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Vulnerability of Amazon forests to storm-driven tree mortality

To cite this article: Robinson I Negrón-Juárez *et al* 2018 *Environ. Res. Lett.* **13** 054021

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Environmental Research Letters



LETTER

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OPEN ACCESS

RECEIVED

30 November 2017

REVISED

16 April 2018

ACCEPTED FOR PUBLICATION

17 April 2018

PUBLISHED

3 May 2018

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Keywords: severe convective systems, winds, demography model

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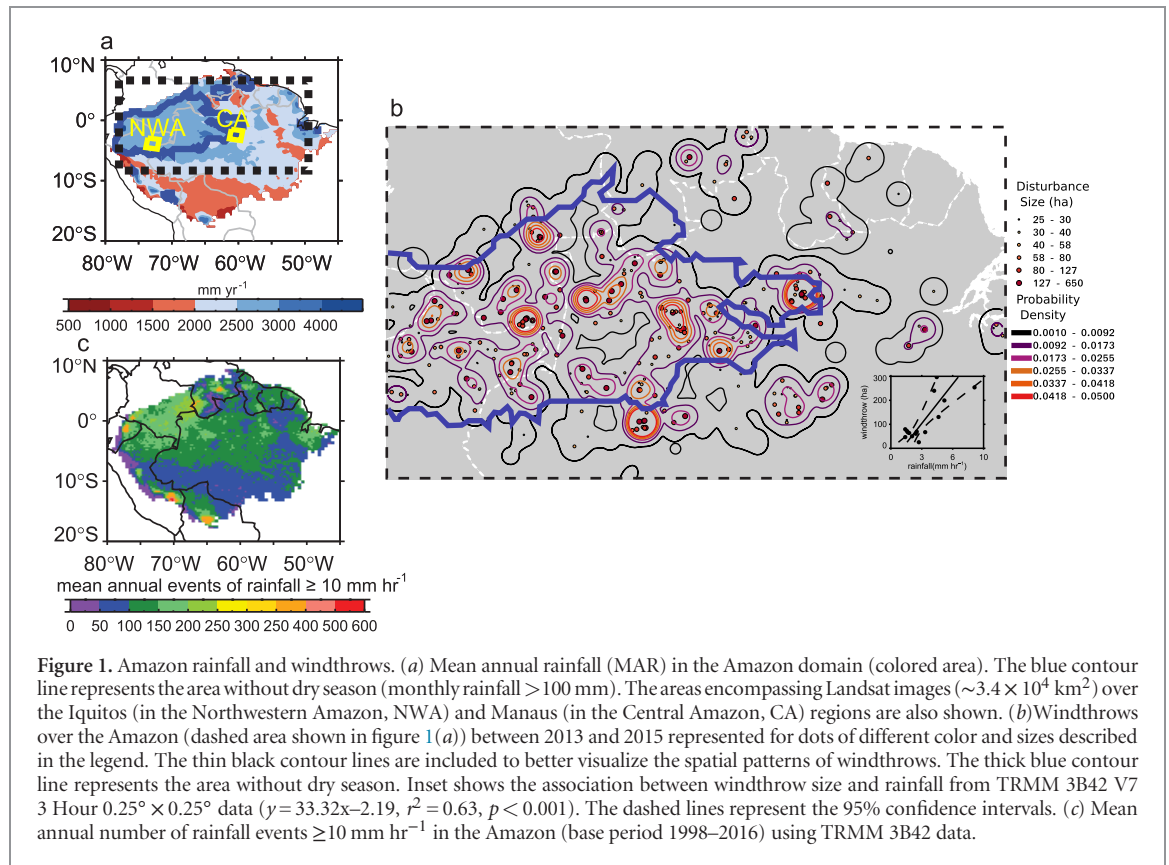
Abstract

Tree mortality is a key driver of forest community composition and carbon dynamics. Strong winds associated with severe convective storms are dominant natural drivers of tree mortality in the Amazon. Why forests vary with respect to their vulnerability to wind events and how the predicted increase in storm events might affect forest ecosystems within the Amazon are not well understood. We found that windthrows are common in the Amazon region extending from northwest (Peru, Colombia, Venezuela, and west Brazil) to central Brazil, with the highest occurrence of windthrows in the northwest Amazon. More frequent winds, produced by more frequent severe convective systems, in combination with well-known processes that limit the anchoring of trees in the soil, help to explain the higher vulnerability of the northwest Amazon forests to winds. Projected increases in the frequency and intensity of convective storms in the Amazon have the potential to increase wind-related tree mortality. A forest demographic model calibrated for the northwestern and the central Amazon showed that northwestern forests are more resilient to increased wind-related tree mortality than forests in the central Amazon. Our study emphasizes the importance of including wind-related tree mortality in model simulations for reliable predictions of the future of tropical forests and their effects on the Earth's system.

1. Introduction

The productivity (22 PgC year⁻¹, or 35% of global terrestrial productivity) (Pan *et al* 2013, Fernandez-Martinez *et al* 2014) and aboveground biomass (AGB, 98 PgC, or 25% of terrestrial biomass) (Pan *et al* 2013, Malhi *et al* 2011) of the Amazon (representing 53% of global tropical forest area; supplementary figure S1 available at stacks.iop.org/ERL/13/054021/mmedia) are well quantified, but the mechanisms affecting their spatial patterns remain uncertain (Stephenson *et al*

2011, Malhi *et al* 2015, Negrón-Juárez *et al* 2015). Tree mortality is an important component of forest dynamics (Kellner and Asner 2009), and affects ecosystem processes (Frelich 2002, dos Santos *et al* 2016) as well as spatial patterns of productivity and biomass (Malhi *et al* 2015, Stephenson *et al* 2014, Negrón-Juárez *et al* 2015, Johnson *et al* 2016). For instance, the less-deforested and rainy northwestern Amazon (NWA) (no dry season, monthly rainfall > 100 mm (Sombroek 2001)) has higher productivity (Aragao *et al* 2009, Malhi *et al* 2004) and lower



biomass (Baker *et al* 2004, Malhi *et al* 2006) than the Central Amazon (CA), which has three months of dry season (consecutive months with rainfall ≤ 100 mm, (Sombroek 2001)). The higher tree mortality in NWA may help explain these patterns (Stephenson and van Mantgem 2005, Galbraith *et al* 2013, Malhi *et al* 2015). Yet, the variation in mortality rates across the Amazon is not fully explained by factors intrinsic to forests (i.e. factors influenced by or resulting from the ecosystem (Wenger 1984)), such as competition, growth, defense strategies, and soil texture and nutrients (Malhi *et al* 2015, Chao *et al* 2008, Stephenson *et al* 2011, Quesada *et al* 2012, Laurance *et al* 1999, Higgins *et al* 2011). Processes producing tree mortality are not fully represented in CMIP5 ESMs (Coupled Model Intercomparison Project Phase 5 Earth System Models) (Taylor *et al* 2012), and may constitute an important and unassessed source of uncertainty.

