Contrasting taxonomic and functional responses of a tropical tree community to selective logging

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Summary

1. Considerable debate surrounds the extent to which tropical forests can be managed for resource extraction while conserving biodiversity and ecosystem properties, which depend on functional composition. Here we evaluate the compatibility of these aims by examining the effects of logging on taxonomic and functional diversity and composition in a tropical forest.

2. Twenty years after selective logging, we inventoried 4140 stems regenerating in logging gaps and adjacent undisturbed areas, and we integrated a database of 13 functional traits describing leaf and wood economics of tropical trees.

3. We found no differences in taxonomic and functional richness among habitats, but logging gaps had significantly higher taxonomic and functional evenness.

4. Logging also effected striking, long-term changes in both species and functional composition. In particular, the xylem density of recruits in logging gaps was 6% less than in unlogged forests, leaves were 11% less tough and had 6–13% greater mineral nutrient concentrations.

5. *Synthesis and applications.* Our results suggest that managers of tropical forests should limit overall surface area converted to logging gaps by creating fewer, larger gaps during selective logging, to reduce impacts on the taxonomic and functional composition of the regenerating stand.

Key-words: canopy gap dynamics, French Guiana, functional diversity, functional evenness, functional traits, disturbance, light partitioning, species richness, tropical rain forest

Introduction

The consequences of global environmental changes include altered community structure and associated ecosystem processes and services (Balvanera *et al.* 2006; Diaz *et al.* 2007). Recent studies have underlined metrics beyond species richness to assess the relationship between biodiversity and environmental changes (Mayfield *et al.* 2005; Moretti *et al.* 2009; Villéger *et al.* 2010). The emerging perception is that conservation and restoration practices can be improved by considering the consequences of management activities for both taxonomic and functional trait diversity (Devictor *et al.* 2010; Mayfield *et al.* 2010), functional traits being the biological attributes of organisms that influence fitness and that shape ecosystem properties (McGill *et al.* 2006; Diaz *et al.* 2007; Suding & Goldstein 2008; Cadotte, Carscadden & Mirotchnick 2011).

The recent expansion in the use of functional traits to study basic and applied questions in ecology has benefited from many methodological advances, particularly for the measure of functional diversity and its comparison with standard indices of taxonomic diversity (Petchey & Gaston 2006; Villéger, Mason & Mouillot 2008; Mouchet *et al.* 2010). Functional diversity metrics complement taxonomic metrics (Petchey & Gaston 2002; de Bello *et al.* 2010) and are particularly sensitive in the face of species extinctions (Devictor *et al.* 2010). How-

ever, there is still no consensus about the relationships between functional diversity metrics and key ecosystem properties and processes (Mayfield *et al.* 2010; Cadotte, Carscadden & Mirotchnick 2011). The performance of functional diversity metrics remains excessively dependent on the *a priori* choice of traits (Lavorel & Garnier 2002; Lavorel *et al.* 2008; Mouchet *et al.* 2010). A comprehensive analysis of community responses to environmental change should therefore include not only measures of functional diversity but also a discussion of functional composition (Moretti *et al.* 2009).

Tropical forests represent a major reservoir of global biodiversity, with an estimated 15 000 tree species occurring in the Amazon region alone (Hubbell *et al.* 2008). Large tracts of forests are at risk from land use change, with more than a quarter of tropical forest area in South America currently under threat (Asner, Loarie & Heyder 2010). Recent attention has advanced our focus beyond deforestation to forest degradation (Foley *et al.* 2007; Putz & Redford 2008), especially logging, which impacts at least 15 000 km^2 of Amazonian forests per year (Asner *et al.* 2005). Several authors have argued that the lack of decrease in tree species diversity they observed in selectively logged forests implies that logging activities are compatible with biodiversity conservation (Plumptre 1996; Cannon, Peart & Leighton 1998; Kariuki *et al.* 2006; Berry *et al.* 2008). These findings merit further evaluation given the ongoing development of metrics of functional diversity. To our knowledge no study has assessed how selective logging impacts both taxonomic and functional composition of tropical tree communities.

Here we examine the long-term impacts of selective logging on a tropical forest tree community via a comprehensive analysis of changes in taxonomic and functional diversity, evenness and composition. We inventoried 4140 stems representing 473 species that recruited into logging gaps and into adjacent undisturbed forest in permanent plots that were monitored for 20 years after logging, and we integrated one of the largest functional trait databases for tropical trees to address the following questions: (i) How does logging disturbance affect tropical tree community structure, in terms of diversity, evenness and composition? (ii) How do the taxonomic and functional responses of tree communities to logging differ? (iii) What guidelines can we give to timber harvesters to improve biodiversity conservation in selectively logged forests?

Our results underline the need to consider not only taxonomy and functional traits, but also measures of both diversity and composition, when describing the impacts of global changes on community structure.

