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Understanding the recruitment response of juvenile Neotropical trees to logging intensity using functional traits

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Abstract. Selective logging remains a widespread practice in tropical forests, yet the long-term effects of timber harvest on juvenile tree (i.e., sapling) recruitment across the hundreds of species occurring in most tropical forests remain difficult to predict. This uncertainty could potentially exacerbate threats to some of the thousands of timber-valuable tree species in the Amazon. Our objective was to determine to what extent long-term responses of tree species regeneration in logged forests can be explained by their functional traits. We integrate functional trait data for 13 leaf, stem, and seed traits from 25 canopy tree species with a range of life histories, such as the pioneer *Goupia glabra* and the shade-tolerant *Iryanthera hostmannii*, together with over 30 yr of sapling monitoring in permanent plots spanning a gradient of harvest intensity at the Paracou Forest Disturbance Experiment (PFDE), French Guiana. We anticipated that more intensive logging would increase recruitment of pioneer species with higher specific leaf area, lower wood densities, and smaller seeds, due to the removal of canopy trees. We define a recruitment response metric to compare sapling regeneration to timber harvest intensity across species. Although not statistically significant, sapling recruitment decreased with logging intensity for eight of 23 species and these species tended to have large seeds and dense wood. A generalized linear mixed model fit using specific leaf area, seed mass, and twig density data explained about 45% of the variability in sapling dynamics. Effects of specific leaf area outweighed those of seed mass and wood density in explaining recruitment dynamics of the sapling community in response to increasing logging intensity. The most intense treatment at the PFDE, which includes stand thinning of non-timber-valuable adult trees and poison-girdling for competitive release, showed evidence of shifting community composition in sapling regeneration at the 30-yr mark, toward species with less dense wood, lighter seeds, and higher specific leaf area. Our results indicate that high-intensity logging can have lasting effects on stand regeneration dynamics and that functional traits can help simplify general trends of sapling recruitment for highly diverse logged tropical forests.

Key words: French Guiana; functional traits; Paracou Forest Disturbance Experiment; recruitment; saplings; selective logging; tropical forest.

Introduction

In the last decade, approximately one-fifth (20.3%) of the world's humid tropical forests (3.9 million km^2) have been subjected to selective timber harvest (Asner et al. 2009*a*). Harvest of tropical hardwoods was estimated at 125 million m^3 in 2007 and nearly doubled to 248 million m^3 in 2015 (ITTO 2009, 2017). About one-quarter (26%) of tropical hardwood production comes from Neotropical forests, with the Brazilian Amazon producing the majority (29 million m^3; ITTO 2017), from an estimated 2 Mha selectively logged each year (Asner et al. 2005, Sist et al. 2012). Furthermore, annual forest carbon dioxide emissions from tropical forests are estimated at 2.1 billion Mg, over one-half (53%) of which is attributed to forest degradation associated with timber harvest (Pearson et al. 2017). Logged Amazonian forest is four times more likely to undergo land use change (e.g., conversion to oil palm plantation) than unlogged areas (Asner et al. 2006, 2009*b*). Therefore, logging poses a significant threat to the long-term conservation of tropical tree species (Royal Botanical Garden Kew 2016).

Reduced Impact Logging (RIL) guidelines have been developed to limit harvest intensities and cutting cycles to protect the remaining forest stand and to decrease the destructive impact of forestry machines (FAO 2004, Sist and Ferreira 2007). RIL practices have been successful in reducing the forest disturbance of selective logging (Putz et al. 2012); for example, RIL operations for *Chlorocardium rodiei* in Guyana reduced understory damage by 65% and decreased canopy treefall gap formation by 40%, without increasing operating costs (Van der Hout 2000, Holmes et al. 2001). Nevertheless, much uncertainty remains around how logging practices, particularly logging intensity, and subsequent forest management techniques (e.g., stand-thinning or poison-girdling of non-timber-valuable trees) impact regeneration dynamics (i.e., regenerating richness and composition; Guariguata and Dupuy 1997, Nepstad et al. 1999, Blanc et al. 2009, Hérault and Piponiot 2018).

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A major impediment to measuring logging impacts in tropical forests has been their high species diversity, and little is known about how tropical tree life histories interact with selective logging to affect the regeneration dynamics of tropical forests over the long term (Asner et al. 2009*b*). A potential solution to this challenge involves the use of functional traits, which can simplify the demographic variation of hundreds of tropical tree species in a community along a few key axes of functional variation (McGill et al. 2006, Shipley et al. 2006). Specifically, functional traits representing physiological trade-offs in plant strategies have been directly related to tree species' ecologies and life histories (Wright et al. 2004, Reich 2014). Early successional species that colonize disturbed forest areas tend to have low seed mass and traits associated with fast growth, such as high specific leaf area (SLA) and low wood density. In contrast, later successional species, with low SLA, dense wood, and larger seeds, have more conservative life-history strategies with slow growth and high survival (Garnier et al. 2016). These three plant traits (seed mass, SLA, and wood density) represent most of the global functional variation that coordinates with the life histories of plant species across ecosystems (Díaz et al. 2016, Kunstler et al. 2016). Therefore, functional traits offer a means to generalize community demographics and species performance to species for which data may not exist, in both space and time (Flores et al. 2014, Muscarella et al. 2017). In this study, we employ a functional trait perspective to examine sapling recruitment over three decades in an experimentally logged forest in French Guiana.

Many studies have related functional traits to tropical tree performance (e.g., Wright et al. 2010, Hérault et al. 2011, Rüger et al. 2012). Notably, Poorter et al. (2008) found strong relationships with wood density and tree growth and mortality rates. More recently, tropical tree performance–functional-trait relationships have been understood to be multidimensional (Kraft et al. 2015), nuanced (Poorter et al. 2018), and plastic with tree size or age (Lasky et al. 2015, Visser et al. 2016). Functional traits also offer great utility in summarizing changes in community composition in relation to forest succession (Lebrija-Trejos et al. 2010, Letcher et al. 2015), but the few studies that have sought to document the long-term effects of RIL on the regeneration success of tropical forest species (Schwartz and Caro 2003, Makana and Thomas 2006) have not taken a trait-based approach. The frequency, intensity, and spatial arrangement of logging directly manipulate stand dynamics, which interact with the complete tree life cycle, including adult tree growth, fecundity, and mortality, seed germination, seedling survival, and the various life-stage transitions in between (Hérault et al. 2010, Baraloto et al. 2012), with potential influence on forest community composition. Generally, functional composition of the understory following logging is homogenized (i.e., becomes more even; Baraloto et al. 2012). Recently, Döbert et al. (2017) examined the functional and phylogenetic composition of understory species in a tropical lowland forest in Borneo and found logging increased functional and phylogenetic dispersion (i.e., more random community composition). They also found a clear, threshold response for the functional dispersion of the understory community of all plants at 65% canopy loss but found no coherent trends with respect to individual traits. Therefore, the question remains, do threshold responses in sapling regeneration exist in relation to selective logging intensity in the Amazon?

