30 Years of Post-disturbance Recruitment in Tropical Forest

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Abstract
Résumé de l'article.

Keywords
Taxonomic and Functional Diversity, Recruitment, Resilience, Tropical Forests, Disturbance Dynamics

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1. Introduction

Determining the response of tropical forests to disturbance is a key to predict their fate in the global changing context. In the last decades, tropical forests experienced a wide range of disturbance, from radical land-use changes for agriculture or mining (Dezecache *et al.*, 2017; Dezécache *et al.*, 2017) to more insidious changes of communities structure, diversity and functioning following anthropogenic activities like selective logging (Baraloto *et al.*, 2012; Hérault & Gourlet-Fleury, 2016) or climate change (Aubry-Kientz *et al.*, 2015). In that respect a vast literature successfully modeled communities response to disturbance in terms of tree growth (Gourlet-Fleury & Houllier, 2000), tree height (Rutishauser *et al.*, 2016), carbon stocks and fluxes (Putz *et al.*, 2012; Martin *et al.*, 2015; Piponiot *et al.*, 2016). Similar approaches regarding forest composition and diversity, however, have been hindered by the huge biological diversity, often focusing on common or mainly commercial species, and the scarcity of long-term monitoring (Sebbenn *et al.*, 2008; Rozendaal *et al.*, 2010; Vinson *et al.*, 2015).

Communites trajectories after disturbance, defined here as the evolution of communities diversity along time, depend on the trees surviving from before disturbance and on those recruited afterward (Hérault & Piponiot, 2018). Because surviving trees proved to mirror the composition of pre-disturbance forest, the response of communities is driven by the diversity and composition of recruited trees that build the future community and determine the resilience of the pre-disturbance forest. The recruitment trajectories are first determined by the composition and diversity of the initial community that partly conditions the pool of recruitable species (Hérault & Piponiot, 2018). Trajectories then depend on the recruitment processes that are either stochastic, like random dispersal, recruitment and death (Hubbell, 2001), or deterministic, like niche-based competition processes (Adler *et al.*, 2007) While stochastic processes build communities as random samples of the larger regional-scale forest, deterministic processes rely on the abiotic environment and filter-out recruited species according to their ecology. To understand the mechanisms of communities trajectories the first point is to estimate the importance of the initial community composition and the balance between stochastic and deterministic processes. Then it is to determine the resilience of communities and the time recover pre-disturbance ecosystem properties in order to adjust exploitation and conservation guidelines (Díaz *et al.*, 2005; Gardner *et al.*, 2007; Schwartz *et al.*, 2017).

The ecological processes shaping communities' trajectories differently affect their functional and taxonomic diversities as the first consider all species equally while the second accounts for species functioning and ecology (Violle *et al.*, 2007; Kunstler *et al.*, 2016). The potential decoupling between functional and taxonomic trajectories is then insightful of the ecological processes at stake, and only a combined approach of functional and taxonomic diver-

sities would reveal the determinant recruitment processes (Fukami *et al.*, 2005). Functional trajectories will rely on deterministic processes oriented towards the use of limiting resources: in tropical forests where the light is limiting forests response would then be a shift from slow-growing, long-living species with "conservative" resource use to fast growing, resource "acquisitve" species (Denslow, 1980; Molino & Sabatier, 2001; Bongers *et al.*, 2009).

Such processes would be detected throught the diversity and composition trajectories of key leaf, wood and life-history functional traits assessing species ecology and resources acquisition strategy (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011). The deterministic processes could filtered-out, decreasing the recruitment functional diversity, or the less competitive ones could be excluded, increasing the functional diversity through the limitation of similarity among species (Ackerly, 2003; McGill *et al.*, 2006).

In this paper we followed the fate of a recruited tree communities (60121 individuals) over 30 years on a large disturbance gradient, with 10 to 60% of forest biomass removed. We assessed the taxonomic and functional diversity of recruited trees, using a large functional trait database covering the leaf, wood and life-history spectra. We compared the observed trajectories to a stochastic recruitment entailing the random sampling of recruites and the randomization of their functional traits. We aimed (i) to assess the role of deterministic processes compared to stochastic recruitment after disturbance, (ii) assess the taxonomic and functional convergence of forest communities and the maintenance of taxonomic composition in the long term, and (iii) determine the degree of resilience of the ecosystem.