One major contributor of tree mortality in the Amazon are downbursts (strong descending winds) associated with severe convective systems as squall lines (Garstang *et al* 1998, Negrón-Juárez *et al* 2017, Cohen *et al* 1989). Downbursts create gaps of uprooted or broken trees, windthrows (Mitchell 2013). Previous studies focused over Brazil used Landsat imagery to identify windthrows ranging in size from a single pixel (30 m × 30 m) to hundreds of hectares (Nelson *et al* 1994, Chambers *et al* 2013, Espirito-Santo *et al* 2010, Negrón-Juárez *et al* 2011). Our objectives in this study are to use: (i) Landsat images

between 2013 and 2015 to identify the spatial occurrence of windthrows (<1 yr old) across the whole Amazon; (ii) surveys of tree mortality over windthrown areas to determine tree mortality rates and floristic composition; and (iii) chronosequences of Landsat images to compare the occurrence of windthrows over NWA and CA. Our final objective is to use these data to inform a modeling experiment of forest response to increased wind-related tree mortality rates likely to accompany projected increases in extreme rainfall events in the Amazon (sections 2.6.2 and 14.8.5 in IPCC 2013).

2. Methods

2.1. Research sites and climate

The study areas are the regions of Iquitos (located in NWA) and Manaus (located in CA) (figure 1(a)). In Iquitos MAR (mean annual rainfall) is ~3000 mm, MAT (mean annual temperature) is 25.9 °C, and June through August are the months with the lowest precipitation ($\sim 183 \pm 10$ mm month⁻¹, figure S2(a)). In Manaus, the MAR and MAT are 2300 mm and 26.2 °C, respectively, and the region experiences three consecutive months of dry season (June through August, $\sim 65 \pm 10$ mm month⁻¹, figure S2(b)). The research sites in Iquitos and Manaus (described in sections 2.2 and 2.5) are lowland old-growth forests with trees ~30–40 m tall where windthrows have occurred.

2.2. Landsat imagery and windthrows

To determine the spatial distribution of recent windthrows ≥ 25 ha across the Amazon (figure 1(a)) 229 Landsat 8 images (L8, each covering $\sim 3.4 \times 10^4$ km², 30 m \times 30 m of pixel resolution) with low cloud cover ($< 20\%$) between 2013 and 2015 were used. Windthrows were identified by their distinctive fan-shape diverging from a central area with radiant corridors separated by standing forest (Nelson *et al* 1994) and spectral characteristics (Negrón-Juárez *et al* 2010). To assess the severity of windthrows, spectral mixture analysis (SMA) (Adams *et al* 1995, Shimabukuro and Smith 1991) was applied to bands 2–7 in L8 scenes. SMA quantifies the per pixel fraction of endmembers which sums to match the full pixel spectrum of the image (Adams *et al* 1995). Image-derived endmembers of photosynthetic (green) vegetation (GV), non-photosynthetic vegetation (NPV), and shade were used. The fractions of GV and NPV were then normalized without shade (Adams and Gillespie 2006) as $GV/(GV+NPV)$ and $NPV/(GV+NPV)$. The normalized NPV images were used to calculate the total area of the selected windthrows (supplementary text S1). With this data we produced a windthrown area weighted 2D Kernel Density Estimate (KDE) with the SAGA geospatial analysis library (www.saga-gis.org) using a quartic kernel with a 100 km radius, resampled to a 1 km resolution. The KDE is plotted as a contour plot showing the probability that a windthrow greater than one hectare will occur within each 1 km² pixel (figure 1(b)).

Chronosequences of Landsat imagery were used to calculate the return frequency of windthrows in Iquitos and compared with frequencies from our previous study over Manaus (Chambers *et al* 2013). Landsat 5 Thematic Mapper images (L5) were obtained from the United States Geological Survey (<http://glovis.usgs.gov>), and atmospherically corrected and converted to reflectance using the Atmospheric CORrection Now (ACORN) software (ImSpec LLC, Boulder, CO). The Carlotto (Carlotto 1999) technique, which corrects for haze and smoke contamination, was applied over the scenes as needed. All anthropogenic areas, water bodies, clouds and their shadows were masked out. We used ten L5 images for five intervals (pairs) for Iquitos (Landsat scene P006R063, 1988–1985, 1991–1989, 1999–1995, 2002–2001, 2009–2005) each on approximately the same day of the year. Paired images were intercalibrated (old image, e.g. 1985, with respect to new image, e.g. 1988) band by band by regressing the encoded radiances using temporally invariant targets (Negrón-Juárez *et al* 2011), and the normalized (without shade) NPV was calculated. Changes in NPV for each period (Δ NPV, a quantitative measure of the changes in dead biomass associated with disturbance (Negrón-Juárez *et al* 2011)) were calculated (normalized $NPV_{\text{newimage}} - \text{normalized } NPV_{\text{oldimage}}$).

The Δ NPV was also used to determine the location of plots (~ 3 ha and divided in 100 subplots of 0.03 ha) for conducting forest inventories over windthrown forest (covering a gradient of disturbance severity) and adjacent undisturbed forests. For each plot, we measured tree diameters for all trees ≥ 10 cm in DBH (diameter at the breast height = 1.3 m above ground or above buttress) and measured trees were identified. We studied two windthrows in the Iquitos region (Allpahuayo, in the Allpahuayo-Mishana National Reserve and Nauta, in the Nauta Research Station, managed by National University of the Peruvian Amazon-UNAP) (Rifai *et al* 2016) and three windthrows in Manaus in research stations managed by the Brazil's National Institute for Amazonian Research-INPA (Tumbira, ZF2 and ZF5) (Magnabosco Marra *et al* 2014, Magnabosco Marra 2016). The windthrow in Allpahuayo extended 50 ha and occurred in 1992. Nauta (300 ha) occurred in 2009, Tumbira (75 ha) occurred in 1987, ZF5 (900 ha) occurred in 1996 and ZF2 (250 ha) occurred in 2005. Supplementary table S1 describes the plots and table S2 the common species in Iquitos. Based on all forest inventory plots we present the twenty most common genera observed in Iquitos and Manaus. The relative density of species was calculated as 100 times the number of individuals of a given species divided by the total number of individuals of all species, and similar for frequency and dominance (Curtis and McIntosh 1950).

2.3. Tropical Rainfall Measuring Mission data

Data from the 3 Hour Multi-satellite Precipitation Analysis (3B42) of Tropical Rainfall Measuring Mission (TRMM) (Huffman *et al* 2007) version 7 for the period 1998 to 2016 was used to determine areas with heavy rainfall as well as the association between heavy rainfall and windthrows (text S2).