In this study, we integrate 30 yr of forest demographic data from experimental logging plots with functional traits to address three research questions:

1) Across species, how does sapling recruitment respond to logging intensity? If tropical tree life-history strategies interact with logging disturbance, we expect variability in recruitment among species in relation to logging disturbance. Generally, sapling recruitment should increase with logging intensity, due to the creation of canopy gaps and increased light in the forest understory.
2) Can species recruitment patterns be generalized using their functional traits? We hypothesize that as logging increases, juvenile tree recruitment will be positively correlated with SLA and negatively associated with wood density and seed mass, because of recruitment selection for species with more pioneer life histories (Paine et al. 2015).
3) Is there a threshold of timber harvest intensity, beyond which community composition of regenerating trees changes? We predict a threshold response at logging intensities representing the extremes practiced in the region, corresponding to removal of more than 40% of forest basal area.

Material and Methods

Study site

The Paracou Forest Disturbance Experiment (PFDE) was established in 1982 in the lowland *terra firme* moist forest (5°18′ N, 52°53′ W) of French Guiana (Maître 1982). Climate is strongly seasonal with the main dry season occurring between August and November and a secondary, more mild, dry season from February to April (Wagner et al. 2011). The average annual temperature is 26°C and average annual rainfall measured 3,041 mm from 1979 to 2001 (Gourlet-Fleury et al. 2004). Soils are highly eroded ferralitic soils atop a transformed loamy saprolite (Gourlet-Fleury et al. 2004, Blanc et al. 2009), with similar carbon and nitrogen content as other eastern South American lowland forest soils, but lower phosphorus content (Baraloto and Goldberg 2004).

In Paracou, adult tree (individuals ≥10 cm diameter at breast height [dbh]) stem density averages 618 individuals/ha, with a mean collective basal area of 31 m^2/ha (Durrieu De Madron 1994). Floristically, species richness is high, totaling over 600 species, with >140 species per hectare having dbh ≥10 cm (Sabatier and Prévost 1990). Species composition is variable depending on topography and soil characteristics (ter Steege et al. 1993). *Terra firme* communities are dominated by species in the Fabaceae, Lecythidaceae, Chrysobalanaceae, Sapotaceae, and Burseraceae, while bottomland areas have higher dominance of palms and species in the Fabaceae and Lauraceae.

Logging treatments and tree census methods

The PFDE is a factorial experiment of three blocks, each with four treatments (Fig. 1). Blocks were established in homogenous forest defined according to forest size structure and the density of timber-valuable and potentially timber-valuable tree species. Prior to the onset of the logging treatments, an initial inventory was conducted in 1984, where 12 6.25-ha permanent tree plots (75 ha area in total) were established, wherein all trees ≥10 cm dbh were identified and measured. Between 1986 and 1988, experimental logging treatments were applied to three-quarters of the plots (9 out of 12) in three logging intensities, with the primary objective of evaluating the effect of various thinning techniques on stand dynamics and populations of commercial species (Gourlet-Fleury et al. 2004). The three treatments, which differ little in the amount of logged biomass, but vary with respect to stand management are T1, selective felling for timber at approximately 10 trees of dbh ≥50–60 cm/ha for 58 potentially timber-valuable species; T2, selective felling for timber at the same logging intensity as T1 plus stand-thinning by poison-girdling of about 30 trees/ha of non-commercial species with dbh ≥40 cm; and T3, selective felling for timber at the same logging intensity as T1 plus fuelwood logging of around 15 trees/ha of non-commercial species with dbh between 40 and 50 cm, followed by poison-girdling of about 20 trees/ha of non-commercial species with dbh ≥50 cm (Table 1).

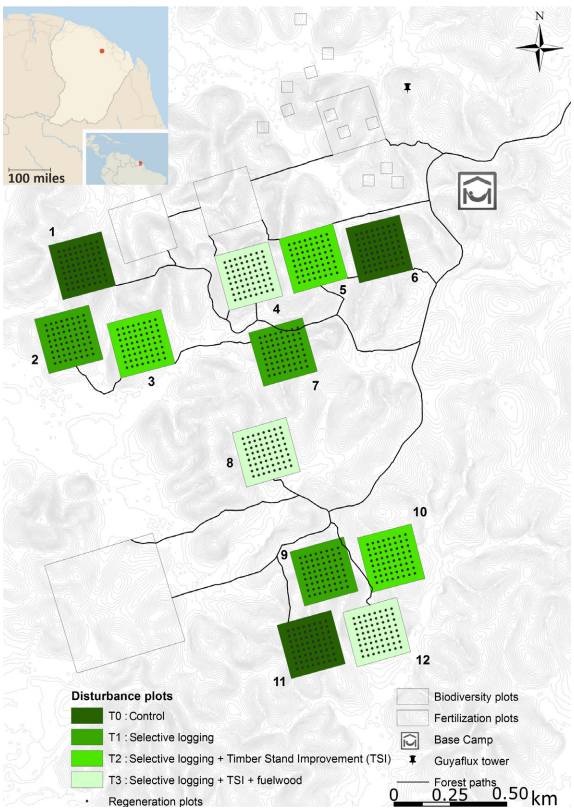

FIG. 1. Map of the Paracou Forest Disturbance Experiment (PFDE), French Guiana. Inset in the top left corner shows the geographic location of the PFDE (red dot) in French Guiana (1 mile = 1.67 km). Treatments are arranged in a randomized block design with three blocks each containing one plot of the four treatments (control plus three logging intensities). Black dots within each plot show the circular sapling regeneration plots (64 per plot). Map modified and reproduced with permission from CIRAD (http://paracou.cirad.fr).

Treatment 1 represents a selectively logged, unmanaged, tropical forest stand. Treatments 2 and 3 represent differences in management strategies, with T3 incorporating less poison-girdled thinning than T2, but coupling it with fuelwood harvest (i.e., selective felling of non-timber species). Although explicitly set up as a replicated experiment (i.e., three replicates of four treatments in a randomized block design), very slight differences in logging implementation within treatments led to a gradient in basal area removed (see Table 1). Juvenile trees (hereafter saplings) were defined as individuals >105 cm tall, but <10 cm in dbh. Beginning in 1992, all saplings were tagged, identified to species, and measured and assessed for damage. Sapling monitoring was done in a series of 768 fixed-radius circular subplots of 50 m^2 arranged in an 8 × 8 grid with 20-m spacing, within each of the 12 treatment plots (68 subplots per plot; Fig. 1). Sapling height and dbh were recorded for 25 focal species (6,872 individuals) chosen to represent commercially harvested and potentially timber-valuable species with a breadth of variation in life-history strategies (Table 2). Subsequent inventories took place in 1993, 1995, 2002, 2005, 2008, 2013, and 2016.

Species abundance dynamics and demographic rates

To explore the variability in sapling demographic responses among species, we first calculated mortality and recruitment rates for saplings of the 25 species in each of the

TABLE 1. The effect of the initial implementation of experimental logging treatments on forest structure at the Paracou Forest Disturbance Experiment, French Guiana.