2. Material and Methods

2.1 Study Site

The Paracou station is located in a lowland tropical rain forest in French Guiana (5°18'N and 52°53'W). Climate is tropical wet with mean annual precipitation averaging 2980 mm.y^{-1} (30-y period) and a 3-months dry season (< 100 mm.$months^{-1}$) from mid-August to mid-November, and a one-month dry season in March (Wagner *et al.*, 2011). Elevation ranges from 5 to 50 m and mean annual temperature is 26°C. Soils are thin acrisols over a layer of transformed saprolite with low permeability generating lateral drainage during heavy rains. The disturbance experiment spread over a network of twelve 6.25ha plots (Table 1) that underwent three disturbance treatments in 1986-1987 (Hérault & Piponiot, 2018). Dominant families are Fabaceae, Chrysobalanaceae, Lecythidaceae and Sapotaceae.

2.2 Inventories Protocol and Dataset Collection

All trees above 10 cm DBH were mapped and measured annually since 1984. During inventories, trees were first identified with a vernacular name assigned by the field team, and afterward with a scientific name assigned by a botanist during regular botanical campaigns. Botanical campaigns have been carried out every 5 to 6 years from 2003 onwards. These changes in identification protocol raised methodological issues as vernacular names usually correspond to dif-

ferent botanical species, resulting in significant taxonomic uncertainties that were propagated to composition and diversity metrics. Vernacular names were replaced through multinomial trials $M_v\left([s_1, s_2, \ldots, s_N], [\alpha_1, \alpha_2, \ldots, \alpha_3]\right)$ based on the observed association probability $[\alpha_1, \alpha_2, \ldots, \alpha_3]$ between each vernacular name v and the species $[s_1, s_2, \ldots, s_N]$ recorded in the inventory. See appendix 1 and Aubry-Kientz *et al.* (2013) for the detailed methodology. To avoid remaining identification caveats, the simulated botanical inventories were reported at genus level.

Eight functional traits were considered, representing leaf economics (leaves thickness, toughness, total chlorophyll content and specific leaf area), wood economics (wood specific gravity and bark thickness) and life history traits (maximum specific height and seed mass). Traits were exctracted from the BRIDGE project [1] where trait values were measured on nine forest plots infrench guianan, including two in Paracou. Missing trait values of the trait database (10%) were filled by multivariate imputation by chained equation using the Mice r package (van Buuren & Groothuis-Oudshoorn, 2011). As traits variability was lower within genus and families, we accounted for the phylogenetic signal of the functional traits by restricting the gap filling processes to samples pertaining to the next higher taxonomic level. As seed mass information corresponded to a classification into discrete mass classes, no data filling process was applied so analysis were performed only considering the 414 botanical species of the seed mass dataset.

2.3 Recruitment trajectories

To disentangle the recruitment processes from overall dynamics, communities were split into per-disturbance surviving trees and those recruited since disturbance. Recruited communities were examined either considering the "punctual recruitment", *i.e.* recruited trees by 2-year intervals, or all recruits since disturbance as the "accumulated recruits". Eventually, in disturbed plots the recruited communities were examined distinguishing the undisturbed and logging gap areas to test the validity of recruitment processes for the whole area.

The taxonomic diversity was assessed through Richness and the Hill number translation of Shannon and Simpson indices (Hill, 1973; Chao & Jost, 2015; Marcon, 2015). The three diversities belong to the set of HCDT or generalized entropy, respectively corresponding to the 0, 1 and 2 order of diversity (q), which grasps the balance between richness and evenness in the community through the value of q that emphasizes common species. Functional trajectories were estimated with the Rao quadratic entropy and completed by the trajectories of traits community weighted means (CWM), representing the average trait value in a community weighted by relative abundance of the species carrying each value (Díaz *et al.*, 2007; Garnier *et al.*, 2004). Seed mass trajectories were reported by the proportion of each class recorded in the inventories. The similarity between the recruited trees and the pre-disturbance forest was measured with the turnover metrics detailed in Podani *et al.* (2013). To estimate the importance of stochastic processes

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[1]http://www.ecofog.gf/Bridge/

Table 1. Intervention table, summary of the disturbance intensity for the 4 plot treatments in Paracou.