2.4. Power law exponent for event size distribution data

A power law function was used to determine the gap size frequency across the Iquitos landscape (Di Vittorio *et al* 2014, Fisher *et al* 2008). The power law exponent ($y = cx^{-\alpha}$) was obtained using an Ordinary Least Squares technique (OLS) (Milojevic 2010) and a Maximum Likelihood Estimator (MLE) (Clauset *et al* 2009). We performed these estimates on two data cases: (1) the remotely sensed data only (windthrow from Landsat), and (2) the remotely sensed data plus inventory plots data (Landsat+plot). These data was multiplied by the total analyzed forested area across the five Iquitos Landsat scene-pairs (31 900 km²) described in section 2.2. Tree mortality data from Landsat included windthrows with more than eight dead trees based on the average mortality rate as function of gap size (figure S3) as well as data from eight-tree events from single-pixel disturbances (Negrón-Juárez *et al* 2011). Plot data include mortality of single trees

(Chao *et al* 2008). The OLS method used log-binned data with the starting bin center at event of eight trees in size, while the MLE method used the data directly. An extensive description of the power law fit method used is described in Di Vittorio *et al* (2014). To directly compare this average mortality event-size distribution with those in Manaus (Chambers *et al* 2013) (that uses the same method) we aggregated the distribution into the same set of discrete event-size bins which were defined in logarithm with base 10 for Manaus, plus one extra bin to cover the larger clusters detected in Iquitos. Probability distribution-function of event size and dead trees is presented. Further details are presented in text S3.

2.5. Comparison of Iquitos and Manaus wind-related tree mortality

The Nauta windthrow (November 2, 2009) in Iquitos was compared with the previously studied ZF2 windthrow in Manaus (Negrón-Juárez *et al* 2010). For the Nauta windthrow, L5 scenes (Path 006/Raw063) from June 27, 2008, and December 07, 2009 were used to calculate Δ NPV. The Δ NPV image was used to randomly select thirty disturbed pixels covering the whole gradient of disturbance. Each pixel was located using a handheld GPS (60CSx GPS, Garmin Ltd.) and a plot of 20 m \times 20 m was installed. The number of live and dead trees with DBH \geq 10 cm was recorded in the surveys. The survey was done 10 months after the occurrence of the windthrow. Dead trees were identified by the direction of fall similar to the predominant direction of the windthrows, presence of leaves, preserved trunk bark, and fresh fiber characterizing snapping. An ANCOVA analysis (using SAS 9.2, SAS Institute Inc., North Carolina, USA) was used to compare the association between tree mortality and Δ NPV in Iquitos and Manaus. The associated downburst velocities for the Nauta windthrow were estimated as 19–31 m s⁻¹ (68–112 km h⁻¹) (figure S4).

2.6. Simulation of forest and windthrows dynamics

We used the ZELIG-TROP model (Holm *et al* 2014) to simulate forest and tree mortality interactions due to increased windthrow events. ZELIG-TROP is an individual-based demographic gap model with trees of varying size and structure, as well as a dynamic vegetation model in that regeneration, growth, and mortality rates all dynamically vary as a function of climate, stand density, canopy openness, and competition for resources. The data used to parameterize the species traits and demographic attributes (such as maximum DBH, age, growth-rate scaling coefficient, stress tolerances, and recruitment rates) was obtained from our inventory plots, RAINFOR data (Lopez-Gonzalez *et al* 2011, date of extraction 16/04/2015), and Holm *et al* (2014) for Manaus. We used the allometric equation from Chambers *et al* (2001) based on DBH to estimate AGB in ZELIG-TROP. Average monthly precipitation and temperature required for

the environmental driving parameters in ZELIG-TROP were from data collected at UNAP, Iquitos, Peru (3.46°S, 73.17°W), from 1988–2011. ZELIG-TROP was parameterized and validated previously for Manaus (Holm *et al* 2014), and here the model was parameterized for tree species typical of Iquitos (see table S2).

We simulated 50 spatially explicit plots, each at the patch-dynamic scale of 400 m² (totaling two hectares). The simulations started from bare ground (as typical for successional-based gap models), thus simulating dynamic and stochastic individual tree-recruitment, growth, and mortality within competing environmental conditions for Manaus and Iquitos. Model simulations were run for 400 yr until the forest reached a mature steady state (compared to field data in table 1), and all results are averaged over the final 50 yr of simulation. The tree mortality rate (% stems yr⁻¹) was simulated to be 2.1% for Iquitos (i.e. control), which is very close to observed values (i.e. \sim 2.3%) (Chao *et al* 2008). The control simulations agreed with observed values of forest attributes (table 1) and predictors of tree mortality (text S4 and figure S5) from a previous tree pulling study (Ribeiro *et al* 2016).

To study how increases in windthrows may affect community composition, the current background mortality (M) in Iquitos (\sim 2%) and Manaus (\sim 1%) was near doubled (2M) (table 1), assuming that all increase in mortality is associated with windthrows. A justifiable value of increased mortality associated with windthrows is not currently possible since model predictions of future climate do not include windthrows as a form of disturbance. To increase mortality to 2M the model randomly selected trees \geq 10 cm DBH to die and are removed from the forest on an annual basis. Control simulations were denoted as Iquitos M and Manaus M, and doubled-mortality simulation as Iquitos 2M and Manaus 2M.

Sixty eight species belonging to 46 genera were used in the Iquitos simulations (table S2). For Manaus simulation, 90 species belonging to 51 genera were used (Holm *et al* 2014). Eighteen genera (figure S6) were found common in both Amazon regions. These 18 common genera accounted for 75% and 47% of the total basal area (BA) in Iquitos and Manaus, respectively. These overlapping genera were used to compare shifts in community composition between the M and 2M simulations in these regions (figure S6 (a) and (b)). Using the 18 common genera allowed for a stricter and standardized basis for comparing compositional shifts and alleviate biases that would manifest when including genera that are only present in one region and not the other.

A non-metric multidimensional scaling (NMDS) ordination analysis (Shepard 1962, Kruskal 1964a, 1964b, Faith *et al* 1987) on genera abundance classified by BA (m² ha⁻¹) was used to analyze the plot data and model results. We used this technique to reduce the multidimensionality of our studied communities

Table 1. Model results for Iquitos. Control outputs over Iquitos (\pm standard deviation) compared against field data and disturbance model outputs. The tree mortality rate for Iquitos is the exponential mortality (2.3%) (Chao *et al* 2008)*, which can be considered the true annual mortality since both differ only by about 0.02% (Sheil *et al* 1995). Since ZELIG-TROP is an individual-based model that prognoses mortality mechanistically, mortality is reported as individual level annual mortality. ANPP = aboveground net primary production.

| | Iquitos field data | ZELIG-TROP iquitos M | ZELIG-TROP iquitos 2M | % Change due to disturbance |
|---|--------------------|-------------------------|--------------------------|--------------------------------|
| Aboveground biomass (AGB, Mg ha ⁻¹) | 247 (\pm 77)* | 249 (\pm 40.2) | 175 (\pm 23.8) | -29.62 |
| Stem density (trees ha ⁻¹) | 597 (\pm 68) | 623 (\pm 185) | 654 (\pm 205) | 4.98 |
| ANPP (MgC ha ⁻¹ yr ⁻¹) | 9.06 (\pm 0.7)* | 9.5 (\pm 2.6) | 8.8 (\pm 2.7) | -7.37 |
| Leaf area Index (LAI) | 5.5 (\pm 0.2)* | 5.4 (\pm 0.7) | 4.9 (\pm 0.5) | -9.26 |
| Mortality Rate (% yr ⁻¹) | 2.3 (\pm 0.31)* | 2.1 (\pm 0.08) | 3.9 (\pm 0.04) | 85.71 |

