Dear Editor,
Please find herewith our revised ms "Environmental control of natural gap size distribution in tropical forests" for re-submission to Biogeosciences. We first would like to thank both reviewers for the high quality and seriousness of their review. We acknowledge them for that and we recognize that their works have contributed to improve the quality of our manuscript. Responses to their comments are in red in the following as well as are changes in the main ms.
We remain at your disposal for any further enquiries.
Youven Goulamoussène,

1 Reviewer 2

In this manuscript y et al. report on an interesting analysis on the environmental drivers behind gap size distribution in tropical forests, using Lidar data. Their methodology builds on previous work by Lobo and Dalling (2014), but they introduce an interesting new method to determine height thresholds and minimum gap sizes.

They rightfully criticize the empirical cutoffs that have been used, and come up with an innovative and interesting alternative. The authors further introduce Lidar-derived environmental parameters to include in the Bayesian model, which enables them to assess the effect of physical environment on gap size distribution.

Although I've enjoyed reading this interesting work, I think the authors could im prove/clarify their manuscript in some parts ; both for science and form/language

A first point would be the height cutoff ; the whole study is dependent on the value you set here. You set up a nice probabilistic model, but then you still go back to an empirical threshold (being 0,001percentile). If you have no theoretical considerations to justify this cutoff, than your method is as such not better than any other empirical threshold used in previous studies. Hence, this would need bit more clarification. I wonder whether you could not use the average of the second (lower) normal distribution as a cutoff. This would, I believe, also increase the applicability of your method in other forest types/regions, since the relative difference between canopy tree height/gap height will shift in other forest types. Even if you have a sound reason to use 0,001perc in this case, you would need to reselect a threshold in other forest types.

Thank you for this comment. If the threshold is chosen from the first distribution, then the expected value of the first law will be too dependant on the frequency of gap formation in time and this dependence is a problem. In other words, with a similar gap generation process (the same drop in height) a frequency of 1% of the forest area that will be transformed in gaps each year will generate a target value (the average of the first law as suggested) mechanically lower than for a landscape where the frequency is 0.5%. In the last case, the lower frequency of young gaps will produce on average a higher target value. We still do not want to depend on this gap frequency at the landscape scale.
We choose this threshold value to keep the maximum of information from the first distribution (gap height) while minmizing biases due to including too much information from the 2nd one (canopy height). Because the whole process needs several hours to be performed, from the GIS works to the model inference, with thousands of gaps, we cannot run a well-performed sensitivity analysis. However, we provide in supplementary informations , the parameter values for 2 additional thresholds (0.0001th and 0.01th). The posterior values of almost all variables are quite similar and thus do not change interpretation : Slope, TRI are always positive whatever the threshold TOPEX, HAND are always negative whatever the threshold DA and HAlt always include zero in the credibility interval

Secondly, I have not been working with Bayesian statistics myself, but I think the manuscript should be clear for the broad readership of Biogeosciences. Some questions related to the rest of your methodology :

— I wonder why you use equation 8 to constrain lambda. What is the reasoning behind an exponential model ?

We have constrained the value of lambda in equation 8 because the linear combination, without the exponential constraint, may have result, during the inference process, in negative lambda values. And Riemann's Zeta function only admits values > 1.

— You explain the interpretation of Lambda on p 5 L 146-150. I think the authors are confused here (or maybe I am...) ; "lambda is not defined when lambda>=1 ? ? ", and "A value close to 1 means there are a large number of small gaps". Both of these statements seem absolutely wrong to me (I would expect the contrary with both), and they are actually vital to the interpretation of this very manuscript. Either I am wrong, but if not, I am a bit worried for the misinterpretation of the results by the authors. Please have a look at this. Maybe this is also at the basis for the contradiction in some of the statements through the manuscript ;
I apologize for this mistake in the manuscrit. Thank you for pointing it out. The error has been corrected at line : "In forests dominated by small canopy openings, values of λ are larger, whereas smaller values of λ increase the frequency of large events (Fisher et al. 2008)". Line : 147

— Discussion (L296-297) : ""We found similar results to Lobo and Dalling in BCI ; i.e., large gaps are more frequent on gentle slopes". Conclusion : "We expected that slope would also play an important role, with steeper slopes leading to larger gap sizes, but found the opposite effect." Please go through the MS again and make sure the interpretations are the same, and are right, everywhere. If not, you fail to give the reader a clear take home message
the text has been modified for each section. Line 10, 305, 345

Thirdly, I have listed some other comments. The list is not complete ; some of these are clear typos or sloppiness. This would need to be avoided for your resubmission ... In general ; make sure results, M and M, and discussion are in the appropriate section, redo your subheadings, avoid typos, avoid repetition...

Specific comments

— P1 L10 : "we plan to scale up"
done line 10
— P2 L23 : a large quantity of leaf and wood litter becomes available. But please rephrase this anyway. It's not a good sentence. Mineralisation and decomposition makes the nutrients available, not the wood and leaf litter available as such.
Rewritten. Line 24
— p4 L90 : the buffer you applied to anthropogenic tracks : is the Approuage an anthropogenic track ? For sure not masking out natural rivers out of your algorithm would hugely affect your results. I think (hope) you did include natural rivers in your buffers, but you would need to rephrase, since these are not anthropogenic...
Line 88 : Approuague is a large natural river. Indeed, we have applied a buffer in order to only account for areas (i) not affected by forest logging and (ii) natural rivers : *In order to remove areas close to natural rivers : a 20 m buffer was first applied to all shorelines. Then a 25 m buffer was applied to anthropogenic tracks.*
— P4 : Sloppiness ; your subtitles have the same rank on this page, while they all fall within the first subtitle 'Environmental data' Page 4 : Paragraphs are now correctly ranked. See the document Line 96
— P5 L 141-142 : what do you define as contiguous ? Diagonal pixels would be contiguous ? You know from the field that some trees may be left standing in certain gaps, so this could be important for your results . Line 144 : contiguous is defined as a pixel that has any contact with another i.e., a contact by edges or by vertices. In our framework, diagonal pixels are indeed considered as contiguous pixels.
— P6 l 153-154 : Please cite both R packages properly. Done. Line 157 : Most of the analysis was performed under R and making use of poweRlaw and VGAM packages.
— P6 L172 : Here you use X as the vector of covariates ; while on the next page in equation 8 you

use varig. Please be consistent to make your MS more comprehensible. The vector of covariates as been properly replaced as X in equation 8.

