

Response of an old-growth tropical rainforest to transient high temperature and drought

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Abstract

Tropical rainforests have experienced episodes of severe heat and drought in recent decades, and climate models project a warmer and potentially drier tropical climate over this century. However, likely responses of tropical rainforests are poorly understood due to a lack of frequent long-term measurements of forest structure and dynamics. We analyzed a 12-year record (1999–2010) of 47 817 annual measurements of canopy height to characterize the response of an old-growth Neotropical rainforest to the severe heat and drought associated with the 1997–1998 El Niño. Well-drained soils on slopes and plateaus experienced a threefold increase in the fraction of the landscape in gaps (≤ 2 m) and a reduction in the fraction in high canopy (> 15 m) causing distributions of canopy height to depart from equilibrium for a period of 2–3 years. In contrast, forests on low-lying alluvial terraces remained in equilibrium and were nearly half as likely to experience upper canopy (> 15 m) disturbance over the 12 years of observation. Variation in forest response across topographic positions suggests that tropical rainforests are more sensitive to moisture deficits than high temperature and that topography likely structures landscape-level variation in the severity of drought impacts.

Keywords: canopy, Costa Rica, drought, global change, La Selva, rainforest

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Introduction

The future structure and spatial extent of tropical rainforests will depend crucially on forest sensitivity to changing temperature and precipitation patterns in the tropics (Phillips *et al.*, 2009). The frequency of extreme heat in the tropics has increased in recent decades, and is projected to further increase over this century (Diefenbaugh & Scherer, 2011). Although rainfall projections for some tropical regions are not consistent across models, reduced rainfall is projected in certain regions, such as Central America. Rainfall is expected to remain unchanged or increase in other regions, including tropical Africa and South and East Asia. However, reduced dry season rainfall may accompany increases in annual rainfall in some regions, such as South Asia. (Christensen *et al.*, 2007). Ongoing deforestation in the tropics is expected to exacerbate temperature increases and precipitation declines (Costa & Foley, 2000) because evapotranspiration from rainforest canopies reduces local surface temperatures (Shukla *et al.*, 1990) and is a substantial source of rainfall in tropical rainforests (Eltahir & Bras, 1994).

Results from coupled climate-carbon cycle models indicate that a warmer, drier tropical climate could lead

to the decline and eventual replacement of tropical evergreen rainforest by seasonal forest (Malhi *et al.*, 2009) or tropical savanna (Cox *et al.*, 2000; Salazar *et al.*, 2007). However, the assumptions concerning forest sensitivity to climatic factors that underlie these projections remain largely untested against field data. This is in part due to the complexity of the physiological and demographic mechanisms that mediate forest response to high temperature and drought. Higher temperatures increase both photosynthesis and respiration, resulting in uncertain net impacts on overall carbon gain (Saxe *et al.*, 2001). Reductions in rainfall decrease tree growth (Nepstad *et al.*, 2002) and increase tree respiration (Metcalf *et al.*, 2010) and mortality (Nepstad *et al.*, 2007). Furthermore, increased evapotranspiration associated with higher temperatures can exacerbate the impacts of reduced rainfall. On the other hand, reduced rainfall could increase plant growth by reducing cloud cover and light limitation (Graham *et al.*, 2003). The net impact of these competing effects at the landscape scale is difficult to predict a priori.

Field studies following El Niño-related droughts in 1998 and 2005 indicate tropical rainforests are vulnerable to water stress with forests experiencing reductions in estimated aboveground biomass (Rolim *et al.*, 2005; Phillips *et al.*, 2009) and increases in tree mortality (Williamson *et al.*, 2000; Phillips *et al.*, 2010). Nepstad *et al.* (2007) conducted a rainfall exclusion experiment

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in the Amazon, excluding 60% of incoming wet season throughfall from treatment plots over a 4-year period. These plots experienced an increase in the mortality of large trees and lianas (Nepstad *et al.*, 2007) and a decrease in canopy water content (Asner *et al.*, 2004) and aboveground net primary production (Nepstad *et al.*, 2002) relative to control plots. Furthermore, remote sensing studies indicate that the widespread 2005 drought in the Amazon increased canopy water stress, probably as a result of reduced night-time water recharge due to soil moisture deficits (Frolking *et al.*, 2011; Saatchi *et al.*, 2013). Nonetheless, the impacts of increased mortality and reduced canopy water content and aboveground biomass on rainforest structure remain unknown. To date, no study has examined the response of forest structure to severe heat and drought using an extended time series of annual field measurements with representative sampling across key physical gradients known to impact plant function, such as soil type and topography.

Here, we characterize the impact of high temperature and drought associated with the 1997–1998 El Niño on forest structure and dynamics at La Selva Biological Station in the Atlantic Lowlands of Costa Rica. The 135-year record of the multivariate ENSO (El Niño–Southern Oscillation) index indicates that the 1997–1998 El Niño was the first or second most severe since 1871 (Wolter & Timlin, 2011). Record high temperatures and record low dry season (January–April) rainfall in 1998 (OTS meteorological data, <http://www.ots.ac.cr/>) caused the largest dry season soil moisture deficit observed in the 14-year record at La Selva (D. A. Clark and S. F. Oberbauer, unpublished data). We used >45 000 annual canopy height measurements acquired over 12 years of observation (1999–2010) to generate canopy height transition matrices and project equilibrium distributions of canopy height. Our methods allowed us to address the following questions concerning forest response to high temperature and drought: (i) Did severe hot and dry conditions in 1997–1998 cause the distribution of canopy height at La Selva to depart from the forest's equilibrium distribution? (ii) How quickly did the distribution of canopy height recover to equilibrium? (iii) Did the magnitude of departure from equilibrium and the rate of recovery differ across edaphic conditions?

Materials and methods

We used annual measurements of canopy height from 18 0.5 ha plots to characterize canopy dynamics in a Neotropical rainforest in the Atlantic lowlands of Costa Rica. The study site, located at the La Selva Biological Station, encompasses flat alluvial terraces and deeply weathered oxisols on undulating

terrain. Plots were sited randomly within old-growth forest and were stratified by edaphic conditions with six plots each sited on alluvial terraces, oxisol slopes, and oxisol plateaus (Clark & Clark, 2000). We measured canopy height (± 1 cm) between 1.50 m and 15.00 m aboveground on a 5×5 m grid in each plot annually between 1999 and 2010 using a Hastings 15 m extendable measuring pole (Hastings Fiber Glass Products, Hastings, Michigan, USA). At each location, we measured the height of the tallest vegetation within a 2×2 m quadrat directly above each grid point. Heights outside the measurable range were recorded as <1.5 m or >15 m. Openings in the canopy smaller than 2×2 m were treated as closed canopy. Each measurement was assumed to represent a height estimate for the 5×5 m cell centered on each grid point. An equivalent assumption is implicit in all sampling-based landscape models, such as canopy height and digital elevation models, as point estimates are taken to represent estimates for larger area grid cells.

