Natural regeneration and environmental relationships of tree species in logging gaps in a Bolivian tropical forest

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Abstract

Successional dynamics and environmental associations of 18 pioneer and 24 commercial tree species were studied in a 4-year chronosequence of logging gaps in a Bolivian tropical forest. Logging gap area ranged from 108 to 1246 m^2. Pioneer regeneration was 71–387 more abundant than that of commercial species in all harvest years. Pioneer saplings ($>$1.5 m tall and $<$10 cm dbh) were more abundant in 2- and 4-year-old gaps than in 1-year-old gaps, but pioneer seedlings ($\leq$1.5 m tall) were more abundant in 1-year-old openings. By contrast, there were no significant differences among harvest years in size class distributions of commercial seedlings or saplings.

Some pioneers (*Acacia polyphylla*, *Urera baccifera*, *Heliocarpus americana*, *Cecropia concolor*, and *Inga edulis*) were associated with large gaps or coarse soils with high herbaceous cover. Among commercial trees, *Ampelocera ruizii*, *Hura crepitans*, and *Pseudolmedia laevis* were associated with fine textured soils, while *Pouteria nemorosa* was associated with high fern cover and rock outcrops. Although most logging gaps were dominated by a few pioneer species, the commercial species *A. ruizii*, *H. crepitans*, *P. nemorosa*, and *Terminalia oblonga* may eventually dominate many gaps. Notably absent among gap regeneration were some of the most commercially valuable tree species, such as *Swietenia macrophylla*, *Cedrela fissilis*, *Cariniana ianeirensis*, and *Ficus boliviana*. Outplanting programs may be needed to ensure successful regeneration of these rare but valuable species.
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1. Introduction

The successful establishment of commercially valuable trees is crucial to the successful long-term management of humid tropical forests. Much of this regeneration will be recruited in logging and tree-fall gaps, whose formation and occupation by new trees

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largely controls the structure and function of forests (Bazzaz, 1991). In managed tropical forests in Bolivia, commercial tree regeneration is generally sparse (Fredericksen et al., 1999; Mostacedo and Fredericksen, 1999; Fredericksen and Licona, 2000; Pariona and Fredericksen, 2003). This is particularly true for the regeneration of shade-tolerant/mid-intolerant commercial tree species in logging gaps. By contrast, non-commercial species, such as *Acosmium cardenasii* or *Acacia* spp. may aggressively colonize gaps in logged forests (Fredericksen and Licona, 2000).

Many factors influence the success of commercial tree regeneration in managed tropical forests. The reduced abundance of seed trees after logging may limit seed supply and restrict seed dispersal (Fredericksen and Licona, 2000). Logged forests may have a higher proportion of their area in gaps because logging gaps are larger than natural treefall gaps (Dickinson et al., 2000; Jackson et al., 2002). Furthermore, as companies expand the range of tree species harvested, a hyperbolic expansion of the total disturbed area occurs (Panfil and Gullison, 1998).

Over time, the changing character of logged forests may affect the relative regeneration success of trees with different dispersal characteristics and degrees of shade tolerance (Denslow, 1980; Whitmore, 1996). Large logging gaps may favor wind-dispersed, shade-intolerant pioneers at the expense of shade-tolerant timber trees that have a competitive advantage in smaller gaps (Denslow, 1987; Bazzaz, 1991). Seed-dispersing birds or mammals may also avoid entering larger logging gaps, restricting regeneration opportunities for animal-dispersed species (Schupp et al., 1989).

Knowledge of seed dispersal, phenology, and the conditions needed for successful regeneration is fragmentary or non-existent for many Bolivian tree species (Mostacedo and Fredericksen, 1999). Forest managers therefore have a very limited knowledge base from which to predict regeneration success or failure in commercial forests. Further study of short- and long-term regeneration dynamics is therefore needed, particularly with respect to the response of tropical tree communities to environmental conditions in logging gaps. In this paper, we investigate the dynamics of commercial and pioneer tree regeneration in a 4 year chronosequence of logging gaps in a Bolivian tropical forest. Our objectives were: (1) describe and compare the distribution of commercial and pioneer tree re-

generation in gaps of various ages, using the chronosequence as a proxy for post-harvest succession, and (2) explore species-environment relationships for commercial and pioneer trees using multivariate analysis.

2. Methods

2.1. Study sites and logging history

Our study area was a 100,000 ha commercial forestry concession managed by Agroindustria Forestal La Chonta Ltda. This forest lies at the southern edge of the Amazon Basin in east-central Bolivia (15°45′S, 62°38′W) in gently rolling terrain. The dominant soils are oxisols, ultisols, and inceptisols. Mean annual temperature is 24.5 °C and mean annual precipitation is 1500 mm (Pinard et al., 1999). The 3–6 month dry season is occasionally broken by Antarctic cold fronts that bring 1–2 days of rain. La Chonta is a seasonally dry humid tropical forest and it supports tree species that are characteristic of both the humid forests of the Amazon Basin and the drier Chiquitano forests to the south.

