LETTER

Pervasive canopy dynamics produce short-term stability in a tropical rain forest landscape

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Abstract

A fundamental property of all forest landscapes is the size frequency distribution of canopy gap disturbances. But characterizing forest structure and changes at large spatial scales has been challenging and most of our understanding is from permanent inventory plots. Here we report the first application of light detection and ranging remote sensing to measurements of canopy disturbance and regeneration in an old-growth tropical rain forest landscape. Pervasive local height changes figure prominently in the dynamics of this forest. Although most canopy gaps recruited to higher positions during 8.5 years, size frequency distributions were similar at two points in time and well-predicted by power-laws. At larger spatial scales (hundreds of ha), height increases and decreases occurred with similar frequency and changes to canopy height that were analysed using a height transition matrix suggest that the distribution of canopy height at the beginning of the study was close to the projected steady-state equilibrium under the recent disturbance regime. Taken together, these findings show how widespread local height changes can produce short-term stability in a tropical rain forest landscape.

Keywords

canopy gap, forest dynamics, global change, light detection and ranging, remote sensing, stability.

Ecology Letters (2009) **12**: 155–164

INTRODUCTION

The size frequency distribution of canopy disturbances is a fundamental property of all forest landscapes (Hubbell & Foster 1986; Sanford *et al.* 1986; Valverde & Silvertown 1997; Cumming *et al.* 2000; Fisher *et al.* 2008). But characterizing forest structure and changes, such as regeneration of canopy gaps in tropical rain forests, has been difficult to accomplish at large spatial scales commensurate with human activities and many biological processes (Clark & Clark 1992; Jones *et al.* 2005; Hardesty *et al.* 2006). Some studies have used data from remote sensing to quantify forest structure on landscapes (Hall *et al.* 1991; Nelson *et al.* 1994; Drake *et al.* 2003; Vepakomma *et al.* 2008), but most of our understanding is from small permanent plots of up to several tens of hectares in size (Hubbell & Foster 1986; Phillips & Gentry 1994; Phillips 1998; Clark & Clark 2000;

Chave *et al.* 2008; Phillips *et al.* 2008). How, or whether, these findings represent forest dynamics at landscape to regional scales is largely unknown (Fearnside 2000; Clark 2004a; Fisher *et al.* 2008).

Previous studies have argued that rates of canopy disturbance are increasing (Phillips & Gentry 1994) and biomass is accumulating (Phillips 1998) throughout large areas of undeveloped lowland rain forest. These findings have been controversial (Clark 2002, 2004b; Wright & Calderon 2006), because inferences are from repeated censuses of small permanent-inventory plots. Methodological bias may have confounded early measurements (Clark 2002; Phillips *et al.* 2002) and data from other sources point toward alternative conclusions (Chave *et al.* 2003; Clark *et al.* 2003; Chave *et al.* 2008). Some studies have suggested that most local sites in any tropical rain forest landscape are recovering from previous disturbance, which could account

for observations of increasing biomass (Fearnside 2000; Clark 2004a; Körner 2004; Chave *et al.* 2008). A recent study demonstrated that local sampling within field-based plots may not produce unbiased estimates of regional forest dynamics (Fisher *et al.* 2008). Whether or not plots provide representative samples depends on the spatial distribution and sizes of canopy gaps at large spatial scales and the size of the area sampled within plots (Fisher *et al.* 2008).

Remote sensing has been used to measure forest structure in temperate and tropical ecosystems (Hall *et al.* 1991; Nelson *et al.* 1994; Clark *et al.* 2004a,b,c; Vepakomma *et al.* 2008). Many of these approaches have used relatively conspicuous features to identify large disturbance patches (Nelson *et al.* 1994; Chambers *et al.* 2007) or biological invasions (Asner *et al.* 2008) and typically provide estimates from a single point in time. However, recent developments in the capacity of airborne light detection and ranging (LiDAR) enable precise measurements of forest structure and changes, providing opportunities to characterize dynamics of forest ecosystems on landscapes (Asner *et al.* 2008; Vepakomma *et al.* 2008). By recording the return-time of reflected laser pulses, aircraft-mounted LiDAR systems provide measurements of canopy height and ground elevation and the vertical and horizontal distribution of biomass. These data can be used to generate spatially-referenced, extensive and fine-grained vegetation height measurements that are objectively acquired, facilitating measurements of the forest canopy that are difficult to obtain from a ground-based perspective.

We quantified the structure and dynamics of an old-growth tropical rain forest landscape using data collected 8.5 years apart from two LiDAR systems. Data from each system were processed to generate imagery with 5 m spatial resolution, where each 5 m pixel contained a local height estimate that corresponded to traditional interpretations of canopy height used in studies of forest dynamics (c.f. Brokaw 1982). We used these data to characterize size frequency distributions of forest canopy gaps and to determine whether a tropical rain forest landscape was close to steady-state equilibrium with the recent disturbance regime.

