2001) emphasized ecological processes, neglecting integration of indigenous agriculture and fallow management (Denevan & Padoch 1987) with secondary forest succession. These two processes are inextricably linked, as indigenous people intensively utilize secondary forests (Denevan & Treacy 1987, Salick 1992, Chazdon & Coe 1999) and can alter the course of natural succession by planting, transplanting, protecting, weeding, or selecting desirable species (Irvine 1989). Furthermore, most studies concentrate on trees and ignore the understory, although many of the products harvested from secondary forests occur there (Salick *et al.* 1995). Finally, most studies stress stages in secondary forest succession, rather than continuous and individualistic species responses to succession (Peet & Christensen 1980).

In Bolivia, indigenous communities still maintain a strong relationship with lowland forests (Toledo & Vroomans 2001). One of these communities is the ethnic group *Los Gwarayo*, who for generations have managed forests and cultivated land with a complex swidden–fallow cycle (Weber 1994). Here, we evaluate secondary forest succession and fallow management by *Los Gwarayo* people across a chronosequence from 1 to 36 yr in a subhumid transitional forest in the Bolivian lowlands. Specifically, we analyzed the plant community structure, species density and diversity, floristic composition, and useful plant species in both over- and understories of different-aged fallows as well as mature forests.

METHODS

STUDY AREA AND PEOPLE.—Field research was conducted in Salvatierra, a village located along the Río Negro (15°30′08″S, 63°01′33″W), Guarayos province, department of Santa Cruz (Fig. 1) at 250 m elevation. Mean annual temperature and rainfall

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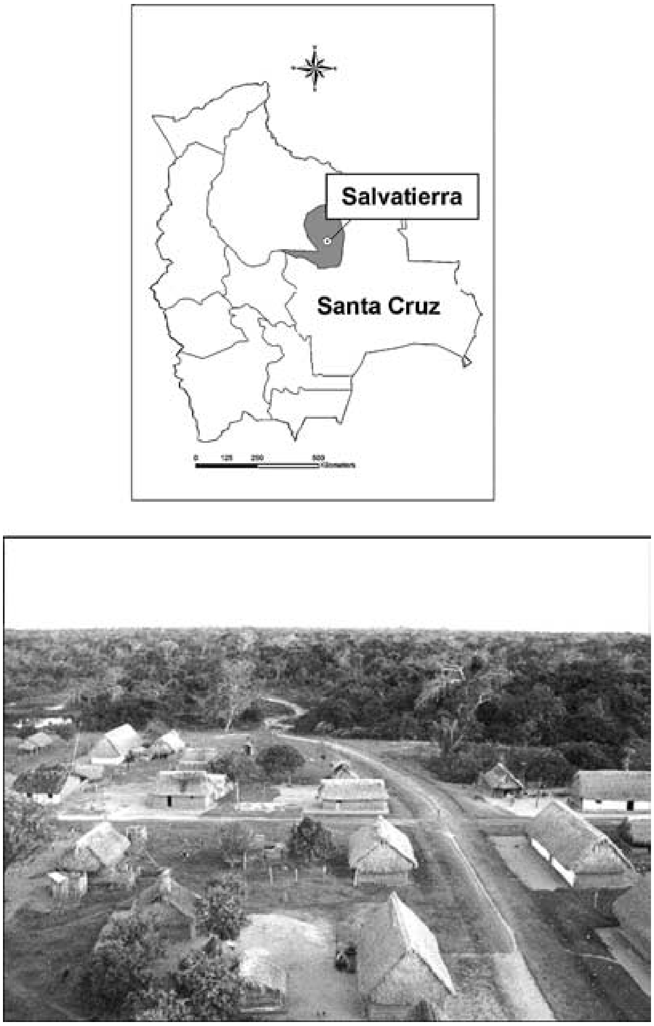

FIGURE 1. Salvatierra village of *Los Gwarayo*, Guarayos province, department of Santa Cruz, Bolivia.

are 25°C and 1200 mm, respectively. There is a warmer/wetter period from October to March (CEASE 2001). Guarayos province is located on two morphostructural geological units—the Precambrian Brazilian Shield in the east and the Chaco-Benian floodplain in the west—with a slightly undulated topography (Guamán 1983, Ballivian & Rojas 1993). The forest is subhumid within an ecotone between northern Amazonian forests and southern dry forests (Beck *et al.* 1993).

Salvatierra is a small village founded in 1938 that still maintains its native language (Gwarayu), which is very similar to the Guaraní from Paraguay. *Los Gwarayo* manage and use the land based on communal ownership. Traditional resource management systems consist of swidden agriculture, hunting, fishing, animal husbandry, and gathering forest products. Recently, a community forestry project with technical support from the Bolivian Sustainable Forestry Project has been established (Cronkleton 2002, Putz *et al.* 2004). The swidden annual cycle is adapted to the seasonality of the climate. Swiddens and different-aged fallows are located within a radius of 7 km and mature forests begin at 8 km from the center of the village.

STUDY DESIGN.—Fieldwork was conducted during the dry season (May–July) of 2003. An initial meeting was held with local authorities to explain the objectives of the study and to receive prior informed consent. Two men with broad knowledge of fallow and mature forests were selected as principal informants to assist with both ecological sampling and ethnobotanical studies. From a map sketched by village informants, sampled stands were selected at random; fallow age was obtained from the most recent swidden farmer.