Treatment	Timber	Thinning	Fuelwood	%AGB lost
Control				0
T1	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha			$[12\% - 33\%]$
T2	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha	DBH $\geq$ 40 cm, non-valuable species, $\approx$ 30 trees/ha		$[33\% - 56\%]$
T3	DBH $\geq$ 50 cm, commercial species, $\approx$ 10 trees/ha	DBH $\geq$ 50 cm, non-valuable species, $\approx$ 15 trees/ha	40 cm $\leq$ DBH $\leq$ 50 cm, non-valuable species, $\approx$ 15 trees/ha	$[35\% - 56\%]$

the recruitment was compared to the trajectories of a random sampling. For the taxonomic trajectories the random sampling was a shuffle of trees among plots that preserved species abundance and tree density, and for the functional diversity it was a shuffling of functional trait values among species.

All composition and diversity metrics correspond to the median and 90% percentile obtained after 50 iterations of the taxonomy uncertainty propagation framework and the gap filling process. The stochastic trajectories were similarily obtained after 50 iterations of the random sampling.

3. Results

3.1 Recruitment Diversity

All the trajectories were identical in disturbed and undisturbed areas, confirming that the recruitment processes applied to whole communities and were not restricted to logging gaps.

3.1.1 Taxonomic Diversity

The diversity trajecctories of punctual recruitment followed a consistent trajectory after disturbance with first an increase of the richness and a decrease of the evenness (Figure (1). For all disturbed plots,both richness and evenness tended to return towards initial values but none had recovered 30 years after disturbance. The accumulated recruits displayed sharp increasing richness (order 0) and decreasing evenness (order 2) after intense disturbance (T3 and some T2, Appendix I, fig. S1).

Punctual and accumulated recruitment diversities were then compared to the stochastic trajectories of a random sampling. Richness (order 0) and evenness (order 2) of punctual recruits remained equivalent or higher than for a random sampling in control plots while both were lower in disturbed plots. Disturbed plots however followed humped-shaped trajectories heading towards a recovery of the initial state (Figure 1). Accumulated recruitment richness and evenness were higher or equivalent to those of the random sampling after low disturbance intensity (plots T1 and some plots T2) but lower after intense disturbance (plots T3 and

a plot T2, Appendix I fig. S1).

3.1.2 Functional Diversity and Composition

Communities functional diversity was measured with the Rao diversity and compared to the stochastic trajectories of a random traits shuffling. In disturbed plots (T2 and T3), the functional diversity decreased until 15 years after disturbance (Figure 2) before recovering towards the initial values. While the recovery was not achieved for the most disturbed plots, the functional diversity of lighter disturbance plots recovered faster and for some T1 plots exceeded the initial values. For all plots, disturbed or not, the observed functional diversity was lower than this of the random model, to the exception of two plots T1.

Trajectories of the functional traits showed a switch in disturbed plots towards species with large exchange surface area, light tissues (high SLA, low leaf toughness and thickness and low wood specific gravity) with smaller maximum height (Figure 3). Functional traits either followed hump-shaped trajectories with an ongoing recovery or an achieved return to the initial state (for SLA,Bark thickness and leaf thickness and Hmax to a certain extent).

3.2 Recruitment Turnover

In control plots species turnover remained highly stable for the 30 sampled years (Figure 4), reflecting a strong similarity between the initial plots composition and the punctual recruits. In disturbed plots, the taxonomic turnover followed a marked hump-backed trajectory, with a maximum value reached around 15 years after disturbance and a maximum positively correlated to the disturbance intensity ($\rho_{spearman} = 0.93$). Thirty years after disturbance the turnover of all disturbed plots had return to low values close to zero.