Annual height measurements were acquired across plots in the same sequence during January–June to ensure approximately 1-year intervals between censuses (mean interval between midpoint of censuses was 365 ± 13 days). Within each 0.5 ha plot (100×50 m), there were 231 height measurements acquired each year. Summed across all 18 plots there were 4158 height measurements in each year except 1999, during which only nine of the plots were sampled. Thus, the analyses described below are based on 47 817 measurements of vegetation height over 12 years. We assessed the precision of height measurements annually by acquiring replicate measurements on two consecutive days at an average of 109 locations. Of 389 replicate measurements <15 m on both days, 317 (95.6%) were within <1 m of each other. Of 915 replicate measurements >15 m on one of the two consecutive days, 904 (98.8%) were >15 m on both days. Lastly, all trees (≥ 10 cm in diameter) in each plot were marked, mapped, and censused annually until confirmed to be dead in successive censuses. During each census, we recorded the number of newly recruited and dead individuals (≥ 10 cm in diameter) in each plot. Details on diameter measurements are given in Clark and Clark (1999).

We defined gaps in the forest canopy using Brokaw's (1982) definition. Gaps were areas where the height of the tallest vegetation was ≤ 2 m aboveground. We used the binomial distribution to construct confidence intervals on the number of grid cells in new canopy gaps in each year. The binomial parameter p_t determines the respective probabilities of two possible outcomes at each grid cell. A new gap can form with probability p_t , or no new gap forms (i.e., the vegetation height remains >2 m) with probability $1-p_t$. Simply stated, p_t represents the probability that vegetation height within a grid cell will decline to ≤ 2 m during year t . We estimated p_t as the ratio of the number of grid cells in new gaps to the number of grid cells that could become gaps in each year (i.e., we excluded from the denominator grid cells that were already in gaps in the previous year $t-1$).

To characterize the size frequency distribution of canopy gaps, we used a power-law probability distribution. Specifically, we used the Zeta distribution, which is a discrete probability density. We determined the size of new canopy gaps

based on the number of adjacent grid cells (including diagonally touching grid cells) with canopy height ≤ 2 m in year t and height > 2 m in the previous year. The smallest observable gap size corresponded to one 25 m² grid cell. Therefore, we defined size classes for new canopy gaps as integer multiples of this minimum gap size (e.g., 25 m², 50 m², 75 m², etc.). If the number of gaps in each size class follows a Zeta distribution with parameter k , the likelihood that gap size equals the integer k is: $f(k) = k^{-\lambda}/\zeta(\lambda)$, where $\zeta(\lambda)$ is the Riemann zeta function and is undefined for $\lambda = 1$. Larger values of λ give distributions dominated by small canopy openings, whereas smaller values increase the frequency of large canopy openings (Fisher *et al.*, 2008). The Zeta distribution is a discrete analog to the continuous Pareto distribution and is appropriate for modeling the frequency of gap sizes in our study (Fisher *et al.*, 2008; White *et al.*, 2008). Because $f(k)$ cannot be solved analytically, we obtained maximum likelihood estimates for λ by minimizing the negative log-likelihood function of the Zeta distribution. Standard errors for λ were calculated using 100 000 nonparametric bootstrap samples (Clark, 2007).

To quantitatively assess canopy dynamics over the 12-year period, we compared the observed distribution of canopy height in each year to the distribution expected in equilibrium. The equilibrium distribution of canopy height is the height distribution a canopy would achieve if the probabilities in the canopy height transition matrix were to remain constant indefinitely. Although changes in canopy height occur in equilibrium, the fraction of the landscape in each height class remains unchanged. The expected equilibrium distribution is given by the dominant right-hand eigenvector of the canopy height transition matrix. Each cell of this 15 × 15 matrix gives the probability of a grid cell transitioning from the column height class to the row height class. The first row and column of the matrix correspond to the ≤ 2 m height class (i.e., gaps). The last row and column correspond to the >15 m height class, which we call ‘high/upper canopy.’ Intermediate rows and columns represent 1 m vertical increments in canopy height between 2 m and 15 m aboveground.

We computed canopy height transition matrices for each annual time step between 1999 and 2010 based on the observed height transitions between years. We also computed matrices based on height transitions pooled across all years. Our analysis indicated that there was a single equilibrium distribution of canopy height for each edaphic site-type over the 12 years of observation. We evaluated this hypothesis by comparing the equilibrium distributions of canopy height computed for each annual time step between 1999 and 2010 for each edaphic site-type. These steady-state distributions did not differ significantly across years (Fig. S1), indicating that the equilibrium distribution of canopy height for each edaphic site-type could be defined using a single matrix with height transitions pooled across all years. Table 1 shows the pooled canopy height transition matrix for alluvial terraces. Pooled height transition matrices for oxisol slopes and plateaus are available in the Supporting Information (Tables S1–S2). We used these pooled transition matrices to derive the equilibrium distributions of canopy height for each edaphic site-type.

Traditional approaches estimate probabilities in the canopy height transition matrix by dividing the number of transitions

Table 1 Canopy height transition matrix for alluvial terraces.