We sampled 38 stands: 28 fallow stands, between 1 and 36 yr since cultivation, and 10 mature forest (MF) stands. Stands were at least 0.5 km distant from each other to assure independence. Samples were stratified by four successional stages (Fig. 2): early stage (ES) = 1–5 yr since cultivation, intermediate stage (IS) = 6–10 yr, advanced stage (AS) = 12–20 yr, and older stage (OS) = 22–36 yr, with seven repetitions in each stage. The term "mature forest" in this study is relative, since forest age and human influences are unknown.

DATA COLLECTION.—In each stand, a 20 × 50 m plot was randomly established to inventory trees and lianas $\geq$5 cm diameter at breast height (DBH at 130 cm) (henceforth overstory). Within this larger plot, three nested subplots 2 × 5 m were randomly established to inventory abundance and identity of regenerating saplings, herbs, shrubs, and climbers (herbaceous and small woody) $<$5 cm DBH (henceforth understory); the three subplots were pooled by stand for analysis. Voucher specimens were identified and deposited in the Museum of Natural History Noel Kempff M. (Santa Cruz, Bolivia) and at the Missouri Botanical Garden (St. Louis, MO, U.S.A.) (Collections M. Toledo 1497–1719). The two principal informants provided local plant names and uses.

In addition, semistructured interviews about fallow management were conducted with 48 of the 54 households of Salvatierra. At the conclusion of the fieldwork, another meeting was arranged with the community to present and discuss preliminary results and to obtain additional information about useful plants.

DATA ANALYSIS.—Canopy height (estimated), total basal area, plant density, growth form density, species density, and Shannon diversity index (H') were calculated for each plot. Parametric data were analyzed with one-way and two-way analysis of variance (ANOVA) and multivariate analysis of variance (MANOVA; Zar 1999, Field 2000). For each statistical analysis, we conducted a Levene test of homogeneity of variance, and data were log-transformed as needed. Statistical differences among groups were tested with the Tukey test for multiple comparisons. For the Shannon diversity index (H'), the nonparametric Kruskal–Wallis test was applied. Because of the large number of statistical tests, only results with $P < 0.005$ were considered statistically significant (Rice 1990, Moran 2003). All statistical analyses were performed with SPSS 12.0 for Windows (SPSS Inc. 2003).

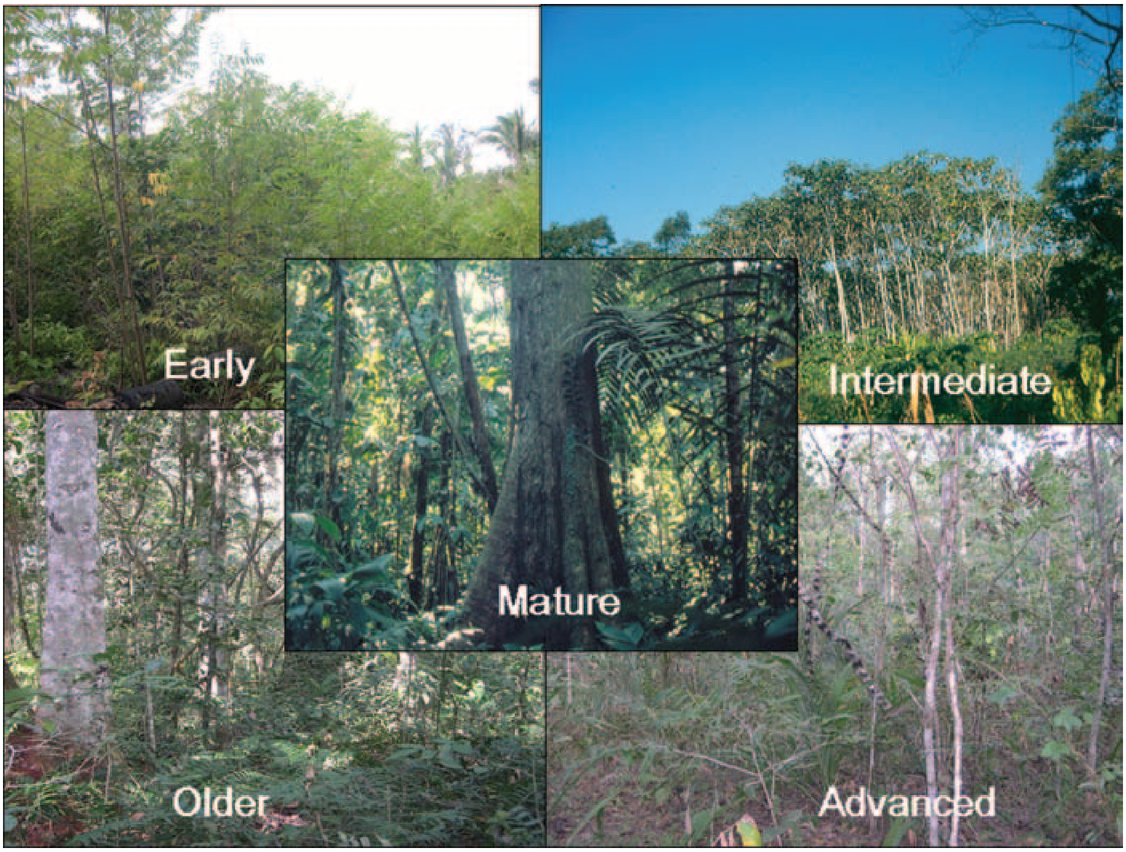

FIGURE 2. Successional stages defined as early (ES = 1–5 yr), intermediate (IS = 6–10 yr), advanced (AS = 12–20 yr), and older (OS = 22–36 yr), and mature forest (MF).

