Running head: Wind disturbance in fragmented forests

Fragmentation increases wind disturbance impacts on forest structure and carbon stocks in a western Amazonian landscape

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Abstract

Tropical second-growth forests could help mitigate climate change, but the degree to which their carbon potential is achieved will depend on exposure to disturbance. Wind disturbance is common in tropical forests, shaping structure, composition, and function, and influencing successional trajectories. However, little is known about the impacts of extreme winds on second-growth forests in fragmented landscapes, though these ecosystems are often located in mosaics of forest, pasture, cropland, and other land cover types. Indirect evidence suggests that fragmentation increases risk of wind damage in tropical forests, but no studies have found such impacts following severe storms. In this study, we ask whether fragmentation and forest type (old vs. second growth) were associated with variation in wind damage after a severe convective storm in a fragmented production landscape in western Amazonia. We applied linear spectral unmixing to Landsat 8 imagery from before and after the storm, and combined it with field observations of damage to map wind effects on forest structure and biomass. We also used Landsat 8 imagery to map land cover with the goals of identifying old- and second-growth forest and characterizing fragmentation. We used these data to assess variation in wind disturbance across 95,596 hectares of forest, distributed over 6,110 patches. We find that fragmentation is significantly associated with wind damage, with damage severity higher at forest edges and in edgier, more isolated patches. Damage was also more severe in old-growth than in second-growth forests, but
this effect was weaker than that of fragmentation. These results illustrate the importance of considering landscape context in planning tropical forest restoration and natural regeneration projects. Assessments of long-term carbon sequestration potential need to consider spatial variation in disturbance exposure. Where risk of extreme winds is high, minimizing fragmentation and isolation could increase carbon sequestration potential.

Key words: tropical forest, second-growth forest, carbon, wind disturbance, forest fragmentation, remote sensing, Amazon, reforestation

Introduction

Tropical second-growth forests, defined here as forests growing on previously cleared land, can recover biomass quickly and sequester large amounts of carbon (Poorter et al., 2016). These forests could play an important role in mitigating climate change; for example, if allowed to grow undisturbed, existing Latin American second-growth forests could accumulate an additional 8.48 Pg C in the next 40 years, enough to offset all carbon emissions from fossil fuel use and industrial processes in Latin America and the Caribbean from 1993-2014 (Chazdon et al., 2016). Many factors, including past land use, climate, and soil characteristics influence rates and quantities of carbon sequestration in second-growth forests (Poorter et al. 2016, Jakovac et al. 2016, Anderson-Teixeira et al. 2013, Uriarte et al. 2016). In particular, exposure to natural disturbances such as extreme winds, fires, or drought can affect successional trajectories in regenerating forests (Flynn et al., 2009; Anderson-Teixeira et al., 2013, Uriarte et al. 2009, Uriarte et al. 2016), influencing the degree to which the carbon sequestration potential of second-growth forests is achieved.
Furthermore, second-growth forests are typically located in landscapes subject to human influence that are mosaics of old growth, second growth, and other land cover types (Brown and Lugo 1990). Regrowth often happens along existing forest margins (Asner et al., 2009; Sloan et al., 2015), making second-growth forests highly exposed to edge effects, impacts of fragmentation, and anthropogenic disturbances such as fire and logging. Accurately predicting biomass recovery in these forests requires that we understand their disturbance ecology and how their disturbance regimes are influenced by the landscapes in which they are situated.

Wind is a major disturbance in the tropics and has both short-term impacts and lasting legacies in tropical forests (Everham & Brokaw, 1996; Laurance & Curran, 2008; Lugo, 2008). Tropical forests are exposed to extreme winds from tropical storms or via convective downdrafts, squall lines and isolated cold fronts. Convective downdrafts and squall lines are relatively common in the Amazon basin (Garstang et al., 1994; 1998), and associated extreme winds can cause large-scale forest disturbance and tree mortality (Espírito-Santo et al., 2010; Negrón-Juárez et al., 2010). Tropical storms and heavy precipitation events are expected to become more intense with climate change (Knutson et al. 2010, Orlowsky and Senevirante, 2012, IPCC 2013), and warming and land use change will affect future convection patterns (Del Genio et al., 2007; Ramos da Silva et al., 2008). Understanding the determinants of forest susceptibility to extreme winds is thus important for modeling and monitoring future impacts of forest disturbance (US DOE, 2012).