REMOTE MEASUREMENT OF FOREST STRUCTURE AND DYNAMICS

The study was conducted in 444 ha of old-growth rain forest at the La Selva Biological Station, in the Atlantic lowlands of Costa Rica (Fig. 1). The site is classified as Tropical Wet Forest in the Holdridge life-zone system and receives *c.* 4 m of rainfall annually. Mean monthly temper-
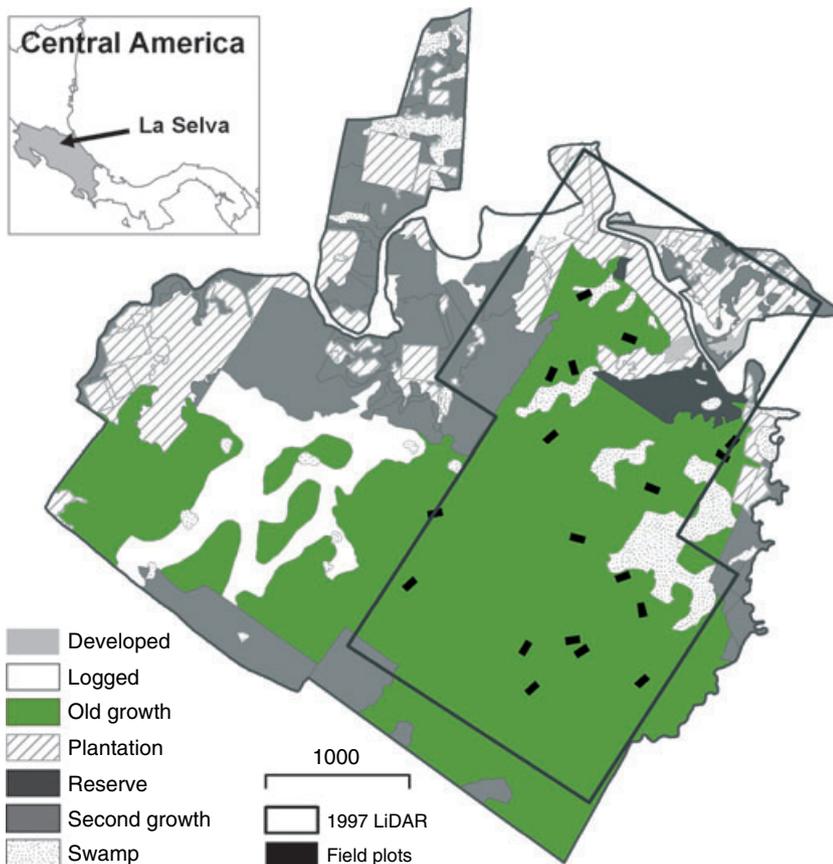

Figure 1 La Selva, Costa Rica. Land use history and locations of field plots and light detection and ranging (LiDAR) coverage. The site has a mixed history of historical land use, including cleared or developed areas, selectively logged forest, old-growth forest, current and abandoned plantations or pastures, second-growth forests and swamps. Remote sensing data were collected in 1997 (rectangular area) and 2006 (entire area). Analyses were restricted to the old-growth forest.

ature is 26 °C and relief ranges from 41–142 m on highly weathered Oxisols (Kleber *et al.* 2007). Mean canopy height is 20.3 m ± 6.9 m SD and the density of stems ≥ 10 cm diameter in terre firme old-growth is 504 ± 22 individuals ha^{-1} (Clark & Clark 2000). Estimated above-ground biomass is 160.5 ± 4.2 Mg ha^{-1} (Clark & Clark 2000). Most of the study site is on undulating upland plateaus for which there is no evidence of extensive historical forest clearing (Kennedy & Horn 2008). A detailed site description is in McDade *et al.* (1994).

We quantified forest structure and dynamics using data collected 8.5 years apart from two LiDAR systems. The FLI-MAP system (John E. Chance and Associates, Lafayette, Louisiana, USA) and Leica ALS50 (Cognocarta GIS LLC, San Jose, Costa Rica) are discrete pulse, scanning laser altimeters. Data were collected for 444 ha of old-growth tropical rain forest on September 12–13, 1997 (Clark *et al.* 2004c) and March 13–14, 2006, respectively. We processed LiDAR data to generate 5 m raster canopy surface models (digital surface model, DSM). Each 5 m pixel contained the mean of all elevation measurements within the given pixel, so that local height estimates would correspond to traditional interpretations of canopy height used in defining gap vs. non-gap areas (Brokaw 1982). To estimate canopy height above ground, we generated raster ground surfaces with 5 m spatial resolution (digital terrain model, DTM) and subtracted the respective DTM from DSM elevation to produce digital canopy models. For the FLI-MAP system, we resampled the 1 m DTM generated by Clark *et al.* (2004c) to 5 m using nearest-neighbour resampling. For the Leica ALS50 we generated a 5 m DTM by applying a natural neighbour interpolation to point elevation estimates that were classified as ground elevation. Because occasional interpolation errors in the DTM will influence canopy height estimates (Vepakomma *et al.* 2008), we excluded 11 pixels in 1997 and 72 pixels in 2006 with negative canopy height estimates and our analyses are based on the remaining 177 750 observations. We used data from extensive field surveys to establish that LiDAR DTM estimates are precise and accurate within the old-growth study area. The relationship between field and LiDAR estimates of ground elevation in 2006 is: field measured elevation (m) = 0.999 × LiDAR predicted elevation (m) − 0.406 m, $P_{\text{intercept}} < 0.001$ $P_{\text{slope}} < 0.001$, $r^2 = 0.994$, root mean squared error (RMSE) = 1.85 m.

To quantify forest dynamics using data from LiDAR, we calculated height changes within 5 m grid cells using LiDAR imagery from 1997 and 2006 and examined the distribution of canopy height change and properties of the transition matrix, A, for 1 m canopy height classes between 0 and 56 m throughout old-growth forest at La Selva. To calculate canopy height changes, we first coregistered LiDAR imagery from 1997 and 2006 using a geographic information system.

The correction was an affine transformation applied to six control points that were well-distributed throughout the old-growth study area. Overall RMSE was 1.24 m (i.e. smaller than the 5 m side length of a single pixel). We then subtracted 1997 from 2006 canopy elevation to produce a model of canopy height change.

The distribution of canopy height change can be used to infer the dynamics of disturbance and regeneration that are operating at large spatial scales. If most local sites are recovering from a previous disturbance, the distribution could be right skewed, as more sites would increase than decrease in height. This could occur, for example, if the old-growth landscape at La Selva is embedded within a larger historical disturbance patch that predates the first census from which recovery is still underway (Nelson *et al.* 1994; Fearnside 2000; Clark 2004a; Körner 2004). In contrast, a landscape that has experienced catastrophic disturbance between height measurements could have a left-skewed distribution of canopy height change, as height losses would occur more frequently than increases under this scenario. This could occur if mortality rates were increasing through time (e.g. Phillips & Gentry 1994), or if disturbance events over the transition interval caused widespread canopy damage. Finally, if the dynamics of disturbance and regeneration are close to the steady-state expectation, height increases and decreases should occur with similar frequency and the distribution of canopy height change would be symmetric with a mean close to zero.