Bray–Curtis ordination (Beals 1984), based on species composition and abundance of only species with $\geq$5 individuals, was performed with PC–Ord 4 (McCune & Mefford 1999). For ordination, we used Sørensen distance measure and variance–regression endpoint selection with general relativization by plots. The Sørensen's Similarity Index (Sørensen 1948) and Importance Value Index (IVI = Σ relative cover, relative density, and relative frequency) were also calculated (Cain *et al.* 1956).

RESULTS

FOREST STRUCTURE.—Mean canopy height increased significantly among successional stages (Table 1; ANOVA, $F_{4,33} = 7.7$, $P = 0.0001$). Similarly, the total basal area of the overstory increased from 2.9 m^2/ha in the early stage to 21.6 m^2/ha in mature forests (ANOVA, $F_{4,33} = 13.9$, $P = 0.0001$). However, plant density of overstory and understory was not different among successional stages. Tree density was significantly different for diameter categories by successional stages (Fig. 3; two-way ANOVA, $F_{19,132} = 9.3$, $P = 0.0001$). Diameter categories were different (ANOVA, $F_{3,132} = 45.9$, $P = 0.0001$), whereas successional stages and their interaction were not.

Growth forms in the overstory differed among successional stages (Table 2; MANOVA, Wilks' Lambda value = 228, $F_{16,92.3} = 3.6$, $P = 0.0001$). This result was attributable to differences in large liana density increasing from secondary to mature forests ($F_{4,33} = 8.7$, $P = 0.0001$), and probably due to growth in size of early-established individuals.

In the understory, herbs and tree seedlings differed among successional stages (Table 2; MANOVA, Wilks' Lambda value = 0.17, $F_{24,98.9} = 2.7$, $P = 0.0001$). Herb density decreased in mature forests ($F_{4,33} = 4.9$, $P = 0.003$). Tree seedlings were most abundant in the early successional stage and mature forest ($F_{4,33} = 5.3$, $P = 0.002$).

SPECIES DENSITY AND DIVERSITY.—Species density differed among successional stages only in the overstory (Table 1; ANOVA, $F_{4,33} = 16.1$, $P = 0.0001$). In the overstory, the lowest species density occurred in the early stage and increased with fallow age; species density was highest in later successional stages (AS 12–20 yr and OS 22–36 yr) and mature forests. Diversity differed significantly among successional stages in both the overstory (Table 1; Kruskal–Wallis, $\chi^2_4 = 23$, $P = 0.0001$) and the understory (Kruskal–Wallis, $\chi^2_4 = 16.9$, $P = 0.002$). The youngest stage had the lowest diversity in the overstory and the highest diversity in the understory, while the

TABLE 1. *Canopy height, total basal area, plant density, species density, and diversity for the over- (≥5 cm DBH) and understories (<5 cm DBH) of different-aged secondary forests. Data are mean ± SE from seven stands for each successional stage: early (ES), intermediate (IS), advanced (AS), and older (OS), and from ten stands for mature forest (MF). Significant Tukey test results for pair-wise comparisons are labeled with letters; NS = nonsignificant with P > 0.001 (adjusted for multiple tests).*

					Overstory species		Understory species	
Successional stages	Canopy height (m)	Overstory total basal area (m^2/ha)	Overstory density (# ind./0.1 ha)	Understory density (# ind./30 m^2)	Sp. density (S)	Diversity (H')	Sp. density (S)	Diversity (H')
ES (1–5 yr)	5.7 ± 0.5^a	2.9 ± 1.2^a	55.4 ± 17.1	239.4 ± 38.1	7.0 ± 0.9^a	5.2	33.1 ± 1.7	33.7
IS (6–10 yr)	8.6 ± 0.9^b	8.9 ± 1.9^{ab}	105.4 ± 20.0	292.0 ± 32.1	16.7 ± 1.7^b	13.3	29.9 ± 1.5	15
AS (12–20yr)	8.6 ± 0.9^b	12.7 ± 2.5^b	82.7 ± 8.7	314.7 ± 32.3	23.6 ± 2.6^{bc}	20.2	30.1 ± 1.8	10.9
OS (22–36 yr)	8.8 ± 0.4^b	12.2 ± 1.1^b	75.9 ± 7.1	232.4 ± 8.6	26.6 ± 2.3^c	28.6	30.1 ± 2.4	18.7
MF	10.5 ± 0.4^b	21.6 ± 2.1^c	69.5 ± 4.6	222.4 ± 8.6	23.6 ± 1.7^{bc}	27	25.1 ± 1.6	19.3
P value	0.0001	0.0001	NS	NS	0.0001	0.0001	NS (0.03)	0.002

overstory was most diverse in old succession and the understory was least diverse in advanced succession.