| | ≤ 2 m | 2–3 m | 3–4 m | 4–5 m | 5–6 m | 6–7 m | 7–8 m | 8–9 m | 9–10 m | 10–11 m | 11–12 m | 12–13 m | 13–14 m | 14–15 m | >15 m |
|------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| ≤ 2 m | 0.333 | 0.029 | 0.075 | 0.029 | 0.000 | 0.035 | 0.011 | 0.012 | 0.033 | 0.009 | 0.009 | 0.000 | 0.000 | 0.005 | 0.003 |
| 2–3 m | 0.098 | 0.114 | 0.075 | 0.014 | 0.025 | 0.012 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.005 | 0.001 |
| 3–4 m | 0.041 | 0.229 | 0.075 | 0.043 | 0.025 | 0.000 | 0.011 | 0.000 | 0.022 | 0.009 | 0.000 | 0.000 | 0.000 | 0.000 | 0.001 |
| 4–5 m | 0.089 | 0.029 | 0.175 | 0.314 | 0.062 | 0.012 | 0.000 | 0.000 | 0.000 | 0.019 | 0.026 | 0.000 | 0.000 | 0.000 | 0.001 |
| 5–6 m | 0.057 | 0.086 | 0.000 | 0.200 | 0.259 | 0.081 | 0.044 | 0.036 | 0.022 | 0.037 | 0.000 | 0.000 | 0.000 | 0.005 | 0.001 |
| 6–7 m | 0.016 | 0.086 | 0.025 | 0.071 | 0.111 | 0.174 | 0.110 | 0.036 | 0.011 | 0.056 | 0.017 | 0.000 | 0.007 | 0.005 | 0.002 |
| 7–8 m | 0.008 | 0.029 | 0.000 | 0.014 | 0.099 | 0.198 | 0.154 | 0.048 | 0.011 | 0.046 | 0.009 | 0.000 | 0.013 | 0.000 | 0.002 |
| 8–9 m | 0.008 | 0.000 | 0.025 | 0.029 | 0.049 | 0.070 | 0.143 | 0.202 | 0.011 | 0.046 | 0.000 | 0.000 | 0.007 | 0.005 | 0.002 |
| 9–10 m | 0.033 | 0.000 | 0.000 | 0.029 | 0.025 | 0.023 | 0.066 | 0.190 | 0.211 | 0.074 | 0.043 | 0.000 | 0.013 | 0.000 | 0.002 |
| 10–11 m | 0.016 | 0.029 | 0.050 | 0.014 | 0.025 | 0.023 | 0.099 | 0.012 | 0.233 | 0.204 | 0.061 | 0.045 | 0.033 | 0.014 | 0.001 |
| 11–12 m | 0.008 | 0.000 | 0.050 | 0.029 | 0.062 | 0.000 | 0.066 | 0.024 | 0.111 | 0.157 | 0.183 | 0.107 | 0.013 | 0.023 | 0.002 |
| 12–13 m | 0.000 | 0.000 | 0.000 | 0.014 | 0.000 | 0.012 | 0.000 | 0.012 | 0.022 | 0.056 | 0.157 | 0.250 | 0.132 | 0.055 | 0.002 |
| 13–14 m | 0.016 | 0.000 | 0.075 | 0.029 | 0.012 | 0.047 | 0.044 | 0.048 | 0.011 | 0.028 | 0.113 | 0.125 | 0.199 | 0.110 | 0.004 |
| 14–15 m | 0.024 | 0.000 | 0.025 | 0.043 | 0.049 | 0.012 | 0.011 | 0.060 | 0.044 | 0.037 | 0.052 | 0.161 | 0.172 | 0.292 | 0.006 |
| >15 m | 0.252 | 0.371 | 0.350 | 0.129 | 0.198 | 0.302 | 0.242 | 0.321 | 0.256 | 0.222 | 0.330 | 0.313 | 0.411 | 0.484 | 0.969 |

Diagonal values in bold are the probabilities of experiencing no change in height. Values below the diagonal represent height increases. Values above the diagonal represent height decreases. Numbers are the transition probabilities from the column to row height class based on observed transitions pooled across all years (1999–2010)

in each cell of the matrix by the column total (e.g., Valverde & Silvertown, 1997; Caswell, 2001; Kellner *et al.*, 2009). We depart from this traditional approach and use a Bayesian statistical framework for three reasons. First, Bayesian methods allow us to quantify uncertainty in height transition probabilities and to propagate this uncertainty through our computations of the projected steady-state equilibrium. Second, using this approach, it is straightforward to handle differences in sample sizes between years (i.e., between 1999, when only half of the plots were sampled, and subsequent years). Third, the Bayesian approach provides a method for handling zero-valued elements that are present in height transition matrices (e.g., Kellner *et al.*, 2009). Zeros in a canopy height transition matrix indicate that no transitions occurred for particular column and row combinations over the period of observation. However, the probability of such height transitions occurring is unlikely to be zero in all cases. Within a Bayesian framework, we can estimate transition probabilities for these zero-valued elements. In all three cases, the advantage of the Bayesian approach over traditional analyses is the ability to evaluate uncertainty in observed transition probabilities, and therefore in the projected equilibrium distributions of canopy height.

We assumed observed transitions from a given height class to all 15 height classes followed a multinomial distribution. The multinomial gives the number of events expected in each of k possible categories (i.e., height classes) over n independent trials given a probability p_k corresponding to each category k . The conjugate prior for a multinomial likelihood is the Dirichlet distribution (Clark, 2007). We assumed an uninformative Dirichlet prior, which assigns equal probability $1/k$ of transitioning from a given column height class to each row height class. This uninformative prior allows the observed height transitions to drive the estimation of the posterior transition probabilities, which make up the columns of the canopy height transition matrix.

To determine whether height classes were in steady-state equilibrium, we compared the observed and equilibrium fractions of the landscape in each height class over the 12-year period (1999–2010). Observed and equilibrium distributions of canopy height are not statistically independent, because observed heights are used to calculate height transitions, and these height transitions determine the projected equilibrium. Therefore, to reduce dependence between observed and equilibrium distributions, we estimated the distributions from separate random plot samples by bootstrapping over the 18 0.5 ha plots. We drew 10 000 random samples of half of the plots within each edaphic site-type to compute the observed fraction of the landscape in each height class, and used the remaining half of plots within each edaphic site-type to estimate transition probabilities from which we compute the projected equilibrium fraction of the landscape in each height class. Therefore, our comparisons of observed and equilibrium height distributions are based on 10 000 statistically independent bootstrap samples. Because three of the six plots within each edaphic site-type lacked height measurements in 1999, we forced each random plot sample to include at least one plot with measurements from 1999. We summarized variability across the 10 000 bootstrap samples by computing

the median and the 95% Bayesian credible intervals for the observed and equilibrium fractions of the landscape in each height class.

We used ordinary least-squares regression to examine the influence of temperature and rainfall on departures from the equilibrium distribution of canopy height. Within each height class, we used the 10 000 bootstrap samples over the period 1999–2010 to regress differences between the observed and equilibrium fractions (O–E) within each height class on a set of five temperature and rainfall variables measured daily at La Selva: annual and dry season (January–April) rainfall and mean annual daily temperature, mean annual minimum daily temperature, and mean annual maximum daily temperature. Mean minimum and maximum temperature values reflect the mean of all daily minima and maxima recorded over the course of each year. Because our canopy height record begins 1 year after the anomalous heat and drought of 1998, we conducted regressions with and without a 1-year lag in the temperature and rainfall variables.

To determine whether transition probabilities differed among edaphic site-types, we made pairwise comparisons (alluvial terraces – oxisol slopes, alluvial terraces – oxisol plateaus, and oxisol slopes – oxisol plateaus) in the above and below diagonal elements of the canopy height transition matrices (Table 1, Tables S1–S2). Values in the matrix below the diagonal represent the probabilities of transitioning from a lower to a taller height class (i.e., growth), and values above the diagonal represent the probabilities of transitioning from a taller to a lower height class (i.e., disturbance). Because equilibrium distributions of canopy height depend solely on the values in the canopy height transition matrix, differences in transition probabilities above or below the diagonal indicate whether differences in equilibrium distributions are likely due to growth or disturbance. We conducted all analyses using the R programming environment for statistical computation version 2.14.1 (R Development Core Team, 2012).