We calculated the steady-state distribution of canopy height under the recent 8.5 year disturbance regime by solving for the dominant right-hand eigenvector of a height transition matrix, A (Caswell 2000). The A matrix has dimensions 56 × 56, one column and row for each 1 m height class. Elements of the A matrix integrate growth and lateral filling, mortality and branch loss that characterize forest dynamics. Each column and row combination contains the empirically estimated probability that the height class at column *i* will enter the height class at row *j* over the 8.5 year transition interval. Thus, columns of the A matrix can be interpreted as prospective height transition probabilities, because they represent the likelihood of occupying future states, given a current height class (Fig. 2). In contrast, rows of the A matrix can be interpreted as retrospective projections of height transitions, because they describe probabilities of occupying past states, given a height class (Fig. 2). An aggregation of the A matrix is in Table 1 and the full transition matrix is in Appendix S1.

Calculation of the dominant right-hand eigenvector associated with the height transition matrix produces the projected distribution of canopy height associated with dynamics over the recent 8.5 year interval. Because our analysis is based on two time points, differences between the observed distributions of canopy height and the steady state
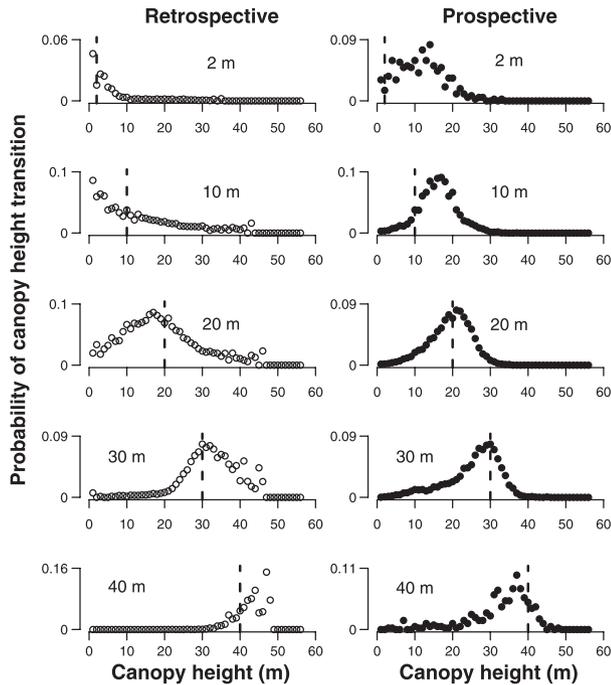
Figure 2 Probabilities of canopy height class transitions in an old-growth tropical rain forest. Data are from columns or rows of a canopy height transition matrix for 444 ha of old-growth tropical rain forest. Right column contains prospective height transition probabilities and left column contains retrospective transition probabilities. These probabilities estimate the likelihood of occupying a future or past height class, given a current height class. Current height classes for each panel are indicated by text labels and vertical dashed lines.

expectation can only decrease through time. We therefore compared the steady-state distribution of canopy height under the recent disturbance regime to the observed height distribution at the beginning of our study in 1997. If these two distributions are similar, it suggests that canopy height at the beginning of the study was consistent with steady-state dynamics. To evaluate the effect of sampling on the projected steady-state distribution, we used a nonparametric bootstrap simulation. Each iteration randomly sampled n height transitions with replacement, where n is equal to the observed number of height transitions in our data ($n = 177\ 750$). We then generated the height transition matrix and calculated the steady-state distribution of canopy height. This procedure was repeated 2000 times to generate a confidence interval for the projected steady-state equilibrium. This analysis assumes that 5 m grid cells have independent height dynamics and that canopy height changes can be modeled by a simple Markov process. That is, the probability of height transition from time t to $t + 1$ is dependent only on the state at time t, but not on previous states. These same assumptions have been made in other analyses of forest dynamics using Markov models (Hubbell & Foster 1986; Hall *et al.* 1991; Tanaka & Nakashizuka 1997; Valverde & Silvertown 1997).

We defined canopy gaps by applying Brokaw's (1982) definition to high-resolution LiDAR imagery. Gaps are openings in the forest canopy extending down to an average height ≤ 2 m above ground (Brokaw 1982). Data from LiDAR are ideal for distinguishing gap vs. non-gap areas, because they minimize the potential for subjective assessments to influence conclusions (see discussion in Clark &

Table 1 An aggregation of the canopy height transition matrix

2006	Canopy height class in 1997									
	< 2	2–5	5–10	10–15	15–20	20–25	25–30	30–35	> 35	n
< 2	**0.061**	0.028	0.008	0.004	0.003	0.002	0.002	0.001	0.000	577
2–5	0.104	**0.079**	0.026	0.013	0.013	0.011	0.008	0.005	0.003	2255
5–10	0.270	0.191	**0.123**	0.082	0.063	0.047	0.036	0.025	0.024	10 321
10–15	0.309	0.374	0.352	**0.272**	0.179	0.111	0.073	0.050	0.036	27 027
15–20	0.190	0.245	0.343	0.395	**0.357**	0.231	0.131	0.079	0.057	45 279
20–25	0.050	0.068	0.116	0.192	0.300	**0.357**	0.263	0.159	0.079	47 448
25–30	0.011	0.012	0.027	0.036	0.076	0.207	**0.342**	0.291	0.162	30 387
30–35	0.006	0.003	0.004	0.004	0.008	0.031	0.132	**0.307**	0.305	11 493
> 35	0.000	0.000	0.001	0.001	0.001	0.002	0.013	0.081	**0.334**	2963
n	538	2739	9475	22 200	42 988	50 127	33 346	12 224	4113	177 750

The study area was 444 ha of terra firme old-growth tropical rain forest at La Selva Biological Station, Costa Rica. Canopy heights were defined as the mean height estimated using light detection and ranging remote sensing within 5×5 m cells ($n = 177\ 750$). Numbers are transition probabilities from the column to row height class over 8.5 years. Diagonal bolded values are the proportion of sites that experienced no net change in height class. Within each column, sites below the diagonal increased in height and sites above the bolded value had height loss. Sample sizes in 1997 and 2006 are shown in the final row and column respectively. The full height transition matrix is in Appendix S1.

Clark 1992) and allow gap definitions to be applied consistently throughout large areas. The smallest gap observable in this study was a 5×5 m cell of 25 m^2 (i.e. a single pixel). Any of its eight neighbours with vegetation height ≤ 2 m were considered part of the same Brokaw gap.