Materials and methods

SITE DESCRIPTION

All inventories were conducted at the Paracou experimental site (5°18′N, 52°55′W), a lowland tropical rain forest near Sinnamary, French Guiana (Gourlet-Fleury *et al.* 2004). The site has a tropical wet climate, driven by the movement of the Inter-Tropical Convergence Zone. Average annual rainfall is 2920 ± 529 mm (mean over

1996–2009; J.-Y. Goret & D. Bonal, unpublished data), with large seasonal variations. A wet season with an average 333 ± 93 mm of rain per month occurs between December and July, followed by a 4-month period with < 100 mm per month. Mean air temperature is 25·5 ± 0·2 °C with very weak daily and seasonal variations.

In 1984, twelve plots of 6·25 ha were established for a complete annual inventory of all trees ≥10 cm in diameter at 1·3 m height (d.b.h.). From 1986 to 1988, the plots underwent three logging treatments according to a randomized block design, with three replicate blocks of four plots. These treatments resulted in a gradient of logging intensity, with 1·56 ha subplots that had from one to more than fifteen trees removed per hectare (16–94 m^3 wood ha^{-1}; Blanc *et al.* 2009).

We quantified logging disturbance using a spatial database in ARCGIS 9.3 (ESRI, Redlands, CA, USA) that was constructed using detailed maps drawn at the time of harvesting activities. We focused on canopy gaps resulting from timber harvesting (Hérault *et al.* 2010). In 1986, these areas were mapped via projection to the ground surface. Open canopy area in the logged 1·56 ha subplots ranged from 0·20 to 0·89 ha (12–58% of surface area). Logging gaps are heterogeneous. In particular, the proportion of edges and centres may differ depending on the gap shape (Broadbent *et al.* 2008; Lopes *et al.* 2009). We thus focused on two habitats, *gap edges* (a 4-m-perimeter band of each gap), and *logging gaps* (gap centres at least 4 m from any edge). Gaps of diameter < 8 m were thus considered to contain only gap edge habitat. We contrasted these habitats with *unlogged* habitats at least 20 m from any logging gap. Skid trails and log landings, where heavy machinery passed to extract logs, were mapped, but we chose not to sample them because the extreme soil compaction often precludes any regeneration (Pinard, Barker & Tay 2000).

SAMPLING DESIGN

We sampled juvenile trees (with 2 cm < d.b.h. < 10 cm) that recruited after logging and represented potential long-term changes to forest composition (Hubbell *et al.* 1999; Molino & Sabatier 2001). We designed our sampling based on two factors that have been found to influence taxonomic composition at the Paracou site. First, three taxonomic blocks of about 50 ha with different dominant families and species occur at the site (Gourlet-Fleury *et al.* 2004). Second, the principal topographic features, hilltops and slopes, differ in their taxonomic composition. Bottomland forests also occur at Paracou, but as they were little impacted by logging activities (Ferry *et al.* 2010) they are not considered here. We therefore stratified our study design such that each habitat was sampled once within each of the six combinations of two topographic positions (hilltop and slope) and three taxonomic blocks, for a total of 18 samples.

The variable shapes and sizes of areas of logging gaps precluded the use of a plot-based sampling approach in this study. Instead, we focused on sampling an equivalent number of individuals across all habitats (Magurran & Queiroz 2010). We first sampled within the logging gap habitats as these were most restricted in spatial coverage; we then sought to replicate the spatial arrangement of these areas in forest undisturbed by logging activities. In doing so, we made no effort to exclude natural treefall gaps. Marking tape was used to reconstruct logging gap and gap edge habitats, using as guides those trees that were present in 1986. In each demarcated zone, we inventoried all woody stems (with 2 cm < d.b.h. < 10 cm). Each stem was marked, its circumference measured to the nearest 1 mm and mapped by triangulation from nearby trees mapped in 1986. For any individual that could not be identified with certainty to species level, we collected a herbarium voucher.

The maximum number of stems occurring in one of the 18 samples was 230. We therefore sampled the 18 habitat*block combinations to sample the same number of individuals ($n = 230$) while maintaining similar spatial distributions of sampled individuals in each habitat (Table S1, Supporting Information).

The resulting database contained 4140 individuals and over 2500 herbarium vouchers. Botanical determinations were made at the Herbier de Guyane (CAY) of the Institut de Recherche pour le Développement, using a reference collection for juvenile trees established by Molino & Sabatier (2001). For those individuals for which we could not arrive at a family determination, we employed DNA barcoding techniques (Gonzalez *et al.* 2009). The DNA barcodes were able to provide clues to family and genus for subsequent herbarium comparisons, and resulted in 98·2% of the individuals being determined to the species level. The remaining individuals were assigned morphospecies numbers within genera and/or families.