Results

There were 232 new gaps formed during the 2000–2010 interval, excluding gaps that already existed in 1999, the first year of our study. Because gaps in our study are represented by 25 m² cells centered on each grid point, the area of forest in new gaps at least once during our study was 5800 m². This represents 6.4% of the 9 ha sample and corresponds to an average annual gap formation rate of 527 m² yr⁻¹ (0.59% yr⁻¹). The annual fraction of the landscape in gaps varied threefold over the duration of the study (Table 2). The fraction in gaps was greatest in 1999 (3.6% ± 0.42, 95% CI = 2.90–4.50%), decreased to 1.2% (±0.18, 95% CI = 0.92–1.60%) by 2001, and remained approximately ≤1% for the duration of the study. The fraction of the landscape in high canopy was lowest in 1999 (77.1% ± 0.94, 95% CI = 75.19–78.97%), increased to 83.6% (±0.58, 95% CI = 82.44–84.71%) by 2001, and remained above 80% for the remainder of the study (Table 2). Mortality

Table 2 Classification of canopy height over 12 years of observation (1999–2010)

| | 1999 | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 |
|-----------------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Gap (≤ 2 m) | | | | | | | | | | | | |
| Alluvial Terrace | 0.023 | 0.017 | 0.014 | 0.010 | 0.004 | 0.009 | 0.009 | 0.004 | 0.006 | 0.002 | 0.002 | 0.003 |
| Oxisol Plateau | 0.045 | 0.038 | 0.012 | 0.010 | 0.006 | 0.004 | 0.017 | 0.005 | 0.002 | 0.004 | 0.003 | 0.002 |
| Oxisol Slope | 0.040 | 0.025 | 0.010 | 0.012 | 0.009 | 0.007 | 0.006 | 0.008 | 0.004 | 0.012 | 0.009 | 0.005 |
| Total | 0.036 | 0.026 | 0.012 | 0.011 | 0.006 | 0.007 | 0.011 | 0.006 | 0.004 | 0.006 | 0.005 | 0.003 |
| Intermediate (2–15 m) | | | | | | | | | | | | |
| Alluvial Terrace | 0.117 | 0.089 | 0.069 | 0.071 | 0.068 | 0.084 | 0.100 | 0.104 | 0.083 | 0.098 | 0.100 | 0.084 |
| Oxisol Plateau | 0.185 | 0.214 | 0.202 | 0.229 | 0.224 | 0.233 | 0.251 | 0.253 | 0.215 | 0.227 | 0.201 | 0.168 |
| Oxisol Slope | 0.263 | 0.173 | 0.174 | 0.163 | 0.136 | 0.146 | 0.139 | 0.139 | 0.120 | 0.123 | 0.111 | 0.115 |
| Total | 0.188 | 0.159 | 0.148 | 0.154 | 0.143 | 0.154 | 0.163 | 0.165 | 0.139 | 0.150 | 0.137 | 0.123 |
| High canopy (>15 m) | | | | | | | | | | | | |
| Alluvial Terrace | 0.860 | 0.894 | 0.916 | 0.918 | 0.928 | 0.907 | 0.892 | 0.892 | 0.911 | 0.900 | 0.898 | 0.913 |
| Oxisol Plateau | 0.771 | 0.748 | 0.786 | 0.761 | 0.770 | 0.763 | 0.732 | 0.742 | 0.783 | 0.769 | 0.797 | 0.830 |
| Oxisol Slope | 0.697 | 0.802 | 0.816 | 0.825 | 0.856 | 0.847 | 0.855 | 0.854 | 0.877 | 0.864 | 0.880 | 0.880 |
| Total | 0.776 | 0.815 | 0.839 | 0.835 | 0.851 | 0.839 | 0.826 | 0.829 | 0.857 | 0.844 | 0.858 | 0.874 |

Values indicate the fraction of the landscape in high canopy (>15 m), intermediate canopy (2–15 m), and gaps (≤ 2 m).

Table 3 Annual new gap formation

| | 2000 | 2001 | 2002 | 2003 | 2004 | 2005 | 2006 | 2007 | 2008 | 2009 | 2010 |
|------------------|------------|------------|------------|-----------|------------|------------|-----------|----------|------------|-----------|-----------|
| Alluvial Terrace | 7 (3–14) | 13 (8–22) | 6 (3–13) | 3 (1–9) | 10 (6–18) | 5 (2–12) | 3 (1–9) | 5 (2–12) | 3 (1–9) | 2 (1–7) | 4 (2–10) |
| Oxisol Plateau | 14 (8–23) | 9 (5–17) | 13 (8–22) | 3 (1–9) | 5 (2–12) | 21 (14–31) | 1 (0–6) | 1 (0–6) | 5 (2–11) | 1 (0–6) | 3 (1–9) |
| Oxisol Slope | 11 (6–19) | 11 (6–19) | 14 (8–23) | 6 (3–13) | 8 (4–16) | 6 (3–13) | 7 (3–14) | 3 (1–9) | 16 (10–26) | 8 (4–16) | 5 (2–12) |
| Total | 32 (22–44) | 33 (23–46) | 33 (23–46) | 12 (7–21) | 23 (15–34) | 32 (22–45) | 11 (6–20) | 9 (5–17) | 24 (16–35) | 11 (6–20) | 12 (7–21) |

Values indicate the number of new grid cells with canopy height ≤ 2 m in each year. Numbers in parentheses indicate the 95% confidence interval for annual gap formation based on a binomial distribution and uninformative prior (Supporting Information).

across all 18 plots was 62.1% higher in 1998 ($3.81\% \pm 0.29$, 95% CI = 3.28–4.39%) and 36.2% higher in 1999 ($3.20\% \pm 0.26$, 95% CI = 2.69–3.74%) relative to the mean ($2.35\% \pm 0.23$, 95% CI = 1.93–2.83%) over the subsequent decade (2000–2009; Table S3). Mortality in 1998 was higher on oxisol slopes and plateaus (oxisol slopes: $4.26\% \pm 0.49\%$, 95% CI = 3.35–5.29%; oxisol plateaus: $5.13\% \pm 0.56\%$, 95% CI = 4.1–6.3%) than alluvial terraces ($1.64\% \pm 0.36\%$, 95% CI = 1.02–2.43%), although mortality was statistically equivalent across site-types in nearly all subsequent years.

The frequency of canopy disturbance also varied by edaphic site-type. The fraction of the landscape that experienced net negative change in height over the 12 years of observation was lower on alluvial terraces ($7.65\% \pm 0.71$, 95% CI = 6.37–9.19) than on oxisol slopes ($10.61\% \pm 0.83$, 95% CI = 9.07–12.34) and plateaus ($12.55\% \pm 0.89$, 95% CI = 10.89–14.40). A larger fraction of the landscape remained in high canopy (>15 m) over the duration of the study on alluvial terraces ($71.57\% \pm 1.20$, 95% CI = 69.03–73.76) than on

oxisol slopes ($54.11\% \pm 1.34$, 95% CI = 51.41–56.68) and plateaus ($47.04\% \pm 1.33$, 95% CI = 44.38–49.58). Comparing transition probabilities across edaphic site-types indicated that the probability of transitioning out of the high canopy to lower height classes was higher on oxisol slopes and plateaus than on alluvial terraces (Table S4). There were no significant differences among edaphic site-types in height transition probabilities associated with lower canopy disturbance (i.e., among canopy positions <15 m in height) and few differences associated with growth (Table S4).