To characterize the frequency distribution of forest canopy gaps, we used a power-law probability distribution. The Zeta distribution is a discrete probability density. If the number of gaps follows a Zeta distribution with parameter λ, the likelihood that gap size equals the integer k is:

$$f(k) = \frac{k^{-\lambda}}{\zeta(\lambda)} \tag{1}$$

where $\zeta(\lambda)$ is the Riemann zeta function and is undefined for $\lambda = 1$. Larger values of λ are associated with disturbance regimes dominated by small canopy openings, whereas smaller values increase the frequency of large events (Fisher *et al.* 2008). Because gap areas in our study cannot take on some integer values (i.e. numbers that are not whole multiples of 25 cannot be observed), we expressed gap area as the number of pixels within each canopy gap. This transformation does not affect the shape of the size-frequency distribution, but does allow correct estimation of the power-law exponent (Edwards *et al.* 2007). This distribution is a discrete analog to the continuous Pareto distribution and is appropriate for modelling the frequency of gaps in our sample (Clauset *et al.* 2007; Edwards *et al.* 2007; Fisher *et al.* 2008; White *et al.* 2008). Because $f(k)$ cannot be solved analytically, we obtained maximum likelihood estimates (MLE) for λ by minimizing the negative log-likelihood function (White *et al.* 2008). Standard errors for λ were calculated using 2000 nonparametric bootstrap samples (Clark 2007).

We evaluated the goodness of fit of the power-law Zeta distribution using 2000 parametric bootstrap simulations. Each simulation generated a distribution of gap sizes under the Zeta distribution with a scaling parameter equal to the MLE from the observed data and sample size equal to the observed sample size. Because the simulated data meet the assumptions of the model, comparison of the observed model likelihood to the distribution of likelihoods from simulated data provides a measure of goodness of fit that is similar to Akaike's information criterion (AIC) (Burnham & Anderson 2002). Smaller values of the negative log likelihood indicate a better fit. If the observed likelihood is significantly larger than the expected value under the simulations, it would suggest a poor fit of the model to the data. We therefore calculated a one-tailed *P*-value by computing the probability of observing a result $\geq$ the observed model likelihood within the 2000 simulations.

We conducted field studies to determine whether data from LiDAR produced results that were consistent with ground-based sampling and to ask whether the frequency distribution of canopy gaps from 0.5 ha plots was representative of landscape forest dynamics. We measured canopy height within 18 0.5 ha plots (Fig. 1). Each plot is 100×50 m, and was randomly sited within old-growth forest but stratified by dominant topographic and fertility gradients (Clark & Clark 2000). Measurements of vegetation height ($\pm$ 1 cm) between 1.50 m and 15.00 m were made on a 5×5 m grid in each plot using a Hastings measuring pole between June and August 2006. At each location on the 5×5 m grid, the height measurement was the maximum vegetation height vertically above the point of measurement. Field technicians visualized a 2×2 m quadrat projected upward to the canopy using a hand-held clinometer. Holes in the forest canopy that were smaller than 2×2 m were treated as closed canopy. Sites with vegetation height outside the measurable range were given discrete classifications (i.e. '< 1.50 m' or '> 15.00 m'). There were 231 height measurements within each 0.5 ha plot and a total of 4158 vegetation height measurements were compared to LiDAR data.

To assess the ability of 0.5 ha plots to obtain unbiased estimates of the gap size frequency distribution, we identified gaps in the forest canopy within each plot using the same criteria applied to LiDAR data. Each site on the 5×5 m field sampling grid within each plot was classified as 'gap' or 'non-gap' based on the point estimate of vegetation height. Sites with field measured vegetation height ≤ 2 m were in Brokaw gaps and adjacent gap sites were part of the same individual gap.

We anticipated that the largest forest gaps might not be represented in 0.5 ha plots (Fearnside 2000; Clark 2004a; Fisher *et al.* 2008). Such an outcome is expected based on the smaller area sampled on the ground (9 ha) compared to the landscape (444 ha), because the largest forest gaps are rare, but could also occur if there is systematic bias between smaller samples and larger spatial scales (Fisher *et al.* 2008). We used simulations to determine whether gap size frequency distributions were significantly different between 0.5 ha plots and the old-growth landscape. Each simulation selected a random sample of *n* Brokaw gaps from the larger number observed using LiDAR in 2006 and estimated the parameter λ of the power-law frequency distribution, where *n* is the number of Brokaw gaps identified within plots using field methods. This process was repeated 2000 times to generate confidence intervals for the expected value of λ under the null hypothesis of no systematic difference between 0.5 ha plots and the old-growth landscape. Because bias should omit the largest forest gaps from plot-based samples, it would produce a larger value for λ in plots relative to the landscape. We therefore computed the one-tailed *P*-value corresponding to the probability of observing a value for λ within the 2000 simulations that is $\geq$ the observed value within plots. The analysis allowed us to test

the hypothesis that the absence of the largest gaps within plots is a sampling artifact. All statistical analyses and simulations were conducted using the R language and environment for statistical computing version 2.7.2 (R Development Core Team, 2008).

RESULTS

Pervasive local height changes figure prominently in the dynamics of this forest (Fig. 2). Thirty-nine percent of the old-growth landscape (173.8 ha) had net height changes > 5 m, of which 18.5% (82.3 ha) were height increases and 20.6% (91.5 ha) height decreases. Most canopy gaps were produced by vegetation below the main canopy and not by taller canopy or emergent trees (Table 1, c.f. values in the first row, i.e. gaps ≤ 2 m in height in 2006, were produced by transitions from lower height classes in 1997). Many height losses were not large enough to form gaps ≤ 2 m after 8.5 years (Table 1, c.f. the relatively high probability of height loss above the diagonal and below the first row). The distribution of canopy height change had *c.* equal numbers of positive and negative transitions and mean change to canopy height between 1997 and 2006 was −0.32 m ± 6.80 SD (Fig. 3).

Less than 1% of the landscape was in Brokaw gaps in both 1997 and 2006. There were 304 gaps within 444 ha of old-growth forest in 1997 and 282 gaps in 2006 (mean gap densities were 0.68 and 0.63 gaps ha^{-1} in 1997 and 2006, Table S1). Gaps were transient features over the 8.5 year study interval. Out of 1.35 ha that were within gaps ≤ 2 m at the beginning of the study, only 0.08 ha were also in gaps after 8.5 years. The remaining 1.26 ha (94%) recruited to higher canopy positions and an additional 1.36 ha of new gaps were formed. Size distributions of gaps identified using LiDAR had medians of 25 m^2 in both years. This is equal to the smallest observable gap size in our data and is commonly observed in gap size frequency distributions (Hubbell & Foster 1986; Fisher *et al.* 2008).