Plot	Treatment	Initial basal area (m^2/ha)	Basal area removed (m^2/ha)	Percent change in basal area (Δ% BA)	Logging intensity (m^3/ha)
1	Control	30.1	0.739†	−2.38†	6.69†
2	T1	29.3	5.985	−19.31	48.68
3	T2	32.7	13.890	−44.81	95.33
4	T3	31.8	13.981	−45.10	81.51
5	T2	30.5	8.810	−28.41	58.68
6	Control	31.1	0.353†	−1.14†	7.95†
7	T1	31.6	5.319	−17.16	40.40
8	T3	31.4	15.951	−51.46	97.57
9	T2	30.8	5.765	−18.60	38.15
10	T1	32.4	11.772	−37.98	80.52
11	Control	31.7	−0.327†	+1.05†	+3.36†
12	T3	33.0	13.279	−42.84	89.54

Notes: Three blocks of four plots each corresponding to one of four treatments, a control plus three intensities of logging: selective logging (T1), selective logging + timber-stand improvement (TSI; T2), selective logging + TSI + fuelwood harvest (T3).

†Changes in basal area and volume of wood in control plots are a function of natural biomass dynamics of the stand, and no timber was removed experimentally.

TABLE 2. Three functional traits: specific leaf area (SLA), twig density, and dry seed mass for the 23 focal species from the Paracou Forest Disturbance Experiment, French Guiana.

Code	Species (Family)	Commercial volume harvested ($m^3 \cdot ha^{-1} \cdot yr^{-1}$)†	Functional traits			Demographic response to logging		
			SLA (m^2/kg)	Twig density (g/cm^3)	Seed mass (g)	Slope of recruitment response	Recruitment response R^2	Recruitment response RMSE
sg	*Symphonia globulifera* L.f. (Clusiaceae)	2.7	10.23	0.61	4.48	−0.00557	0.1469	0.1792
mo	*Moronobea coccinea* Aubl. (Clusiaceae)	—	33.4	0.65	6.23	−0.00425	0.0328	0.3082
dth	*Iryanthera hostmannii* (Benth.) Warb. (Myristicaceae)	—	31.87	0.54	0.65	−0.00327	0.2941	0.0676
wa	*Vouacapoua americana* Aubl. (Fabaceae)	2.9	38.99	0.64	12.67	−0.00242	0.0542	0.135
wg	*Recordoxylon speciosum* (Benoist) Gazel ex Barneby (Fabaceae)	—	45.47	0.62	0.178	−0.00082	0.0023	0.2284
sy	*Symphonia sp. 1* (Clusiaceae)	—	29.76	0.65	1.18	−0.00075	0.0256	0.062
ko	*Sterculia pruriens* (Aubl.) K.Schum. (Malvaceae)	13.2	28.98	0.43	0.44	−0.00021	0.0004	0.1427
bo	*Bocoa prouacensis* Aubl. (Fabaceae)	—	24.01	0.77	1.07	−0.00004	0.0003	0.032
to	*Iryanthera sagotiana* (Benth.) Warb. (Myristicaceae)	—	33.01	0.49	2.02	0.00038	0.038	0.0254
eg	*Eperua grandiflora* (Aubl.) Benth. (Fabaceae)	—	22.7	0.66	27.61	0.00154	0.0047	0.2983
da	*Tachigali melinonii* (Harms) Zarucchi & Herend. (Fabaceae)	—	26.91	0.74	0.186	0.00193	0.0176	0.1925
ca	*Carapa surinamensis* Miq. (Meliaceae)	—	28.39	0.52	7.71	0.00277	0.0445	0.1715
ef	*Eperua falcata* Aubl. (Fabaceae)	—	38.31	0.55	3.18	0.00278	0.0251	0.2312
an	*Dicorynia guianensis* Amshoff (Fabaceae)	—	31.73	0.55	0.346	0.00556	0.0735	0.2633
gr	*Sextonia rubra* (Mez) van der Werff (Lauraceae)	2.7	27.74	0.53	1.17	0.00614	0.145	0.1988
sr	*Andira coriacea* Pulle (Fabaceae)	2.5	26.31	0.8	40.63	0.00179*	0.5478	0.0217
ya	*Virola michelii* Heckel (Myristicaceae	—	32	0.47	1.74	0.00594*	0.5968	0.0651
ys	*Virola surinamensis* (Rol. Ex Rottb.) Warb. (Myristicaceae)	—	29.63	0.47	0.81	0.00594*	0.5968	0.0651
ki	*Pradosia cochlearia* (Lecomte) T.D.Penn (Sapotaceae)	—	20.54	0.61	0.954	0.00712*	0.5817	0.0805
sc	*Schefflera decaphylla* (Seemann) Hanns (Araliaceae)	—	20.23	0.52	0.006	0.00798*	0.6469	0.0787
go	*Qualea rosea* Aubl. (Vochysiaceae)	5.2	17.53	0.53	0.096	0.00851*	0.4841	0.1172
ja	*Jacaranda copaia* (Aubl.) D.Don (Bignoniaceae)	—	30.48.	0.38	0.005	0.00908*	0.7659	0.067
gi	*Goupia glabra* Aubl. (Goupiaceae)	3.6	34.48	0.62	0.002	0.01942*	0.8164	0.1229

Notes: Codes correspond to the species labels near points in Figs. 2 and 3. Cells with a dash indicate where commercial timber harvest volumes for species are unknown. RMSE, root mean-squared error.
*Statistically significant slopes at $\alpha = 0.05$.
†Harvest volumes obtained from Guitet et al. (2016).

12 plots over each of the seven census intervals (see Appendix S1: Fig. S1), using the following equations:

$$\text{Mortality rate} = [\ln N_t - \ln(N_t - \#\text{dead}_{t+1})]/\ \#\ \text{months} \quad (1)$$

$$\text{Recruitment rate} = [\ln(N_t + \#\text{recruits}_{t+1}) - \ln N_t]/\#\text{months} \quad (2)$$

where N is the number of individuals and t is a given census. As a side note, recruitment rates are sapling in-growth rates to the diameter size class ≥1 cm or height class >105 cm, so that recruitment and growth are nearly the same in this case, eliminating the need to look at growth and recruitment of saplings independently. We were cautious in the interpretation of these rates as direct metrics of logging effects of species demographics, since forest inventory data did not start until ~4 yr after implementation of the experimental treatments and methodological inconsistencies existed at the initial stage of the experiment. Additionally, natural, background recruitment took place even in the control treatments for some species, at various time intervals, making it difficult to use these demographic rates as the exclusive metric. We therefore sought to develop a novel metric, which we term "the recruitment response." Two of the 25 species (*Sterculia speciosa* and *Platonia insignis*) had very low abundances (i.e., were not found in one-half of the plots; see Appendix S1: Fig. S1 bottom-right most panels) and were therefore excluded from the recruitment response analyses.