Although the frequency of disturbance depended on edaphic conditions, the annual fraction of the landscape in new canopy gaps was not statistically different across edaphic conditions (Table 3; Fig. S2). Fitting the discrete Pareto distribution to size frequency distributions of new canopy gaps indicated that gap size frequency distributions were also not statistically different among edaphic site-types (alluvial terraces: $\lambda = 2.94 \pm 0.35$, 95% CI = 2.32–3.68, oxisol plateaus: $\lambda = 3.02 \pm 0.32$, 95% CI = 2.45–3.72, oxisol slopes: $\lambda = 2.81 \pm 0.25$, 95%

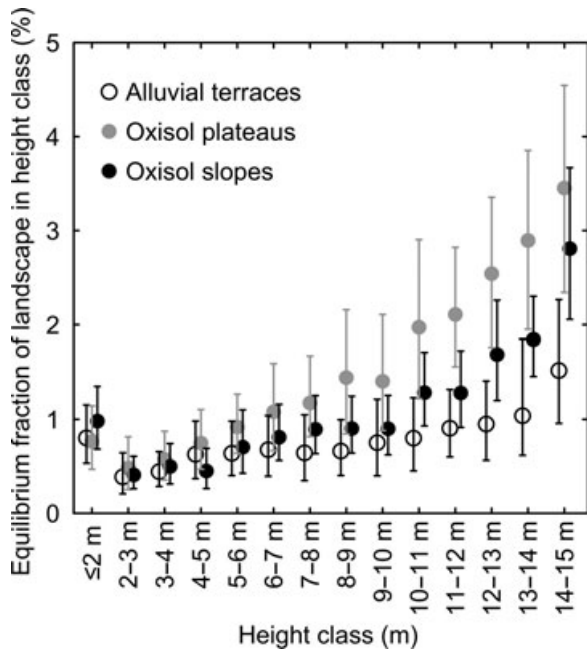


Fig. 1 Equilibrium fraction of the landscape in each height class, excluding high canopy (>15 m), for alluvial terraces (open circles), oxisol plateaus (gray), and oxisol slopes (black). Error bars show the 95% confidence interval from 10 000 bootstrap samples.

CI = 2.37–3.36). The maximum likelihood estimate of $\lambda \approx 3$ for all edaphic site-types indicates that disturbance events were typically small in area. The mean size of new canopy gaps was 33 m².

However, equilibrium distributions of canopy height depended on edaphic conditions. At intermediate canopy positions (6–15 m aboveground), the projected equilibrium fractions in each height class were largest on oxisol plateaus, intermediate on oxisol slopes, and smallest on alluvial terraces (Fig. 1). Differences in equilibrium high canopy (>15 m) cover were more pronounced, but the rank order was reversed. The equilibrium fraction of the landscape in high canopy was greatest on alluvial terraces (88.93% ± 1.73, 95% CI = 85.31–91.91), followed by oxisol slopes (84.44 ± 1.39, 95% CI = 81.55–86.89) and oxisol plateaus (78.34 ± 3.14, 95% CI = 72.13–83.98). In short, equilibrium distributions on alluvial terraces had a larger fraction of the landscape in high canopy (>15 m) relative to oxisol slopes and plateaus and a smaller fraction in intermediate height classes (6–15 m). Excluding years potentially impacted by the 1997–1998 El Niño from the computation of equilibrium distributions does not substantially alter predicted equilibrium distributions (Fig. S3). Using all 12 years of height transition data represents a conservative estimate of the equilibrium for each edaphic site-type. Departures from this

conservative equilibrium prediction are therefore more likely to reflect real departures rather than random noise or departures due to a particular selection of years.

Observed distributions of canopy height were in equilibrium for the majority of the 12 years of observation on all three edaphic site-types. However, transient departures from equilibrium occurred in 1999, and the magnitude of departure depended on edaphic site-type (Figs 2 and 3). Height classes on oxisol slopes and plateaus departed from equilibrium values for a period of 2–3 years beginning in 1999 (Fig. 2). In contrast, observed distributions on alluvial terraces remained in equilibrium for the duration of the study. Departures from equilibrium on oxisol slopes and plateaus occurred in the gap height class (≤2 m) and the tallest two height classes (14–15 m and >15 m). In 1999, the fraction of the landscape in gaps was higher relative to equilibrium on both oxisol slopes [observed (%)–equilibrium (%) = 3.20% ± 1.69, 95% CI = 0.59–6.58%] and plateaus (3.72% ± 0.53, 95% CI = 2.64–4.77%; Fig. 3). The fraction of the landscape in high canopy (>15 m) in 1999 was lower relative to equilibrium on oxisol slopes (–15.53% ± 6.14, 95% CI = –5.24 to –27.46%), whereas the fraction in the 14–15 m height class was lower relative to equilibrium on oxisol plateaus (–2.56% ± 0.74, 95% CI = –1.22 to –4.02%; Fig. 3).

Departures from equilibrium were correlated with the previous year's dry season rainfall and mean annual minimum daily temperature across the three edaphic site-types (Fig. 4). Larger departures from equilibrium (observed–equilibrium) were associated with higher minimum daily temperature (≤2 m height class: intercept = –13.84, slope = 0.677, $P < 0.001$; >15 m height class: intercept = 42.17, slope = –2.05, $P < 0.001$); and lower dry season rainfall (≤2 m height class: intercept = 1.76, slope = –0.00153, $P < 0.001$; >15 m height class: intercept = –4.25, slope = 0.00379, $P < 0.001$). These relationships depended entirely on observations associated with the hot and dry El Niño year (Fig. 4). If temperature and rainfall observations from 1998 and the associated departures from equilibrium in 1999 were excluded, the regression lines were flat. Departures from equilibrium were uncorrelated with lagged total annual rainfall, lagged mean annual daily temperature, lagged mean annual maximum daily temperature, and all nonlagged temperature and rainfall observations (Fig. S4).