The frequency of gap sizes was well-predicted by a power-law (*P* for 1997 gap sizes = 0.482, *P* for 2006 gap sizes = 0.511, *P* for 2006 field measurements = 0.450, goodness of fit tests based on 2000 bootstrap simulations; Fig. 4). Most gaps in the forest canopy were small (Table S2). Maximum likelihood estimates of λ were 2.34 ± 0.07 (SE), 2.24 ± 0.08 (SE) and 2.68 ± 1.09 (SE) in 1997, 2006 and 2006 field measurements respectively. There were 30 gaps identified within 18 0.5 ha plots using field methods and median gap size was 25 m^2. Comparison of frequency distributions of gaps from field and LiDAR data shows that the proportion of gaps of smaller sizes within plots was representative of their abundance throughout the landscape (Figs. 4, 5), although gaps > 125 m^2 were not represented within field data. However, simulations
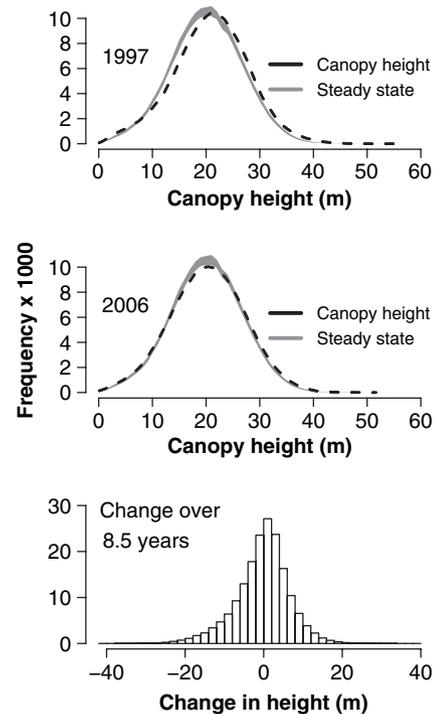

Figure 3 Distributions of canopy height and canopy height change in and old-growth topical rain forest. Dashed lines are the observed distributions of canopy height in 1997 and 2006 using data from light detection and ranging (LiDAR) remote sensing. The shaded region shows the minimum and maximum values for the expected steady-state equilibrium based on the dominant right-hand eigenvector of a height transition matrix and 2000 nonparametric bootstrap simulations. The histogram is the distribution of changes to canopy height from 177,750 observations of net height change over 8.5 years.

demonstrate that the absence of gaps > 125 m^2 within plots is probably a consequence of the smaller area sampled (9 ha vs. 444 ha), rather than systematic bias, because larger gaps are rare within the old-growth landscape and the MLE of the power-law exponent is marginally significantly different between plots and the old-growth landscape in 2006 (one-tailed *P* = 0.069, based on 2000 nonparametric bootstrap samples). No comparison was made between field measurements and 1997 LiDAR data because our plot-based field measurements did not commence until after the 1997 LiDAR data collection.

The dominant right-hand eigenvector of the height transition matrix was similar to the observed distribution of canopy height in 1997 (Fig. 3). Because our analysis is based on two time points, differences between the observed distributions of canopy height and the steady state expectation can only decrease through time (Fig. 3). However, similarity between the distribution of canopy height in 1997 and the steady-state expectation suggests that canopy height at the beginning of our study was consistent with steady-
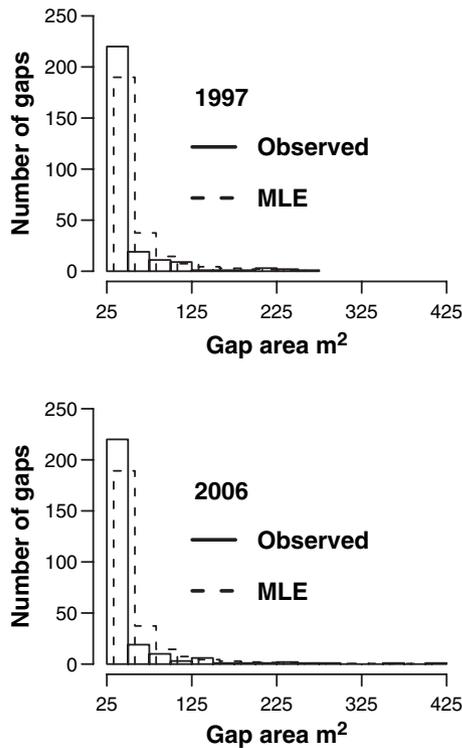
Figure 4 Size frequency distributions of canopy gaps in an old-growth tropical rain forest. The expected number of gaps of each size is indicated by dashed lines, with a small horizontal offset for clarity. Expected values are based on the maximum likelihood estimate for the power-law Zeta distribution fitted to the data and the observed sample size.
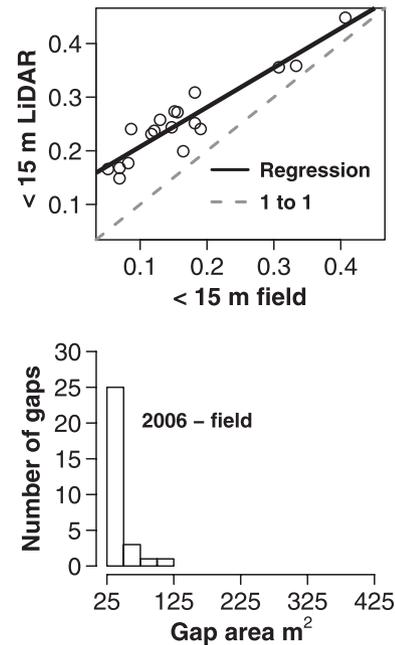

Figure 5 Validation of remote measurements in an old-growth tropical rain forest. The proportion of canopy height measurements < 15.00 m within 18 0.5 ha plots is highly correlated using field measurements and light detection and ranging (LiDAR) remote sensing. Canopy gaps > 125 m² were not represented in plots, but simulations suggest this is an artifact of the smaller area sampled, because larger gaps are rare within the old-growth landscape and the MLE of the power-law exponent is marginally significantly different between plots and the old-growth landscape (one-tailed $P = 0.069$, based on 2000 nonparametric bootstrap samples).

state dynamics. Although absolute differences between the observed distributions of canopy height and the steady-state expectation were small in magnitude, simulations indicate that observed height distributions differed from the steady-state expectation at some canopy positions (Fig. 3). Equilibrium mean canopy height under the recent 8.5-year disturbance regime is 19.6 m ± 6.7 SD, a height loss of 1.3 m from the observed distribution in 1997 and 0.7 m from 2006 (Fig. 3). Height variance was greater in 1997 (7.1 SD) and 2006 (6.9 SD) than the equilibrium expectation (6.7 SD).