Timber harvesting was concentrated on *Swietenia macrophylla* (mahogany) and *Cedrela fissilis* (Spanish cedar) until 1997. As these species are now scarce, logging has shifted to a broader range of potentially valuable species. Thirteen additional species are now harvested, the most commercially important of which include *Ficus boliviano*, *Hura crepitans*, and *C. ianeirensis*.

2.2. Field methods

During the 2001 dry season, we surveyed logging gaps adjacent to forest inventory transects in areas harvested in 1997, 1999, and 2000. Along each transect, we sampled 2–4 gaps that were at least 100 m apart and 50 m away from major haul roads. Twenty logging gaps were located in each harvest area for a total sample of 60 gaps.

Gap borders were defined by the vertical projection of the edges of mature tree crowns (i.e. those definitely present before logging) bordering the gap. Natural regeneration and environmental variables were sampled along four transects that bisected gap centres at 45° to each other. Gap area was estimated as the sum

of the areas of eight triangles formed by adjacent half transects.

Twenty-four commercial or potentially commercial trees and 18 non-commercial species considered to be pioneers (Whitmore, 1998) were sampled (Table 1). Juvenile trees were divided into two classes: those ≥10 cm tall (the minimum size for which certain identifications could be made) and ≤1.5 m tall (seedlings), and those ≥1.5 m tall and <10 cm dbh (saplings). Seedlings were sampled in a 1 m belt on either side of the central line of each transect, while saplings were sampled 2 m to either side of the central line.

Environmental variables describing physical gap characteristics, vegetation and canopy development were collected in each gap (Table 2). Gap area, mineral soil texture, and an index of topographic exposure were used to describe the physical gap environment. Vegetation cover was broken down into the percent cover of lianas, *Philodendron* sp. (an herbaceous hemi-epiphyte), giant herbs (*Heliconia* spp. and *Costus* spp.), ferns, other herbs, grasses, palms and shrubs. These variables were measured in 1 m^2 quadrats placed at 4 m intervals along the transects (20–33 per gap, depending on gap area). Percent cover of coarse woody debris (CWD), exposed mineral soil, and rocks were also estimated in the 1 m^2 quadrats.

Canopy cover was also assessed from the 1 m^2 quadrats. Cover was estimated for height categories of 0–1, 1–2, 2–4, 4–8, and >8 m above the ground by counting the number of covered squares and half squares on a 20 cm × 20 cm grid inscribed on a clear plastic sheet. The grid was divided into 25 4 cm × 4 cm squares, and for cover estimation, was held approximately 20 cm from the viewer's eyes. Cover in the >8 m height class occasionally included residual trees within the gap borders.

A modified Gower similarity coefficient (Legendre and Legendre, 1998) was calculated to measure the degree of association between the community of juvenile trees in each gap and the equivalent community of potential seed trees bordering gaps (Table 2). Potential seed trees were counted only if they belonged to the 42 species community of juvenile trees, if they were clearly a part of the canopy-tree community prior to gap formation, and if they were growing within 20 m of the gap edge. Because mature and juvenile trees differed widely in abundance, raw counts were reduced to a simplified set of four numerical states to reflect the approximate probabilities that species would be present at different densities in a gap (Legendre and Legendre, 1998). No attempt was made to separate male from female trees in calculating Gower indices. However, among the trees studied, only *Pseudolmedia laevis* and *Batocarpus amazonicum* were dioecious.

2.3. Data analysis

Commercial and pioneer trees were analyzed as separate seedling and sapling data sets. Differences in raw abundance (numbers of stems per 100 m^2 of transect), species richness, and species evenness (Legendre and Legendre, 1998) were compared across the chronosequence. We also ranked the importance values (Mueller-Dombois and Ellenberg, 1974) of the pooled pioneer and commercial species to describe the relative dominance of commercial versus pioneer trees in different harvest years.

Between harvest year differences in environmental variables were analyzed by one-way ANOVA. Contrasts between group means were calculated using the Tukey–Kramer method ($\alpha = 0.05$, Mathsoft Inc., 1997). Species abundance data failed to conform to the assumptions of ANOVA. Between harvest year differences for each of the commercial and pioneer data sets were therefore tested with Kruskal–Wallis rank sum tests. Significance levels were adjusted using Bonferroni corrections for multiple independent tests, and Mann–Whitney U-tests were used to test for pairwise differences between harvest year rank sums (Sokal and Rohlf, 1981).

2.3.1. Multivariate ordination

Multivariate analyses were used to investigate community relationships among juvenile trees and to explore species-environment associations. Species responses to environmental gradients were assumed to be linear because the three primary axes of an exploratory detrended correspondence analysis (DCA) spanned ≤2 S.D. each (ter Braak, 1995). Redundancy analysis (RDA), an ordination technique based on multiple linear regression, was therefore used as the principle ordination technique (Legendre and Legendre, 1998). Sequential partial RDAs (pRDAs) were used to extract the influence of harvest year from the species community-environment relationship (Borcard et al., 1992).