The spatial distribution and size of blowdowns have important consequences for understanding biomass dynamics in tropical forests (Fisher et al., 2008; Chambers et al., 2009; Di Vittorio et al., 2014, Marra et al. 2016). A number of studies have quantified the frequency, return interval, rotation period, and carbon impacts of large blowdowns in the

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Amazon across expanses of old-growth forest (Nelson et al., 1994; Negrón-Juárez et al., 2010; Chambers et al., 2013; Espírito-Santo et al., 2014). However, little is known about the impacts of extreme winds in the fragmented, mosaic landscapes in which tropical second-growth forests occur. If forest fragmentation increases the impacts of wind disturbance, this difference could affect estimates of potential carbon sequestration in tropical second-growth forest.

Impacts of extreme wind on both individual trees and stand-level carbon balance differ depending on species composition and forest structure. Damage is most severe for pioneer species, species with low wood density, taller trees, and trees with higher slenderness coefficient, i.e. a larger height for a given diameter (Zimmerman et al., 1994; Curran et al., 2008; Canham et al., 2010; Uriarte et al., 2012; Rifai et al. 2016, Putz et al., 1983; Everham & Brokaw, 1996; McGroddy et al., 2013, Mitchell 2012, Ribeiro et al. 2016). Stand structure characteristics such as canopy height, canopy density, basal area, and median diameter are positively correlated with the amount of wind damage in a stand (Everham & Brokaw, 1996; Uriarte et al., 2004; McGroddy et al., 2013). Susceptibility to damage also increases with stand age in earlier stages of succession, but may decline in older stands (Everham & Brokaw, 1996). These shifts are due to both changes in forest structure and changes in species composition: though canopy height, density, and basal area increase over succession, species composition often shifts away from low wood-density pioneers towards late-successional species with higher wood density (Bazzaz & Pickett, 1980; Lohbeck et al., 2013).

Though second-growth forests are often highly fragmented and located in mosaic landscapes, few studies have considered the influence of landscape and patch structure on wind damage. Fragmentation may influence exposure to strong winds because landscape

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variability influences the way wind moves, and generates heterogeneity in wind speeds and wind exposure through a number of mechanisms. Wind speeds vary with surface roughness, with winds gaining more speed over low-roughness vegetation such as open grassland, brush, or agricultural crops (Fons, 1940; Oliver, 1971; Davies-Colley et al., 2000). Accordingly, wind speeds decline with distance from forest-pasture edges (Davies-Colley et al., 2000), and there is strong wind turbulence at high-contrast forest edges (Somerville, 1980; Morse et al., 2002) (Quine and Gardiner 2007). Wind also moves more quickly though open forest (Somerville, 1980; Kanowski et al., 2008). Forest edges have lower biomass and a more open canopy (de Casaneve et al., 1995; Laurance et al., 1997b; Harper et al., 2005), implying that wind speeds should be higher at forest edges than in the interior. Furthermore, pioneer species are more common close to forest edges, elevating the vulnerability of edge forest to windthrow (Oosterhoorn & Kappelle, 2000; Laurance et al., 2006).

Despite variation in exposure and vulnerability to extreme winds, evidence for impacts of fragmentation on wind damage in tropical forests is lacking. Several studies in temperate silvicultural systems have detected edge effects on wind damage (Peltola, 1996; Talkkari et al., 2000; Zeng et al., 2004) but this effect has been more challenging to detect in diverse tropical forests. The Biological Dynamics of Forest Fragments experiment in the Brazilian Amazon found high tree mortality close to forest edges, with uprooting more frequent relative to standing dead trees (Ferreira & Laurance, 1997; Laurance et al., 1997a; Mesquita et al., 1999). However, this mortality was not linked to specific extreme wind events and could have resulted from other factors (e.g., desiccation). Several studies have examined fragmentation effects on wind damage after tropical storms, and have found little evidence that damage varies with fragmentation (Catterall et al., 2008; Grimbacher et al., 2008). The degree to which fragmentation increases the risk of damage from extreme winds
in tropical forests thus remains an open question.