Based on a data set of 4184 ground-surveyed control points, the relationship between field and LiDAR estimates of ground elevation is: field measured elevation (m) = 0.999 × LiDAR predicted elevation (m) − 0.406 m, $P_{\text{intercept}} < 0.001$ $P_{\text{slope}} < 0.001$, $r^2 = 0.994$, RMSE = 1.85 m. There was a strong positive relationship between the proportion of vegetation height < 15.00 m identified using LiDAR and field measurements within 18 0.5 ha plots: proportion from LiDAR = 0.134 + 0.737 × proportion from field measurements, $P_{\text{intercept}} < 0.001$ $P_{\text{slope}} < 0.001$, $r^2 = 0.859$, RMSE = 0.027, $n = 18$ (Fig. 5).

DISCUSSION

We used data from airborne LiDAR remote sensing to quantify the structure and dynamics of an old-growth tropical rain forest landscape. These sensors provide spatially detailed measurements of canopy height and ground elevation by recording the return-time of reflected laser pulses and generate opportunities to characterize the dynamics of forest ecosystems on landscapes. Our results demonstrate that pervasive canopy height changes figure prominently in the dynamics of this forest (Fig. 2). Most canopy gaps were produced by vegetation that was shorter than the main canopy layer and not by taller canopy trees, suggesting that repeated disturbance events contribute to formation of gaps ≤ 2 m in height. However, at larger spatial scales (hundreds of ha), size frequency distributions of canopy gaps were similar at two points in time separated by 8.5 years (Fig. 4) and changes to canopy height that were analysed using a height transition matrix demonstrate that the distribution of canopy height at the beginning of our study was close to the steady-state equilibrium expectation (Fig. 3).

Characterizing the distribution of canopy height change on a forested landscape provides insights into the dynamics of disturbance and regeneration at large spatial scales. We developed predictions for the shape of the distribution of canopy height change under three simple scenarios of disturbance and regeneration that could be operating in the Atlantic lowlands of Costa Rica. If the old-growth landscape is recovering from previous disturbance, most height changes would be positive, and the distribution could be right skewed. In contrast, a landscape that has experienced catastrophic disturbance between height measurements could have a left-skewed distribution of canopy height change, as height losses associated with canopy damage and mortality would occur more frequently than increases under this scenario. If changes to canopy height were close to the steady-state equilibrium, height increases and decreases should occur with similar frequency and the distribution would be symmetric with an expected value close to zero. The empirical distribution of changes to canopy height calculated using data from LiDAR over 8.5 years most closely resembled our prediction for steady-state dynamics. Height increases and decreases occurred with similar frequency throughout the old-growth landscape and the mean change to canopy height was − 0.32 m over 8.5 years (Fig. 3).

These findings suggest differences may exist in the dynamics of disturbance and regeneration in the Atlantic lowlands of Costa Rica and elsewhere in the Neotropics, where studies have argued that mortality rates are increasing and biomass accumulating throughout large areas (Phillips & Gentry 1994; Phillips 1998). Our findings and other recent work at this site (Clark *et al.* 2003), suggest that canopy height in the old-growth landscape is close to the projected steady-state equilibrium under the recent disturbance regime. Comparison of the steady-state distribution of canopy height with the observed distribution at the beginning of our study indicates small, though potentially meaningful, differences. If transition probabilities observed over the 8.5-year interval remain similar, subcanopy sites would increase in frequency and mean canopy height would decrease through loss of the tallest forest trees (Fig. 3). This indicates that the tallest trees lost height or died during the 8.5 year study and have not yet been replaced.

There are at least three caveats to our interpretation of canopy height changes. First, the degree of natural variability in canopy dynamics for an old-growth landscape is almost completely unknown. Small but ecologically meaningful changes could be obscured by our data and more frequent or longer term observations may be required to identify significant trends. For example, the observed 0.32 m decrease to mean canopy height between 1997 and 2006 is probably approaching the degree of measurement error in our study. Under ideal conditions, LiDAR height measurements are unbiased and precision is < 15 cm. But old-

growth rain forests on undulating terrain are not ideal conditions. Extensive field studies and comparison of 4184 field measurements of subcanopy ground elevation and 4158 field measurements of canopy height to data from LiDAR demonstrate that LiDAR measurements of ground elevation and canopy height are highly precise and accurate under the range of conditions within old-growth forest in this study, but we lack the capacity to obtain field measurements that are sufficiently more precise than LiDAR data, as well as a process-based sampling model, to fully characterize the consequences of measurement error from two LiDAR systems on our conclusions. Nonetheless, if the observed rate of decrease in canopy height (3.7 cm year^{-1}) continued for several decades, it would have significant impacts on forest structure and carbon balance.

Second, whereas most previous studies of forest dynamics are based on measurements of diameter growth and individuals in permanent inventory plots, our conclusions are from changes to canopy height observed using LiDAR remote sensing. These two approaches may not produce similar inferences if changes to mean canopy height are not associated with productivity as measured by diameter growth. It seems likely that changes to productivity should be associated with canopy dynamics. Positive allometric relationships between tree height, stem diameter and biomass are the basis for inferring above-ground biomass from diameter measurements (Brown 1997; Enquist & Niklas 2001) and numerous remote sensing studies have shown that canopy height can be a strong predictor of field-measured above-ground biomass under a wide range of structural conditions (Lefsky *et al.* 2002; Drake *et al.* 2003).