Table 2. Binned mortality event size distribution and stem mortality in Iquitos. The binned probabilistic distribution functions (PDFs) provide the fraction of total mortality in each event class. Text S3 provide further details about the production of this table.

| Minimum event PDF | Maximum event PDF | Average event PDF | Trees per event | Normalized # of events (# events ha ⁻¹ yr ⁻¹) | Area return frequency (ha yr ⁻¹) | Normalized # of dead trees (# trees ha ⁻¹ yr ⁻¹) | Percentage of annual tree mortality (%) |
|----------------------|----------------------|----------------------|-----------------|---|--|---|---|
| 0.6875406 | 0.7559586 | 0.7321610 | 1 | 11.17362 | 0.09 | 11.174 | 34.1 |
| 0.1435392 | 0.1290837 | 0.1349253 | 2 | 2.05911 | 0.49 | 4.118 | 12.6 |
| 0.1054770 | 0.0804218 | 0.0894581 | 4 | 1.36523 | 0.73 | 5.461 | 16.7 |
| 0.0383210 | 0.0234811 | 0.0283769 | 8 | 0.43306 | 2.31 | 3.465 | 10.6 |
| 0.0143309 | 0.0071449 | 0.0093377 | 16 | 0.14250 | 7.02 | 2.280 | 7.0 |
| 0.0074081 | 0.0029711 | 0.0042158 | 33 | 0.06433 | 15.54 | 2.123 | 6.5 |
| 0.0023191 | 0.0007123 | 0.0011184 | 84 | 0.01706 | 58.59 | 1.434 | 4.4 |
| 0.0007295 | 0.0001717 | 0.0002982 | 210 | 0.00455 | 219.71 | 0.956 | 2.9 |
| 0.0002850 | 0.0000492 | 0.0000961 | 637 | 0.00146 | 681.54 | 0.935 | 2.9 |
| 0.0000421 | 0.0000047 | 0.0000108 | 2900 | 0.00016 | 6054.60 | 0.479 | 1.5 |
| 0.0000070 | 0.0000004 | 0.0000013 | 16788 | 0.00002 | 48805.20 | 0.344 | 1.0 |

into a two dimensional-ordination space and assess possible differences in genera composition. The NMDS from 124 inventory plots distributed in Iquitos and Manaus (supplementary table S1) was compared against simulations. For M and 2M simulations, the NMDS analysis was based on 20 plots per region. Stress scores (that represents the difference between the reduced and the complete multidimensional space) < 0.3 indicates a good representation of data in the reduced dimensions.

3. Results

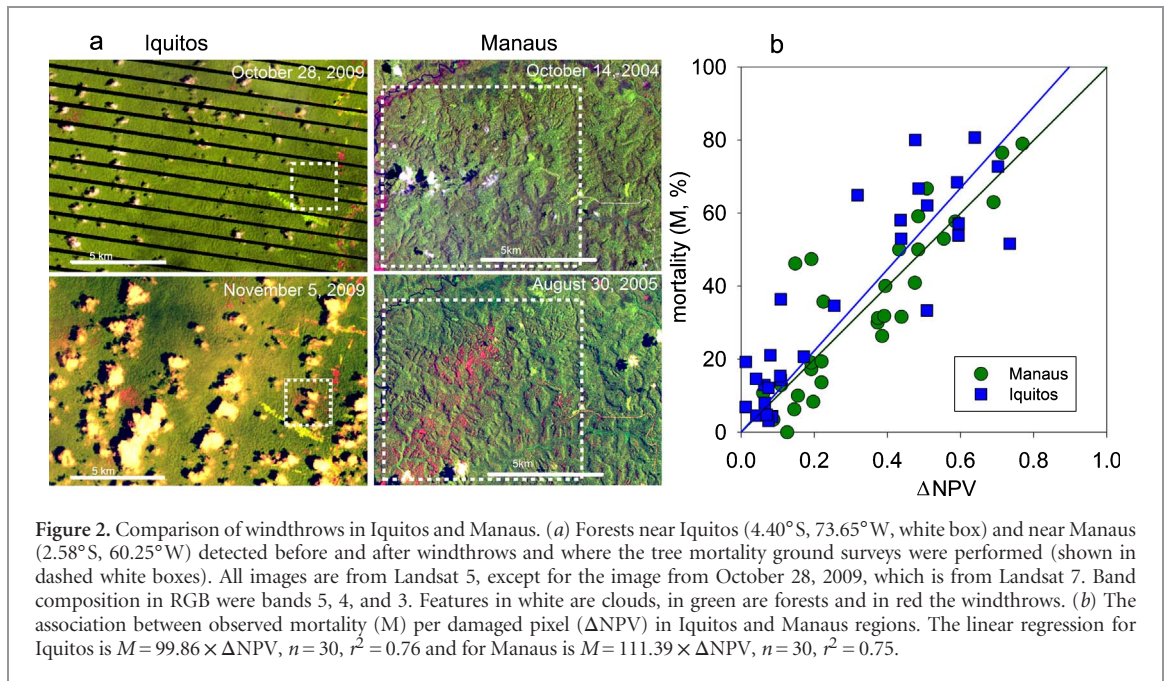
Between 2013 and 2015, the areas of the Amazon basin without dry season (figure 1(a)) were most affected by windthrows (figure 1(b)). These areas, which include northwestern Peru, southern Colombia, southern Venezuela, and the central and western regions of the Brazilian Amazon, also experience more frequent and intense hourly rainfall rate events (figure 1(c)). A positive association was found between hourly rainfall rates and windthrows (inset in figure 1(b)).

The Iquitos power law exponents range from -2.26 to -2.55 , with a mean value of -2.44 (figure S7) which are outside the range of the Manaus exponent (-2.71 and -2.97) (Chambers *et al* 2013, Di Vittorio *et al* 2014). These power law exponents do not change substantially between methods (OLS and MLE) or data used (Landsat and Landsat+ plot data) (figure S7) and show that windthrows are more frequent in Iquitos. In

Iquitos 37% of annual tree mortality associated with windthrows occurred in gaps formed from the death of eight or more trees (bins ≥ 8 trees) (table 2). This proportion is more than double the rate previously estimated for CA (17%) (Chambers *et al* 2013).

The downburst speeds that produced the Nauta windthrow (figure 2(a)) were less intense (estimated as $68\text{--}112$ km h⁻¹, figure S4) than over the ZF2 forest (estimated as $93\text{--}147$ km h⁻¹) (Negrón-Juárez *et al* 2010) that was expected since slower moving system (12 m s⁻¹ in Nauta (figure S4) vs 19 m s⁻¹ in ZF2 (Negrón-Juárez *et al* 2010)) produce lower downburst velocities (Garstang *et al* 1998). A strong linear relationship ($p < 0.001$ and $r^2 = 0.8$; figure 2(b)) was found between observed tree mortality and Δ NPV in Nauta and ZF2. The ANCOVA analysis showed that the slopes (112 ± 6.0 (SE) and 99 ± 5.6 for Nauta and ZF2) were not statistically different ($F = 2.38$, $p = 0.12$), even for the unforced through origin case ($F = 0.16$, $p = 0.69$). Despite the fact that downburst speeds were lower during the Nauta windthrow than the ZF2 windthrow, the tree mortality per area associated with these storms was similar suggesting that trees in Iquitos had a higher sensitivity to winds.