— P7 L191-193 : For clarity I would rename the transformed variables. Also in eq 6 you use the HA as the new variable, and the hydraulic altitude in full as the old, while in 2.1.6. on p 4 you already use the HA abbreviation. Please correct these small errors for your future readers. Done. Transformed variables have a new name. Line 195 : Halt, Topex

— P7 l 204 : investigated ; Material and methods should be in past tense. Please correct Done. Line : 207

— Figure 4 : This figure does not have a lot of information. I would leave it out and describe in text instead. We prefer maintaining this fig in the text but remains open to suggests from the editor.

— P14 L285 : why don't you show the values from the Kellner studies in brackets, like you do for Lobo and Asner ?Line 295, Done

— P14 L300 : Please add reference to your 75% statement. Line 306 : We changed this sentence

— P 14 l 309-311 : "Together with : : :" I don't get this sentence. Please rephrase : : : Line 320 : In agreement with Asner et al., (2013), our results suggest that we can effectively extend these results to bottomlands, where we already know that aboveground biomass and mean wood density are 10% lower than on hilltops (Ferry et al., 2010).

— P 15 l 330-331 : Really ? The first study ? And what about Lob and Dallin (a study which served as a basis for your study) Please review the reference list. Line 340 : Rewritten. "To our knowledge, this is the first study where the precise environmental descriptors associated to each canopy gap were explicitly taken into account in the general model likelihood. We were able to do so because we wrote general model likelihood as the product of all the single likelihoods (*i.e.* each gap had its own likelihood depending on the environmental covariate values). Doing so, we were able to predict gap size distribution from the fine environmental covariates, an impractical task when the scale exponent is estimated once at the forest level (*i.e.* mixing all the found gaps together) and compared between forests *a posteriori*"

2 Supplementary information

TABLE 1 – List of environmental variables, abbreviations, units, and values of the posteriors in univariate models for a height threshold equal to the 0.0001*th* percentile of the height distribution of the canopy.

Parameter	Abbreviation	Unit	Posterior value	Confidence interval (CI 95%)
Slope	Slope	°	0.119	[0.0416 ; 0.208]
Terrain Ruggedness Index	TRI	-	0.119	[0.083 ; 0.157]
TOPographic EXposure	TOPEX	-	-0.128	[-0.188 ; 0.00202]
Drained Area	DA	m^2	0.0843	[-0.0574 ; 0.179]
The Hydraulic Altitude	HAlt	m	-0.0135	[-0.04 ; 0.042]
HAND	HAND	-	-0.0615	[-0.152 ; 0.0162]

TABLE 2 – List of environmental variables, abbreviations, units, and values of the posteriors in univariate models for a height threshold equal to the $0.001th$ percentile of the height distribution of the canopy.

Parameter	Abbreviation	Unit	Posterior value	Confidence interval (CI 95%)
Slope	Slope	$^\circ$	0.0735	[-0.02 ; 0.15]
Terrain Ruggedness Index	TRI	-	0.0718	[0.04 ; 0.10]
TOPographic EXposure	TOPEX	-	-0.082	[-0.12 ; -0.05]
Drained Area	DA	m^2	-0.0176	[-0.09 ; 0.05]
The Hydraulic Altitude	HAlt	m	-0.0177	[-0.05 ; 0.02]
HAND	HAND	-	-0.003	[-0.08 ; 0.09]

TABLE 3 – List of environmental variables, abbreviations, units, and values of the posteriors in univariate models for a height threshold equal to the $0.01th$ percentile of the height distribution of the canopy.

Parameter	Abbreviation	Unit	Posterior value	Confidence interval (CI 95%)
Slope	Slope	$^\circ$	0.0975	[-0.02 ; 0.17]
Terrain Ruggedness Index	TRI	-	0.089	[0.05 ; 0.12]
TOPographic EXposure	TOPEX	-	-0.012	[-0.03 ; -0.32]
Drained Area	DA	m^2	-0.004	[-0.08 ; 0.05]
The Hydraulic Altitude	HAlt	m	0.063	[-0.04 ; 0.08]
HAND	HAND	-	-0.01	[-0.09 ; 0.06]

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Environmental control of natural gap size distribution in tropical forests

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Abstract. Natural disturbances are the dominant form of forest regeneration and dynamics in unmanaged tropical forests. Monitoring the size distribution of treefall gaps is important to better understand and predict the carbon budget in response to land use and other global changes. In this study, we model the size frequency distribution of natural canopy gaps with a discrete power law distribution. We use a Bayesian framework to introduce and test, using Monte Carlo Markov Chain and Kuo-Mallick algorithms, the effect of local physical environment on gap size distribution. We apply our methodological framework to an original Light Detecting and Ranging dataset in which natural forest gaps were delineated over 30000 ha of unmanaged forest. We highlight strong links between gap size distribution and environment, primarily hydrological conditions and topography, with large gaps being more frequent in floodplains and on wind-exposed areas. In the future, we plan to scale up testing our methodology with satellite data. Additionally, although gap size distribution variation is clearly under environmental control, gap process variation over time should be tested against climate variability.

1 Introduction

Natural disturbances caused by forest gaps play an important role in tropical rainforest dynamics. Canopy gaps caused by the death of one or more trees are the dominant form of forest regeneration because the creation of canopy openings continuously reshapes forest structure as gaps are filled with younger trees (Whitmore, 1989). The first, and perhaps most important, effect of gap occurence is an immediate increase in light intensity (Hubbell et al., 1999a), allowing sunlight to penetrate the understory. This phenomenon has been widely studied because the opening of gaps contributes to the establishment and growth of light-demanding trees (Denslow et al., 1998), thus contributing to the maintenance of biodiversity. Another effect of canopy gaps is the local modification of the forest nutrient balance (Rüger et al., 2009). When canopy gaps are created, large amounts of dead leaves and wood will be decomposed and mineralised so that the availability of soil nutrients for neighboring trees will increase (Brokaw, 1985). These nutrient patches are also linked to small-scale spatial variations in forest carbon balance, as shown by Feeley et al. (2007). The relationship between gap formation and the population dynamics of trees or lianas is also quite well understood, with increased liana basal area (Schnitzer et al., 2014) allowing low-wood-density pioneer species to recruit exclusively in newly formed gaps (Molino and Sabatier, 2001).