FUNCTIONAL TRAIT ASSIGNMENT

We calculated functional diversity and functional composition in our samples by integrating data for 13 functional traits (see Table 2) describing leaf economics (Wright *et al.* 2004) and wood economics (Chave *et al.* 2009) that were collected in nine permanent plots in French Guiana, including two at Paracou (Baraloto *et al.* 2010a). For species from the Paracou inventories that had not been sampled for functional traits, we substituted the mean values for all individuals pertaining to the next higher taxonomic level, as these traits show weak but significant phylogenetic signal (Baraloto *et al.* 2012). The number of species for which trait values were substituted were equally represented among the postlogging habitats (ANOVA $P = 0·63$). Trait values were applied to each individual in the sample by taxonomic correspondence. Family level and genus level mean values were applied to 9% and 39% of individuals, respectively.

DATA ANALYSES

Here, we report species richness and we estimated species evenness using the Pielou index (Pielou 1975). For comparison with the published literature, we also calculated Fisher's alpha, the Gini-Simpson index, and the Hill number translation of the Shannon index (Jost 2006) (Table S2, Supporting Information). Indices were computed using the relative number of stems in each sample.

Multiple measures have been developed for estimating functional diversity (reviewed in Mouchet *et al.* 2010). Among these, three indices have been recommended to provide complementary information. Functional Richness (FRic) represents the amount of trait space occupied by a community and represents the extreme trait values independent of species relative abundances (Cornwell, Schwilk & Ackerly 2006). Functional Divergence (FDiv) incorporates species relative abundances to weight species deviances from the centre of functional trait space (Villéger, Mason & Mouillot 2008). FDiv can provide contrasting information to FRic by discriminating between cases where the most abundant species have the most extreme traits combinations (i.e. specialist species) and cases where generalist species are most abundant (Mouchet *et al.* 2010). Functional Evenness (FEve) incorporates abundance to weight the average distance among pairs of species in functional trait space (Villéger, Mason & Mouillot 2008). FEve can therefore be contrasted with species evenness (Pielou's J) and FDiv to determine the extent to which functional distances among species are regular.

All functional diversity indices are influenced greatly by the choice of functional traits and the correlations among these traits (Lavorel *et al.* 2008; Mouchet *et al.* 2010). We calculated functional diversity measures based on the first two principal components because they represent overall trait strategies of leaf and wood economics (Baraloto *et al.* 2010b) and because their orthogonality limits overweighting of the more numerous correlated leaf traits. For comparison with the published literature, we also calculated the Rao index of quadratic entropy (Botta-Dukat 2005) (Table S2, Supporting Information).

Functional composition is most often calculated as the average of trait values in a community, weighted by the relative abundance of species, giving the community-weighted mean (CWM) for a functional trait (Lavorel & Garnier 2002; Moretti *et al.* 2009). We calculated the CWM for each of the 13 traits in each sample, and we computed principal component scores of each sample derived from correlation matrices among the traits in principal components analysis (PCA), to simplify traits to the leaf economics and wood economics spectra (Baraloto *et al.* 2010b).

We examined differences in taxonomic and functional diversity indices among the habitat types using analysis of variance (ANOVA), with penalty-corrected probability values to interpret multiple tests.

We evaluated changes in taxonomic composition using redundancy analysis (RA) followed by detrended correspondence analysis (DCA) to alleviate the horseshoe-type effect present in the RA; the significance of compositional differences among habitats was assessed by permuted ANOVA analyses (Oksanen *et al.* 2012).

We used two approaches to assess effects of postlogging habitats on functional composition. First, we assessed univariate differences of CWM traits among the habitats using ANOVA with penalty-corrected probabilities. We also evaluated differences among the habitats for multivariate trait space using ANOVA on the PCA axis scores of each sample.

LOGGING INTENSITY AND LOGGING GAPS

To extrapolate our results to potential landscape scale patterns of logging impacts, we developed a relationship to predict the surface area converted to the gap habitats we studied from the intensity of selective logging. We calculated harvest intensity as the volume of wood that was removed from the forest in 1986–1987. Each 2-m section of roundwood harvested at Paracou was measured for basal and apical circumference and its fate was recorded as left in the forest or skidded to the log landing with subsequent transport to the sawmills (Blanc *et al.* 2009). The volume of wood removed from each forest plot was calculated as the sum of the volumes skidded out of a plot. We estimated relationships between logging intensity (volume skidded) and the surface area converted to gap edge and gap centre using linear models.

All analyses were conducted in the R statistics 2.13 platform (R Core Development Team 2012).