Table 1
Characteristics of commercial and pioneer species sampled at La Chonta, Bolivia.

Species code	Scientific name	Spanish name	Commercial or pioneer	Seed production[a]	Dispersal mode[a]	Relative shade tolerance[b]	Sub-strate[a]
Amru	*A. ruizii*	Blanquillo	C	G	A	T[*]	FF
Ascy	*Aspidosperma cylindrocarpon*	Jiquituriqui	C	G	W	M	FF
Boam	*B. amazonicum*	Mururé	C	G[*]	A[*]	T[*]	FF[*]
Cado	*Cariniana domestica*	Yesquero bianco	C	G	W	M	FF
Caia	*C. ianeirensis*	Yesquero bianco	C	G	W	M	FF
Caes	*C. estrellensis*	Yesquero negro	C	G	W	M	FF
Ceod	*Cedrela odorata*	Cedro 1	C	G[*]	W[*]	I	DS[*]
Cefi	*C. fisilis*	Cedro 2	C	G[*]	W[*]	I	DS[*]
Cemi	*Centrolobium microchaete*	Tarara amarilla	C	P	W	I	DS
Coal	*C. alliodora*	Picana negra	C	G	W	I	DS
Capl	*Caesalpinia pluviosa*	Momoqui	C	G	G	M	DS
Figl	*Ficus glabrata*	Bibosi colorado	C	G	A	M	DS/E
Gain	*G. integrifolia*	Ajo ajo	C	G	W	M[*]	FF
Hucr	*H. crepitans*	Ochoo	C	G	G[c]	I	Any
Hyco	*Hymenaea coubaril*	Paquió	C	F	A	M	FF
Psla	*P. laevis*	Ojoso colorado	C	GE	G	T	FF
Pone	*P. nemorosa*	Coquino	C	F[*]	A/G[*]	M[*]	FF[*]
Ptni	*Pterogyne nitens*	Ajunao	C	F[*]	W[*]	I[*]	DS[*]
Spmo	*S. mombin*	Ocorocillo	C	G	A	M	DS
Scpa	*S. parahyba*	Serebó	C/P[d]	G	W	I	DS
Swfr	*S. fruticosa*	Manì	C	P[*]	W[*]	I[*]	F[*]
Swma	*S. macrophylla*	Mara	C	G	W	I	DS
Teob	*T. oblonga*	Verdolago	C	G	W	I	FF
Tase	*T. serratifolia*	Tajibo amarillo	C	G	W	I	FF
Acpo	*A. polyphylla*	CariCari	P	G[*]	W	M[*]	DS[*]
Alsp	*Albizia* sp.		P	G[*]	W	I[*]	DS[*]
Ceco	*C. concolor*	Ambaibo	P	G[*]	A	I[*]	EI
Cepo	*C. polystachia*	Ambaibo macho	P	G[*]	A	I[*]	DS[*]
Cybl	*Cyclolobium blanchetianum*	Cacha	P	G[*]			
Guul	*Guazuma ulmifolia*	Coco	P	G[*]	A/G	M[*]	FF/DS[*]
Haga	*H. gargatea*	Gargatea	P	G[*]	A	I[*]	DS[*]
Heam	*H. americanus*	Baboso	P	G[*]	W	I[*]	DS[*]
Ined	*I. edulis*	Pacay peludo	P	G[*]	A	M[*]	FF[*]
Inma	*I. marginata*	Pacay rosario	P	G[*]	A	T[*]	FF[*]
Mati	*Madura tinctoria*	Mora	P	G[*]	A	I[*]	DS[*]
Pisp	*Piptadenia* sp.	CarCari colorado	P	G[*]	W	I[*]	DS[*]
Popr	*P. procera*	CariCari bianco	P	G[*]	W	I[*]	DS[*]
Poce	*P. cecropifolia*	Ambaibauva	P	G[*]	A	I[*]	DS[*]
Sasp	*Sapium* sp.	LecheLeche	P	G[*]		I[*]	DS[*]
Trmi	*T. micrantha*	Uvillo	P	G[*]	A	I[*]	DS[*]
Urba	*U. baccifera*	Pica Pica	P	G[*]	A	M[*]	DS[*]
Zasp	*Zanthoxylum* sp.	Sauco	P	G[*]	A	I[*]	DS[*]

Scientific names are as in Killeen, 1993.

[a] Codes taken from Fredericksen et al., 2000; Mostacedo and Fredericksen, 1999, and Pinard et al., 1999, except for [*] (established in consultation with Todd Fredericksen). Seed production: G, good (>1000 sound seeds/tree); F, fair (200–1000 seeds/tree); P, poor (<200 seeds/tree). Dispersal mode: W, Wind; A, animal; G, gravity. Eexcept for *H. crepitans*, in which gravity is aided by explosive dispersal; Substrate (for regeneration): FF, forest floor; DS, disturbed soils; E, epiphytic on other trees.