Third, interpretation of the distribution of canopy height change is sensitive to the timing of previous disturbance. If a severe event produced widespread canopy damage prior to the first census in our study and the landscape were recovering from this disturbance, most sites would increase in height during our transition interval. However, even if a disturbance occurred after the first canopy height census and the landscape were recovering for most of the study, most net height changes could be negative, even though the landscape had been gaining height and is thus regenerating in our terms.

The pervasive local height changes observed in this study were unanticipated based on a classical understanding of the gap disturbance regime (Brokaw 1982, 1985; Hubbell & Foster 1986). We examined properties of a height transition matrix whose elements describe the empirical probability of transition between 1 m column and row height classes. Columns of the transition matrix can be interpreted as prospective height transition probabilities, because they represent the likelihood of occupying future states, given a current height class (Fig. 2). Rows can be interpreted as retrospective projections of height transitions, because they

describe probabilities of occupying past states, given a current height class (Fig. 2). Out of the 3136 height class transitions that were possible, 1788 of them were observed during 8.5 years (Appendix S1). Because these transition probabilities are calculated using net height changes over the study interval, they underestimate the total frequency of height transitions that occurred. For example, for sites > 20 m tall in 1997, the probability of producing a canopy gap ≤ 2 m in height is only 0.005 (Table 1). The true figure is probably higher, as vertical height growth of 1–4 m per year is common in high-light environments at La Selva (Clark & Clark 2001) and small gaps created early in the study interval are likely to have become filled through upward or lateral growth. Nonetheless, canopy gaps were more likely to be produced by vegetation that was shorter than the main canopy layer, rather than by taller canopy trees. This finding is consistent with earlier work at the same site that has shown erratic trajectories characterize upward height growth in juvenile trees (Clark & Clark 2001). Many height changes also occurred in the upper canopy and were not severe enough to form openings that extended to ground level after 8.5 years. Thus, canopy height and canopy height changes are continuously distributed in nature and gaps at ground level are near one extreme in a spectrum of forest dynamics.

This study demonstrates the capacity of LiDAR remote sensing to produce measurements of forest structure and dynamics that are consistent with ground-based field data in a lowland Neotropical rain forest. Our findings show how pervasive canopy dynamics can generate short-term stability in a tropical rain forest landscape. The power of the approach is in its ability to rapidly generate spatially explicit measurements of canopy height that are objectively acquired at large spatial scales. Integration of this technology with long-term field studies will provide insights into the causes and consequences of ongoing global changes to forested landscapes.

REFERENCES

Asner, G.P., Hughes, R.F., Vitousek, P.M., Knapp, D.E., Kennedy-Bowdoin, T., Boardman, J., Martin, R.E., Eastwood, M. & Green, R.O. (2008). Invasive plants transform the three-dimensional structure of rain forests. *Proc. Natl Acad. Sci. USA*, 105, 4519–4523.

Brokaw, N.V.L. (1982). The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica*, 14, 158–160.

Brokaw, N.V.L. (1985). Gap-phase regeneration in a tropical forest. *Ecology*, 66, 682–687.

Brown, S. (1997). Estimating biomass and biomass change of tropical forests: a primer. *Forestry Paper 134*, FAO, Rome.

Burnham, K.P. & Anderson, D.R. (2002). *Model Selection and Multi-Model Inference*. Springer Science + Business Media Inc., New York.

Caswell, H. (2000). *Matrix Population Models: Construction, Analysis, and Interpretation*, 1st edition, Sinauer Associates Inc., Sunderland, MA, USA.

Chambers, J.Q., Fisher, J.I., Zeng, H.C., Chapman, E.L., Baker, D.B. & Hurtt, G.C. (2007). Hurricane Katrina's carbon footprint on U. S. Gulf Coast forests. *Science*, 318, 1107–1107.

Chave, J., Condit, R., Lao, S., Caspersen, J.P., Foster, R.B. & Hubbell, S.P. (2003). Spatial and temporal variation of biomass in a tropical forest: results from a large census plot in Panama. *J. Ecol.*, 91, 240–252.

Chave, J., Condit, R., Muller-Landau, H.C., Thomas, S.C., Ashton, P.S., Bunyavejchewin, S. *et al.* (2008). Assessing evidence for pervasive alteration in tropical tree communities. *PLoS Biol.*, 6, e45. doi:10.1371/journal.pbio.0060045.

Clark, D.A. (2002). Are tropical forests an important carbon sink? Reanalysis of the long-term plot data *Ecol. Appl.*, 12, 3–7.

Clark, D.A. (2004a). Sources or sinks? The responses of tropical forests to current and future climate and atmospheric composition *Philos. Trans. R. Soc. Lond., B, Biol. Sci.*, 359, 477–491.

Clark, D.A. (2004b). Tropical forests and global warming: slowing it down or speeding it up? *Frontiers .Ecol. Environ.*, 2, 73–80.

Clark, J.S. (2007). *Models for Ecological Data*. Princeton University Press, Princeton.

Clark, D.A. & Clark, D.B. (1992). Life-history diversity of canopy and emergent trees in a Neotropical rain-forest. *Ecol. Monogr.*, 62, 315–344.

Clark, D.B. & Clark, D.A. (2000). Landscape-scale variation in forest structure and biomass in a tropical rain forest. *For. Ecol. Manage.*, 137, 185–198.

Clark, D.A. & Clark, D.B. (2001). Getting to the canopy: tree height growth in a neotropical rain forest. *Ecology*, 82, 1460–1472.

Clark, D.A., Piper, S.C., Keeling, C.D. & Clark, D.B. (2003). Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proc. Natl Acad. Sci. USA*, 100, 5852–5857.

Clark, D.B., Castro, C.S., Alvarado, L.D.A. & Read, J.M. (2004a). Quantifying mortality of tropical rain forest trees using high-spatial-resolution satellite data. *Ecol. Lett.*, 7, 52–59.

Clark, D.B., Read, J.M., Clark, M.L., Cruz, A.M., Dotti, M.F. & Clark, D.A. (2004b). Application of 1-M and 4-M resolution satellite data to ecological studies of tropical rain forests. *Ecol. Appl.*, 14, 61–74.