Discussion

Previous field studies have demonstrated that high temperature and drought increase mortality and decrease growth (Nepstad *et al.*, 2002; Clark *et al.*, 2003,

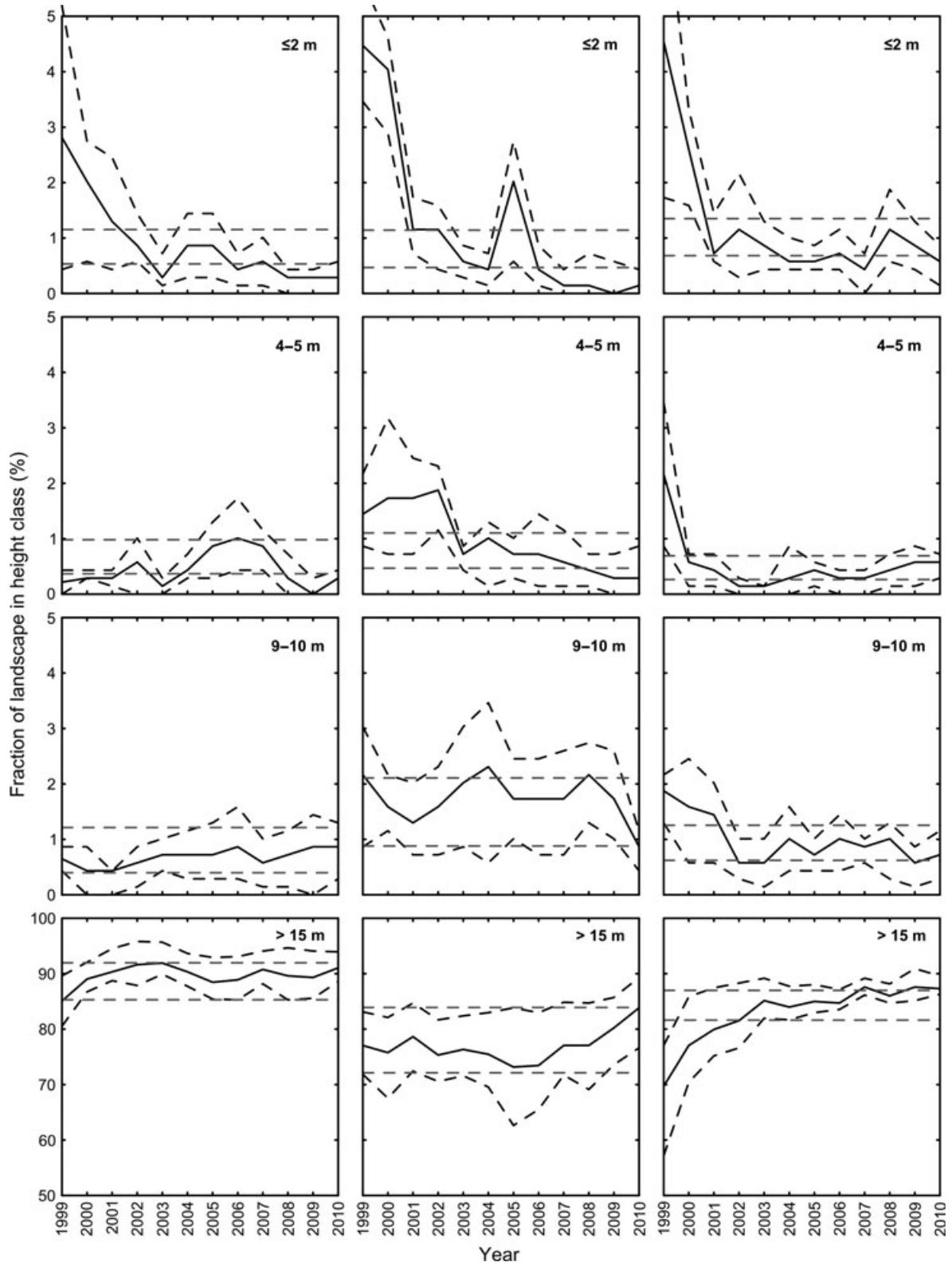


Fig. 2 Observed and equilibrium distributions of canopy height for alluvial terraces (left), oxisol plateaus (center), and oxisol slopes (right). Dashed lines show the 95% confidence interval on the observed (black) and equilibrium (gray) fractions of the landscape in each height class. Solid black lines show the median estimate of the observed fraction of the landscape in each height class from 10 000 bootstrap samples.

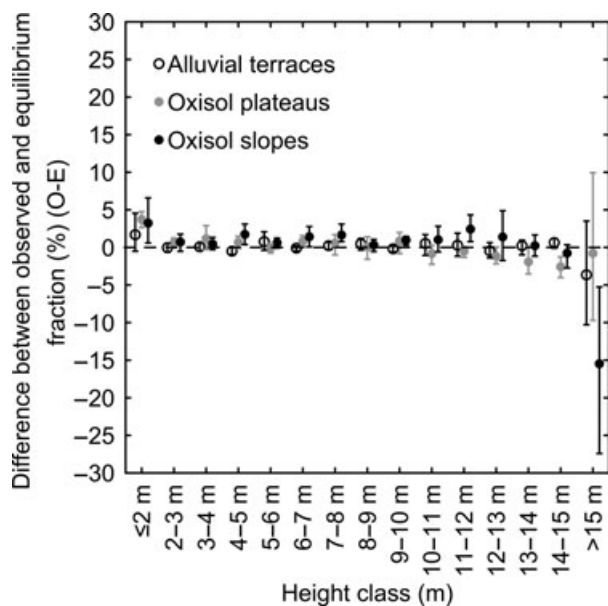


Fig. 3 Departure from equilibrium fraction [observed (%)–equilibrium (%)] of the landscape in each height class in 1999 for alluvial terraces (open circles), oxisol plateaus (gray), and oxisol slopes (black). Error bars show the 95% confidence interval from 10 000 bootstrap samples.

2010) and aboveground biomass (Nepstad *et al.*, 2002; Rolim *et al.*, 2005; Phillips *et al.*, 2009) in tropical rainforests. Satellite measurements further indicate that the severe 2005 drought in the Amazon reduced canopy water content throughout the basin (Frolking *et al.*, 2011; Saatchi *et al.*, 2013). Such findings underlie projections of rainforest decline under a warmer, potentially drier tropical climate. However, the impacts of heat and moisture stress on the structure of tropical rainforests are not well understood. This uncertainty persists in part due to a lack of long-term measurements of tropical rainforest dynamics with representative sampling across key physical gradients.

We analyzed >47 000 annual measurements of canopy height during 1999–2010 to characterize the structural response of an old-growth tropical rainforest to record heat and drought associated with the 1997–1998 El Niño. In 1999, the fraction of the landscape in gaps was nearly three times larger than during the subsequent decade (Table 2). The increased disturbance caused distributions of canopy height to depart from equilibrium on oxisol slopes and plateaus, whereas forests on alluvial terraces remained in equilibrium. All departures were transient with recovery to equilibrium conditions within 2–3 years (Figs 2 and 3). These findings indicate that heat and drought can substantially alter short-term height dynamics in an old-growth tropical rainforest.