[b] Relative shade tolerance: IE, intolerant pioneer; I, intolerant, M, medium tolerance; T, tolerant.

[c] Gravity dispersal aided by explosive ejection from seed capsule (Condit, 2003).

[d] *S. parahyba* is considered both a commercial and pioneer species.

Table 2
Environmental variables measured once in each logging gap at La Chonta, Bolivia

Variable	Acronym	Description
Slope (%)	Slope	Percent slope measured looking down-slope
Aspect	SloDir	Azimuth of dominant direction of downward-facing slope
Slope position	SloPos	Slope position on a eight-point scale, one being a flat Plateau and eight being the valley bottom
Slope index	SloInd	Cos(315 − A) + 1, where A = aspect, and 315 = angle of maximum exposure to the southern sun
Exposure index	ExpInd	Slope index + Sin of slope + 1/slope position, this index was modified from (Beers et al., 1966 #271) and (Callaway and Davis, 1993 #574)
Soils	Soils	Mineral soil texture on an 11-point scale from one (sand) to 11 (heavy clay)
Gap area	GapA	In square meters calculated from eight similar triangles calculated from transect data
Liana	Liana	Percent cover averaged over all sub-plots. Includes all lianas and vines except *Philodendron* sp.
Philodendron	Phyllo	Percent cover of *Philodendron* sp.
Heliconia	Helico	Percent cover of *Heliconia* and *Costus* spp (classed together because of similar life forms)
Ferns	Fern	Percent cover of ferns
Herbs	Herbs	Percent cover of herbaceous plants (including grasses)
Shrubs/small trees	Bush	Percent cover of shrubs and small trees without the potential to become canopy trees (i.e. *Piper*, *Celtis* spp.)
Palms	Palm	Percent cover of palms
Exposed mineral soil	ExpMin	Percent cover exposed mineral soil
Coarse woody debris	CWD	Percent cover of coarse woody debris
Total canopy cover	OneTwo, TwoFour etc.	Percent cover at 0–1, 1–2, 2–4, 4–8, and >8 m (five variables)
Rock	Rock	Percent cover of rocks (not used much!)
Gower index (Legendre and Legendre, 1998)	GowerC (commercial) or GowerP (pioneer)	$S_{BL} = \sum_{i=1}^{p}(1 - [|y_{Bi} - y_{Ti}|/R_{BiTi}])/\sum_{i=1}^{p} w_{bt} + \sum_{i=1}^{p}(1 - [|y_{Li} - y_{Ti}|/R_{LiTi}])/\sum_{i=1}^{p} w_{bt}$, similarity index where between juveniles and border trees; takes a maximum value of two, where y_{Bi} and y_{Li} = abundance codes for seedling and sapling species, respectively; y_{Ti} is the abundance of each tree species and the R_s are the maximum differences between the abundance codes for trees and seedlings or trees and saplings; the binary variables, w_{bt} or w_{lt} = 1 where species are represented by a juvenile, a tree or both, and zero if both juveniles and adult trees are absent

Of the 42 pioneer and commercial trees, 17 commercial and 15 pioneer trees that were present in ≥5% of the gaps were included in the pRDAs. An initial pRDA which included all 20 environmental variables was used to arrive at a subset of variables to use in the final analysis. Thirteen environmental variables with eigenvectors ≥50% of the positive or negative gradient lengths of the first two RDA axes comprised the final set of independent variables. The significance of each pRDA model was tested using 9999 random permutations of the species data residuals in CANOCO 4.0 (ter Braak and Smilauer, 1998).

3. Results

3.1. Gap characteristics

Gap area averaged 395 m² and ranged from a 108 m² gap caused by felling a small diameter *H. crepitans* to a 1246 m² gap produced by felling a *F. boliviano*. (Fig. 1). Average slopes were <10%, and exposure indices indicated that no gaps were excessively drought-prone. There were no significance differences between harvest years in gap area, exposed mineral soil, rock cover, or the percent cover of lianas, giant herbs, ferns, and
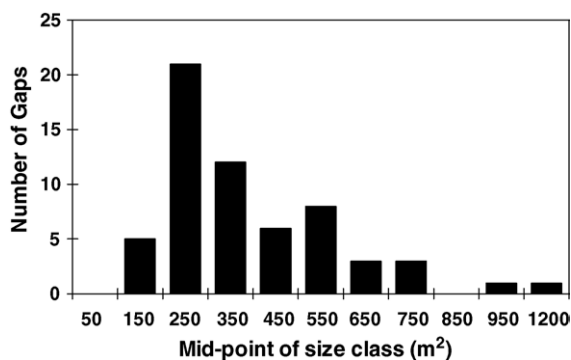

Fig. 1. Distribution of gap sizes at la Chonta, Bolivia.

shrubs. Soils in 1-year-old gaps were coarser-textured than those in 2- or 4-year-old gaps ($p = 0.002$). However, soil-texture spanned a narrow range from sandy-loam to silty-clay loam; therefore, no gaps appeared to suffer from excessive or impeded drainage. *Philodendron* and palms were more abundant ($p < 0.001$) in 2-year-old gaps than in 1- or 4-year-old gaps, and herbs were more abundant in 4-year-old gaps than in the other 2 years ($p = 0.001$).