Results

EFFECTS ON TAXONOMIC AND FUNCTIONAL DIVERSITY

In total, we inventoried 4140 stems 2–10 cm in d.b.h. and encountered 473 species, with high local diversity of 93–141 species per 230 individuals sampled (Fig. 1).
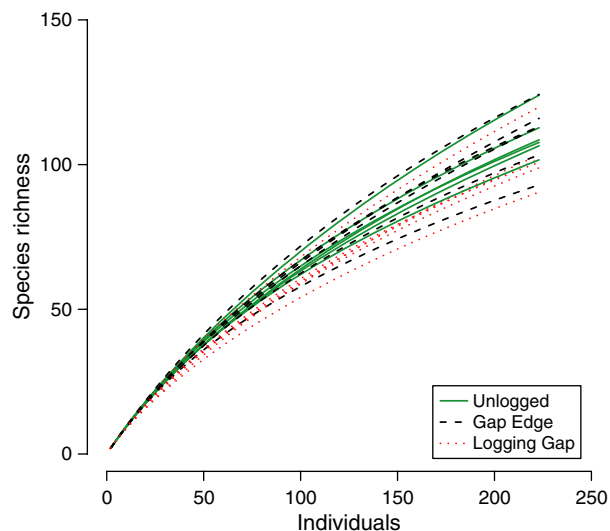
Fig. 1. Species individual accumulation curves for postlogging habitats. Each line represents a sample of 230 individuals in one of three classes of logging matrix habitats. Complete details contrasting diversity indices for the habitats are presented in Table S3 (Supporting Information).

We found no difference among logging habitats in taxonomic or FRic, with high richness in each of the three habitats (Fig. 2a, Table 1). This finding was congruent for both the FRic index and the FDiv index (Table S2, Supporting Information), the latter of which integrates species relative abundances (Table 1).

In contrast, we observed lower species evenness, as estimated by Pielou's J, and much lower FEve, as estimated by Villéger's FEve, in unlogged relative to logged habitats (Fig. 2b, Table 1).

EFFECTS ON TAXONOMIC AND FUNCTIONAL COMPOSITION

We observed very strong differences in taxonomic and functional composition between logged and unlogged habitats. DCA revealed striking taxonomic segregation on Axis 1 (42% of variance) between the logged and unlogged samples (Fig. 3a). Individuals recruited into logged sites had very different taxonomic composition from those recruited in intact forest. Some shade-tolerant species and some canopy taxa (Table 2) simply did not recruit into logged sites, even after
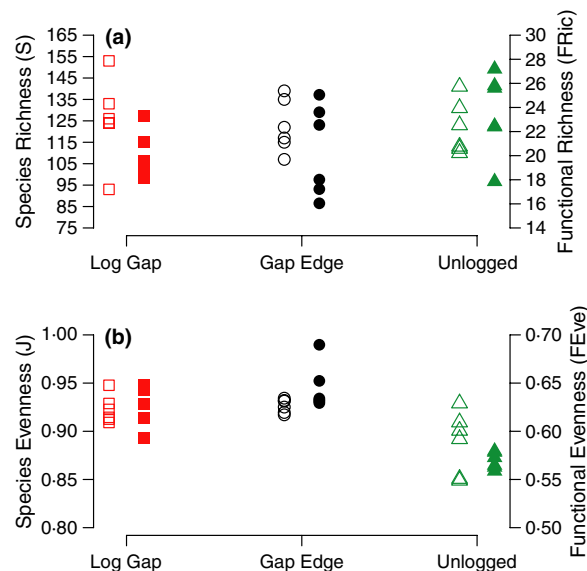

Fig. 2. Effects of logging disturbance on taxonomic and functional diversity across six samples in each of three postlogging habitats. (a) Taxonomic diversity estimated by species richness (open symbols) and functional diversity estimated as Villéger's functional richness (closed symbols). (b) Taxonomic evenness estimated by Pielou's J (open symbols) and functional evenness (FEve) estimated by Villéger's FEve (closed symbols) evenness. Full details of analyses of variance among habitats are given in Table 2.

20 years. To a lesser extent, gap edges discriminated slightly from gap centres, with a particular complement of heliophilic species (Table 2).

These changes in taxonomic composition were accompanied by marked shifts in community functional composition, with clear distinction between logging gaps and gap edges on one hand, and unlogged habitats on the other (Fig. 3b). Tree communities in logged gap and edge habitats differed from unlogged habitats along both leaf and wood economics spectra (Table 3, Fig. 3b). In particular, the xylem density of recruits in logging gaps was 6% less than in unlogged forests, and leaves were 11% less tough, and had 6–13% greater mineral nutrient concentrations (Table 3, Fig. S1, Supporting Information). We found no evidence for effects of logging on composition for water use efficiency, as estimated by leaf carbon isotope discrimination, nor for descriptors of leaf morphology including leaf thickness, specific leaf area (SLA) and laminar surface (Table 3, Fig. S1, Supporting Information).