FLORISTIC COMPOSITION.—The influence of succession on floristic composition and species abundance of the overstory is presented by ordination (Fig. 4a). The Bray–Curtis ordination accounted for 26.4 percent of the variation on the first axis and distinguished mature forests, with the oldest fallow (36 yr) clearly separated from successional stages (ANOVA, $F_{4,33} = 50.2$, $P = 0.0001$). The oldest fallow had plant species similar to mature forest (*Pseudolmedia laevis* and *Licaria triandra*) and it did not have *Cecropia* individuals. The second axis explained only 9.3 percent of the variation, separating early stands from other successional stages (ANOVA, $F_{4,33} = 12.8$, $P = 0.0001$) due to *Trema micrantha* abundance in the early stage.

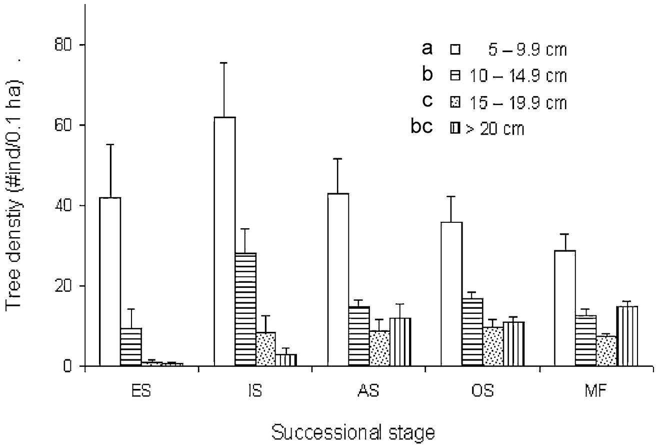

FIGURE 3. Tree density of the overstory (≥5 cm DBH) for four tree size categories in different-aged secondary forests. Data are mean ± SE from seven stands for each of the successional stages: Early (ES = 1–5 yr), intermediate (IS = 6–10 yr), advanced (AS = 12–20 yr), and older (OS = 22–36 yr), and ten from mature forest (MF). Significant Tukey test results for pair-wise comparisons among size classes are labeled with letters.

Similar floristic patterns were found in the understory's successional stages (Fig. 4b). The variation explained by the first two axes of the ordination was 33.8 percent (axis 1 = 24.1%, axis 2 = 9.7%). Mature forests and early stages were separated from other successional stages (ANOVA, axis 1, $F_{4,33} = 24.4$, $P = 0.0001$; axis 2, $F_{4,33} = 7.7$, $P = 0.0001$). Plant species such as *Iresine diffusa, Axonopus compressus,* and *Conyza bonarienses* had the highest abundance in early stages, while *Bolbitis serratifolia* and *Piper aleyreanum* were most abundant in mature forests.

Species distribution of the overstory (Fig. 5a, Table 3) and understory (Fig. 5b, Table 3) showed individualistic responses during succession. Similarities of floristic composition between stands varied largely as expected among successional stages: secondary forests with similar ages tended to be more similar in floristic composition than those separated by two or more stages.

USEFUL PLANT SPECIES.—A total of 123 species (44% of all species) were considered useful by *Los Gwarayo*, and 30 species had more than one use. The overstory had 52 percent (82 of 157) and the understory 43 percent (98 of 226) useful species. The highest percentage of useful plants was found in the youngest stage for both overstory (72%) and understory (50%).

In the overstory, species density of useful plants differed among successional stages and use categories (Table 4; two-way ANOVA, $F_{29,198} = 10.6$, $P = 0.0001$). Useful species density was lower in the youngest stands, increased with successional stage, and declined again in mature forests ($F_{4,198} = 31.2$, $P = 0.0001$). The overstory had significantly more edible, medicinal, and construction plant species than those plants used for other purposes ($F_{5,198} = 28.8$, $P = 0.0001$).

In the understory, useful species density also differed among successional stages and use categories (Table 4; two-way ANOVA, $F_{29,198} = 9.7$, $P = 0.0001$). Most useful species were found in early and later successional stages ($F_{4,198} = 9.6$, $P = 0.0001$). Medicinal,

TABLE 2. *Plant density for growth forms of the overstory (mean of the number of individuals/0.1 ha ± SE) and the understory (mean of the number of individuals/30 m^2 ± SE) in early (ES), intermediate (IS), advanced (AS), and older (OS) successional stages and mature forests (MF) in the Bolivian lowlands. Significant Tukey test results for pair-wise comparison are labeled with letters. NS = nonsignificant with $P > 0.001$ (adjusted for multiple tests).*

Overstory (≥5 cm DBH)

Successional stages	Growth form			
	Tree	Palm	Shrub	Liana
ES (1–5 yr)	52.4 ± 17.3	2.7 ± 1.3	0.3 ± 0.2	0^{a}
IS (6–10 yr)	97.0 ± 20.5	4.1 ± 1.1	4.0 ± 1.5	0.3 ± 0.2^{a}
AS (12–20 yr)	71.0 ± 8.2	4.3 ± 0.9	6.9 ± 4.6	0.6 ± 0.2^{a}
OS (22–36 yr)	69.0 ± 7.9	3.0 ± 1.0	1.0 ± 0.8	2.9 ± 1.1^{a}
MF	53.7 ± 5.6	8.5 ± 1.5	0.2 ± 0.1	7.1 ± 1.6^{b}
P value	NS	NS (0.01)	NS	0.0001

Understory (<5 cm DBH)