Mean canopy cover at 0–1 m was virtually identical in gaps of all ages, but there was significantly higher cover at 1–2 m in 2- and 4-year-old gaps ($\bar{x} = 46$ and 42%, respectively) than in 1-year-old gaps ($\bar{x} = 33\%$). This pattern was repeated for the 2–4 m height class (42 and 46% cover in 2- and 4-year-old gaps, respectively, versus 29% cover in 1-year-old gaps). Cover in the 4–8 m height class was higher in 4-year-old gaps than in 1- or 2-year-old gaps, but canopy cover >8 m varied as much within harvest years as between them.

3.2. Distribution of regeneration across harvest years

3.2.1. General patterns

The majority of stems in each harvest year were comprised of a small number of species, most of which were pioneers. *Urera baccifera* and *Acacia polycephala* dominated the pioneer community in all harvest years, with *U. baccifera* being both more numerous and frequent in gaps logged in years 2 and 4 than those logged in year 1 (Fig. 2). Only the shade-tolerant *Ampelocera ruizii* and *P. laevis* ranked consistently among the ten most important species in each harvest year, where they accounted for 43–59% of commercial stems. *Schizolobium parahyba*, a wind-dispersed shade-intolerant tree that produces abundant seed crops, ranked seventh in importance in 2-year-old gaps, while *Terminalia oblonga* and *H. crepitans* (moderately shade-tolerant), respectively ranked ninth and 10th in importance in 4-year-old gaps.

3.2.2. Statistical differences

There were no significant differences in mean densities of commercial seedlings or saplings among harvest years (Bonferroni-adjusted $p > 0.0125$; Table 3 and Fig. 3A and B). Numbers of commercial stems per gap varied widely, but averages varied little
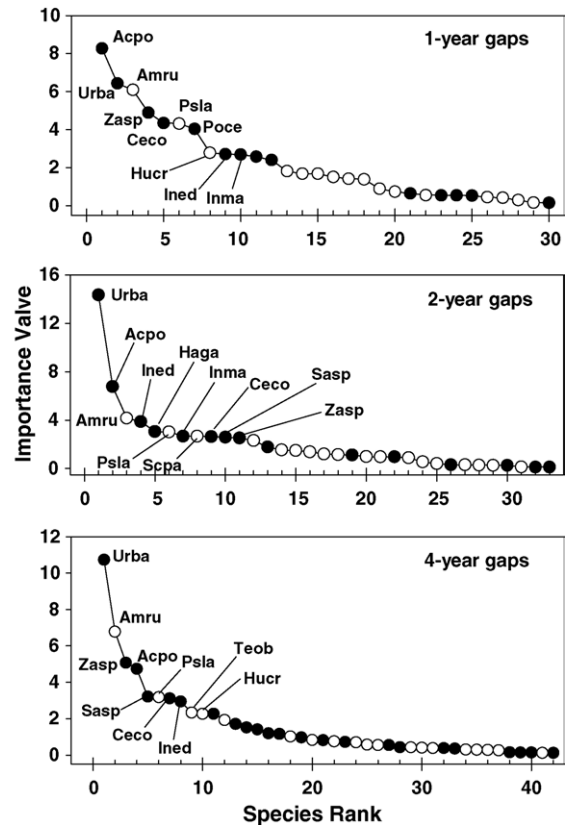

Fig. 2. Ranked species importance values (%) for commercial (white circles) and pioneer (black circles) tree populations at La Chonta, Bolivia. The top 10 ranked species are shown for each harvest year. Codes are as written in Table 1.

among harvest years (9.0–13.7 for commercial seedlings and 2.0–3.2 stems 100 m^{-2} for commercial saplings). There were also no significant between harvest-year differences in commercial species richness or evenness.

By contrast, there were highly significant differences in pioneer seedling and sapling densities among harvest years (Fig. 3C and D). Pioneer seedlings were less abundant in 4-year-old gaps ($\bar{x} = 9.1$ stems 100 m^{-2} relative to 1- and 2-year-old gaps ($\bar{x} = 29.0$ and 29.1 stems 100 m^{-2}, respectively). Pioneer sapling abundance averaged 4.5, 15.5 and 23.4 stems 100 m^{-2} 2 in 1-, 2-, and 4-year-old gaps, respectively. Species richness (but not evenness) of pioneer seedlings and saplings was significantly greater in 4-year-old gaps than in 2- or 1-year-old gaps (Table 3).