4. Discussion

4.1 On the underlyings of the hump-shaped trajectories

Along the 30 years, the recruitment richness and species turnover compared to the initial composition, and the trajectories of key functional traits (SLA and bark thickness)
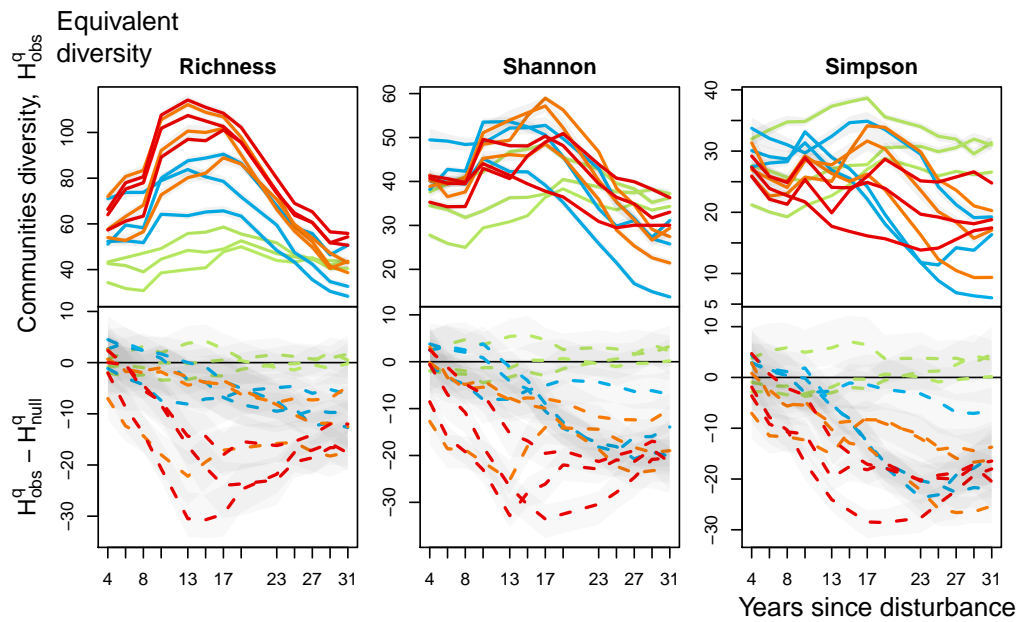
Figure 1. Trajectories of Richness, Shannon and Simpson diversity for 2-years laps punctual recruitment (upper panels) and divergence to null model (lower panels). Lines colors refer to the perturbation regime: green for control, blue for T1, orange for T2 and red for T3 disturbance treatments. Plain lines correspond to the median observed after uncertainty propagation and are given along with the 95% confidence interval (grey envelope).
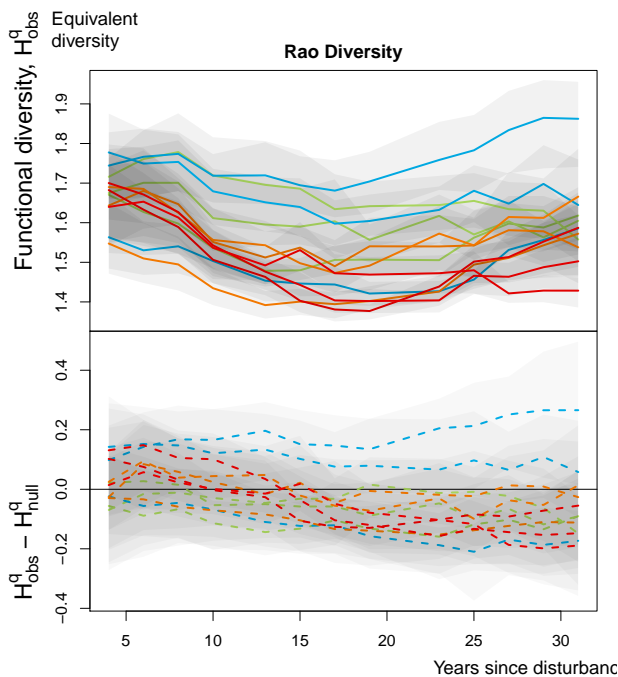
Figure 2. Functional diversity of punctual recruited trees from the considered functional traits and divergence to null model. Values reported correspond to the plot-level median and the 95% confidence interval obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database gap-filling processes and 50 run of the null model. Lines colors correspond to the logging treatment initially applied (green for control, blue for T1, orange for T2 and red for T3).

exhibited clear hump-shaped trajectories, revealing three distinct recruitment phases. Communities trajectories involved an interplay between stochastic and deterministic recruitment, advocating that disturbance effectively maintained forests diversity (Molino & Sabatier, 2001; Sheil & Burslem, 2003).