Table 1. Taxonomic and functional diversity and evenness (mean ± SD of six samples of 230 individuals each) in each of the three sampled postlogging habitats. *F*-statistic values follow analysis of variance for the effect of habitat type on each index. Functional indices were calculated based on the first two principal components of the 13 traits described in Table 2

Index	Log gap	Gap edge	Unlogged	*F*
Species richness (S)	123 (12)	126 (19)	122 (12)	0·11
Pielou evenness (J)	0·93 (0·01)	0·92 (0·01)	0·89 (0·03)	6·07*
Functional richness (FRic)	20·4 (2·0)	19·9 (3·8)	23·5 (3·4)	2·37
Functional divergence (FDiv)	0·69 (0·03)	0·66 (0·03)	0·68 (0·05)	1·05
Functional evenness (FEve)	0·64 (0·02)	0·63 (0·02)	0·57 (0·01)	26·5***

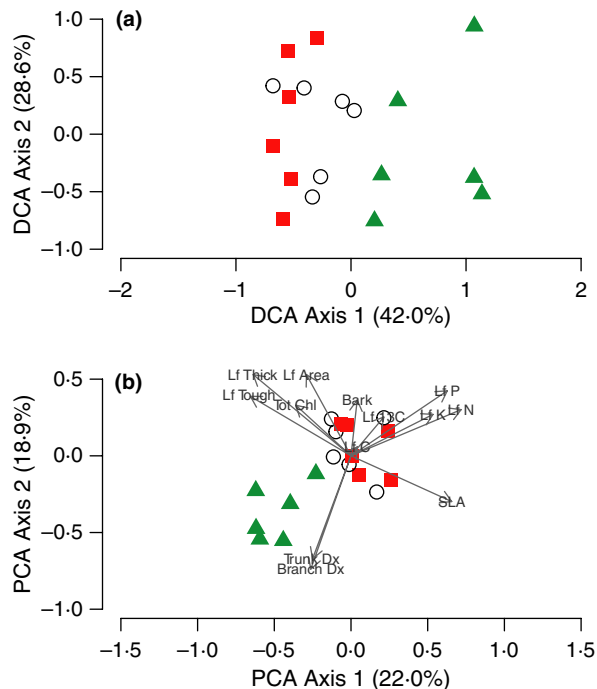*P < 0·05, **P < 0·01, ***P < 0·001.

Fig. 3. Effects of logging disturbance on taxonomic and functional composition across six samples in each of three postlogging habitats. (a) Ordinations of taxonomic composition on the first two axes of a detrended correspondence analysis (DCA). Logging gaps (squares) and gap edges (circles) had significantly different species composition from unlogged samples (triangles) along the first axis (ANOVA on DCA axis 1, $P < 0.001$). (b) Principal component analysis (PCA) ordination of functional composition of postlogging habitats. Logging gaps (squares) and gap edges (circles) had significantly different functional composition from unlogged samples (triangles) for traits related to leaf economics (ANOVA on PCA axis 1, $P < 0.001$) and stem economics spectra (ANOVA on PCA axis 2, $P = 0.001$). Full details of analyses of variance among habitats are given in Table 3.

LOGGING INTENSITY AND CONVERSION TO GAP HABITATS

We found strong relationships between the intensity of logging, measured as the volume of timber skidded from each 1·56 ha subplot at Paracou, and the proportion of surface area converted to the two logging habitats (Fig. 4). Above about 40 m³ ha⁻¹ (about 8 logged trees per ha) we note a strong difference in these relationships, as the higher intensity results in an increased accumulation of area converted to larger gaps with a greater centre to edge ratio.

Discussion

CONTRASTING TAXONOMIC AND FUNCTIONAL DIVERSITY AND COMPOSITION

Our study responds to the recent literature calling for complementary analyses of both taxonomic and functional diversity to characterize community response to environmental changes (Diaz *et al.* 2007; Suding & Goldstein 2008). In particular, our results underline the need to consider not only taxonomic and functional diversity, but also different aspects of each, including richness, evenness and composition.

Several studies have suggested that the decreases in functional diversity observed following disturbance imply significant risks to the provisioning of ecosystem services, even when no corresponding decrease in taxonomic diversity was observed (Ernst, Linsenmair & Rodel 2006; Flynn *et al.* 2009; Villéger *et al.* 2010). Our results further imply that communities may be altered by disturbance in ways significant to ecosystem processes, even when some measures of functional diversity do not change. For example, we found no difference

Table 2. Species with significant associations with each of the three postlogging habitats. Shown are the indicator species values after Dufrene & Legendre (1997), and the probability of obtaining as great an indicator value as observed over 1000 iterations