Quantifying the recruitment response

An issue when approaching the question of species response to logging over time is how to appropriately account for time and repeated measures across multiple tree

censuses. To control for repeated measurements over multiple tree censuses, we looked at the absolute recruitment response for species, effectively standardizing effects of time. We quantified the recruitment response of each of the remaining 23 species, as the quotient of the natural log of the maximum abundance found in each of the logged plots over the 30-yr period and the natural log of average maximum abundance across the three control plots

$$\text{Recruitment response}_s = \frac{\ln(\text{Abundance Logged Plot}_{s,\max} + 1)}{\ln(\text{Abundance Control Plot}_{s,\max} + 1)} \quad (3)$$

where s is species. We chose to take the natural log of the abundance plus one for both the numerator and denominator because it allows for the calculation of the metric in plots where the species is not present. Taking the maximum abundance in any of the logged plots, and not averaging across them, estimates the maximum potential response to logging for that species and mitigates the effect of differing abundances of species across treatments (i.e., among blocks). Recruitment response values greater than one indicate an increase in abundance of that species in response to the logging treatment in that plot, while values less than one indicate an abundance decrease. Recruitment response values for each of the nine logged plots were regressed against the amount of basal area removed from each plot during the establishment of the PFDE (Δ% BA; see Table 1). The slope of this linear relationship represents the magnitude of the response to increasing logging intensity for that species. To better understand the interspecific variation in response to logging intensity, we solved linear regressions for the recruitment response for each species at three logging intensities: low (a 20% reduction in stand basal area), medium (a 40% reduction), and high (a 60% reduction). These logging intensities were chosen from the literature and our knowledge of common logging practices (irrespective of the PFDE treatments) to represent realistic conditions of logging in the Amazon. In other words, fitted linear regressions for species recruitment responses were solved linearly at ΔBA 20%, 40%, and 60% (see Appendix S1) and then regressed against functional traits.

Application of functional traits

For the French Guiana community, tree wood density ranges from 0.26 to 1.29 g/cm^3, seed mass ranges from 10 μg to 120 g (ter Steege and Hammond 2001), and SLA ranges from 1.77 to 47.41 cm^2/g (Baraloto et al. 2012). Plant functional traits were measured directly on individuals for all 25 species across 13 plots at Paracou (the 12 associated with PFDE and a larger permanent monitoring plot) as part of the BRIDGE project for 12 functional traits representing leaf and stem economics (see Baraloto et al. [2010] for details). The traits measured were leaf area, specific leaf area (SLA), leaf thickness, leaf toughness, leaf nitrogen content, leaf carbon content, leaf carbon isotope (C_{13}) content, leaf potassium content, leaf chlorophyll, sapwood density, twig density, and bark thickness. Seed mass data were previously collected (see Baraloto and Forget 2007).

A principal components analysis revealed that more than one-half of the variance in the 13 functional traits across the 25 species could be explained by two axes (Appendix S2: Fig. S1). Correlations of the first two PCA eigenvectors showed that the first axis was related to leaf economics, mainly leaf thickness, leaf toughness, and SLA; and the second to stem economics, chiefly sapwood and twig density (Appendix S2). Leaf thickness was the strongest correlated trait with axis 1 but can be difficult to understand in terms of leaf economics its relationship with tropical tree life histories, so we chose SLA because of its popularity and interpretability. Therefore, we simplified subsequent analyses by using SLA as the main functional trait representing species trade-offs in leaf economics and twig density as the main functional trait characterizing species trade-offs in stem economics. We chose twig density because of greater data coverage for the study species; however, twig density has been shown to be highly correlated with wood density for the French Guiana plant community (Sarmiento et al. 2011), making inference using twig density applicable to a similar variation in wood density. We added seed mass as a third trait representing an axis of whole-plant strategy variation (Díaz et al. 2016) and given its importance to species life histories for the French Guiana tree community (Baraloto et al. 2005, 2006, Baraloto and Forget 2007). The slopes of the recruitment response and the predicted values of the recruitment response at low, medium, and high logging intensity were regressed against these three functional traits (SLA, twig density, and seed mass) to examine general patterns between species recruitment responses to logging and their functional trait values.

Generalized linear mixed model: looking for a threshold

Lastly, we modeled the sapling regeneration dynamics, using sapling abundance data for all 25 species, over time in the PFDE based on the interaction of logging intensity and the three chosen functional traits (SLA, twig density, and seed mass). The goal was to identify a possible threshold in sapling regeneration to the logging treatments. A negative binomial generalized linear mixed model (glmm) with a logistic link function was used. Sapling abundance data were roughly Poisson distributed; we chose a negative binomial glmm due to the computational ease of fitting a negative binomial glmm vs. a Poisson glmm (Zuur et al. 2013).

Prior to model fitting, seed mass data were log-transformed, and all explanatory variables were scaled and centered. We modeled sapling abundance per plot per species (using all 25 focal species) as a function of logging intensity, SLA, twig density, time, and seed mass as fixed effects and random intercept terms for plot, block (i.e., replicate, to account for spatial differences in community composition, see Fig. 1) and species. Stepwise model selection was performed based on model AIC_c (Akaike information criterion corrected for sample size) followed by model validation (visualization of residuals, examination and plotting of the fixed and random effects and the interaction terms, and evaluation of model fit using glmm R^2; Nakagawa and Schielzeth 2013), and the model was used to predict sapling abundances per species per plot. Analyses were conducted in R v.3.3.3 (R Development Core Team 2017) using the lme4,

MuMIN, r2glmm, sjPlot, and effects packages (Fox 2003, Bartoń 2013, Bates et al. 2014, Jaeger 2017, Lüdecke 2017).

Results

Sapling demographic responses to logging intensity

Stem abundances and mortality and recruitment rates were dynamic through time in response to the experimental logging treatments. Among species, mortality rates greater than zero ranged from 0.001 to 0.36 stems/yr with a median value of 0.002, while recruitment rates greater than zero varied between 0.001 and 0.6 stems/yr with a median value of 0.004 (Appendix S1: Fig. S1). Mortality rates were zero in 66% of the cases (plot × census combinations), while recruitment rates were zero in 50% of the cases. So, over the 30 yr of sapling monitoring, recruitment of saplings outweighed mortality, and recruitment increased until about two decades following the implementation of the experimental logging treatments (Fig. 2). Sapling recruitment rates were highest in the first two census intervals (1992 and 1993); thus, the majority of sapling recruitment occurred in the first 8 yr following logging (Appendix S1: Fig. S1). This is evident in the changes in stem densities in the logged plots, which increased until 2008 and then thinned to densities similar to those in the control plots (Fig. 2).

The recruitment response metric shows high variability in sapling response to logging across the experimental gradient; 8 of 23 species exhibited significantly increased recruitment in response to logging and seven species exhibited significantly decreased recruitment (Appendix S1). Slopes of the linear recruitment response for the 23 focal species ranged between −0.005 (*Symphonia globulifera*) and 0.009 (*Jacaranda copaia*, *Qualea rosea*), with varying goodness of fit among species and coefficients of determination averaging 0.26. Of the statistically significant linear regressions, the model for *Goupia glabra* fit the best (R^2 = 0.82) and the model for *Qualea rosea* fit the poorest (R^2 = 0.48). The average residual mean-squared error (RMSE) of the linear models was 0.14, ranging from the best fitting model (*Andira coriacea*) with a RMSE of 0.022 to the poorest fitting model (*Moronobea coccinea*) with a root mean-squared area (RMSE) of 0.31 (Table 2). Of the seven species that had negative slopes in recruitment response, meaning they responded with decreased sapling recruitment to the logging treatments, none were statistically significant; statistically significant recruitment responses were found only for species responding positively to increasing logging intensity (Table 2; Appendix S3).