Successional stages	Growth form					
	Tree	Palm	Shrub	Climber	Fern	Herb
ES	48.9 ± 6.8^{a}	7.1 ± 1.6	15.0 ± 6	31.6 ± 7.3	24.6 ± 8.5	112.1 ± 24.9^{ab}
IS	27.7 ± 3.7^{b}	4.4 ± 1.4	7.3 ± 2.1	25.4 ± 5.2	47.6 ± 10.7	179.3 ± 33.5^{a}
AS	19.6 ± 2.7^{b}	7.0 ± 2.1	9.0 ± 2.4	26.3 ± 2.7	41.7 ± 21.6	211.1 ± 40.5^{a}
OS	25.4 ± 4.1^{b}	4.8 ± 1.9	2.6 ± 0.9	29.0 ± 6.3	46.7 ± 9.5	123.9 ± 13.5^{ab}
MF	37.2 ± 5.1^{ab}	5.3 ± 1.0	2.6 ± 0.8	10.5 ± 1.2	92.3 ± 15.3	74.1 ± 9.9^{b}
P value	0.002	NS	NS (0.02)	NS (0.01)	NS (0.02)	0.003

edible, construction, and other use categories had the highest species density ($F_{5,198} = 42.6$, $P = 0.0001$).

INDIGENOUS FALLOW MANAGEMENT.—Indigenous swidden agriculture of *Los Gwarayo* people of Salvatierra creates a complex land use mosaic including field rotations, different-aged fallows, and sections of mature forests. Swiddens are prepared from either mature forests or less frequently older fallows. Most of *Los Gwarayo* mentioned that they prefer mature forests (83%) because weeds are fewer and productivity higher. However, some people prefer fallows (13%) because smaller trees take less time to cut and fallows are closer to the village than the mature forests. *Los Gwarayo* clearly recognize that fallows start immediately when they stop tending crops (especially by weeding). They usually leave fallows from 5 to 10 yr before another cropping cycle. Crops remain in younger fallows, especially fruit trees such as mango, citrus (50% of people), and *Inga* species (other crops include plantain 58%, manioc 31%, banana 12%, and sugarcane 12%). Native useful plants like palms are protected as long as they produce fruit. Fallows can be managed by weeding, implanting, maintaining useful plants, and experimenting with new species and crops. *Los Gwarayo* consider fallows valuable for supplying crops (79% of people) and other useful species (23%), for regenerating timber species (9%), and for preparing new swiddens (52%).

DISCUSSION

Many of our results on forest structure, species density and diversity, and floral composition are comparable with the growingly robust generalizations on tropical secondary succession (*e.g.,* Finegan 1996, Guariguata & Ostertag 2001, DeWalt *et al.* 2003). These similarities in themselves suggest that *Los Gwarayo* are observably managing secondary forest succession. How much comparable human impact are other secondary forests with similar succession patterns experiencing? Nonetheless, at least three exceptional patterns in our study are worth particular note. In studying tropical secondary succession, few researchers have gathered appropriate data on understory as well as overstory changes, on continuous rather than phase change, or on the integration of succession with indigenous fallow management and plant uses. These are extremely important issues when considering the human dimensions of biodiversity as well as theory.

UNDERSTORY SUCCESSION.—Although most of the successional patterns that we observed in the overstory have been described elsewhere, the understory responded very differently to succession, as did human use of the understory. The highest species diversity in the understory of Guarayos was obtained in the youngest successional stage. This pattern was also observed by Salick *et al.* (1995), who noted that high density in younger secondary forests is due both

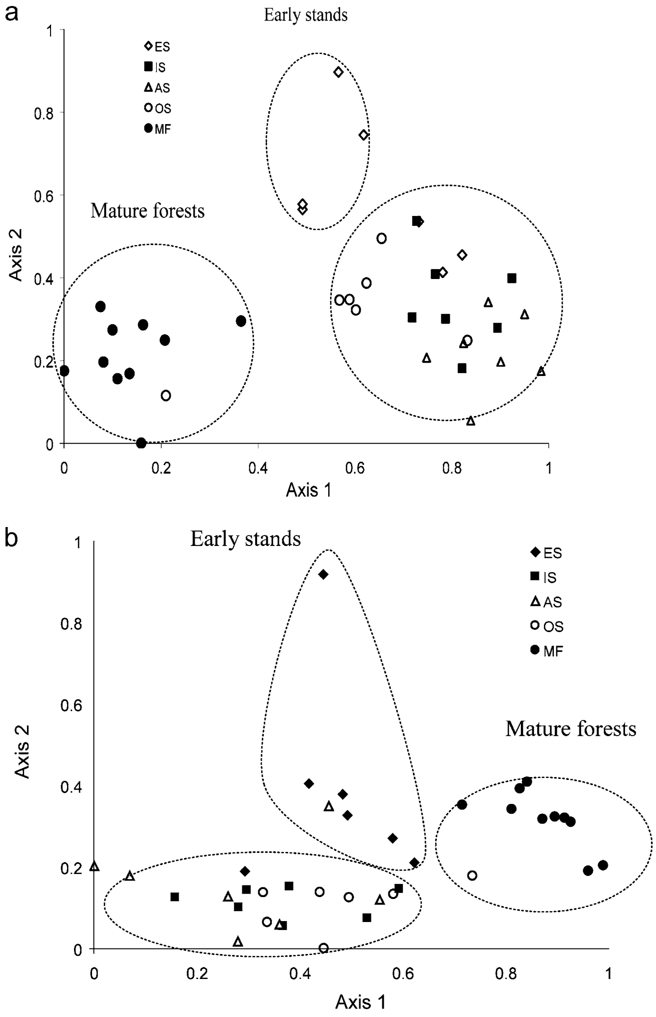

FIGURE 4. Bray–Curtis ordinations of (a) overstory species ($\geq$5 cm DBH) and (b) understory species ($<$5 cm DBH) in successional forests in the Bolivian lowlands. Forest stands are plotted according to their scores along the first two axes of the ordination. Successional stages are early (ES = 1–5 yr), intermediate (IS = 6–10 yr), advanced (AS = 12–20 yr), and older (OS = 22–36 yr), and mature forest (MF).