Species (family)	Preferred habitat	Indicator value	P
Protium opacum (Burseraceae)	Logging gap	0·667	0·029
Miconia sp. 2 (Melastomataceae)	Logging gap	0·667	0·013
Quiina integrifolia (Quiinaceae)	Logging gap	0·667	0·015
Cupania scrobiculata (Sapindaceae)	Logging gap	0·651	0·004
Inga sarmentosa (Fabaceae)	Logging gap	0·600	0·031
Xylopia nitida (Annonaceae)	Logging gap	0·579	0·023
Rhodostemonodaphne grandis (Lauraceae)	Logging gap	0·556	0·024
Tapirira obtusa (Anacardiaceae)	Gap edge	0·714	0·008
Inga paraensis (Fabaceae)	Gap edge	0·667	0·016
Protium tenuifolium (Burseraceae)	Gap edge	0·641	0·023
Jacaranda copaia (Bignoniaceae)	Gap Edge	0·583	0·045
Sterculia pruriens (Malvaceae)	Gap Edge	0·529	0·044
Oxandra asbeckii (Annonaceae)	Unlogged	0·737	0·012
Heisteria densifrons (Olacaceae)	Unlogged	0·611	0·024
Astrocaryum sciophilum (Arecaceae)	Unlogged	0·606	0·029
Duguetia calycina (Annonaceae)	Unlogged	0·598	0·039
Anaxagorea dolichocarpa (Annonaceae)	Unlogged	0·583	0·026
Rheedia benthamiana (Clusiaceae)	Unlogged	0·542	0·049
Talisia guianensis (Sapindaceae)	Unlogged	0·524	0·018

Table 3. Functional traits and their mean values (community-weighted means of all species) in each of the three sampled postlogging habitats. Also shown are *F*-values for ANOVA tests of habitat type on mean trait values, with false-discovery-corrected probabilities for univariate trait tests

Attribute (Abbreviation)	Unit	Log gap	Gap edge	Unlogged	*F*
Leaf thickness (Lf thick)	μm	238	242	245	3·76
Leaf toughness (Lf tough)	N	1·66	1·76	1·88	12·4**
Laminar surface (Lf area)	cm^2	185	181	171	1·74
Total chlorophyll (Tot Chl)	$\mu g\ mm^{-2}$	74·7	75·5	74·6	0·257
Specific leaf area (SLA)	$m^2\ kg^{-1}$	29·5	29·5	28·3	1·51
Foliar N (Lf N)	%	2·12	2·13	2·01	13·2***
Foliar C (Lf C)	%	47·8	47·9	47·8	0·145
Foliar P (Lf P)	‰	0·71	0·71	0·62	51·4***
Foliar K (Lf K)	‰	5·85	5·95	5·29	9·48**
Foliar $\delta^{13}C$ composition (Lf ^{13}C)	‰	−32·1	−32·1	−32·2	1·29
Trunk xylem density (Trunk Dx)	$g\ cm^{-3}$	0·638	0·645	0·676	12·8**
Branch xylem density (Branch Dx)	$g\ cm^{-3}$	0·604	0·608	0·641	16·2***
Bark thickness (Bark)	mm	4·28	4·28	4·14	1·22
PCA axis 1 – leaf economics		0·078	0·005	−0·483	25·1***
PCA axis 2 – stem economics		0·047	0·058	−0·371	11·2**

PCA, principal components analysis.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
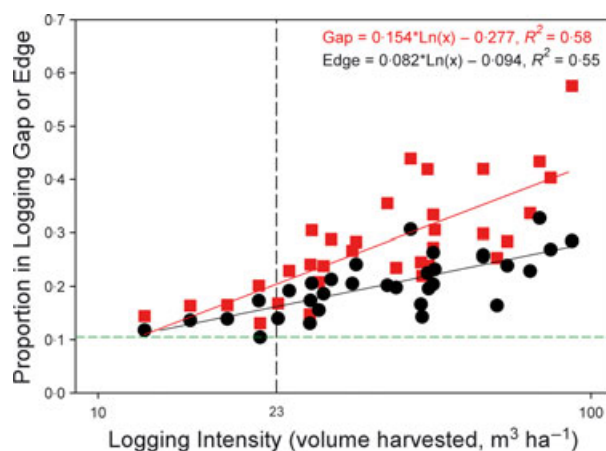
Fig. 4. The proportion of surface converted to logging gaps and gap edges as a function of timber harvest intensity at Paracou (log-scale). The dashed vertical line is a reference for average logging intensity practiced in the Amazon basin (23 $m^3\ ha^{-1}$; Asner *et al.* 2005), at which an estimated 20% of forest surface is converted to gaps. The dashed horizontal line indicates an additional baseline of 10·5% of surface area that is observed in natural treefall gaps in this forest type (C. Baraloto, unpublished data).

among habitats in FRic or in FDiv, but much lower values of FEve in unlogged forest (Table 2). In concert with the slightly lower species evenness values in unlogged forests (Table 2), we may conclude that unlogged forests differ not only in terms of the relative abundance of species with contrasting functional strategies, but also in the regularity of spacing of those species in functional trait space (Villéger, Mason & Mouillot 2008). In this way, the functional diversity index approach allows a more nuanced understanding of potential ecosystem recovery, beyond that provided by indices of taxonomic diversity (Villéger *et al.* 2010).