Table 3
Kruskal–Walks rank-sum tests (A) and ANOVA statistics (B) for commercial and pioneer species × harvest year at La Chonta, Bolivia.

(A) Abundance (stems per 100 m^2)	χ^2	p-value	Signed rank statistic p-value		
			Year 1 vs. year 2	Year 1 vs. year 4	Year 2 vs. year 4
Commercial seedlings	1.92	0.3828	–	–	–
Commercial saplings	4.727	0.0941	–	–	–
Pioneer seedlings	19.84	0.0000	0.0200	0.0000	0.1054
Pioneer saplings	18.24	0.0001	0.812	0.0002	0.0001

(B) Species diversity (based on species per stem)	F-statistic	p-value	Tukey–Kramer p-values		
			Year 1 vs. year 2	Year 1 vs. year 4	Year 2 vs. year 4
Commercial seedling richness	0.448	0.6412	–	–	–
Commercial sapling richness	1.808	0.1732	–	–	–
Pioneer seedling richness	8.541	0.0006	<0.05	<0.010	<0.001
Pioneer saplings richness	10.428	0.0001	<0.05	<0.001	<0.001
Commercial seedling evenness	0.061	0.9407	–	–	–
Commercial saplings evenness	0.840	0.4369	–	–	–
Pioneer seedlings evenness	4.982	0.0101	<0.05	<0.001	<0.05
Pioneer saplings evenness	1.865	0.1642	–	–	–

Species richness and evenness were tested with one-way ANOVA because the data conformed to the assumptions of analysis of variance. Contrasts were only reported if the global test was significant. Global tests are considered significant at a Bonferroni-corrected level of 0.0125 for either the rank-sum or ANOVA.
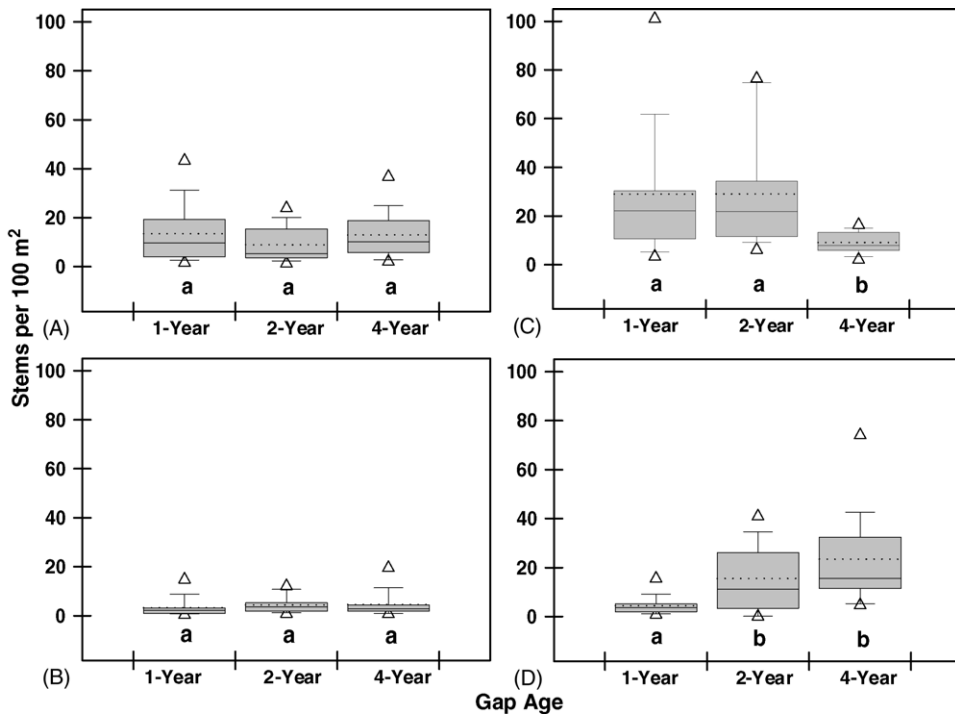

Fig. 3. Box plots showing density distributions of: (A) commercial seedlings, (B) commercial saplings, (C) pioneer seedlings, and (D) pioneer saplings at La Chonta, Bolivia. Plots show treatment means (dotted lines), medians (solid line), 25th and 75th percentiles (upper and lower borders of box), 10th and 90th percentiles (bounded by error bars), and outliers (triangles). Different lower-case letters beneath boxes indicate significantly different treatments (Mann–Whitney U-test, $p \leq 0.05$). Note the different scales used for the y-axes of commercial and pioneer species.

3.3. Multivariate analysis

Thirteen environmental variables explained 28.6% of the variation in the species data. There was also a small but significant effect of harvest year on overall species composition (explained variation = 8.7%, $p \leq 0.05$). Covariance between the environment and harvest year was slight (1.9%), and 65.6% of total species variation remained unexplained. All pRDA models were statistically significant ($p \leq 0.05$).