Departures from equilibrium occurred primarily in the gap (≤ 2 m) and high canopy (14–15 m and >15 m) height classes with the fraction of the landscape in gaps increasing relative to equilibrium and the fraction in high canopy declining relative to equilibrium (Figs 2 and 3). The magnitude of departure was correlated with the previous year's dry season rainfall and minimum daily temperature. Although departures were larger with higher minimum daily temperature and lower dry season rainfall, the actual relationship does not appear to be linear. If the El Niño-related observations are excluded, the correlation disappears (Fig. 4), suggesting that temperature and rainfall changes of the severity of the 1997–1998 El Niño are necessary to perturb the canopy from equilibrium. The 1997–1998 El Niño drought was the most severe recorded at La Selva in at least the last 50 years. Dry season rainfall (January–April) in 1998 (395.8 mm) was 55.8% below the 49-year mean (1963–2011) at La Selva and 64.4% below the mean over the 12 years of our study (Table S5), causing the lowest soil moisture levels observed in the 14-year record at La Selva (D. A. Clark and S. F. Oberbauer, unpublished data). The 1997–1998 El Niño also caused a transient increase in night-time temperatures. Mean minimum daily temperature in 1998 was 0.27 °C above the 30-year mean (1982–2011) at La Selva and was the highest recorded over the 12 years of our study (1.2 °C above the 12-year mean, Table S5).

The interpretation of a causal role for the 1997–1998 El Niño assumes the forest at La Selva was not already recovering from a large disturbance event that predated the first census in our study. However, this alternative explanation is unlikely, as long-term records of tree growth and mortality at La Selva dating back to 1983 do not show evidence of previous large-scale disturbance (Clark & Clark, 1994; Clark *et al.*, 2010). Pollen and charcoal records indicate agricultural activity may have been present along peripheral alluvial terraces at La Selva several hundred to several thousand years ago (Kennedy & Horn, 2008), but our alluvial terrace plots were in equilibrium throughout the 12 years of our study. Furthermore, a recent study of canopy dynamics at La Selva using airborne LiDAR-derived height measurements acquired in 1997 and 2006 showed that the canopy height distribution was approximately in equilibrium in 1997, 2 years prior to the start of our canopy height record (Kellner *et al.*, 2009). Taken together, these findings suggest that historic disturbance predating the 1997–1998 El Niño is unlikely to explain the departures from equilibrium canopy height distributions observed in 1999.

The observed dependence of departures from equilibrium on dry season rainfall and minimum daily tem-

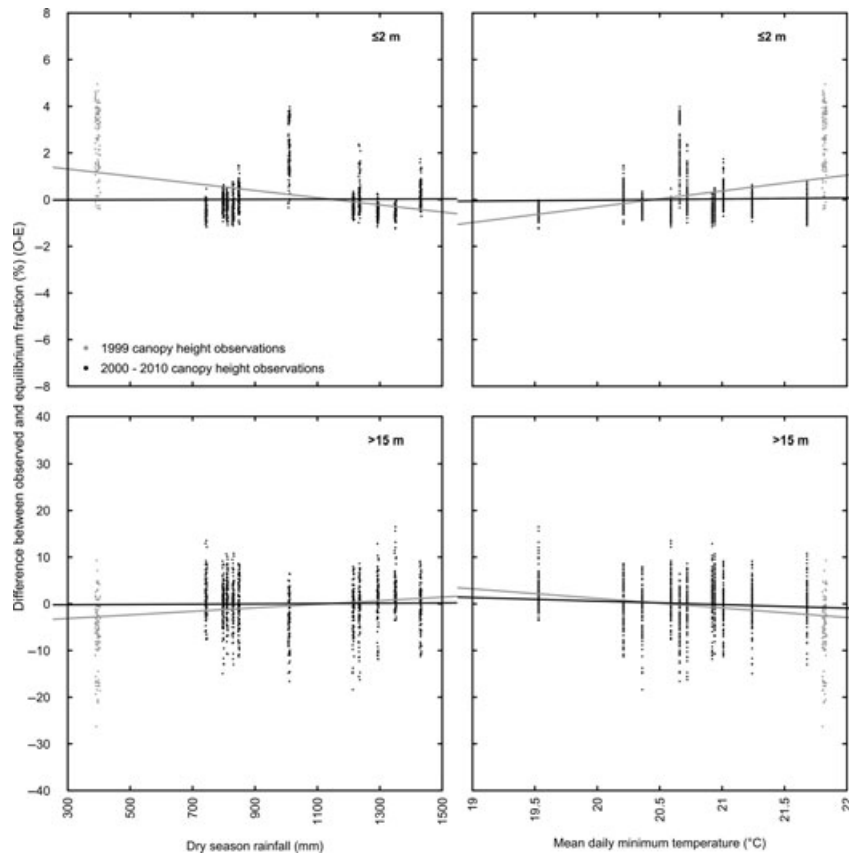


Fig. 4 Scatter plots of departure from equilibrium fraction [observed (%)–equilibrium (%)] of the landscape in the ≤ 2 m and >15 m height classes from 10 000 bootstrap samples across all 18 0.5 ha plots. For visual clarity, each panel plots a random sample of 100 bootstrap samples for each year, rather than the full 10 000 bootstrap samples. Points are also jittered by a small factor. Panels on the left plot departures from equilibrium against lagged annual dry season (January–April) rainfall (mm). Panels on the right plot departures from equilibrium against lagged mean annual minimum daily temperature ($^{\circ}\text{C}$). Rainfall and temperature observations from the 1998 El Niño year (departures from equilibrium in 1999) are plotted in gray. Gray lines show estimated relationship from ordinary least-squares regression including the El Niño-impacted observations. Black lines show estimated relationship excluding the El Niño-impacted observations.

perature is consistent with the findings of Clark *et al.* (2010), which found that tree mortality was significantly correlated with prior-year dry season rainfall and minimum daily temperature over 24 years of observation at La Selva. Increased tree mortality (Table S3) and branch loss in 1998 would be expected to result in a lower fraction of the landscape in high canopy and a higher fraction in canopy gaps and intermediate height classes in 1999 (Table 2). Elevated mortality and canopy damage are well-documented impacts of both actual droughts and rainfall exclusion experiments in the wet tropics (Nakagawa *et al.*, 2000; Nepstad *et al.*, 2002, 2007; Phillips *et al.*, 2010). In a meta-analysis of drought impacts across 39 tropical rainforest sites, Phillips *et al.* (2010) found that stem mortality remained above predrought levels for an average of 2 years after a drought. Our findings similarly show that mortality returned to nondrought levels within 2 years (Table S3), and that

canopy height distributions returned to equilibrium within 2–3 years (Fig. 2).