Beyond diversity indices, we also recommend that comprehensive assessments of anthropogenic impacts on plant communities should also monitor changes in taxonomic and functional composition so that changes in particular species and/or traits and their impacts on ecosystem processes may be followed (Lavorel & Garnier 2002; Bellwood *et al.* 2006). Functional diversity indices are notably sensitive to the choice of traits (Lavorel & Garnier 2002; Lavorel *et al.* 2008; Mouchet *et al.* 2010). Indeed, we found contrasting results with FEve on the 13 traits rather than the two derived PCA axes (Table S2, Supporting Information), which we hypothesize is due either to the inclusion of multiple traits that represent redundancy in leaf or wood tissue strategies (Fig. 3b), or to the ecological meaning that is captured in the 40% of variance in trait composition captured by the two principal components, which we know represent ecological strategies in tropical forest trees (Baraloto *et al.* 2010b). In fact, logging habitats remained similar to unlogged habitats for CWM values of many leaf traits (Table 3, Fig. S1, Supporting Information) including those soft traits such as SLA and leaf area that are commonly used in analyses of plant functional diversity (Lavorel *et al.* 2008).

DISTURBANCE AND TREE DIVERSITY IN MANAGED TROPICAL FORESTS

The changes in floristic composition we observed in logging gaps (Fig. 2a) confirms previous observations that moderate disturbance intensities can modify the composition of tropical tree communities (Plumptre 1996; Vandermeer *et al.* 2000; Molino & Sabatier 2001; Laurance *et al.* 2006; Bongers *et al.* 2009). Nevertheless, all of these studies, including ours, must be interpreted in light of the temporal and spatial scales of analyses (Sheil & Burslem 2003; Cadotte 2007).

The ultimate impact of disturbance on community composition in long-lived organisms depends not only on initial changes in community composition but rather changes

in composition among stems that will live to reproduce and contribute to subsequent generations (Shea, Roxburgh & Rauschert 2004; Haddad *et al.* 2008). Indeed several tests of the intermediate disturbance hypothesis in tropical trees (e.g. Hubbell *et al.* 1999; Molino & Sabatier 2001) have been criticized because they focus on regenerating communities within several years of disturbance (Sheil & Burslem 2003). We report less pronounced contrasts in diversity than that observed in the same site by Molino & Sabatier (2001), probably in part because some short-lived pioneer species that were present in their study (inventory 10 years after logging in 1995–1997) did not persist to the time of our study (in 2007–2008). For example, the pioneer genera *Apeiba* Malvaceae and *Cecropia* Urticaceae were three times less common in our study than in theirs (0·13% and 0·16% of stems vs. 0·37% and 0·53%, respectively).

The consequences of any disturbance regime for community structure must also be considered across a range of spatial scales (Hamer & Hill 2000; Cadotte 2007; Bongers *et al.* 2009). As in several previous studies (e.g. Hubbell *et al.* 1999), we focused on the fine scale of a treefall gap, and we further separated between gap edges and gap centres as edge effects may limit colonization and establishment for some understory species (Denslow 1987). We found no strong evidence for a distinction at this fine spatial scale, however. Gap edges and gap centres had different common species (Table 2) but largely overlapping species and functional composition (Fig. 2). Still, by focusing on these three contrasting and widespread habitats, we did not sample extreme disturbances to both canopy and soil such as those found on log landings or skid trails where we would expect decreases in diversity (Pinard, Barker & Tay 2000). Approaches using plot-based analyses in which these habitats are mixed even at small spatial scales would likely result in higher levels of taxonomic and functional diversity than those we report here (Plumptre 1996; Molino & Sabatier 2001).

Likewise, the impacts of disturbance on diversity also depend on the distribution of disturbed sites across a landscape (Sheil & Burslem 2003; Cadotte 2007; Bongers *et al.* 2009). Indeed, in some communities where disturbance reduces or has no effect on diversity at small spatial scales, diversity at larger spatial scales is actually enhanced because a matrix of sites favouring species with complementary ecological requirements is created (Cadotte 2007; Berry *et al.* 2008). The pertinent scale of this effect is likely determined by the dispersal abilities of the study organism (Shea, Roxburgh & Rauschert 2004; Haddad *et al.* 2008), and for trees we expect infrequent colonization events beyond several hundred metres up to several kilometres (Nathan & Muller-Landau 2000; Sheil & Burslem 2003). Therefore, it is important to consider the spatial distribution of gaps in the studied forest, especially when assessing appropriate interventions for forest management. The logging gap habitats we studied were separated by distances within the range of dispersal of most species 30–2500 m, but this distribution would be considerably more scattered

for natural treefall gaps in unlogged forests (e.g. Hubbell *et al.* 1999). The effects we note within particular habitats therefore need to be considered relative to the proportion of surface area they cover and its distribution in space, particularly as a function of management interventions such as harvest intensity (Fig. 4).