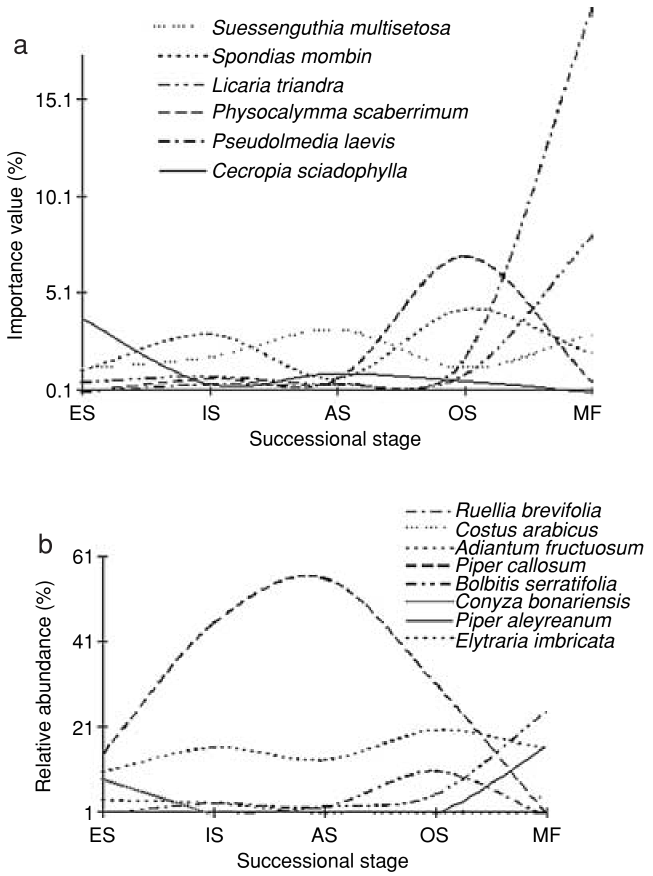

FIGURE 5. Individualistic responses of some important (a) overstory species ($\geq$5 cm DBH) and (b) understory species ($<$5 cm DBH) in successional forests in the Bolivian lowlands. Successional stages are early (ES = 1–5 yr), intermediate (IS = 6–10 yr), advanced (AS = 12–20 yr), and older (OS = 22–36 yr), and mature forest (MF).

to the abundance of previously established tree seedlings and the influx of secondary species. Unfortunately, few successional studies pay attention to the understory where much of the diversity resides (Guariguata *et al.* 1997, Peña-Claros 2003). Our results are important for the management of natural forest regeneration and nontimber forest products.

Whereas most useful species in the overstory were found in older fallows (see also Gavin 2004), in the understory, the great majority was found in early fallows. Between the over- and the understories, there is a continuous supply of useful species. Similar results of a productive fallow period that lasts 20 yr or more were found with a Runa Indian community in Ecuador (Irvine 1989). Denevan and Treacy (1987) indicated that most useful species in the Peruvian Amazon were found in fallows of less than 10 yr. The Amuesha from Peru use both secondary and primary forests intensively (Salick 1992). Thus, by paying equal attention to over- and understories, we conclude that different-aged fallows and mature forests are equally useful, with a mosaic of secondary forest patches continuously providing different species and useful plant products.

INDIVIDUALISTIC TEMPORAL RESPONSES.—Although we set up our ANOVA experimental design based on previous concepts of phase changes in secondary succession, in analyzing our data we began to see another pattern. Rather than phase changes, we saw individualistic species responses in forest succession (Fig. 5a,b). Analogous to the individualistic responses that Gleason (1926) and Whittaker (1967) found over spatial gradients, species abundance in Salvatierra showed individualistic patterns over time. As proposed by Peet & Christensen (1980), a temporal gradient occurs with different species varying in their establishment and mortality rates. We suggest that concepts of phase changes in forest succession have obscured these more basic demographic processes in plant population ecology, which are highly individualistic.

TABLE 3. *Use categories, relative importance value index (IVI) for overstory, and relative abundance for understory of the most abundant species. Use categories: E = edible, C = construction, F = fuel, M = medicinal, T = timber, O = others. Successional stages: ES = early (1–5 yr), IS = intermediate (6–10 yr), AS = advanced (12–20 yr), and OS = older (22–36 yr), and MF = mature forests. Species are presented in alphabetical order by family.*