Many studies have investigated the effect of treefall gaps on biodiversity, particularly animal movement and species composition (Bicknell et al., 2014; Puerta-Piñero et al., 2013), carbon cycles, and forest dynamics. Some authors use field data to study natural gap dynamics, usually at plot scale (Hubbell et al., 1999b). As these studies are quite limited in spatial extent (< 50 ha) and because gap formation is largely unpredictable (Hubbell et al., 1999a; Lloyd et al., 2009), optical satellite imagery has been widely promoted and proven adequate for monitoring forest gaps over space and time (Frolking et al., 2009). At high resolution (< 10 m), IKONOS satellite images may be well suited for evaluating gap dynamics (Espírito-Santo et al., 2014). In French Guiana, the SPOT-4 satellite (20 m spatial resolution) has successfully detected canopy gaps (Colson et al., 2006) using a combination of several spectral bands, such as near and short-wave infrared. However, topographical variation, gap shape, and shade may influence and bias gap detection with optical products. Moreover, persistent cloud cover, common in many tropical forest basins, limits their utility.

Airborne Light Detecting and Ranging (LiDAR) platforms therefore offer a solution to this problem. Recent developments in LiDAR have significantly advanced our ability to derive accurate measurements of canopy forest structure, to detect gaps, and to assess the effect of spatial and temporal variation in carbon balance (Asner and Mascaro, 2014). Kellner and Asner (2009) used remote LiDAR sensing to quantify canopy height and gap size distributions in five tropical rain forest landscapes in Costa Rica and Hawaii. They showed that canopy gaps can be observed with the help of LiDAR-derived digital canopy models (DCMs) and that gap size frequency distribution (GSFD) can be fit with a power law distribution, suggesting a surprising similarity in canopy gap size frequency distributions on diverse soil types associated with diverse geologic substrate ages. Asner et al. (2013) also used LiDAR data to analyze whether gap size frequency distribution is modified by topographic and geologic characteristics and again showed that canopy gap size distribution is largely invariant between forests on erosional terra firme and depositional floodplain substrates in the Peruvian Amazon basin. Finally, using airborne LiDAR, Lobo and Dalling (2014) have recently explored the effect of forest age, topography, and soil type on canopy disturbance patterns across central Panama. For the first time, they highlighted significant effects of slope and of forest age, with a higher frequency of large gaps associated with old-growth forests and gentle slopes.

In this study, we use a DCM derived from airborne LiDAR across a 30000 ha tropical forest landscape in the Régina forest in French Guiana. This approach provides high-resolution maps of canopy gaps and helps us to understand the environmental determinism of gap occurrence in tropical forests. Our specific aims were therefore:

- to define canopy gaps from canopy height data using a probabilistic approach
- to model gap size distribution by inferring a likelihood-explicit discrete power law distribution in a Bayesian framework
- to introduce the environment into the scaling parameter of the power law distribution and test its predictive ability

2 Materials and Methods

The study site is located in the Régina forest (4°N, 52°W), where the most common soils are ferralitic. The site is located on slightly contrasting plateau-type reliefs that are rarely higher than 150 m on average. The forest is typical of French Guianese rainforests. Dominant plant families in the Régina forest include *Burseraceae*, *Mimosoideae*, and *Caesalpinoideae*. The site receives 3,806 mm of precipitation per year, with a long dry season from mid-August to mid-November, and a short dry season in March (Wagner et al., 2011).

2.1 Data source

2.1.1 LiDAR data

LiDAR data were acquired by aircraft in 2013 over 30,000 ha of forest by a private contractor, Altoa (http://www.altoa.fr/), using a Riegl LMS-Q560 laser. This system was composed of a scanning laser altimeter with a rotating mirror; a GPS receiver (coupled to a second GPS receiver on the ground); and an inertial measurement unit to record the pitch, roll, and heading of the aircraft. The laser wavelength was near-infrared (from about 800 nm to 2500 nm). Flights were conducted at 500 m above ground level with a ground speed of 180 km.h^{-1}, and each flight derived two acquisitions. The LiDAR was operated with a scanning angle of 60° and a 200 kHz pulse repetition frequency. The laser recorded the last reflected pulse with a precision better than 0.10 m, with a density of 5 pulses.m^{-2}.

The DCM was derived from the raw scatter plot consisting of the pooled dataset from the two acquisitions. Raw data points were first processed to extract ground points using the TerraScan (TerraSolid, Helsinki) ground routine, which classifies ground points by iteratively building a triangulated surface model. Ground points typically made up less than 1% of the total number of the return pulses. The DCM has a resolution of 1 m. In order to remove areas close to natural rivers, a 20 m buffer was first applied to all shorelines. Then a 25 m buffer was applied to anthropogenic tracks.

2.1.2 Environmental data

We use six environmental variables to synthesize the observed environmental gradients. All variables were computed from a LiDAR digital terrain model (DTM) with 5 m^2 cells.

Slope

The slope was derived from the LiDAR DTM. Slope was computed at a grid cell as the maximum rate of change in elevation from that cell to its 8 neighboring cells over the distance between them.

Topographic exposure

We use the TOPographic EXposure (TOPEX) index to measure topographic exposure to wind (Chapman, 2000). TOPEX is a variable that represents the degree of shelter assigned to a location. It was derived from quantitative assessment of horizon inclination. The values of this index are closely correlated with wind-shape index (Mikita and Klimánek, 2012). Exposure is calculated based on the height and distance of the surrounding horizon, which are combined to obtain the inflection angle. We use this angle to quantify topographic exposure (pixel resolution 5 m$\times$ 5m). When a large topographic feature, like a mountain, is far off in the distance the inflection angle is low. When the same mountain is closer, the inflection angle is higher. Therefore, a higher inflection angle is equal to lower exposure or higher sheltering (Mikita and Klimánek, 2012).

Drained area

Drained area (DA) measures the surface of the hydraulic basin that flows through a cell. A low value indicates that a cell is located at the border between two basins, whereas high values indicate cells located downstream.

Hydraulic altitude

The hydraulic altitude (HA) of each cell, its altitude above the closest stream of its hydraulic basin, was computed from the 3rd order hydraulic system. Low values, including 0, indicate that the forest plot is potentially temporarily flooded, whereas high values indicate that it is located on a hilltop.