As a first step (0-8 years), recruited trees showed low turnover compared to the initial composition and matched the functoinal diversity of a stochastic recruitment process. This first recruitment phase mirroring the old-growth pre-disturbance community then likely involved already grown saplings (DBH <10cm) immediately benefitting from the increased enlightment and the alleviated competition induced by disturbance (Hérault *et al.*, 2010).

A second phase then fall into place, corresponding to marked changes in several functional traits trajectories and to a decrease in the evenness and functional diversity of the recruited species. These changes revealed during the second phase a restriction in the pool of recruited species, likely selected based on their functional strategy. Indeed after intense disturbance, sharp changes in the SLA, wood density and leaf thickness trajectories revealed the prominent recruitment of short-lived, fast growing hard pioneers species with competitive and efficient light acquisition (Figure **?**(fig:Turnover)) (Wright *et al.*, 2004; Chave *et al.*, 2009; Hérault *et al.*, 2011; Reich, 2014).

The second phase likely incorporated true recruits, *i.e.* trees germinated from the seed bank, selected according to their resource acquisition strategy. The stochastic recruitment observed in the first place were therefore balanced with deterministic, niche-based competition processes. Along time diversity trajectories returned towards the initial state and the values of stochastic recruitment, revealing a reversed balance where stochastic recruitment progressively prevail-

Punctual recruits CWM
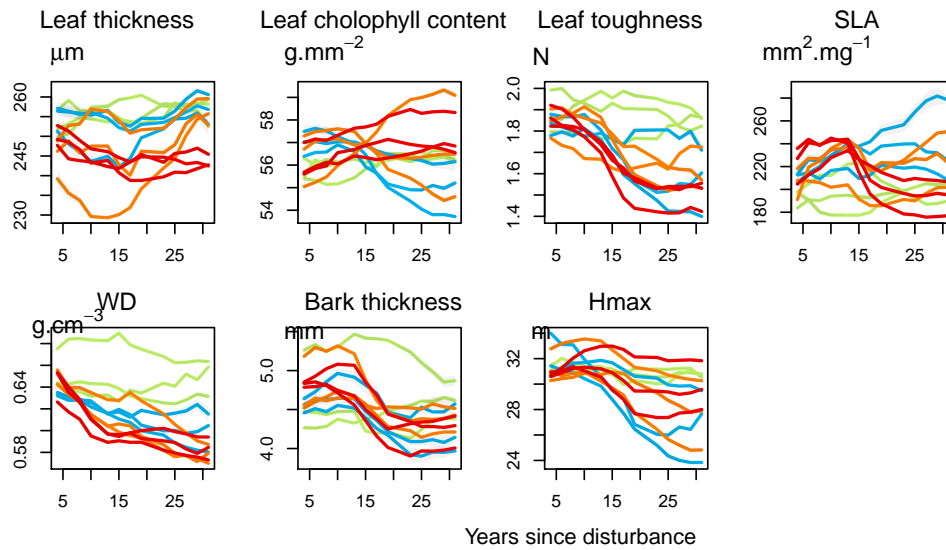
Figure 3. Community weighted means (CWM) of the four disturbance treatment for the four leaf traits, the two stem traits and the specific Hmax. Values reported correspond to the plot-level median obtained after 50 repetition of the taxonomic uncertainty propagation and the functional database gap-filling processes. Lines colors correspond to the disturbance intensity (green for control, blue for T1, orange for T2 and red for T3).
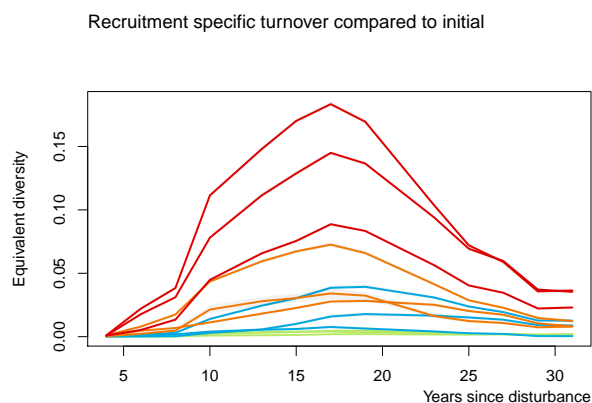
Figure 4. Trajectories over the 30 sampled years of the abundance-based turnover between recruited trees and intial communities before disturbance. Grey envelopes correspond to the 0.025 and 0.975 percentiles of the uncertainty propagation procedue and lines to the median in green for control, blue for T1, orange for T2 and red for T3).