Family	Scientific name	Uses	ES	IS	AS	OS	MF
Overstory (≥*5cm DBH*)							
Acanthaceae	*Suesenguthia multisetosa*		1.24	1.81	3.22	1.25	2.99
Anacardiaceae	*Spondias mombin*	E,M,T	1.09	2.97	0.68	4.25	2
Asteraceae	*Salmea scandens*	M	2.2	0.51	–	–	–
Bignoniaceae	*Clitostoma uleanum*	O	–	–	–	0.9	4.13
Bignoniaceae	*Tabebuia serratifolia*	C	2.07	–	0.31	–	0.35
Boraginaceae	*Cordia alliodora*	CO	–	1.98	2.78	4.48	0.45
Cecropiaceae	*Cecropia polystachya*	E	31.28	39.17	38.99	7.55	–
Cecropiaceae	*Cecropia sciadophylla*		3.75	0.42	0.96	0.55	–
Combretaceae	*Terminalia oblonga*	C,T	–	1.47	1.28	2.34	0.75
Euphorbiaceae	*Hura crepitans*	T	–	–	–	0.62	5.45
Fabaceae (Caes.)	*Diptychandra aurantiaca*	M	–	1.89	0.29	0.29	–
Fabaceae (Caes.)	*Schizolobium parahyba*	T	8.72	0.72	1.55	0.89	0.82
Fabaceae (Mim.)	*Inga edulis*	E,F	1.58	3.01	1.63	1.09	–
Fabaceae (Mim.)	*Inga* sp1.	E	1.09	3.29	1.15	3.38	–
Flacourtiaceae	*Banara* sp.	F	–	0.44	2.65	0.51	–
Lauraceae	*Licaria triandra*	F	–	–	0.38	0.89	8.07
Lecythidaceae	*Cariniana estrellensis*	T	–	–	–	–	3.38
Lecythidaceae	*Cariniana ianeirensis*	T	–	–	–	–	3.21
Lythraceae	*Physocalymma scaberrimum*	C,M,F	–	0.69	0.66	6.97	0.48
Moraceae	*Pseudolmedia laevis*	E	–	0.39	0.41	1.75	19.83
Nyctaginaceae	*Neea* sp1.		–	1.84	2.52	1.83	0.88
Piperaceae	*Piper aduncum*		–	1.78	4.51	0.57	–
Rutaceae	*Zanthoxylum fagara*	C	–	1.05	2.71	3.58	–
Sapotaceae	*Pouteria macrophylla*	E	–	0.79	2.73	1.75	1.82
Sapotaceae	*Pouteria nemorosa*	E,C	–	–	0.29	0.98	3.83
Tiliaceae	*Heliocarpus americanus*	C	4.29	12.14	3.39	7.02	0.51
Ulmaceae	*Ampelocera ruizii*		–	–	–	0.82	2.84
Ulmaceae	*Trema micrantha*	F	30.71	2.09	–	–	–
Urticaceae	*Urera baccifera*	M	5.31	1.01	1.53	2.57	0.77
Total other species			6.7	20.54	25.38	43.17	37.44
Total			100	100	100	100	100
Understory (<*5cm DBH*)							
Acanthaceae	*Elytraria imbricata*		3.58	2.89	–	–	–
Acanthaceae	*Ruellia brevifolia*	O	0.36	2.89	2.18	10.39	–
Amaranthaceae	*Iresine diffusa*	M,O	2.86	–	–	–	–
Asteraceae	*Conyza bonariensis*	M	8.65	–	–	–	–
Costaceae	*Costus arabicus*	M	0.48	0.29	0.32	0.55	4.72
Heliconiaceae	*Heliconia marginata*	O	–	2.74	–	–	6.16
Heliconiaceae	*Heliconia rostrata*	O	2.86	1.32	1.54	0.43	1.38
Hippocrateaceae	*Hippocratea volubilis*		0.65	1.17	0.68	1.11	1.79
Lomariopsidaceae	*Bolbitis serratifolia*		–	–	–	–	24.6
Piperaceae	*Piper aleyreanum*	M	–	–	–	–	15.9
Piperaceae	*Piper callosum*	M	14.68	45.25	55.79	30.92	0.35
Poaceae	*Axonopus compressus*		2.74	–	–	–	–
Poaceae	*Olyra latifolia*	O	2.68	1.08	0.73	–	–
Pteridaceae	*Adiantum fructuosum*		10.26	15.95	13.03	20.04	15.73
Sapindaceae	*Serjania larnotteana*	O	–	1.91	1.32	0.06	–
Total other species			50.2	22.71	24.41	36.51	28.16
Total			100	100	100	100	100

TABLE 4. *Useful species density for the over- and understories of different-aged secondary forests in Bolivian lowlands. Species density data (mean ± SE) are compared between use categories ($P = 0.0001$) and successional stages ($P = 0.0001$): Early (ES = 1–5 yr), intermediate (IS = 6–10 yr), advanced (AS = 12–20 yr), older (OS = 22–36 yr), and mature forest (MF). Significant Tukey test results for pair-wise comparisons are labeled with letters.*