Detecting effects of fragmentation on wind damage may be difficult with a field sampling approach. Extreme winds can be highly patchy (Bellingham et al., 1992; Imbert et al., 1996; Grove et al., 2000; Pohlman et al., 2008). Detecting spatial patterns within heterogeneous, patchy phenomena requires large sample sizes, and inadequate sampling can make it difficult or impossible to detect patterns (Loehle, 1991). Estimates of landscape level mortality based on field plot observations may miss up to 17% of mortality (Chambers et al., 2013), and field plot studies may lack the statistical power to detect the effect of fragmentation on wind damage (Grimbacher et al., 2008). However, remote sensing allows detection of patterns that may be unfeasible or impossible in ground-based studies (Chambers et al., 2007). Recently developed remote sensing techniques can detect small blowdowns (Negrón-Juárez et al., 2011). Unlike plot-based approaches, remote sensing allows estimation of wind damage across broad areas, and in combination with field data can improve our understanding of disturbance and carbon dynamics in tropical mosaic landscapes.

Here, we use remotely sensed data to quantify damage from a mesoscale convective storm system across a fragmented production landscape in the Peruvian Amazon. We use these data in combination with land cover maps to ask:

1) Are second-growth forests more severely fragmented than old-growth forests?
2) How does fragmentation influence forest vulnerability to extreme winds?
3) Does wind damage severity vary in old-growth versus second-growth forests?

We predict that second-growth forests in our study area will be more severely fragmented than old-growth forests, and hypothesize that severity of wind damage will be highest in small, isolated forest fragments and close to forest edges. We expect that second-growth
forests, which have a higher proportion of pioneer species with low wood density, will suffer more severe damage than old-growth forests, composed of less vulnerable high wood density species. This variability could affect forest succession in dynamic, fragmented landscapes, with forest patch and landscape characteristics influencing rates of biomass recovery via effects on exposure and vulnerability to wind disturbance.

Methods

Study area

The city of Pucallpa, the capital of the Ucayali region of Peru, is the largest Amazonian city connected to the national capital, Lima, by road. As a result, Pucallpa is an important transport center, and in recent years has been a hotspot of forest disturbance, deforestation, and fire in the Peruvian Amazon (Oliveira et al., 2007, Schwartz et al., 2015, Uriarte et al., 2012). This research focuses on an area of 2,158 km$^2$ near Pucallpa, surrounding the highway from Lima to Pucallpa. The landscape is heterogeneous, with patches of old growth and second-growth forest surrounded by pastures, oil palm plantations, and smallholder farms (Gutierrez-Velez et al., 2013; Figure 1). Elevation ranges from 150 to 250 m a.s.l and total annual precipitation ranges from about 1500-2500 mm, with a dry season from July to September.

On November 30, 2013, a mesoscale convective system (MCS) passed through the study area, resulting in widespread blowdowns and tree mortality. Though there is insufficient meteorological station data available from the study area to characterize the storm severity, data processed from the GOES-13 satellite using the method described in Bedka and Khlopenkov (2016) indicates high overshooting top probability during the
November 30 storm in the study area (Figure S1). Overshooting tops indicate regions where strong updrafts were present within the MCS. Strong downdrafts are often present near to these updrafts in regions of heavy precipitation. Storms with overshooting tops often generate winds that exceed 58 mph, the criterion for “damaging wind” by the U.S. NOAA National Weather Service (Dworak et al. 2012). Given the heterogeneity in land cover, forest age, and patch size, this landscape offers an ideal opportunity to study how impacts of damaging winds vary with fragmentation and landscape context.