RECOMMENDATIONS FOR TIMBER HARVEST AND BIODIVERSITY CONSERVATION

An important contribution made by our study is a quantification of the functional degradation that selective logging can impose. Even though we found no important effects of logging on taxonomic or FRic (Fig. 2), we found strong shifts in FEve and trait composition between logging gaps and the unlogged gap-phase successional continuum (Fig. 2, Tables 1 and 3). These trait shifts underline the need to cautiously manage the rate of conversion to these habitats, especially if we consider that they may be reinforced with subsequent cutting cycles in areas that are already functionally degraded (Foley *et al.* 2007). In particular, the lower wood density and leaf toughness and greater leaf-nutrient concentrations suggest that communities in logging gaps may have reduced capacities for carbon storage, drought tolerance and increased palatability to predators (Hurokawa, Peltzer & Wardle 2010; Markesteijn *et al.* 2011). The potential cascading results to other trophic levels might be illustrated by an analysis of reproductive traits pertinent to animal communities (e.g. Lopes *et al.* 2009). Unfortunately, these are currently not available for our forest. We discuss later two very important caveats to the generality of our results to other forests – the way forests are logged, and the initial state of the forest.

Logging impacts crucial to regenerating tree communities include changes in seed sources and modifications of the environment to a forest matrix that includes logging gaps, skid trails and log landings (Pinard, Barker & Tay 2000; Broadbent *et al.* 2008). Our study focused on the conversion to logging gaps because the rate of this conversion can be mitigated directly by managers, given its strong positive correlation with harvest intensity (Fig. 4). In the light of our results demonstrating significant long-term shifts in functional composition in logging gaps, we would thus recommend a moderate rate for this conversion. At Paracou, 20·4% of the forest surface was converted to logging gaps in plots logged at the average Amazonian harvest intensity of 23 m^3 ha^{-1} (Fig. 3), a conversion rate similar to that observed in the Brazilian Amazon (Asner *et al.* 2005). Depending on the spatial distribution of converted patches of forest and local management objectives, managers may accept this or even higher rates of conversion to potentially degraded forest. Nevertheless, the entire logged area at the Paracou experimental site covers only about 100 ha within an undisturbed surrounding area of several thousand hectares. In contrast, most logging concessions in the Neotropics cover several thousand hectares (Asner *et al.* 2005). It may be expected that larger forest concessions lead to larger reductions in densities of animals responsible for seed dispersal and/or predation (Hamer & Hill 2000; Clark *et al.* 2009) and

therefore may demonstrate more contrasted results (Plumptre 1996; Berry *et al*. 2008).

Our study further suggests that the creation of larger gaps (*c*. 1·5 ha) does not degrade the functional composition of the forest more than a similar area across several smaller gaps (*c*. 0·1 ha). Gap edges and gap centres showed similar compositional shifts (Fig. 3), which was not owing to any potential bias of sampling edges and centres of the same gaps (Fig. S2, Supporting Information) as the sampling structure balanced spatial sampling among habitats (Table S1, Supporting Information). We therefore recommend that a 'single large' strategy for logging gaps may represent the best option to preserve functional composition for a given harvest intensity, as it can often be achieved with a lower proportion of accompanying surface area converted to skid trails (Putz *et al*. 2008). However, this recommendation must be weighed against other management objectives. Commercial tree growth and carbon accumulation may be achieved more rapidly by creating multiple smaller gaps with higher edge/centre surface area ratios (Hérault *et al*. 2010); and fire risk may increase in areas with greater conversion to larger gap habitats (Asner *et al*. 2005).

Reduced impact logging (RIL) can mitigate the impacts of logging by protecting seed trees, by limiting the surface area converted to skid trails and log landings via directional felling and planning maps, and by limiting the surface area converted to logging gaps per unit harvested by limiting wasted wood left in the forest (Putz *et al*. 2008). Given that functional changes are likely to be even more extreme in log landings and skid trails, the extent of which can be limited by RIL techniques (Putz *et al*. 2008), we endorse RIL to slow forest degradation in selectively logged tropical forests.

Conclusions

Selective logging is responsible for the conversion of at least 15 000 km^2 of primary tropical forest in the Amazon each year (Asner *et al*. 2005; Asner, Loarie & Heyder 2010), and the resulting consequences for important ecosystem services including carbon storage and water and nutrient cycles remain unknown. Our results support a growing literature suggesting that selectively logged tropical forest can retain important value for biodiversity conservation (Hamer *et al*. 2003; Clark *et al*. 2009; Berry *et al*. 2010). Nevertheless, our analysis of functional composition adds an important caution to previous studies focusing on taxonomic diversity. We suggest this approach as a basis towards developing a more complete framework to analyse the impacts of global changes, including multiple disturbances and drought events, across tropical forests.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Effects of logging disturbance on functional trait values of recruited tree communities.

Fig. S2. A validation that compositional patterns observed in Fig. 3 were not due to sampling effects.

Table S1. A validation of the equal spatial distribution of sampling points among the six replicate samples in each habitat.

Table S2. Complementary taxonomic and functional diversity and evenness (mean ± SD of six samples of 230 individuals each) in each of the three sampled post-logging habitats.

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