Terrain ruggedness index

The terrain ruggedness index (TRI) captures the difference between flat and mountainous landscapes. TRI was calculated using SAGA GIS SAGA (2013) as the sum of the altitude change between a pixel and its eight neighboring pixels (Riley, 1999).

The height above the nearest drainage

The height above the nearest drainage (HAND) model normalizes topography with respect to drainage network by applying two procedures to the DTM. The initial basis for the HAND model came from the definition of a drainage channel: perennial streamflow occurs at the surface, where the soil substrate is permanently saturated. It follows that the terrain at and around a flowing stream must be permanently saturated, independently of the height above sea level at which the channel occurs. Streamflow indicates the localized occurrence of homogeneously saturated soils across the landscape. The second basis for the HAND model came from the distinctive physical features of water circulation. Land flows proceed from the land to the sea in two phases: in restrained flows at the hillslope surface and subsurface, and in freer flows (or discharge) along defined natural channels. (Nobre et al., 2011)

2.2 Forest gap definition

2.2.1 Height threshold

To identify discrete canopy gaps, we had to choose a gap threshold height. Some authors define this threshold at 2 m (Brokaw, 1982). Runkle (1982) defines a gap as the ground area under a canopy opening that extends to the base of the surrounding canopy trees, these usually being considered to be taller than 10 m, with a trunk diameter at breast height (DBH) $>$ 20 cm. However, in practice, defining gap boundaries is a tricky issue, even in the field. Here, we develop a probabilistic method for detecting canopy gaps from LiDAR data. We used the DCM to model canopy height distribution considering a mixture distribution of two ecological states: the natural variation of canopy height in mature forests, modeled as a normal distribution, and the presence of forest gaps, which lead to a new normal distribution with lower values. We consider that the threshold between the two states is equal to the $0.001th$ percentile of the height distribution of the canopy (our results appeared robust to the threshold value, see supplementary information). We then define canopy gaps as contiguous pixels at which the vegetation height is less than or equal to the height threshold. Contiguous pixels are defined as pixels that have any contact contact by edges or by vertices.

2.2.2 Minimum gap size

In our study, we define the minimum area of a gap as x_{min}. We model the gap size frequency distribution with a power law distribution. We use the Pareto distribution in a discrete power law probability density function (Virkar and Clauset, 2014). These distributions have a negative slope and their size frequencies are plotted on logarithmic axes, allowing us to observe the scaling parameter λ. A value close to 1 means there are a large number of large gaps. In other word, in forests dominated by small canopy openings, values of λ are larger, whereas smaller values of λ increase the frequency of large gap events (Fisher et al., 2008). In a discrete power law with parameter λ, the probability for gap size x is given by:

$$p(x) = \frac{x^{-\lambda}}{\zeta(x_{min}, \lambda)}, \quad (1)$$

where x_{min} is the lower truncation point and λ is the scaling parameter.

Most of the analysis was performed under R (Team et al., 2013) and making use of poweRlaw (Clauset et al., 2009) and VGAM (Yee et al., 2010) packages.

We use a Kolmogorov-Smirnov (KS) distance criterion order to determine the error between the observed distribution and the Pareto distribution. KS is defined as the maximum distance between the cumulative distribution functions (CDFs) of the data and the fitted function (Virkar and Clauset, 2014). We retain, for the remainder of this study, a minimum gap size area x_{min} = 104 m^2, which minimized the KS distance in our dataset.

2.3 Modeling gap size distribution

Having set the height threshold and minimum gap size, the GSFD is modeled with a discrete Pareto distribution frequency.

2.3.1 Model inference

We use a Bayesian framework to estimate model parameters. Here, the value of a parameter is estimated by its posterior distribution, which by definition, is proportional to the product of the likelihood of the model and the parameter prior distribution. The prior distribution is based on prior knowledge of the possible values of a parameter. The posterior densities of the different parameters were estimated using a Monte Carlo Markov Chain algorithm (MCMC).

2.3.2 Metropolis-Hastings algorithm

As the model contains many parameters, we built a Metropolis-Hastings (MH) algorithm in which all parameters are updated together. Details on the algorithm are given below:

- $Y = y_1, y_2, \ldots, y_n$ is the gap size vector
- $X = x_{g1}, x_{g2}, \ldots, x_{gi}$ is the vector of covariates (environmental variables) for gap g
- $\theta = \theta_1, \theta_2, \ldots, \theta_i$ is the model parameter vector

The first values of the parameter vector are initialized as $t = 1$, $\theta^t \sim \pi^0_\theta$.

For each step t, a new parameter value is sampled from the proposition distribution and a new vector of theta candidates is generated.

$$\theta^{cand} \sim \pi^{prop} \quad (2)$$

Acceptance or rejection of the new candidate θ^{cand} is determined by computing the likelihood ratio of the two discrete Pareto distributions:

$$\rho(\theta^t, \theta^{cand}) = \underbrace{\frac{\mathcal{L}(Y|X, \theta^{cand})}{\mathcal{L}(Y|X, \theta^t)}}_{\text{likelihood}} \underbrace{\frac{\pi^0_\theta(\theta^{cand})}{\pi^0_\theta(\theta^t)}}_{\text{prior}} \underbrace{\frac{\pi^{prop}(\theta^t)}{\pi^{prop}(\theta^{cand})}}_{\text{proposal}} \tag{3}$$

The candidate θ^{cand} is accepted or rejected as follows:

$$u \sim \mathcal{U}_{[0,1]}, \theta^{cand} \begin{cases} \theta^{t+1} & if \quad u < \rho(\theta^t, \theta^{cand}) \\ \theta^t & if \quad u > \rho(\theta^t, \theta^{cand}) \end{cases} \tag{4}$$

The algorithm is run for 1000 iterations. We use the median of the posterior densities to estimate parameter values, and the distribution of the posterior densities to estimate parameter credibility intervals.

2.3.3 Univariate environmental effects

Variable transformation

To improve model inference, parameter significance and interpretation, we first transformed some environmental variables:

$$Slope = sqrt(slope) \tag{5}$$

$$HAlt = log(HA + 1) \tag{6}$$

$$Topex = |max(TOPEX) - (TOPEX)| \tag{7}$$

The environmental variables are then centered and scaled with R function : "scale".