Remote sensing of wind damage

We obtained Landsat 8 OLI scenes covering the study area (path-row 06-066 and 07-066) from 2013 (pre-storm) and 2014 (post-storm; Table S1) at 30 m resolution. All scenes were acquired with atmospheric corrections from the Landsat CDR archive (LaSRC product; USGS 2016) via USGS Earth Explorer (http://earthexplorer.usgs.gov/). The LaSRC product includes a cloud mask band, generated with the FMASK algorithm (Zhu & Woodcock, 2012). We used this band to mask pixels that were cloudy in 2013 or 2014. 1023 ha were masked out due to cloud cover, equal to 0.5% of the study area. Because the atmospheric composition between multi-temporal images differs, especially regarding water vapor and ozone, we applying a radiometric normalization (Hall et al., 1991) to normalize the 2014 scene to the 2013 scene, using the MAD algorithm (Canty and Nielsen, 2008). All remote sensing data processing was conducted in ENVI (Exelis Visual Information Solutions, Boulder, Colorado) unless otherwise indicated.

To map wind damage we follow the approach outlined by Negron-Juarez et al. (2010, 2011), which uses spectral mixture analysis (SMA) to map the change in non-photosynthetic vegetation (NPV) fraction across pixels. SMA assumes that every pixel is a
linear combination of some number of target endmember spectra, such as vegetation, shade, NPV, and/or bare soil, and quantifies the per-pixel fraction of each endmember (Adams & Gillespie, 2006). Wind damage increases the amount of wood, dead vegetation, and litter exposed to the sensor, and so the change in NPV fraction is associated with the amount of wind damage.

We applied linear spectral unmixing to each image using endmembers for green vegetation (GV), NPV, and shade. Endmembers were identified from the 2013 scene using the Pixel Purity Index algorithm (Boardman et al., 1995) available in ENVI (Figure S2). Following unmixing, we normalized the fraction of NPV without shade as NPV/(GV+NPV) so that fractions reflected only relative proportions of NPV and GV, and not differences due to effects of shading (Adams & Gillespie, 2006). Change in NPV (ΔNPV) was calculated by subtracting the normalized NPV fraction in 2013 from 2014.

Field data collection: Wind damage was measured in the field to assess whether ΔNPV provided an adequate approximation of damage. Because previous studies (Negron-Juarez et al. 2011, Rifai et al. 2016) had validated the relationship between ΔNPV and wind damage in old-growth forests, we focused our validation and field data collection on second-growth forest. During the months of July and August of 2014 and 2015, we established 30-0.1 ha forest plots (Figure 1). We used satellite images to identify forest patches, and from those, chose sites where we could locate and get permission from the landowners to access their property. Within these areas, plot locations were selected to encompass a range of ΔNPV. Because plots were slightly larger than a Landsat pixel, plot-level ΔNPV was calculated as the weighted mean of ΔNPV in pixels overlapped by the plot. We determined age of the forest plots from a 28-year land cover time series (Schwartz et al. in press), as the number
of years since the last year that the plot location was classified as non-forest. Though all forest plots were located within forest classified as second growth (see below), not all had been observed as having been clear-cut during the 30 year satellite record, and plot ages ranged from 3 years to >30 (i.e. never cleared). Plots were geolocated using a Garmin GPSMAP 62sc.

In each plot we measured diameter at breast height (dbh) of all trees greater than 5 cm, and coded each tree as damaged (uprooted, trunk snapped, or severe branch loss) or undamaged. Downed or damaged trees that were severely rotted were marked as such, since these trees were likely damaged prior to the 2013 storm. We conducted all analyses including and excluding these previously damaged individuals and it did not significantly affect our results; reported results exclude these trees. Measures of damage include both stems directly thrown by wind and trees that were damaged by other trees, because it is difficult to distinguish between these two types of damage in the field. We calculated aboveground biomass (AGB) using the following allometric equation developed for secondary forest species in the central Amazon (Nelson et al. 1999):

\[ \ln(\text{biomass}) = -1.9968 + 2.4128 \times \ln(\text{DBH}) \]