The control simulations predicted the community composition in both regions accurately (figure S6(a) and figure S6(b) compared to figure 3(a) and (b)), with an exception of the lower dominance of *Eschweilera* (Lecythidaceae) in Manaus. The control simulations also reproduced the differences in genera composition observed between Manaus and Iquitos (figure 3(c)),



as indicated by the distances between genera similarity derived from the NMDS ordination (i.e. separation of red and blue points in figure 3(d)). Iquitos 2M resulted in a significant, yet smaller decrease in biomass compared to the biomass decrease in Manaus 2M (29.6%; two sample t test, $t_{(99,1.97)} = 186.20$, $p < 0.001$ vs. 41.9%; two sample t test, $t_{(99,1.97)} = 108.98$, $p < 0.001$, respectively).

Iquitos 2M did not lead to a significant shift in genera composition with respect to Iquitos M (figure 3(d)) (Wilcoxon rank sum, $Z = 0.33$, $p = 0.74$, and also seen in a cluster analysis in figure S8(a)). In contrast, Manaus 2M had significant shifts in the genera composition with respect Manaus M (Wilcoxon rank sum, $Z = 2.28$, $p = 0.02$, figure S8(b)). Furthermore, Manaus 2M had community similarities to Iquitos M (figure 3(d) and figure S8(c)) but differences exist (Wilcoxon rank sum, $Z = 1.03$, $p = 0.3$). Text 5 summarize model changes in AGB, NPP, BA and diversity index associated with doubling the mortality rate. In both Iquitos 2M and Manaus 2M the model predicted that emergent trees had the largest decrease in basal area (after weighting by abundance) (figure S6(c)). This decrease was stronger in Manaus 2M (19%) compared to Iquitos 2M (14%).

4. Discussion

We found that windthrows are spatially more common in NWA (north of the Ecuadorian Amazon, northeast of Peru, and northwest of Brazil) (figure 1(b)) consistent with and expanding on previous studies focused on Brazil (Nelson *et al* 1994, Espirito-Santo *et al* 2014, Espirito-Santo *et al* 2010).

Our inventory plots vary in important attributes (e.g. biomass, size-distribution of trees, tree height,

stem density and community mean wood density (Quesada *et al* 2012, Feldpausch *et al* 2011, Mitchard *et al* 2014, Baker *et al* 2004)) that characterize the typical gradient across the Amazon driven by climatic, edaphic and ecological aspects (Quesada *et al* 2012). Thus, our inventory plots in Iquitos and Manaus may be considered representatives of NWA and CA respectively.

The power law analysis (figure S7) suggests that windthrows occur more frequently in NWA than in CA (table 1 in Chambers *et al* 2013) across all size classes. NWA and CA have distinctive community composition, which partially can be related to tree-mortality patterns, as discussed in previous studies (Chao *et al* 2008, ter Steege *et al* 2006, ter Steege *et al* 2013, Magnabosco Marra 2016). We found that NWA is more vulnerable to wind-related tree mortality that may be related to a number of factors including tree stem density, tree size, species composition, wood density, soil type, root architecture, and topographic exposure (Boose *et al* 2004, Vandermeer *et al* 2000, Chao *et al* 2008, de Toledo *et al* 2011, Magnabosco Marra 2016, Ribeiro *et al* 2016). The similarities in tree density (supplementary table S1) and tree size-distribution (supplementary figure S9) in NWA and CA suggest that these structural attributes are unlikely to be major contributors of the observed differences in tree mortality, in agreement with previous studies (Chao *et al* 2008).

Winds produce tree mortality by uprooting (more likely associated with soil characteristics) or breaking (more likely associated with mechanical failure) (Rankin-de Merona *et al* 1990, Korning and Balslev 1994). The soils in the NWA are dominantly Acrisols with low infiltration rates that limit root growth due to high soil compaction, while soils in CA are primarily Ferrasols which have physical properties that allow development of deeper root systems (Hengl *et al* 2014).