ing again. The balance along time between deterministic and stochastic processes was determined by the initial disturbance intensity. After light disturbance (T1 plots), although the pool of recruited species was restricted by the competitive exclusion for resources the turnover compared to initial state remained low. Recruited trees then still mirrored the pre-disturbance communities but recruited species were more pioneers and light demanders, with strategies of efficient resource acquisition (high SLA and leaf chlorophyll content) and inexpensive, short-lived tissues (low leaf thickness and thoughness, small Hmax and low wood density and bark thickness) (Hubbell *et al.*, 1999; Sheil & Burslem, 2003; Bongers *et al.*, 2009). At this disturbance intensity the recruitment evenness and functional diversity remained high so despite the selection of more light-demanding species the recruitment was not overwhelmed by hard pioneers. This might be explained by the recruitment and dispersal limitations due to the short dispersal distance observed for tropical trees, specifically in Paracou with the genetic clumping of some pioneers (Leclerc *et al.*, 2015; Scotti *et al.*, 2015).

After intense disturbance in contrast (T2 and T3 plots), the recruitment rapidly differed from the pre-disturbance composition and corresponded to a sharp increase of the SLA and bark thickness reflecting an overhelming recruitment of hard pioneers. In this case the second recruitment phase largely dominated by hard pioneers lasted for 15 years, before the pool of recruited species enlarged again. The first decrease in the recruitment functional diversity was followed by a progressive recovery revealing a third phase of more diversified recruitment. The third recruitment phase remained dominated by light-demanding species, which revealed the selection of species through deterministic competition processes, but increasingly mirrored the pre-disturbance community, suggesting a progressive recov-

ery of stochastic recruitment processes.

4.2 On the resilience of the recruitment process

After 30 years, although taxonomic and functional diversity had recovered initial values, the recruitment remained more restricted than with the stochastic recruitment of undisturbed plots. Despite the settlement after intense disturbance of long-lived pioneers, recruitment processes proved resilient but slow to recover.

The recovery of recruitment processes meant the convergence of communities towards the initial state. More than commonly thought, the taxonomic trajectory of ecosystems would then rely on their pre-disturbance characteristics and concur to maintain the initial taxonomic differences among local communities (Anderson, 2007). In contrast the trajectories of traits and functional diversity were essentially similar among treatments, arguing for the confluence of communities in the functional space despite their divergence in taxonomic composition (Fukami *et al.*, 2005). This confirmed previous results from the Paracou experiment, conducted 10 years (Molino & Sabatier, 2001) and 20 years (Baraloto *et al.*, 2012) after disturbance, where the early signs of the resilience of taxonomic and functional composition had been detected. Still, the functional diversity and several traits CWM values remained altered 30 years after disturbance, suggesting the long-term impact of disturbance. Both taxonomic and functional recovery therefore spread over long periods, i.e. several decades, and to involve the germination of trees from the seed bank and therefore affect the stock of recruitable species and communities response and resilience to additional disturbance (Norden *et al.*, 2009).

5. Conclusion

The hindsight of the 30 years of forest monitoring highlighted a two-phased disturbance response, distinguished by the balance between stochastic and determinisitic recruitment processes. Communities trajectories were first driven by the stochastic recruitment of already-grown saplings mirroring the predisturbance state before it is dominated by true recruits from the seed bank selected based on their resource acquisition strategy. Both communities taxonomy and functioning recovered in the long term but while all communities followed similar trajectories in the funcional space, their taxonomic trajectories relied upon communities composition and diversity and maintained initial local differences. Although resilient within the range of applied disturbance, communities followed a decade-long recovery and probably underwent compositional changes of their seed bank which entailed great caution regarding the forest conservation and exploitation guidelines if the pursued objectives are a complete recovery of pre-disturbance ecosystem properties.

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