	Use categories					
Successional stages	Edible	Medicinal	Construction	Fuel	Timber	Others
Overstory ($\geq$*5cm DBH*)	a	b	ab	c	c	c
ES^{a}	2.7 ± 0.5	2.0 ± 0.5	1.7 ± 0.5	1.3 ± 0.3	0.7 ± 0.2	1.3 ± 0.4
IS^{b}	5.6 ± 0.4	4.1 ± 0.4	3.7 ± 0.8	1.7 ± 0.4	1.3 ± 0.4	2.3 ± 0.4
AS^{c}	6.3 ± 0.7	4.9 ± 0.8	6.6 ± 1.1	3.3 ± 0.6	1.6 ± 0.3	2.9 ± 0.6
OS^{d}	6.1 ± 0.6	6.6 ± 0.9	7.6 ± 0.8	3.4 ± 0.4	3.7 ± 0.6	3.7 ± 0.4
MF^{bc}	5.8 ± 0.4	3.2 ± 0.5	5.5 ± 0.5	2.7 ± 0.6	3.2 ± 0.4	3.4 ± 0.5
Understory ($<$*5cm DBH*)	ab	b	a	c	d	a
ES^{a}	5.3 ± 0.3	6.9 ± 0.3	4.9 ± 0.7	2.9 ± 0.4	1.9 ± 0.4	4.9 ± 0.5
IS^{bc}	4.3 ± 0.6	5.1 ± 0.9	3.7 ± 0.3	2.3 ± 0.5	0.6 ± 0.2	3.9 ± 0.6
AS^{ab}	4.1 ± 0.9	5.6 ± 0.5	4.1 ± 0.4	2.3 ± 0.4	0.9 ± 0.3	5.3 ± 0.7
OS^{ab}	4.0 ± 0.6	5.1 ± 0.8	5.0 ± 0.9	2.9 ± 0.4	1.1 ± 0.5	5.4 ± 0.7
MF^{c}	4.8 ± 0.4	3.9 ± 0.4	2.3 ± 0.4	1.9 ± 0.2	0.8 ± 0.3	2.5 ± 0.4

USEFUL PLANT SPECIES.—*Los Gwarayo* people of Salvatierra identified 64% of the species as useful ($\geq$5 cm DBH) in 1 ha of mature forest. The percentage of species used was similar to other indigenous groups located in Brazil (Ka'a por 77%, Tembé 61%), Venezuela (Panaré 49%), and Bolivia (Chácobos 60%, Tacanas 62%) based on ethnobotanical quantitative inventories (Prance *et al.* 1987, Boom 1987, DeWalt *et al.* 1999). Although it is widely accepted that mature forests offer a high variety of timber and nontimber products (Peters *et al.* 1989, Prance 1998), ethnobotanical studies of secondary forests (Unruh & Alcorn 1987, Unruh & Flores-Paitán 1987, Grenand 1992, Salick 1992, Hernandez & Benavides 1995, Melchor 1998, Pacheco *et al.* 1998) conclude that these forests are very important for peasants and indigenous people, and are used more intensively than old growth forests. Our results on abundance of medicinal and other nontimber products in secondary forests support the findings of Salick *et al.* (1995) and Chazdon and Coe (1999). Furthermore, extraction of forest products from fallows is facilitated by their proximity to human settlements (Brown & Lugo 1990).

INDIGENOUS FALLOW MANAGEMENT.—Indigenous resource management systems are a major theme in ethnobotany. Like *Los Gwarayo*, most ethnic inhabitants of tropical regions use the swidden agriculture to produce their food (*e.g.*, Peru: Salick 1989, Brazil: Bahuchet 1992, Borneo: Pierce *et al.* 1997, Indonesia: De Jong *et al.* 2001, Thailand: Schmidt-Vogt 2001). Swidden agriculture is the first stage of an agroforestry system that presents a wide variety of opportunities for local inhabitants (Irvine 1989, Dubois 1990). Several studies argue that this agricultural system is both complex and nondestructive, causing only small-scale disturbances (Salick 1989, Pierce *et al.* 1997, Hamlin & Salick 2003). People cultivate land for a few years and then let it revert gradually into forest through a combination of natural succession and indigenous management (Posey 1984, Balée & Gély 1987, Balée 1989, Irvine 1989, Gómez-Pompa & Kaus 1990, Alcorn 1995). For *Los Gwarayo*, this management includes harvesting, weeding, implanting, maintaining useful plants, and experimenting with new species and crops. *Los Gwarayo* people consider fallows valuable for supplying crops and other useful species, for regenerating timber species, and for preparing new swiddens.

Although many farmers prefer secondary to primary forests for making swiddens (Nations & Nigh 1978), in Salvatierra, most of *Los Gwarayo* preferred mature forest to older fallows because there are fewer weeds and higher productivity. Yet, a *Los Gwarayo* minority preferred fallows to make new swiddens because they are both close to the village and easy to slash. They wait about 5–10 yr before cutting their fallows, similar in Peru to the Bora (Denevan & Treacy 1987) and the Amuesha farming uplands (Salick 1989).

Although in Salvatierra, *Los Gwarayo* still practice their traditional system of resource management, they are gradually changing with the demands of the cash economy. Recently, timber production has been established in Salvatierra through a community forestry project (Cronkleton 2002, Putz *et al.* 2004). A key component to achieve sustainable management of forests is the regeneration of timber species (Mostacedo & Fredericksen 2000). In Salvatierra, the most abundant timber regeneration was found in the early successional stage.

Secondary forests are an inexpensive and appropriate form of reforestation with high regenerative potential (Emrich *et al.* 2000). In Salvatierra, secondary forests contribute to the availability of timber yields for future generations. Additionally, *Los Gwarayo* harvest crops and nontimber forest products from secondary forests. Fallow management of *Los Gwarayo* is successful in regenerating natural forest rapidly and in maintaining high levels of species diversity.

It is important not to lose sight of indigenous agroforestry within secondary forest succession; through agroforestry, secondary forests are directly related to rural livelihoods.

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