Edaphic site-type influenced both the equilibrium distributions of canopy height and the magnitude of departure from equilibrium associated with the 1997–1998 El Niño. Equilibrium high canopy cover was greater on alluvial terraces than on oxisol slopes and plateaus, and intermediate canopy cover was less (Fig. 1). Differences in equilibrium conditions were the result of differences in disturbance, rather than growth. The probability of transitioning from the high canopy (>15 m) to intermediate height classes (located above the diagonal of the canopy height transition matrix) was lower on alluvial terraces than oxisol slopes and plateaus, whereas transition probabilities associated with growth (located below the diagonal) were not statistically different among edaphic site-types (Table S4). Previous studies at La Selva have also

reported lower disturbance on alluvial terraces as evidenced by smaller losses in aboveground biomass between repeat censuses (Dubayah *et al.*, 2010) and smaller pools of coarse woody debris (Clark *et al.*, 2002). However, the annual rate of gap formation and the size frequency distributions of new gaps were statistically equivalent across edaphic site-types (Table S3, Fig. S2), underscoring the limited scope of gap formation as a measure of disturbance. Disturbances that reduce canopy height to ≤ 2 m aboveground are instances of extreme canopy damage that are statistically rare relative to small reductions in canopy height, which are more frequent. Unlike gap-based measures, our analysis of height transition matrices is able to capture differences in disturbance across edaphic site-types by examining changes in forest structure throughout the canopy profile.

Because departures from the equilibrium distribution of canopy height depended on edaphic site-type, we hypothesize that drought rather than high temperature was the primary driver of departures from equilibrium. Although temperature should not vary substantially across the three site-types, topographic variation in soil moisture may explain why the largest departures occurred on oxisol slopes followed by oxisol plateaus, whereas alluvial terraces remained in equilibrium. Soil water content at La Selva over a 5-year period (1998–2003) was consistently higher on alluvial terraces than oxisol plateaus (Schwendenmann *et al.*, 2003; Schwendenmann & Veldkamp, 2006; Espeleta & Clark, 2007). Studies at Barro Colorado Island, Panama also demonstrate that soil and plant water potentials are more negative on plateaus than slopes, suggesting that plateaus are drier than slopes (Becker *et al.*, 1988; Daws *et al.*, 2002). We hypothesize that reductions in soil moisture during the 1997–1998 El Niño represented a larger departure from baseline conditions on oxisol slopes than on the already-drier oxisol plateaus. Moreover, higher baseline soil moisture levels along low-lying alluvial terraces likely limited moisture stress on alluvial terraces in comparison to oxisol slopes and plateaus. Such topographic variation in soil moisture would produce the pattern of disturbance severity observed in response to the 1997–1998 El Niño with the largest departures from equilibrium occurring on oxisol slopes followed by oxisol plateaus and alluvial terraces (Fig. 3).

Observed distributions of canopy height were stable on each edaphic site-type following recovery from the 1997–1998 El Niño. The stability of canopy height distributions is not consistent with increasing rates of recruitment and mortality, which have been reported for long-term plots in the Amazon (Phillips

et al., 2004). Excluding the drought-impacted years (1998 and 1999), there was no evidence of a temporal trend (slope = -0.45 , $P = 0.84$) in mortality across the 18 plots at La Selva over the remainder of our study (1999–2009). We also found no evidence of a temporal trend in recruitment (new individuals ≥ 10 cm in diameter) (slope = -0.79 , $P = 0.55$). Increases in mortality and recruitment rates over time would increase transition probabilities associated with canopy height reductions and canopy height gains and thus alter the projected equilibrium distributions of canopy height. However, equilibrium distributions of canopy height were statistically invariant over the 12 years of the study, corroborating the finding of stable mortality and recruitment rates in the years after the 1997–1998 El Niño (Fig. S1).

The long-term annual canopy height measurements employed in this study were crucial to detecting forest response to the high temperature and drought associated with the 1997–1998 El Niño. Using LiDAR-derived measurements of canopy height collected in 1997 and 2006, Kellner *et al.* (2009) previously showed that the old-growth forest at La Selva was in structural equilibrium (Fig. 2) during the 9-year interval between measurements, Kellner *et al.* (2009) did not detect transient departures from equilibrium due to the severe heat and drought in 1998. Although LiDAR-measured height distributions were roughly equivalent between 1997 and 2006, forest biomass likely declined over the interval due to the increase in mortality (Table S3) and canopy damage (Table 2) during the El Niño. Long intervals between canopy height measurements can thus obscure carbon fluxes associated with transient increases in disturbance.

Although canopy height distributions recovered to equilibrium within 2–3 years of the 1997–1998 El Niño, forest biomass likely recovers over longer periods of time (Rolim *et al.*, 2005). Pyle *et al.* (2008) projected biomass stocks in an Amazonian forest would require 10–15 years to return to equilibrium levels following a 25% reduction in standing biomass. As our gridded canopy height measurements do not represent the heights of individual trees, we cannot estimate biomass changes at La Selva following the 1997–1998 El Niño. However, our findings indicate that tropical rainforests are likely to experience departures from present-day equilibrium distributions of canopy height if episodes of severe heat and drought become more frequent over this century and that underlying topographic variation will likely structure the magnitude of departures across forest landscapes.

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Supporting Information

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

Figure S1. Equilibrium fraction of the landscape in the gap (≤ 2 m), 4–5 m, 9–10 m, and high canopy (>15 m) height classes computed from annual height transition matrices for alluvial terraces (left), oxisol plateaus (center), and oxisol slopes (right).

Figure S2. Fraction of landscape in new canopy gaps on alluvial terraces (open circles), oxisol plateaus (gray), and oxisol slopes (black).

Figure S3. Observed and equilibrium distributions of canopy height for alluvial terraces (left), oxisol plateaus (center), and oxisol slopes (right).

Figure S4. Scatter plots of departure from equilibrium fraction [observed (%)–equilibrium (%)] of the landscape in the ≤ 2 m and >15 m height classes from against non-lagged dry season rainfall and mean annual minimum daily temperature 10 000 bootstrap samples across all 18 0.5 ha plots.

Figure S5. Scatter plots of departure from equilibrium fraction [observed (%)–equilibrium (%)] of the landscape in the ≤ 2 m and >15 m height classes from 10 000 bootstrap samples across all 18 0.5 ha plots against all non-lagged climate variables.

Table S1. Canopy height transition matrix for oxisol plateaus. Numbers are the transition probabilities from the column to row height class based on observed transitions pooled across all years (1999–2010).

Table S2. Canopy height transition matrix for oxisol slopes. Numbers are the transition probabilities from the column to row height class based on observed transitions pooled across all years (1999–2010).

Table S3. Annual tree mortality ($\% \text{ yr}^{-1}$). Values indicate the mortality rate for stems ≥ 10 cm dbh in each year.

Table S4. Pairwise comparison of height transition probabilities among edaphic site-types: (alluvial terraces–oxisol plateaus) and (alluvial terraces–oxisol slopes).

Table S5. ENSO index and temperature and rainfall values at La Selva over the interval 1998–2010.