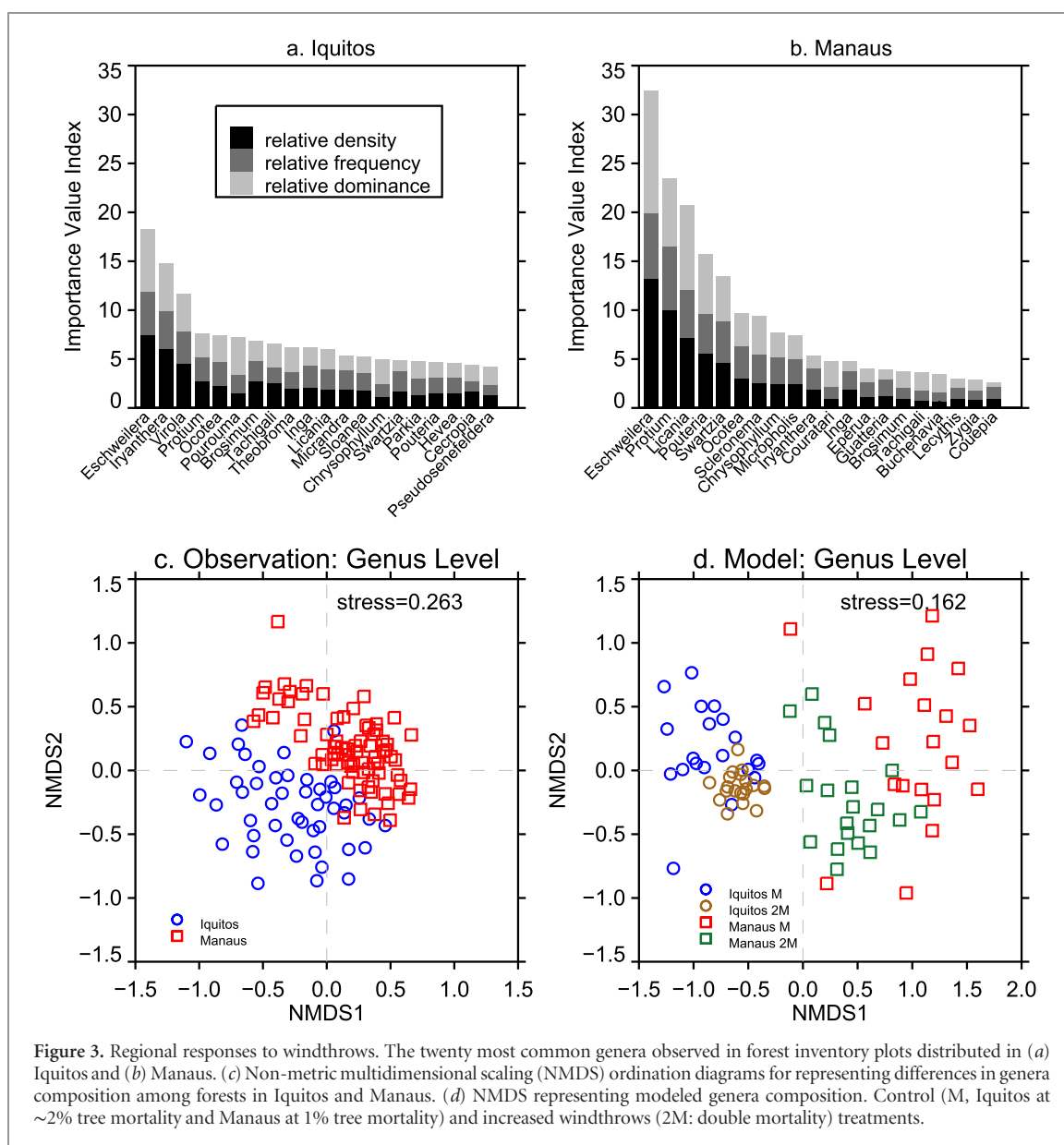


Figure 3. Regional responses to windthrows. The twenty most common genera observed in forest inventory plots distributed in (a) Iquitos and (b) Manaus. (c) Non-metric multidimensional scaling (NMDS) ordination diagrams for representing differences in genera composition among forests in Iquitos and Manaus. (d) NMDS representing modeled genera composition. Control (M, Iquitos at ~2% tree mortality and Manaus at 1% tree mortality) and increased windthrows (2M: double mortality) treatments.

These soil characteristics correspond with gradients of root depth across the region (Ichii *et al* 2007, Nogueira Lima *et al* 2012). Furthermore, in NWA light limitation, abundant rainfall and soil conditions (Nemani *et al* 2003, Malhi and Davidson 2009, Malhi *et al* 2004, ter Steege *et al* 2006, Baker *et al* 2004, Quesada *et al* 2012) promote rapid vertical growth (Stephenson *et al* 2011) and shallow root systems (Quesada *et al* 2012). Frequent extreme rainfall events in NWA (figure 1(c)) might also result in saturated soils (Foster 1988) and strong wind loads affecting the mechanical stability of trees by swaying (Gardiner *et al* 2016). These characteristics (individually or combined) limit the anchoring of trees into soil and may make NWA trees more sensitive to winds (figure 2(b)). Tree-pulling experiments in Iquitos, similar to those we have conducted in Manaus (Ribeiro *et al* 2016), are needed to test these assumptions.

Our modeling results suggest that community composition in Manaus is more vulnerable to an increase

in windthrows with respect to Iquitos, consistent with previous studies showing that forests with low mortality rates are more sensitive to increases in mortality rates (Schiatti *et al* 2016, de Toledo *et al* 2013, Johnson *et al* 2016). Manaus 2M predicted community similarities to Iquitos M, but differences exist. These differences may be related to either individual or combined effects, such as (i) differences in soil characteristics and nutrients (Quesada *et al* 2012); (ii) local effects of disturbances; or (iii) model limitations, as the model cannot incorporate all complex and diverse plant physiological processes (Wright 2002), all of which are challenging data to collect in the tropics.

Our modeling results suggest that the community composition in Iquitos did not significantly change with increases in tree mortality associated with windthrows. The higher frequency of windthrows in Iquitos (with respect to Manaus) may have resulted in a forest that is more resilient (as defined by Holling 1973) to increases in tree mortality rates from windthrows.

This resiliency was represented by the overlap of Iquitos M vs. Iquitos 2M points in figure 3(d), as well as the smaller decrease in biomass in Iquitos 2M. Iquitos might only see a significant change in community composition with a larger increase in mortality or different drivers of mortality.

Our results shows that Landsat and Landsat+plot data do not produce changes in the power law exponent suggesting that an important fraction of plot level tree mortality is produced by winds. However, we emphasize the need for additional field observations of different mortality agents for proper region-specific attributions of cause and effect, as well as vulnerability, resistance, and responses of different species to those agents. Such observations would improve understanding of forest dynamics beyond the importance of general tree mortality in explaining patterns of biomass and productivity in the Amazon. Our results directly address the need to incorporate the effects of wind-related tree mortality on ecosystem processes in ESMs to reduce uncertainties of carbon and climate projections.

5. Conclusions

We found that windthrows are common in the region extending from the northwest Amazon (northeastern Peru, southern Colombia and Venezuela and northwest Brazil) to central Brazil, with the highest occurrence of windthrows found in northwest Amazon. The more frequent extreme winds associated with more frequent severe convective systems in NWA may explain the higher tree mortality observed in this region. The higher frequency of windthrows in NWA may have resulted in a forest that is more adapted to these disturbances. Our model results suggest that increases in the occurrence of windthrows may produce a shift in composition in CA but not in NWA.

Acknowledgments

We thank crew members at the National University of the Peruvian Amazon (UNAP) for their logistic support through the project Muro Huayra (RD N° 321–2009 FCF-UNAP, RR N° 1389–2010-UNAP), and staff at the Brazil's National Institute for Amazonian Research for all their dedicated field work. We thank Marilyn Saarni for her editorial review on the submitted and revised version of this manuscript. Landsat Imagery was analyzed using Google Earth Engine: A planetary-scale geospatial analysis platform, Google Earth Engine Team 2015, <https://earthengine.google.com>. This research was supported as part of the Next Generation Ecosystem Experiments-Tropics, funded by the US Department of Energy, Office of Science, Office of Biological and Environmental Research. This research was partially or fully supported through the Reducing Uncertainties

in Biogeochemical Interactions through Synthesis and Computation Scientific Focus Area (RUBISCO SFA) under contract to LBNL, which is sponsored by the Regional and Global Climate Modeling (RGCM) Program in the Climate and Environmental Sciences Division (CESD) of the Office of Biological and Environmental Research (BER) in the US Department of Energy Office of Science. Data collection in Manaus, Brazil, was supported by the Brazilian Council for Scientific and Technological Development (CNPq) within the projects Woods of the Amazon (INCT Madeiras da Amazonia) and Succession After Windthrows (SAWI) (MCTI/No 14/2012, Proc. 473357/2012-7). Data collection in Iquitos, Peru, was supported by NASA Biodiversity.