With the influence of harvest year removed, Axis 1 of a pRDA spanned a gradient from small gaps characterized by shrubs or ferns to large gaps with high liana cover and high Gower similarity values (Fig. 4). The gradient in Axis 2 had gaps with fine textured soils on the positive side of the axis, and gaps
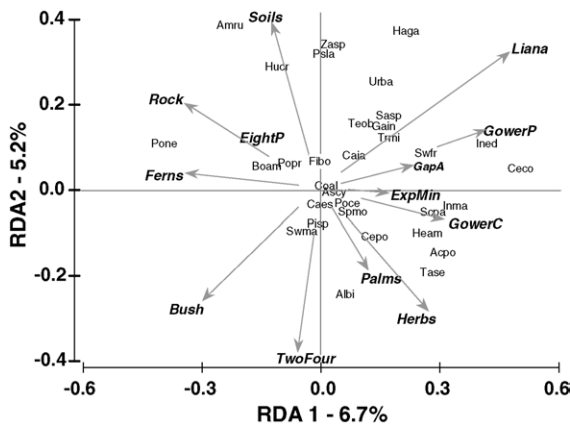

Fig. 4. Partial RDA of combined commercial and pioneer seedling and sapling data sets at La Chonta, Bolivia. Species codes: Amru, *A. ruizii*; Boam, *B. amazonicum*; Caes, *Cariniana estrellensis*; Caia, *C. ianerensis*; Coal, *Cordia alliodora*; Fibo, *F. boliviano*; Gain, *Gallesia integrifolia*; Hucr, *H. crepitans*; Pone, *P. nemorosa*; Psla, *P. laevis*; Scpa, *S. parahyba*; Spmo, *S. mombin*; Swfir, *Sweetia fruticosa*; Swma, *S. macrophylla*; Tase, *T. serratifolia*; Teob, *T. oblonga*; Acpo, *A. polyphylla*; Alsp, *Albizia* sp.; Ceco, *C. concolor*; Cepo, *Cecropia polystachia*; Haga, *Hacaratia gargatea*; Heam, *H. americanus*; Ined, *I. edulis*; Inma, *Inga marginata*; Pisp, *Piptadenia* sp.; Poce, *Pourouma cecropifolia*; Popr, *Porpygia procera*; Sasp, *Sapium* sp.; Trmi, *Trema micrantha*; Urba, *U. baccifera*; Zasp, *Zanthoxylum* sp. Environmental variable codes: gapA, gap area; GowerP, Gower similarity: pioneers; GowerC, Gower similarity: commercial species; soils, mineral soil texture; rock, percent rock outcrops; ExpMin, percent exposed mineral. Liana, herbs, palms, bush, and ferns indicate percent cover of lianas, herbs, palms, bushes, and ferns. TwoFour, and EightP indicate canopy strata at 2–4, and >8 m, respectively.

with high herb, shrub, and 2–4 m high canopy cover with coarse-textured soils on the negative side.

In general, wind-dispersed species occupied the right hand side of the ordination, where larger gap areas combined with a weak vector for exposed mineral soil implied a more disturbed environment. Wind-dispersed intolerant and mid-tolerant pioneers, such as *Acacia polyphylla*, and *Albizia* sp. were also associated with high herbaceous cover, palms, and coarser textured soils, as was the commercial species, *Tabebuia serratifolia*. However, many species clustered close to the origin, indicating no specific environmental affinities on the primary pRDA axes.

Among commercial species, shade-intolerant *H. crepitans*, in which seed is disseminated explosively from the seed capsule (Condit, 2003), was closely associated with fine-textured soils, as were the gravity- and animal-dispersed shade-tolerants, *P. laevis* and *A. ruizii* (Fig. 4). Animal-dispersed pioneers with abundant seed, *Inga edulis* and *Cecropia concolor*, were closely associated with GowerP, and *S. parahyba* was closely associated with the GowerC. Only one species, the animal-dispersed *Pouteria nemorosa*, had a close association with fern cover and rock outcrops, and no species were associated with high levels of shrub cover.

4. Discussion

Trees designated as non-commercial pioneers dominated post-harvest logging gaps in all harvest years. Pioneer seedlings were rapidly recruited into the sapling layer and contributed greatly to increased canopy cover in 2- and 4-year-old gaps. Pioneer species richness was also greater in 4-year-old gaps. This result implies either that seeds of different species in the seedbank were germinating continuously over the 4-year period, or that seeds were arriving and germinating successfully in gaps for several years after gap formation.