Relationships of sapling recruitment response to logging with functional traits

For the 23 species for which we calculated recruitment responses (see Table 2), median SLA measured 29.0 m^2/kg and ranged from 10.2 to 39.0 m^2/kg, median seed mass was 1.09 g and ranged from 0.0015 to 40.63 g, and median twig density was 0.55 g/cm^3 and ranged from 0.38 to 0.80 g/cm^3. Relationships between functional traits and the slope of the recruitment response were weak but significant with respect to seed mass (R^2 = 0.18, P = 0.041) and not significant for twig density and SLA (Appendix S3, Fig. 3). When we investigated the relationship of the three traits to species recruitment response at low (a 20% reduction in basal area), medium (a 40% reduction in basal area), and high (a 60% percent reduction in basal area) logging intensities, a more nuanced pattern emerged (Fig. 3). Species with high SLA tended to have higher recruitment responses at lower logging intensities, a trend that attenuated with an increase in the intensity of logging (Fig. 4, left panels). However, this

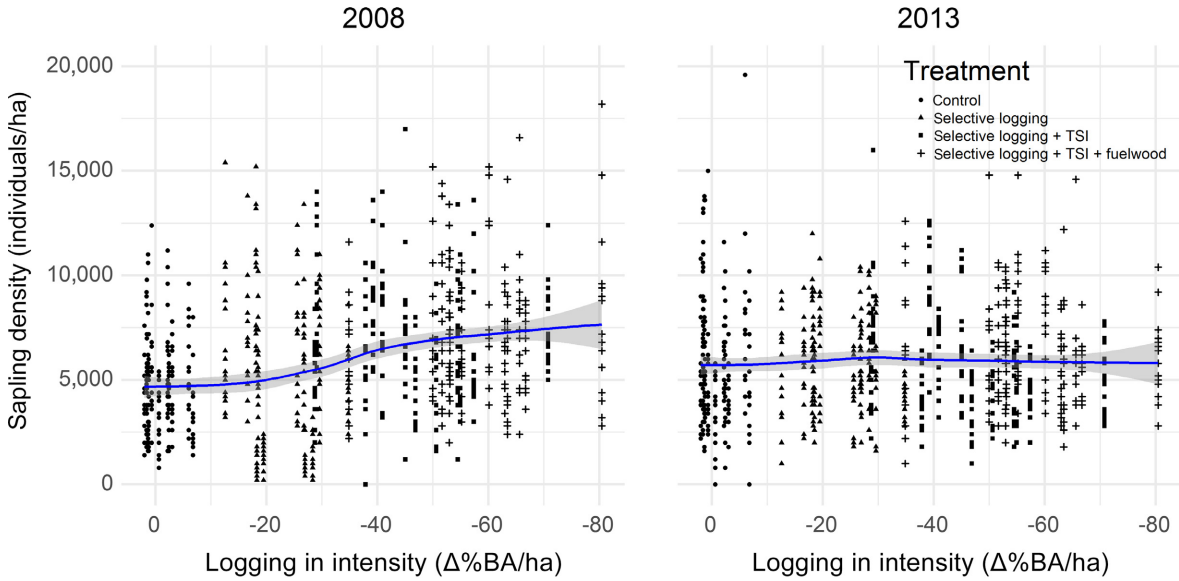

Fig. 2. Sapling stem densities across the logging gradient, shown as the change in percent basal area (Δ% BA; where BA is measured in m^2/ha; x-axis) at the PFDE in 2008 and 2013. Points are total stem densities from the 768 circular subplots of 50 m^2, scaled up to per-hectare values. Plotting symbols represent the treatments, and blue lines are LOESS smoothers fit to the data. Initial stem densities for saplings were not measured when the PFDE was established, but initial stem densities of adults can be found in Table 1.

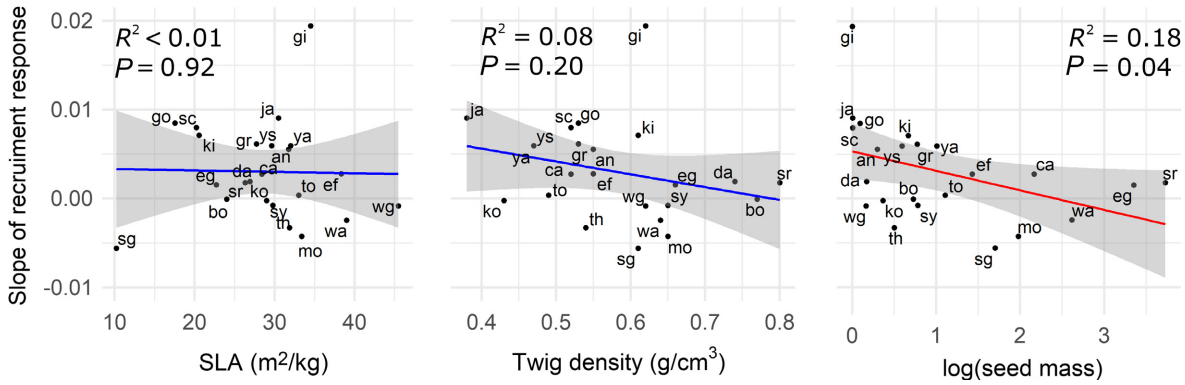

FIG. 3. Relationships between recruitment response to logging intensity and three functional traits: specific leaf area (SLA), twig density, and log-transformed seed mass (g), for 23 focal species of the PFDE. Red lines show statistically significant regressions while blue lines show non-significant ones. Coefficients of determination (R^2) and their associated probabilities given for each regression. Species codes correspond to Table 2.

relationship was not statistically significant and decreased in strength with increasing logging intensity (R^2 = 0.02–0.11, P = 0.13–0.51). Sapling recruitment response relationships to twig density and seed mass varied little with the reduction in stand basal area (i.e., stand thinning and poison girdling; Fig. 4 middle and right panels). These relationships were statistically significant for seed mass (R^2 = 0.17–0.25, P = 0.02–0.05), but not for twig density (R^2 = 0.05–0.09, P = 0.18–0.33) (Fig. 4, Appendix S3).

Modeling sapling dynamics as a function of logging intensity and functional traits; a threshold response?

Using a mixed-effects model that incorporated logging intensity, time, SLA, seed mass, and twig density as explanatory variables, we were able to marginally capture sapling abundance dynamics at the PFDE. The best-fitting glmm included fixed effects for all three functional traits, logging intensity, time, interaction terms between logging intensity (ΔBA) and all three traits and time, and interaction terms between time and seed mass and twig density (Table 3; Fig. 5). Including an interaction term between seed mass and twig density, which were weakly correlated (r = 0.52), did not improve model fit. The model fit was satisfactory (R^2_{glmm} = 0.45). SLA had the greatest fixed effect, accounting for about 75% of the variance explained by fixed effects in the model (R^2_{effect} = 0.32). Seed mass explained the remainder of the variability in sapling demographics for the fixed effects (R^2_{effect} = 0.12), leaving the effect of twig density very small. The model associated most of the random variability in sampling demographics in relation to logging intensity to species differences ($\tau_{00,\ \text{species}}$ = 1.43), with some minor differences between plots and less so between experimental blocks.