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References

- Adams J B and Gillespie A R 2006 *Remote Sensing of Landscapes with Spectral Images: A Physical Modeling Approach* (Cambridge: Cambridge University Press)
- Adams J B, Sabol D E, Kapos V, Almeida R, Roberts D A, Smith M O and Gillespie A R 1995 Classification of multispectral images based on fractions of endmembers—application to land-cover change in the Brazilian amazon *Remote Sens. Environ.* **52** 137–54
- Aragao L E O C *et al* 2009 Above- and below-ground net primary productivity across ten Amazonian forests on contrasting soils *Biogeosciences* **6** 2759–78
- Baker T R *et al* 2004 Variation in wood density determines spatial patterns in Amazonian forest biomass *Glob. Change Biol.* **10** 545–62
- Boose E R, Serrano M I and Foster D R 2004 Landscape and regional impacts of hurricanes in Puerto Rico *Ecol. Monogr.* **74** 335–52
- Carlotto M J 1999 Reducing the effects of space-varying, wavelength-dependent scattering in multispectral imagery *Int. J. Remote Sens.* **20** 3333–44
- Chambers J Q, dos Santos J, Ribeiro R J and Higuchi N 2001 Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest *Forest Ecol. Manage.* **152** 73–84
- Chambers J Q, Negrón-Juárez R I, Marra D M, Di Vittorio A, Tews J, Roberts D, Ribeiro G H P M, Trumbore S E and Higuchi N 2013 The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape *Proc. Natl Acad. Sci. USA* **110** 3949–54
- Chao K-J, Phillips O L, Gloor E, Monteagudo A, Torres-Lezama A and Vasquez Martinez R 2008 Growth and wood density predict tree mortality in Amazon forests *J. Ecol.* **96** 281–92
- Clauset A C, Shalizi C R and Newman M E 2009 Power-law distributions in empirical data *Soc. Ind. Appl. Math. Rev.* **51** 661–703
- Cohen J, Silva Dias M A F and Nobre C A 1989 Climatological aspect of Amazon squall lines *Climanalise, Boletim de monitoriamento e análise climatico* **4** 34–40
- Curtis J T and McIntosh R P 1950 The interrelations of certain analytic and synthetic phytosociological characters *Ecology* **31** 434–55

- de Toledo J J, Magnusson W E and Castilho C V 2013 Competition, exogenous disturbances and senescence shape tree size distribution in tropical forest: evidence from tree mode of death in Central Amazonia *J. Veg. Sci.* **24** 651–63
- de Toledo J J, Magnusson W E, Castilho C V and Nascimento H E M 2011 How much variation in tree mortality is predicted by soil and topography in central Amazonia? *Forest Ecol. Manage.* **262** 331–8
- Di Vittorio A V, Negron-Juarez R I, Higuchi N and Chambers J Q 2014 Tropical forest carbon balance: effects of field- and satellite-based mortality regimes on the dynamics and the spatial structure of Central Amazon forest biomass *Environ. Res. Lett.* **9** 034010
- dos Santos L T, Marra D M, Trumbore S, de Camargo P B, Negron-Juarez R I, Lima A J N, Ribeiro G, dos Santos J and Higuchi N 2016 Windthrows increase soil carbon stocks in a central Amazon forest *Biogeosciences* **13** 1299–308
- Espirito-Santo F D B *et al* 2014 Size and frequency of natural forest disturbances and the Amazon forest carbon balance *Nat. Commun.* **5** 3434
- Espirito-Santo F D B, Keller M, Braswell B, Nelson B W, Frolking S and Vicente G 2010 Storm intensity and old-growth forest disturbances in the Amazon region *Geophys. Res. Lett.* **37** L11403
- Faith D P, Minchin P R and Belbin L 1987 Compositional dissimilarity as a robust measure of ecological distance *Vegetatio* **69** 57–68
- Feldpausch T R *et al* 2011 Height-diameter allometry of tropical forest trees *Biogeosciences* **8** 1081–106
- Fernandez-Martinez M, Vicca S, Janssens I A, Luyssaert S, Campioli M, Sardans J, Estiarte M and Penuelas J 2014 Spatial variability and controls over biomass stocks, carbon fluxes, and resource-use efficiencies across forest ecosystems *Trees-Struct. Funct.* **28** 597–611
- Fisher J I, Hurtt G C, Thomas R Q and Chambers J Q 2008 Clustered disturbances lead to bias in large-scale estimates based on forest sample plots *Ecol. Lett.* **11** 554–63
- Foster D R 1988 Species and stand response to catastrophic wind in central New England, USA *J. Ecol.* **76** 135–51
- Frelich L E 2002 Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests *Cambridge Studies in Ecology. Forest Dynamics and Disturbance Regimes: Studies from Temperate Evergreen-deciduous Forests* (Cambridge: Cambridge University Press) pp 1–266
- Galbraith D *et al* 2013 Residence times of woody biomass in tropical forests *Plant Ecol. Divers.* **6** 139–57
- Gardiner B, Berry P and Moulia B 2016 Review: wind impacts on plant growth, mechanics and damage *Plant Sci.* **245** 94–118
- Garstang M, White S, Shugart H H and Halverson J 1998 Convective cloud downdrafts as the cause of large blowdowns in the Amazon rainforest *Meteorol. Atmos. Phys.* **67** 199–212
- Hengl T *et al* 2014 SoilGrids 1 km-global soil information based on automated mapping *PLoS ONE* **9** e105992
- Higgins M A, Ruokolainen K, Tuomisto H, Llerena N, Cardenas G, Phillips O L, Vasquez R and Rasanen M 2011 Geological control of floristic composition in Amazonian forests *J. Biogeogr.* **38** 2136–49
- Holling C S 1973 Resilience and stability of ecological systems *Annual Review of Ecology and Systematics* ed R F Johnston vol 4 (Palo Alto, CA: Illus. Map. Annual Reviews Inc.) pp 1–23
- Holm J A, Chambers J, Collins W D and Higuchi N 2014 Forest response to increased disturbance in the Central Amazon and comparison to Western Amazonian forests *Biogeosciences* **11** 5773–94
- Huffman G J, Adler R F, Bolvin D T, Gu G J, Nelkin E J, Bowman K P, Hong Y, Stocker E F and Wolff D B 2007 The TRMM multisatellite precipitation analysis (TMPA): Quasi-global, multiyear, combined-sensor precipitation estimates at fine scales *J. Hydrometeorol.* **8** 38–55
- Ichii K, Hashimoto H, White M A, Potters C, Hutyrá L R, Huete A R, Myneni R B and Nemanis R R 2007 Constraining rooting depths in tropical rainforests using satellite data and ecosystem modeling for accurate simulation of gross primary production seasonality *Glob. Change Biol.* **13** 67–77
- IPCC 2013 Climate change 2013: the physical science basis *Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* ed T F Stocker *et al* (Cambridge: Cambridge University Press) p 1535
- Johnson M O *et al* 2016 Variation in stem mortality rates determines patterns of above ground biomass in Amazonian forests implications for dynamic global vegetation models *Glob. Change Biol.* **22** 3996–4013
- Kellner J R and Asner G P 2009 Convergent structural responses of tropical forests to diverse disturbance regimes *Ecol. Lett.* **12** 887–97
- Korning J and Balslev H 1994 Growth-Rates and mortality patterns of tropical lowland tree species and the relating to forest structure in amazonian ecuador *J. Trop. Ecol.* **10** 151–66
- Kruskal J B 1964a Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis *Psychometrika* **29** 1–27
- Kruskal J B 1964b Nonmetric multidimensional scaling: a numerical method *Psychometrika* **29** 115–29
- Laurance W F, Fearnside P M, Laurance S G, Delamonica P, Lovejoy T E, Chambers J and Gascon C 1999 Relationship between soils and Amazon forest biomass: a landscape-scale study *Forest Ecol. Manage.* **118** 127–38
- Lopez-Gonzalez G, Lewis S L, Burkitt M and Phillips O L 2011 ForestPlots.net: a web application and research tool to manage and analyse tropical forest plot data *J. Veg. Sci.* **22** 610–3
- Magnabosco Marra D 2016 Effects of windthrows on the interaction between tree species composition, forest dynamics and carbon balance in Central Amazon *Institute of Biology* (Leipzig: Leipzig University) p 210
- Magnabosco Marra D, Chambers J Q, Higuchi N, Trumbore S E, Ribeiro G H P M, dos Santos J, Negron-Juarez R I, Reu B and Wirth C 2014 Large-scale wind disturbances promote tree diversity in a Central Amazon Forest *PLoS ONE* **9** e103711
- Malhi Y *et al* 2004 The above-ground coarse wood productivity of 104 Neotropical forest plots *Glob. Change Biol.* **10** 563–91
- Malhi Y and Davidson E A 2009 *Amazonia and Global Change* ed M Keller *et al* (Washington, DC: American Geophysical Union) pp 293–7
- Malhi Y, Doughty C and Galbraith D 2011 The allocation of ecosystem net primary productivity in tropical forests *Phil. Trans. R. Soc. London B Biol. Sci.* **366** 3225–45
- Malhi Y *et al* 2015 The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests *Glob. Change Biol.* **21** 2283–95
- Malhi Y *et al* 2006 The regional variation of aboveground live biomass in old-growth Amazonian forests *Glob. Change Biol.* **12** 1107–38
- Milojevic S 2010 Power law distributions in information science: making the case for logarithmic binning *J. Am. Soc. Inform. Sci. Technol.* **61** 2417–25
- Mitchard E T A *et al* 2014 Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites *Glob. Ecol. Biogeogr.* **23** 935–46
- Mitchell S J 2013 Wind as a natural disturbance agent in forests: a synthesis *Forestry* **86** 147–57
- Negrón-Juárez R I, Chambers J Q, Guimaraes G, Zeng H, Raupp C F M, Marra D M, Ribeiro G H P M, Saatchi S S, Nelson B W and Higuchi N 2010 Widespread Amazon forest tree mortality from a single cross-basin squall line event *Geophys. Res. Lett.* **37** L16701
- Negrón-Juárez R I, Chambers J Q, Marra D M, Ribeiro G H P M, Rifai S W, Higuchi N and Roberts D 2011 Detection of subpixel treefall gaps with landsat imagery in central Amazon forests *Remote Sens. Environ.* **115** 3322–8