We first consider each environmental covariate independently. These covariates are included one-by-one in the model to constrain the exponent λ. We use the exponential function to constrain λ, because the Riemann's zeta function only admits $\lambda > 1$.

$$\lambda_i = 1 + \exp(\theta_{0i} + \theta_i \times X) \tag{8}$$

where λ_{ig} is the λ value dependent on the value of environmental variable i in gap g, θ_{0i} is the intercept, and θ_i quantifies the effect of covariates var on the gap size distribution var_{ig}.

2.3.4 Multivariate model

Principal component analysis

We first investigated the collinearity of environmental data through principal component analysis (PCA) on the normalized environmental dataset.

Model

To build the final model, we used the results of the univariate model (Table 1) and the PCA (Figure 3) and set:

$$\lambda = 1 + \exp(\theta_0 + \theta_1 \times Slope + \theta_2 \times Topex \\ + \theta_3 \times HAlt + \theta_4 \times HAND) \tag{9}$$

Variables selection

To select the significant covariates and build the final model, we used the method proposed by Kuo and Mallick (1998) (KM). This method consists of associating an indicator with each variable var_i and parameter θ_i. This indicator can take two values: 1 or 0. If it is set to 1, the variable is included in the model, but if the value is set to 0, it is not. We used the MH and KM algorithms to estimate the indicators I and infer their *a posteriori* distribution in addition to θ.

We start the KM algorithm with $t = 1$, $\theta^t \sim \pi^0_\theta, I^t_j \sim \mathcal{B}er(0.5)$ for j = 1,..., i. For each covariate j (selected in random order), we use the MH algorithm to update θ_j. To update I_j, we compute the ratio ρ (eq10) and generate I_j^{t+1} from a Bernoulli distribution $\mathcal{B}$ern(ρ):

$$\rho = \frac{1}{1 + \frac{\mathcal{L}(Y|\tilde{X},\theta^t,I_j=0,I^t_{-j})}{\mathcal{L}(Y|\tilde{X},\theta^t,I_j=1,I^t_{-j})}} \tag{10}$$

Model inference and data analysis were conducted with R software (R-Core-Team 2012). All maps and geographical information were computed with SAGA (SAGA, 2013) and ArcGIS 10.1.

3 Results

3.1 Gap delineation

In this study, we used a forest canopy height mixture model to define the maximum height of a given pixel to be included in a forest gap. This probabilistic method produced results that fit the observed canopy height distribution. We retained the 11 m threshold that corresponds to the 0.001th percentile of the canopy height distribution (Figure 1). Given this height, we retained the surface x_{min} = 104 m^2 that minimized the KS distance between predictions and observations. Here, our gap definition was therefore defined as an area $>$ 104 m^2, in which the LiDAR measured canopy height is always $\leq$ 11 m.

3.2 Basic statistics

We mapped 12,293 gaps with vegetation $\leq$ 11 m in height. The mean gap size was 236 m^2 with a minimum gap size of 104 m^2 and a maximum of 29,063 m^2. The total gap area was about 290 ha, or 1% of the whole surveyed area. The observed gap size distribution was modeled with a Pareto distribution (Figure 2), leading to a scaling parameter $\lambda_{x_{min}}$ of 2.6.

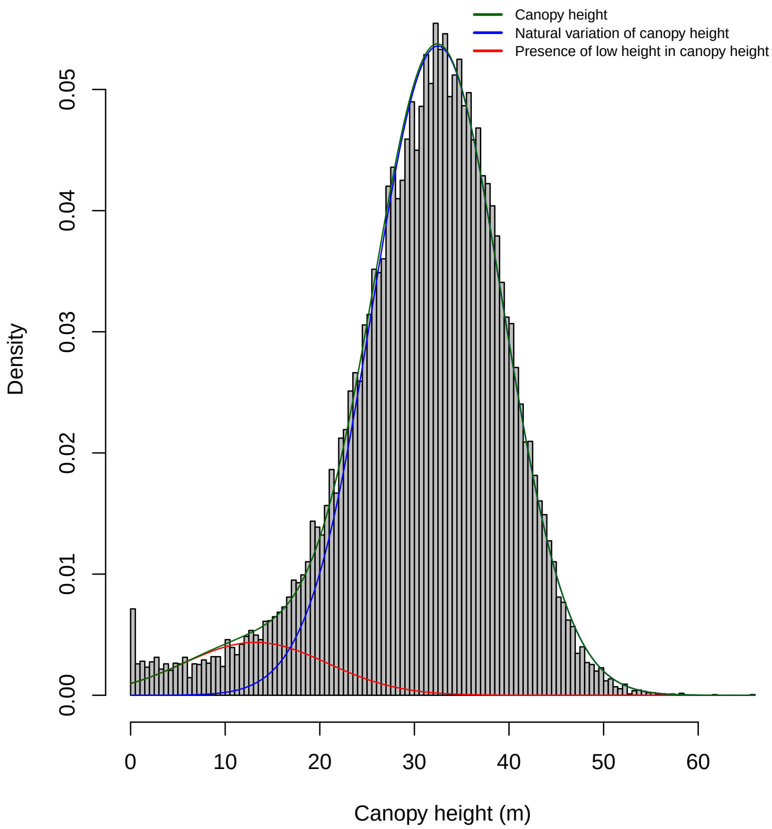

Figure 1. Canopy height distribution. Canopy height considered as a mixture distribution of two ecological features. The first (blue curve) is the natural variation in canopy height, modeled as a normal distribution. The second (red curve) is linked to the presence of low heights in the total canopy height distribution, likely to be due to a forest gap. We set the gap threshold to the 0.001th percentile of the blue curve density, *i.e.*, 11 m.

3.3 Univariate models

All variables had an effect on gap size distribution (Table 1). The scaling coefficient λ is related to the ratio of small gaps to large gaps, with values close to 1 indicating a higher frequency of large gaps and vice versa. Parameter estimates for slope and TRI show high occurrence of small gaps for large values of the two variables. Contrarily, the effect of DA, HAND, HAlt, and Topex on λ are clearly negative, meaning that the frequency of large gaps increases with large values.