DISCUSSION

Effects of logging in the PFDE

Logging treatments reduced stem densities and overall tree basal area and biomass (Table 1; Blanc et al. 2009). After a decade, the logging treatments resulted in an average 2.3 m reduction in total canopy height of adult trees, 2.0 m of which was attributed to reduction in main stem height due to a change in the allometry of the trees in logged areas, causing a 2–13% reduction overall tree biomass and a 3–17% reduction in stem basal area, depending on the treatment (Rutishauser et al. 2016). In 1988 after logging had ceased, Favrichon and Maître (1998) showed that stand basal area was recovering at a rate of about 2% yr^{-1}. Effects of the logging treatments on seedling establishment have been shown to be negligible after 12 yr of logging at the PFDE, with no single species exhibiting differential germination in response to logging (Baraloto and Forget 2004).

How variable was the recruitment response among species?

Sapling recruitment in response to logging increased to a zenith at the 8-yr mark then stabilized (Appendix S3: Fig. S1). Several studies have reported that forest structure, defined as the stand diameter size distribution, in selectively logged areas is indiscernibly similar to unlogged areas by the 8-yr mark (Cannon et al. 1994, 1998, Peña-Claros et al. 2008). Nevertheless, the recovery of forest composition can take much longer, since often times shade-tolerant species can be slow to recruit in the many small forest gaps following selective logging (Peña-Claros et al. 2008, Hérault et al. 2010). Rankin- Mérona and Montpied (2004) examined sapling dynamics 8 yr following the implementation of the treatments in the same study site and found slight differences in sapling abundances across species. Saplings of two species (*Qualea rosea* and *Iryanthera sagotiana*) showed immediate increases in abundance following logging, and saplings of all but three species (*Bocoa proucacensis*, *Moronobea coccinea*, and *Eperua grandiflora*) showed a delayed increase in abundance following logging. The magnitude of increase in sapling abundances following logging ranged from very strong (such as *Virola* spp. and *Jacaranda copaia*) with the species increasing in abundance in all three logging treatments to weak where the species only responded to logging at one intensity (e.g., *Iryanthera hostmanii* to the low-intensity treatment and *Schefflera decaphylla* to the high-intensity treatment).

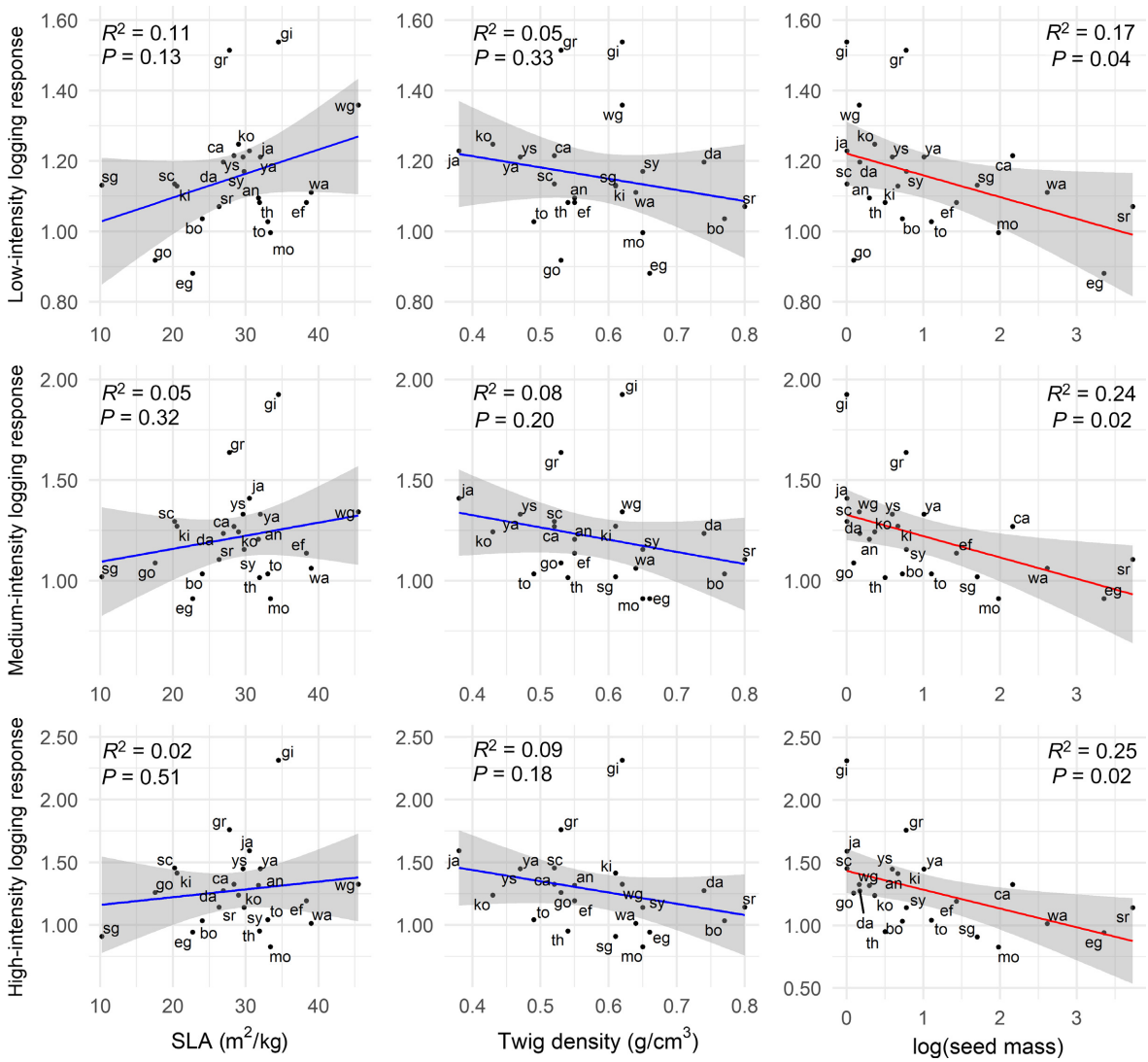

FIG. 4. Recruitment response for saplings at low (a 20% reduction in stand basal area), medium (a 40% reduction in stand basal area), and high (a 60% reduction in stand basal area) logging intensities, for 23 species plotted against three functional traits: specific leaf area (SLA), twig density, and log-transformed seed mass (g). Red lines show statistically significant regressions while blue lines show non-significant ones. Coefficients of determination (R^2) and their associated probabilities given for each regression. Species codes correspond to Table 2.