Clark, M.L., Clark, D.B. & Roberts, D.A. (2004c). Small-footprint lidar estimation of sub-canopy elevation and tree height in a tropical rain forest landscape. *Remote. Sens. Environ.*, 91, 68–89.

Clauset, A., Shalizi, C.R. & Newman, M.E.J. (2007). *Power-Law Distributions in Empirical Data*. E-print, http://arxiv.org/abs/0706.1062v1.

Cumming, S.G., Schmiegelow, F.K.A. & Burton, P.J. (2000). Gap dynamics in boreal aspen stands: is the forest older than we think? *Ecol. Appl.*, 10, 744–759.

Drake, J.B., Knox, R.G., Dubayah, R.O., Clark, D.B., Condit, R., Blair, J.B. *et al.* (2003). Above-ground biomass estimation in closed canopy Neotropical forests using lidar remote sensing: factors affecting the generality of relationships. *Glob. Ecol. Biogeogr.*, 12, 147–159.

Edwards, A.M., Phillips, R.A., Watkins, N.W., Freeman, M.P., Murphy, E.J., Afanasyev, V. *et al.* (2007). Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature*, 449, 1044–1048.

Enquist, B.J. & Niklas, K.J. (2001). Invariant scaling relations across tree-dominated communities. *Nature*, 410, 655–660.

Fearnside, P.M. (2000). Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. *Clim. Change.*, 46, 115–158.

Fisher, J.I., Hurtt, G.C., Thomas, R.Q. & Chambers, J.Q. (2008). Clustered disturbances lead to bias in large-scale estimates based on forest sample plots. *Ecol. Lett.*, 11, 554–563.

Hall, F.G., Botkin, D.B., Strebel, D.E., Woods, K.D. & Goetz, S.J. (1991). Large-scale patterns of forest succession as determined by remote sensing. *Ecology*, 72, 628–640.

Hardesty, B.D., Hubbell, S.P. & Bermingham, E. (2006). Genetic evidence of frequent long-distance recruitment in a vertebrate-dispersed tree. *Ecol. Lett.*, 9, 516–525.

Hubbell, S.P. & Foster, R. (1986). Canopy gaps and the dynamics of a neotropical forest. In: *Plant Ecology* (ed. Crawley, M.J.). Blackwell Scientific Publications, Oxford, pp. 77–96.

Jones, F.A., Chen, J., Weng, G.J. & Hubbell, S.P. (2005). A genetic evaluation of seed dispersal in the neotropical tree Jacaranda copaia (Bignoniaceae). *Am. Nat.*, 166, 543–555.

Kennedy, L.M. & Horn, S.P. (2008). A late Holocene pollen and charcoal record from La Selva biological station, Costa Rica. *Biotropica*, 40, 11–19.

Kleber, M., Schwendenmann, L., Veldkamp, E., Rößner, J. & Reinhold, J. (2007). Halloysite versus gibbsite: silicon cycling as a pedogenetic process in two lowland neotropical rain forest soils of La Selva, Costa Rica. *Geoderma*, 138, 1–11.

Körner, C. (2004). Through enhanced tree dynamics carbon dioxide enrichment may cause tropical forests to lose carbon. *Philos. Trans. R. Soc. B. Biol. Sci.*, 359, 493–498.

Lefsky, M.A., Cohen, W.B., Harding, D.J., Parker, G.G., Acker, S.A. & Gower, S.T. (2002). Lidar remote sensing of above-ground biomass in three biomes. *Glob. Ecol. Biogeogr.*, 11, 393–399.

McDade, L.A., Bawa, K.S., Hespenheide, H.A. & Hartshorn, G.S. (eds.) (1994). *La Selva: Ecology and Natural History of a Neotropical Rain Forest*. The University of Chicago Press, Chicago.

Nelson, B.W., Kapos, V., Adams, J.B., Oliveira, W.J., Braun, P.G. & do Amaral, I.L. (1994). Forest disturbance by large blow-downs in the Brazilian Amazon. *Ecology*, 75, 853–858.

Phillips, O.L. (1998). Changes in the carbon balance of tropical forests: evidence from long-term plots. *Science*, 282, 439–442.

Phillips, O.L. & Gentry, A.H. (1994). Increasing turnover through time in tropical forests. *Science*, 263, 954–958.

Phillips, O.L., Malhi, Y., Vinceti, B., Baker, T., Lewis, S.L., Higuchi, N. *et al.* (2002). Changes in growth of tropical forests: Evaluating potential biases. *Ecol. Appl.*, 12, 576–587.

Phillips, O.L., Lewis, S.L., Baker, T.R., Chao, K.J. & Higuchi, N. (2008). The changing Amazon forest. *Philos. Trans. R. Soc. B. Biol. Sci.*, 363, 1819–1827.

R Development Core Team (2008). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at: URL http://www.R-project.org, last accessed 12/04/2008.

Sanford, R.L., Braker, H.E. & Hartshorn, G.S. (1986). Canopy openings in a primary neotropical lowland forest. *J. Trop. Ecol.*, 2, 277–282.

Tanaka, H. & Nakashizuka, T. (1997). Fifteen years of canopy dynamics analyzed by aerial photographs in a temperate deciduous forest, Japan. *Ecology*, 78, 612–620.

Valverde, T. & Silvertown, J. (1997). Canopy closure rate and forest structure. *Ecology*, 78, 1555–1562.

Vepakomma, U., St-Onge, B. & Kneeshaw, D. (2008). Spatially explicit characterization of boreal forest gap dynamics using multi-temporal lidar data. *Remote. Sens. Environ.*, 112, 2326–2340.

White, E.P., Enquist, B.J. & Green, J.L. (2008). On estimating the exponent of power-law frequency distributions. *Ecology*, 89, 905–912.

Wright, S.J. & Calderon, O. (2006). Seasonal, El Nino and longer term changes in flower and seed production in a moist tropical forest. *Ecol. Lett.*, 9, 35–44.

SUPPORTING INFORMATION

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

Table S1 Size frequency distribution of canopy gaps in 1997 and 2006.
Table S2 Cumulative percent of the number of gaps and cumulative percent of the area in gaps.
Appendix S1 Canopy height transition matrix for 444 ha of old-growth tropical rain forest at La Selva, Costa Rica.

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