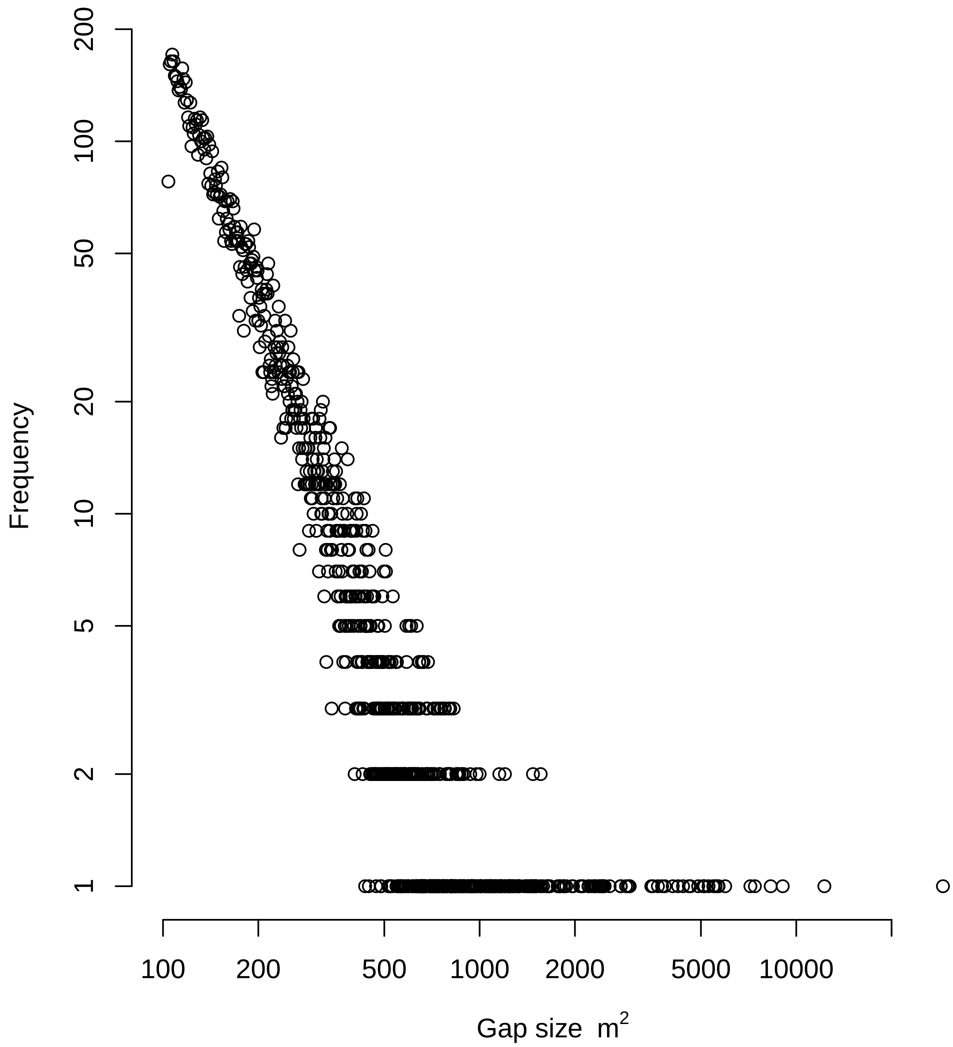

Figure 2. The observed gap size frequency distributions modeled as a power law function with $\lambda = 2.6$.

3.4 The multivariate model

To define the final multivariate predictive model, we used the significant results of the univariate models together with the output of the PCA, in order to avoid multicollinearity.

3.4.1 Variable selection

The first three PCA axes explained more than 80% of the data variance. The first axis, which accounted for 36.45% of the variance, was positively correlated with relative HAlt and negatively correlated to HAND and DA, and thus clearly highlighted the local altitudinal gradient. The second

Table 1. List of environmental variables, abbreviations, units, and values of the posteriors in univariate models.

Parameter	Abbreviation	Unit	Posterior value	Confidence interval (CI 95%)
Slope	Slope	°	0.0735	[-0.02 ; 0.15]
Terrain Ruggedness Index	TRI	-	0.0718	[0.04 ; 0.10]
TOPographic EXposure	TOPEX	-	-0.082	[-0.12 ; -0.05]
Drained Area	DA	m^2	-0.0176	[-0.09 ; 0.05]
The Hydraulic Altitude	HA	m	-0.0177	[-0.05 ; 0.02]
HAND	HAND	-	-0.003	[-0.08 ; 0.09]

axis explained an additional 28.5% of variance and was positively correlated with the TRI and Slope. The third axis explained a further 15.2% of the variance and was correlated only with Topex (Figure 3). The multivariate model was created using a Bayesian framework including four environmental variables: slope, Topex, HAND, and HAlt, the explanatory variables that had an effect on λ. Finally, the KM methodological framework was used to select the most parsimonious model.

Environmental covariates with posterior KM values close to 1, namely Slope, Topex, and HAND (eqn 9) were retained in the final model (Figure 4). Parameter estimates of the final model indicated that the greatest effects on gap size distribution were caused by Topex and HAND.

4 Discussion

4.1 Methodology

4.1.1 Gap Detection

Delineating forest gaps is a persistent challenge for foresters and ecologists, among whom Brokaw (1982) gap definition has remained extensively used, in which "a 'hole' in the forest extending through all levels down to an average height of 2 m above the ground," must be defined by an experienced observer. There are several studies that do not use this 2m-threshold definition of gaps, for instance 10 m (e.g. Hubbell et al., 1999; Meer and Bongers, 1996; Welden et al., 1991). However, in this study we have decided to use a probabilistic approach, modeling height distribution as a mixture of two normal laws. We found a height, 11 m, which is much higher than that in Brokaw's definition, but is consistent with our field experience, where woody debris, dead canopy tree boles, and residual saplings (*i.e.*, remnants that survive the gap formation event) may rise well above 2 m. For example, Hubbell et al. (1999a) showed that small stems frequently remained in gaps up to 4-5 m in height, while Lieberman et al. (1985) reported broken and damaged stems up to 10 m tall within a gap. The choice of the values of height and threshold may be adapted to different forest types and