Our analyses confirm these results, in that we found a decreased recruitment in one-third of the study species, one-third with increased recruitment, and one-third with no effect. Although the slopes of the recruitment responses for the species with decreased recruitment were not statistically significant (Table 2), those species still regenerated at lower rates than in control plots (Appendix S3: Fig. S1). The species with increased recruitment tended to share functional strategies of high SLA and low seed mass (Fig. 3), and the difference in recruitment across functional strategies was most pronounced at low logging intensity (Fig. 4). Overall, our results are congruent with previous research into the dynamics of forest structural recovery following selective logging (Cannon et al. 1998, Nepstad et al. 1999), including those from Paracou (Rankin- Mérona and Montpied 2004, Blanc et al. 2009, Hérault et al. 2011, Baraloto et al. 2012, Flores et al. 2014). We build on these findings with our result that even after 30 yr of stand recovery, sapling recruitment dynamics favored species with higher SLA and less dense wood. This makes sense ecologically but largely remains unconsidered in tropical forest management given that most logging companies and forest managers rely solely on data from adult trees and rarely incorporate functional perspectives. At least an additional 30 yr of monitoring is needed to determine whether the differential recruitment of such species leads to a shift in community composition of larger trees. Certainly, in congruence with the extensive literature on tree species responses to logging, pioneer species tended to benefit; however, we also provide some evidence that saplings of shade-tolerant species are at a disadvantage in the most intense logging treatment at the PFDE. This is likely harder to detect in adult tree inventory data, due to the lagged effects of decreasing population dynamics (e.g., extinction debt), explaining some of the weak (i.e., marginally or non-significant) signals in our analyses.

TABLE 3. Generalized linear mixed model coefficients for sapling abundance per species per plot modeled using a negative binomial data distribution and log link function.

	B	Wald CI	P	R^2 effect	Random parts	Variance, ICC, random effect number
Fixed parts						
(Intercept)	2.649	2.171 to 3.128	<0.001		$\tau_{00,\ species}$	1.430
Δ%BA	−0.148	−0.219 to −0.077	<0.001	0.044	$\tau_{00,\ plot}$	0.014
log(seed mass)	−0.297	−0.838 to 0.246	0.281	0.124	$\tau_{00,\ block}$	0.003
SLA	0.475	0.003 to 0.946	0.049	0.323	$N_{species}$	25
Time	0.090	0.067 to 0.113	<0.001	0.017	N_{plot}	12
Twig density	0.004	−0.536 to 0.544	0.988	0.000	N_{block}	3
Δ%BAlog(seed mass)	0.094	0.068 to 0.119	<0.001	0.014	$ICC_{species}$	0.751
Δ%BA:SLA	−0.033	−0.058 to −0.008	0.009	0.002	ICC_{plot}	0.003
Δ%BA:time	0.067	0.044 to 0.089	<0.001	0.009	ICC_{block}	0.001
Δ%BA:twig density	0.034	0.009 to 0.059	0.008	0.002	Observations	2400
log(seed mass):time	0.037	0.013 to 0.061	0.002	0.003	AIC_c	16846.641
SLA:time	−0.019	−0.045 to 0.006	0.127	0.001	−2 log-likelihood	16814.413
					Deviance	2544.626
					Family	negative binomial (θ = 4.4789) (log)

Notes: Coefficient slope, Wald confidence interval, statistical probability, and R^2 effect shown for the fixed parts of the model and the variance (τ), intra-class correlations (ICC), and random effect number (N) are given for the random parts of the model. AIC_c, Akaike information criterion corrected for sample size. Model R^2_{glmm} = 0.450.

Can sapling recruitment response be predicted using functional traits?

The recruitment response metric we employed adequately characterized general trends in species regeneration. Due to performance differences (i.e., growth rates) at the seedling to sapling life-stage transition, we expected sapling recruitment to be dominated by species with pioneer-associated functional trait values (Sterck et al. 2006, 2011, Wright et al. 2010). As expected, species with more resource-conservative leaves (e.g., lower SLA, longer leaf life span, greater leaf C:N) had reduced recruitment at higher logging intensities. Our result confirms the effects of logging on increasing the SLA of the resultant community (Flores et al. 2014, Kusumoto et al. 2015, Döbert et al. 2017). A similar trend, although much weaker in its explanatory ability, was illustrated with respect to stem and whole-plant economics, with species characterized by higher twig densities and larger seeds having reduced recruitment in treatments where more basal area was removed. Twig density and seed mass showed consistent trends in the recruitment response analysis at low, medium, and high logging intensities, probably because they are more conserved across the variation in life history of species in this study, whereas SLA can be more plastic with

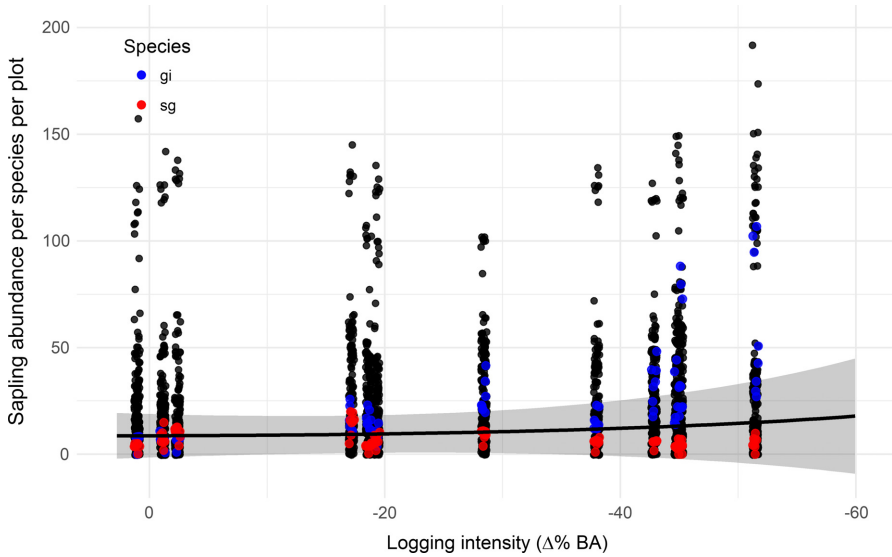

FIG. 5. Predicted model fit for the negative binomial generalized linear mixed model (glmm) displaying model-predicted sapling abundance per species per plot in relation to logging intensity (shown as the change in percent basal area; Δ% BA). See Table 3 for model coefficients. The species with the greatest positive recruitment response, *Goupia glabra* (gi), is shown in blue and the species with the most negative recruitment response, *Symphonia globulifera* (sg), is shown in red. Abundances of these two species diverge with increasing logging intensity.

light environment and ontogeny (Lusk et al. 2008, Lasky et al. 2015, Visser et al. 2016).

We concur with Paine et al. (2015) that relating performance (in this case, regeneration in response to logging) to functional traits for saplings is especially difficult, for several reasons. First, functional traits and their relationship with performance change with the size (or age) of tropical tree species (Lasky et al. 2015, Visser et al. 2016); however, it is difficult to quantify ontogenetic trait variation because it requires extensive sampling (see Poorter et al. 2018). Our results also caution against the interpretation of community dynamics using a single trait. We advocate for the use of multiple traits or "trait syndromes" in trait-based approaches to complement a deeper understanding of tree species ecologies and life histories (Kraft et al. 2015). Specifically, the timber-valuable pioneer species in the Paracou community do not possess one single trait that aptly describes their life-history strategy (Baraloto et al. 2010, Fortunel et al. 2012), but rather most possess a suite of traits that when viewed comprehensively describe the strategy of a fast-growing timber-valuable canopy tree and the functional trait variability within.