A. polyphylla and *U. baccifera* dominated most early successional logging gaps. However, *A. ruizii*, *P. laevis*, and, to a lesser extent, *S. parahyba*, *T. oblonga* and *H. crepitans*, also ranked relatively highly in the pooled pioneer and commercial species community. This finding concurred with the results of surveys in unmanaged Bolivian forests (Smith and Killeen,

1995), and on logging roads (Nabe-Nielsen et al., 2005) in La Chonta. Geoff Blate (unpublished data) also showed that *P. laevis*, *A. ruizii*, *H. crepitans*, and *P. nemorosa* constituted nearly 79% of the regeneration found on several survey transects in closed forest at La Chonta. *T. oblonga*, *H. crepitans*, and *S. parahyba* were also common on the roadbeds and edges of logging roads (Nabe-Nielsen et al., 2005). The common occurrence of some of these species in both logging gaps (Fig. 2) and closed forest implies that many observed saplings may have been established prior to logging. Their persistence in managed Bolivian forests may be further facilitated by the establishment of haul roads and skid trails that accompany logging operations.

4.1. The role of environment

The association of some species with specific environmental characteristics contrasts with studies in which the species composition of gaps was reportedly unpredictable. For example, Eysenrode (2003) found that individual gaps in an Ecuadorian humid forest supported almost unique species communities. Citing similar results from Barro Colorado in Panama, Hubbell et al. (1999) suggested that recruitment limitation (limitations on seedling establishment imposed by seed availability) could account for most of the variation in juvenile-tree communities in natural gaps.

The large logging gaps at La Chonta will receive more sunlight and experience greater evapotranspiration than the smaller natural gaps reported from Ecuador and Panama. Our study area also experiences a more intense dry season than either Panama or Ecuador. Under these circumstances, the environmental affinities of species, such as *H. crepitans*, which has varieties that grow preferentially on very moist alluvial soils (Francis, 1990), may become accentuated. By contrast, gaps with coarser soils in La Chonta will experience greater seasonal drought, and are more likely to be colonized by dry forest-affiliated trees, such as *A. polyphylla*, *Albizia* sp., and the dry forest affiliated commercial species, *T. serratifolia* (Fig. 4).

Disturbance by logging machinery also differentiates logging from natural gaps. Disturbed soils (Dickinson et al., 2000) and mound and pit topography from uprooted trees (Putz, 1983) are rare in unlogged

tropical forests, but skidders cause considerable direct soil disturbance in and around gaps. Commercially valuable species in two Bolivian forests were three times more abundant in the parts of gaps scarified by skidders compared to areas unaffected by skidder traffic (Fredericksen and Pariona, 2002). The ability to occupy disturbed ground may also explain the dominance of *U. baccifera* in 2- and 4-year-old gaps, since this species is a known to occupy disturbed sites, such as those burned in forest fires (Francis, 2001).

Although our analysis demonstrated that environmental factors play a role in structuring regeneration communities, over 65% of species community variation remained unexplained. A substantial role therefore remains for unmeasured environmental variables, stochastic variation and recruitment limitation to mold species communities in logging gaps. For example, trees that produce abundant, wind-dispersed seed, such as *T. oblonga*, can become dominant in gaps even where they are rare (Dalling et al., 2002). Mammals and birds travel through logging gaps more than undisturbed forest at La Chonta (Flores et al., 2001; Fredericksen and Fredericksen, 2002), implying a significant but unmeasured role for animal- and bird-dispersed species to be transported into gaps from a distance.

4.2. Implications for forest management

Early successional dominance by non-commercial pioneers may not prevent commercial trees from eventually growing into the canopy of many logging gaps in our study area. Dominant pioneers, such as *U. baccifera*, *A. polyphylla* and *I.nga* spp. grow no higher than the mid-canopy, whereas all commercial species are long-lived canopy trees. Therefore, provided they survive and receive enough light to grow, commercial trees have the potential to replace pioneers as the tallest stems in recovering gaps.

On the other hand, logging disturbance leaves up to 25% of the forest in gaps at La Chonta (Jackson et al., 2002). This proportion will increase as more tree species become commercially valuable (Panfil and Gullison, 1998), and will be accompanied by a concurrent decrease in the density of commercial seed trees. Species, such as *C. fissilis* and *S. macrophylla* are already represented by <1 tree $\geq$20 cm dbh ha^{-1} at La Chonta because of previous overharvesting.

Among the more valuable commercial species, only *H. crepitans* was present at 3.7 stems ha^{-1} (Fredericksen et al., 2000). The most common commercial trees in the future forest could therefore be low value shade-intolerant species with no serious recruitment limitations (e.g. *T. oblonga*). Commercial species that germinate on disturbed soil (e.g. *S. parahyba*) and dry forest affiliates, such as *T. serratifolia* may also become more common in large logging gaps.

The rarity of high value commercial trees and species-specific environmental associations justify basing silviculture on the environmental requirements of individual species or species guilds. Treatments, such as soil scarification improve regeneration of some commercial species, including *S. parahyba*, *Spondias mombin*, *T. serratifolia*, and *T. oblonga* (Fredericksen and Pariona, 2002). However, planting programs may be needed to establish rare commercial species (e.g. *S. macrophylla*, *Cariniana* spp.). To conserve shade-tolerant species, careful logging techniques may have to be used to produce smaller gaps and to conserve advance regeneration.

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