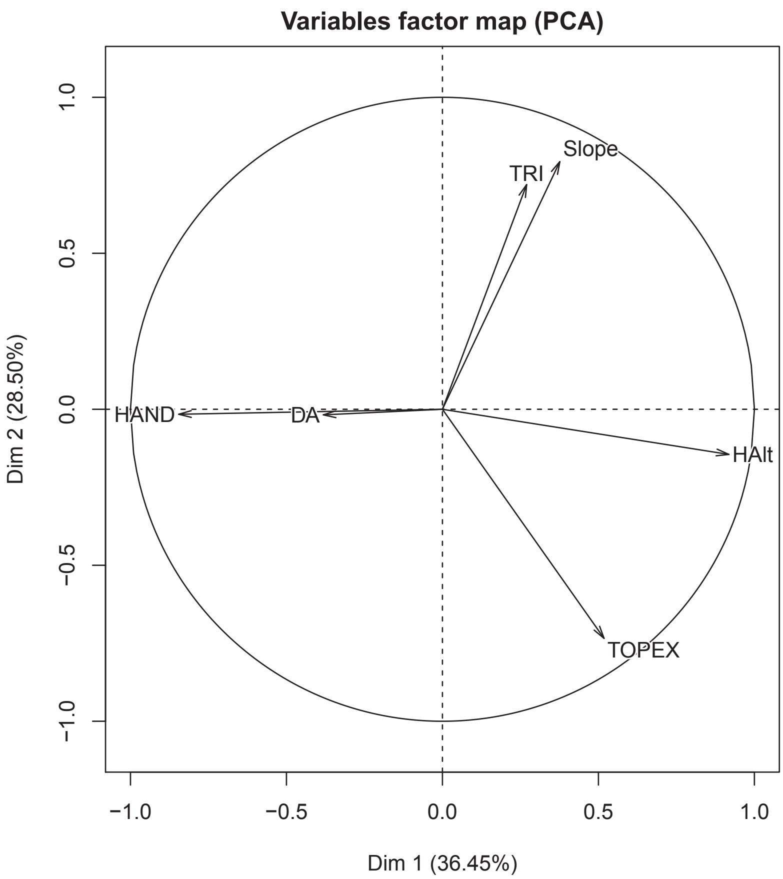

Figure 3. Results of the principal component analysis on the environmental variables

topographic characteristics. In our case, the choice was fully data-driven using the DCM and DEM and no ecological knowledge. Within our framework it is likely that in waterlogged areas, areas covered with mature trees that do not exceed the height thresholds may appear in our analysis as forest gaps. In order to clarify this question, an approach using time-series would allow to identify

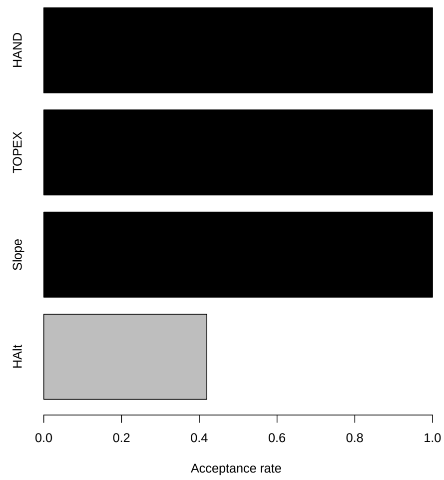

Figure 4. Results of the Kuo-Mallick algorithm for variable selection. Variables were included in the final model when their value was close to 100%: $Slope$, $Topex$ and $HAND$

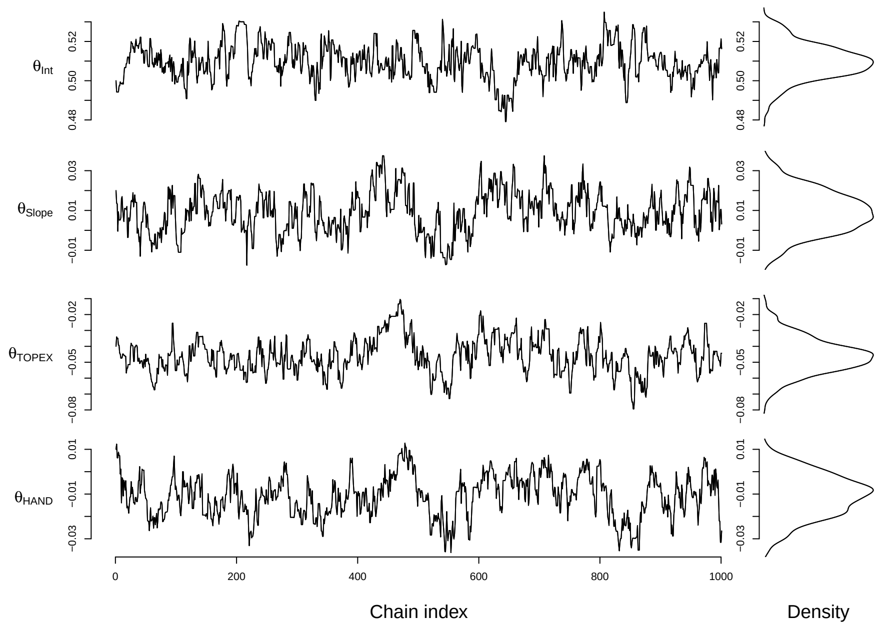

Figure 5. Posterior distribution of the environmental variables in the final multivariate model.

280 these 'false' gaps that never get filled and thus are not part of the forest endogeneous dynamics. These are not gaps in the ecological meaning.

Defining minimum gap size is also a delicate proposition. Some authors, working with high-definition LiDAR data, have considered a minimum gap size (x_{min}) of 1 m^2 (Asner et al., 2013) (Kellner and Asner, 2009). This minimum gap size is unrealistic from an ecological perspective given that a hole of several square meters in the canopy may simply reflect the distance between two crowns. Brokaw recommended a range from 20 m^2 to 40 m^2 based on his field experience. We have worked with a minimum gap size of 104 m^2, and based this value on the minimized Kolmogorov-Smirnov distance between observed and predicted values.

We built on previous studies that show that gap size distribution follows a power law distribution. However, the underlying mechanisms that control this distribution are still unclear. The Bayesian framework we developed allowed us to detail the contributions of each environmental variable to the size of each individual gap. Because the precise environmental variables were explicitly taken into account in the model likelihood of each gap, we were able to predict gap size distribution from environmental covariates, a difficult task when the scale exponent is estimated once, at the forest level, and compared between forests. The global scale exponent that we estimated for an average environment ($\lambda = 2.6$), is consistent with some previous studies (Kellner and Asner, 2009; Kellner et al., 2011), though slightly larger than those of others Lobo and Dalling (2014) [1.97 ; 2.15] and Asner et al. (2013) [1.70 ; 2.03].

4.2 Environmental effects on gap size frequency distribution

For the first time, gap size distribution integrates environmental variables as a linear combination of the scale parameter (λ) of a discrete Pareto distribution frequency. Our results suggest that three covariates drive the gap size frequency distribution in our forest: $Slope$, $HAND$, and $TOPEX$ (Figure 5).