For example, *Goupia glabra*, with low seed mass, high SLA, but intermediate twig density, shows the typical small seeds and low-cost lightweight leaves of a pioneer species but has denser branch wood than the typical tropical forest pioneer species. Despite this, when considered in unison, using the generalized linear mixed model, effects of SLA as an explanatory trait, outweighed the trends observed in the recruitment response of the community for twig density and seed mass. And the analyses of recruitment response to low-, medium-, and high-intensity logging with respect to SLA showed this relationship to weaken with increasing logging intensity. This suggests that when considered in conjunction with other traits, SLA appears to be the most informative single trait for predicting life-history-related demographics of tropical trees to any driver. Despite the known variation of SLA to small-scale variation in forest light environment and across tree ontogeny (Rozendaal et al. 2006), the SLA effect, in this case, is driven by demographic changes in the sapling community. This result implies that variation in traits associated with the leaf economic spectrum (Wright et al. 2004) best explains the sapling dynamics for these 25 tree species at the PFDE.

Modeling sapling dynamics using functional traits: preferential species regeneration

We explored whether sapling recruitment responded differentially to logging intensity using a negative binomial glmm that modeled per-species sapling abundance per plot as a function of the percent reduction in stand basal area, time, and three functional traits. Notably, the two species with low abundances that we excluded when calculating the recruitment response had the most negative random effect values. Logging intensity had a negative effect on sapling recruitment, but time had a positive one, showing that regeneration dynamics in logged stands do recover over time, in this case after two to three decades. However, it undoubtedly takes much longer to recover the wood volume needed for subsequent timber harvest, an estimated 49 yr at the low-intensity logging (10 trees/ha) and over a century at higher intensities (21 trees/ha; estimates using data from PFDE; Sist et al. 2012). SLA was positively related to, and twig density and seed mass were negatively related to, sapling regeneration, confirming our recruitment response analyses that, with increasing logging intensity, sapling regeneration favors species with more resource-acquisitive, pioneer life histories (Reich 2014). Comparable results are corroborated in the literature (Flores et al. 2014, Kusumoto et al. 2015, Döbert et al. 2017). In fact, a recent study showed that, after 49 yr, the species composition of intensively managed tropical forest timber stands in Australia remained distinct (Hu et al. 2018).

In the mixed-effects model, we found little evidence for a clear threshold response of sapling regeneration across the experiment logging treatments at the PDFE (Fig. 5). An explanation is that the treatments represent an incomplete gradient, and even the most intensive logging treatment probably does not remove enough biomass to induce such a threshold. The threshold in the functional dispersion of understory plant documented by Döbert et al. (2017) occurred at a 65% reduction in canopy cover beyond which a major shift occurred toward more random plant assemblages via the integration of more non-woody plant species. A 65% reduction in canopy cover expectedly removes at least one-half of the basal area of a stand, probably more. Methodologically, piecewise regression, as implemented in other studies looking for threshold responses (e.g., Döbert et al. 2017), was explored but determined to be inadequate due to the variability of species responses to logging that we highlight. Future directions in the sustainability of logged forests that use data from juvenile trees could incorporate methods that can project long-term population dynamics to time-scales relevant for subsequent timber harvest (i.e., 60–80 yr; see Needham et al. 2018).

Application of findings for tropical timber-stand management

High-intensity selective logging (i.e., selective felling of the largest timber-valuable trees with timber-stand improvement and fuelwood harvest) either (1) reduces potential seed sources for species regeneration within the logged area (Guariguata and Pinard 1998); (2) depletes the replenishment of those species into the soil seed bank affecting the sustainability of seedling establishment and sapling recruitment (Schupp et al. 1989); and/or (3) adversely changes the behavior of seed dispersers decreasing seed dispersal into the logged areas (Wunderle 1997, Markl et al. 2012). Flores et al. (2006) found dispersal limitation and species shade tolerance to significantly interact with the abiotic light environment and changes in stand structure related to logging intensity (i.e., canopy openness, plant area index, and total basal area and biomass), suggesting complex interplay in abiotic and biotic mechanisms in sapling responses to logging. Notably, sapling recruitment at the PFDE might exceed natural levels of recruitment in non-experimental logged areas in the Guiana Shield because the plots are relatively small and embedded in a matrix of a well-conserved area, likely experiencing some degree of rescue effects at the metapopulation level.

The directional shift in the functional assemblage of species in the most intensively logged plots is a result of increasing functional evenness (Baraloto et al. 2012), driven by

decreased recruitment of long-lived timber-valuable species with low SLA and large seeds in the plots that used timber-stand improvement (i.e., thinning of non-timber-valuable trees) techniques. Poison-girdling, although improving basal area accumulation of the established individuals of timber-valuable species (De Graaf et al. 1999), has a negative effect on their regeneration over the long-term, based on our findings from the T2 and T3 plots. This could be due to the interaction of selective logging and poison-girdling, being that despite increased mortality of non-timber-valuable species poison-girdling effectively increases the recruitment of species with "faster" life histories (i.e., lower wood density).

Conclusion

As selective logging continues in tropical forests, often in an unmanaged context, the need to understand the trade-offs for species regeneration with increased logging intensity has become more urgent. Our trait-based analyses using data from the Paracou Forest Disturbance Experiment, French Guiana, indicate that low-intensity logging (i.e., removing up to 30% of the stand biomass) has a relatively negligible effect on the regeneration dynamics, and the functional composition, of saplings, 30 years following timber extraction, provided the stand is allowed to recover. Logging at higher intensities (i.e., removing over 40% of the stand biomass and thinning the remaining community), however, preferentially selects for tree species with more pioneer-type life histories, which shifts community composition saplings toward species with lower twig densities and smaller seeds. This effectively reduces the sustainability of the selective logging practice, by decreasing the regeneration of species with lower specific leaf area and denser wood.

Using data from the Paracou Forest Disturbance Experiment, we have identified that logging at higher intensities, utilizing thinning by poison-girdling and fuelwood harvest, is responsible for this shift; likely, it is related to complex biotic interactions across all life stages of timber-valuable species in the forest. We advocate for tropical timber companies to ensure that they log less than half of the total forest basal area, only selectively harvesting the largest individuals of timber-valuable species and allowing the stand to recover for at least 60–80 yr. We advocate against the use of timber-stand improvement techniques, such as thinning and fuelwood harvest and especially poison-girdling, as our results show that they alter remnant understory communities and select against the regeneration of the timber-valuable species with dense wood. Adhering to these recommendations will help conserve the naturally regenerating community of timber-valuable species throughout the Amazon, as logging practices continue.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1776/full

Data Availability

Data are available from the Dryad Data Repository: https://doi.org/10.5061/dryad.h9083.