- Negrón-Juárez R I *et al* 2017 Windthrow variability in central Amazonia *Atmosphere* **8** 28
- Negrón-Juárez R I, Koven C, Riley W, Knox R and Chambers J 2015 Observed allocations of productivity and biomass, and turnover times in tropical forests are not accurately represented in CMIP5 Earth system models *Environ. Res. Lett.* **10** 064017
- Nelson B W, Kapos V, Adams J B, Oliveira W and Braun O 1994 Forest disturbance by large blowdowns in the Brazilian Amazon *Ecology* **75** 853–8
- Nemani R R, Keeling C D, Hashimoto H, Jolly W M, Piper S C, Tucker C J, Myneni R B and Running S W 2003 Climate-driven increases in global terrestrial net primary production from 1982–1999 *Science* **300** 1560–3
- Nogueira Lima M *et al* 2012 Allometric models for estimating above- and below-ground biomass in Amazonian forests at Sao Gabriel da Cachoeira in the upper Rio Negro, Brazil *Forest Ecol. Manage.* **277** 163–72
- Pan Y, Birdsey R A, Phillips O L and Jackson R B 2013 The structure, distribution, and biomass of the world's forests *Ann. Rev. Ecol. Evol. Syst.* **44** 593–622
- Quesada C A *et al* 2012 Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate *Biogeosciences* **9** 2203–46
- Rankin-de Merona J, Hutchings R W and Lovejoy T 1990 *Four Neotropical Forests* ed A Gentry (New Haven: Yale University Press) pp 573–84
- Ribeiro G *et al* 2016 Mechanical vulnerability and resistance to snapping and uprooting for central Amazon tree species *Forest Ecol. Manage.* **380** 1–10
- Rifai S W, Munoz J D U, Negrón-Juárez R I, Arevalo F R R, Tello-Espinoza R, Vanderwel M C, Lichstein J W, Chambers J Q and Bohlman S A 2016 Landscape-scale consequences of differential tree mortality from catastrophic wind disturbance in the Amazon *Ecol. Appl.* **26** 2225–37
- Schiatti J *et al* 2016 Forest structure along a 600 km transect of natural disturbances and seasonality gradients in central-southern Amazonia *J. Ecol.* **104** 1335–46
- Sheil D, Burslem D and Alder D 1995 The interpretation and misinterpretation of mortality-rate measures *J. Ecol.* **83** 331–3
- Shepard R N 1962 The analysis of proximities: multidimensional scaling with an unknown distance function *Psychometrika* **27** 125–40
- Shimabukuro Y E and Smith J A 1991 The least-squares mixing models to generate fraction images derived from remote-sensing multispectral data *IEEE Trans. Geosci. Remote Sens.* **29** 16–20
- Sombroek W 2001 Spatial and temporal patterns of Amazon rainfall—Consequences for the planning of agricultural occupation and the protection of primary forests *Ambio* **30** 388–96
- Stephenson N L *et al* 2014 Rate of tree carbon accumulation increases continuously with tree size *Nature* **507** 90
- Stephenson N L and van Mantgem P J 2005 Forest turnover rates follow global and regional patterns of productivity *Ecol. Lett.* **8** 524–31
- Stephenson N L, van Mantgem P J, Bunn A G, Bruner H, Harmon M E, O'Connell K B, Urban D L and Franklin J F 2011 Causes and implications of the correlation between forest productivity and tree mortality rates *Ecol. Monogr.* **81** 527–55
- Taylor K E, Stouffer R J and Meehl G A 2012 An overview of CMIP5 and the experiment design *Bull. Am. Meteorol. Soc.* **93** 485–98
- ter Steege H *et al* 2006 Continental-scale patterns of canopy tree composition and function across Amazonia *Nature* **443** 444–7
- ter Steege H *et al* 2013 Hyperdominance in the Amazonian tree flora *Science* **342** 325
- Vandermeer J, de la Cerda I G, Boucher D, Perfecto I and Ruiz J 2000 Hurricane disturbance and tropical tree species diversity *Science* **290** 788–91
- Wenger K F 1984 *Forestry Handbook* (New York: Wiley)
- Wright S J 2002 Plant diversity in tropical forests: a review of mechanisms of species coexistence *Oecologia* **130** 1–14