4.2.1 Slope

Steep slopes are well-known to directly impact tropical forest canopy structure (Bianchini et al., 2010). In this study, we found similar results to Lobo and Dalling (2014) in BCI, *i.e.*, large gaps (smallest λ) are more frequent on the lowest slopes. This may seem counter-intuitive at first, as treefall may be (i) more prone to induce cascading effects when slopes are steep and (ii) more frequent in slopes where soils are shallow with lateral drainage (Gourlet-Fleury et al., 2004), impeding deep rooting of trees. However, the forest turnover is more important in bottomlands where slopes are gentle (Durrieu de Madron, 1994). Considering that large gaps may be created solely by contiguous and independent treefalls, larger gaps may then be expected in bottomlands from a pure probabilistic approach. And given the positive link between wood density and steep slopes (Ferry et al., 2010), trees may be more resistant to cascading effects than they are in bottomlands.

4.2.2 Water Saturation

$HAND$ is a binary variable that takes the value 1 on water-saturated soils. Because λ decreases when $HAND$ equals 1, the frequency of large gaps increases in floodplains and bottomlands. These results support the findings of (Korning and Balslev, 1994), highlighting more dynamic forests in floodplains subject to large flooding events that lead to cascading treefall events. Together with (Asner et al., 2013), our results suggest that we can effectively extend these results to bottomlands, where we already know that aboveground biomass and mean wood density are 10% lower than on hilltops (Ferry et al., 2010). Given its ease of implementation on a land-surface model and its high predictive power, HAND covariates present great potential applicability for gap size distribution prediction.

4.2.3 Topographic Exposure

The effect of topographic exposure on λ is consistent with our *a priori* hypothesis that wind-exposed areas would have a greater relative frequency of large gaps. Although hurricane damage does not occur in continental equatorial regions of the Amazon (Nelson et al., 1994), here we demonstrate that tree exposure has a large impact on gap size distribution. Lobo and Dalling (2014) observed no clear effect of TOPEX, and suggested that this index has a slight negative effect on gap size distribution. The results of this study are in line with the pioneering work of (Negrón-Juárez et al., 2014), which showed that wind exposure is related to higher elevations that inflate the occurrence of larger gaps. However, coastal French Guianese forests exhibit different landscapes and landforms (Guitet et al., 2013). Our study area is made of dissected plateaus characterized by simple forms resembling hills (Guitet et al., 2013). It is possible that these characteristics, leading to unique combinations of landform elevations, may create complex terrain interactions that increase wind local speed and, in turn, cause large gaps. We conclude that topographic exposure is an appropriate index for predicting gap size distribution, but this must be confirmed in other landscape types.

5 Conclusions

To our knowledge, this is the first study where the precise environmental descriptors associated to each canopy gap were explicitly taken into account in the general model likelihood. We were able to do so because we wrote the general model likelihood as the product of all the single likelihoods (*i.e.* each gap had its own likelihood depending on the environmental covariate values). Doing so, we were able to predict gap size distribution from the fine environmental covariates, an impractical task when the scale exponent is estimated once at the forest level (*i.e.* mixing all the found gaps together) and compared between forests *a posteriori*. We also put forward an innovative method to define a height threshold and minimum gap size using two probabilistic approaches. The modeled distribution of canopy height as mixture of two distributions provides a clear height threshold, while the minimization of KS distance between observed and predicted data proves to be efficient for setting the minimum gap size. We use a Bayesian framework in which the model likelihood of each gap is expressed as a function of the unique environment local to the gap, highlighting the predominant role of the topographic exposure and waterlogging in determining gap size distribution. We expected that slope would also play an important role, with steeper slopes leading to larger gap sizes. However we found that a steeper slope lead to smaller gaps, as already highlighted by (Lobo and Dalling, 2014). We suggest that our modeling approach can be a basis for the development of large-scale methodologies using satellite data to understand gap phase dynamics at a regional scale, combining LiDAR and RaDAR remote sensing tools.

6 Supplementary information

Table 2. List of environmental variables, abbreviations, units, and values of the posteriors in univariate models for a height threshold equal to the 0.0001*th* percentile of the height distribution of the canopy.

Parameter	Abbreviation	Unit	Posterior value	Confidence interval (CI 95%)
Slope	Slope	°	0.119	[0.0416 ; 0.208]
Terrain Ruggedness Index	TRI	-	0.119	[0.083 ; 0.157]
TOPographic EXposure	TOPEX	-	-0.128	[-0.188 ; 0.00202]
Drained Area	DA	m^2	0.0843	[-0.0574 ; 0.179]
The Hydraulic Altitude	HAlt	m	-0.0135	[-0.04 ; 0.042]
HAND	HAND	-	-0.0615	[-0.152 ; 0.0162]

Table 3. List of environmental variables, abbreviations, units, and values of the posteriors in univariate models for a height threshold equal to the 0.001*th* percentile of the height distribution of the canopy.

Parameter	Abbreviation	Unit	Posterior value	Confidence interval (CI 95%)
Slope	Slope	°	0.0735	[-0.02 ; 0.15]
Terrain Ruggedness Index	TRI	-	0.0718	[0.04 ; 0.10]
TOPographic EXposure	TOPEX	-	-0.082	[-0.12 ; -0.05]
Drained Area	DA	m^2	-0.0176	[-0.09 ; 0.05]
The Hydraulic Altitude	HAlt	m	-0.0177	[-0.05 ; 0.02]
HAND	HAND	-	-0.003	[-0.08 ; 0.09]

Table 4. List of environmental variables, abbreviations, units, and values of the posteriors in univariate models for a height threshold equal to the $0.01th$ percentile of the height distribution of the canopy.

Parameter	Abbreviation	Unit	Posterior value	Confidence interval (CI 95%)
Slope	Slope	°	0.0975	[-0.02 ; 0.17]
Terrain Ruggedness Index	TRI	-	0.089	[0.05 ; 0.12]
TOPographic EXposure	TOPEX	-	-0.012	[-0.03 ; -0.32]
Drained Area	DA	m^2	-0.004	[-0.08 ; 0.05]
The Hydraulic Altitude	HAlt	m	0.063	[-0.04 ; 0.08]
HAND	HAND	-	-0.01	[-0.09 ; 0.06]

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