We divided biomass by two so that estimates were in terms of kg C instead of kg biomass, under the assumption that C makes up 50% of biomass (Brown and Lugo, 1982). To characterize plot-level damage, we calculated total damaged biomass, proportion biomass damaged, total stems damaged, and proportion of stems damaged for each plot. We assessed the relationship between ΔNPV and wind damage by calculating linear regressions of ΔNPV vs. field measurements of wind damage in the 30 forest plots. To estimate AGB loss across the study area, we used the parameters from the linear model of ΔNPV vs. total AGB lost in field plots (Figure S6c), and applied it to each forest pixel to calculate lost biomass.
Based on a pixel’s NPV. Because allometries based on secondary forest species yield lower estimates of biomass, using an allometric equation designed for secondary forest species across the whole study area is likely to underestimate biomass lost in old-growth forest. Furthermore, wind damage tends to increase with age (Figure 3), and so old-growth forests likely experienced more severe damage than second-growth forests. However, because we measured wind damage in second-growth forests only, we are extrapolating using parameters derived from the relationship between damage and AGB in second-growth forests. Therefore, our estimates represent a conservative estimate of biomass lost across in the study area’s forests, particularly for old-growth forests.

Remote sensing of land cover: We developed a land cover classification at 30 m resolution for use in generating predictor variables related to fragmentation and masking analyses to forested areas. The classification expanded on the approach laid out in Gutierrez-Velez and DeFries (2013). Land use classes were old-growth forest, second-growth forest, mature oil palm (> 3 years old), and “other,” which included young oil palm (< 3 years old), bare ground, burned non-forest areas, fallow, pasture, degraded pasture, and bodies of water. Training data were collected in the field, and for the training data, second-growth forests were identified as tree-dominated vegetation growing in areas that had previously been cleared, with significantly lower basal area than old-growth forests in the study area (Gutiérrez-Vélez et al., 2011). Old-growth forests were identified as predominantly residual forest from logging and extraction of non-timber resources, but they have significantly higher basal area and biomass than second-growth forests (Gutiérrez-Vélez et al., 2011). Ultimately, whether a pixel was classified as old-growth or second-growth depends on its spectral properties, which do not always coincide with its land-use history.
We classified Landsat 8 OLI images (Table S1) and with a random forest classification built with several spectral indices and spectral transformations: i) NDVI, ii) bare soil, vegetation, and shade fractions from SMA, iii) brightness, greenness, and third from a tasseled cap transformation, and iv) first- and second-order texture measures. Components i-iii were shown to be effective for classifying the non-oil palm land cover classes in a land cover classification from the same study area (Gutiérrez-Vélez & DeFries, 2013). Component iv, the texture measures, were useful for distinguishing oil palm plantations, which are spectrally similar to secondary forests but appear more uniform in satellite images due to even-aged planting. Training and testing data for land cover classes were collected during a 2015 field campaign and included 2198.52 ha total, divided among classes (Table S2). For more details about the classification, see Appendix S1.

The land cover map from 2014 was used to mask analyses to forested areas (old growth and second growth). We also masked areas near known anthropogenic disturbance, since spillover disturbance from recent forest clearing might bias results along forest edges. To do so, we identified recently deforested areas – areas that were classified as forest in 2013 and as non-forest in 2014 – and masked all pixels within 60 m to prevent anthropogenic disturbance biasing results (Figure S3).

**Characterizing forest fragmentation:** We used Fragstats (McGarigal et al. 2012) to characterize forest patch fragmentation. Old-growth and second-growth forests were all treated as a single forest category for the purpose of characterizing patches. Fragmentation has three key axes: area, edge, and isolation (Fahrig, 2003; Haddad et al., 2015). We calculated one Fragstats metric to represent each of these axes (Figure 2). Patch area (ha) represents patch size. Edginess is quantified with the shape index, which is calculated as:
\[
SHAPE = \frac{0.25p}{\sqrt{a}}
\]

where \(p\) is the patch perimeter and \(a\) is the patch area. Shape index increases as the perimeter of a patch gets more complex, and equals 1 if a patch is a perfect square. We quantified isolation with the proximity index. The proximity index takes into account the area and distance of forest within a particular radius around the focal patch, and increases from zero with the upper limit determined by the search radius. For a given patch \(l\), proximity index is calculated as:

\[
PROX = \sum_{j=1}^{n} \frac{a_{ij}}{h_{ij}^2}
\]

where \(a_{ij}\) is the area \((m^2)\) of patches \(j=1...n\) within specified neighborhood radius \((m)\) of focal patch \(i\) and \(h_{ij}\) is the distance \((m)\) between patch \(i\) and patch \(j\). Using this formulation assumes that larger and closer patches decrease patch isolation more than smaller or more distant ones, a reasonable assumption. We calculated proximity index with several radii \((250\ m, 500\ m, 1000\ m, 2000\ m, 4000\ m\ and\ 10000\ m)\), but these indices were highly correlated and there was no significant different in model performance depending on the distance, so we used the 1000 m radius in our final models. So that higher values represented increasing isolation, we multiplied proximity index by -1.

Statistical analysis: We compared sizes of damaged vs. undamaged trees, and fragmentation variables in old- vs. second-growth forest using t-tests. To test the relationship between wind damage, forest fragmentation, and forest age (old vs second growth), we fit a generalized linear model to predict \(\Delta NPV\) at the pixel scale (Table 1). Pixels with \(\Delta NPV\) less than 0 were excluded from analysis, because a decline in NPV cannot represent negative

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damage and instead likely represents changes due to forest succession or recovery from prior disturbance. Both pixel characteristics and patch characteristics were included as predictors. Pixel level predictors were distance from forest edge and a binary predictor for second-growth forest (0 = old growth, 1 = second growth). Patch level predictors were area, edginess, and isolation of the patches in which pixels were located. Because the total number of pixels was large (461,610) and ΔNPV was highly left skewed, we stratified pixels according to ΔNPV (0-0.05, 0.05-0.15, 0.15-0.25, >0.25) and randomly sampled 2000 pixels from each stratum for use in statistical analyses (Figure S4). The sample was bootstrapped 200 times. ΔNPV was log-transformed to meet the assumption of normality. Distance from edge was also log-transformed because it was highly left-skewed. To facilitate interpretation, all predictors were scaled to unit standard deviation by subtracting the mean and dividing by the standard deviation (Gelman and Hill, 2007). To test for collinearity among predictors we calculated variance inflation factors (VIF; Fox & Monette, 1992) and condition indices (Belsley 1991). VIF values greater than ~5 indicate strong collinearity (Dormann et al., 2012), though values as low as 2 can have impacts on parameter estimates (Graham 2003). VIF for all predictors was < 4 with the exception of edginess (VIF = 5.2). To address this potential collinearity issue we ran the model with all predictors other than patch area, which was correlated with the other fragmentation predictors and was the predictor with the weakest effect in the full model. The maximum VIF in this partial model was 2.2, and the parameters for all remaining predictors were qualitatively the same as in the full model. We followed the same steps, removing edginess, which had the highest VIF at 2.2. In this partial model, the maximum VIF was 1.4 and still, parameters were qualitatively the same. Condition indices greater than 30 indicate substantial collinearity (Belsley 1991). All condition indices in our model were < 5. We tested for spatial autocorrelation among model residuals by calculating Moran’s I and found...
no spatial autocorrelation in the model residuals (Moran’s I = 0.0003, p = 0.45). Model parameters reported are the median estimates of the 200 bootstrapped models and 95% bootstrapped confidence intervals. Statistical analyses were conducted in R (R Core Team, 2016).

Results

Overview: linking field and remote sensing data

Validation of ΔNPV with field observations: Mean pre-damage AGB in field plots was 62.04 Mg C ha⁻¹ (s.d. = 13.31, Table S4). Mean AGB damaged was 17.5 Mg C ha⁻¹ (s.d. = 18.7), or 24.6% of pre-storm AGB (s.d. = 25.1%). Mean stem density in field plots was 1286 stems ha⁻¹ (s.d. = 342.6), with an average 16.5% of stems damaged (s.d. = 15.7). Damaged stems were significantly larger than undamaged stems (Figure S5, t = -9.73, p < 0.0001).

ΔNPV was strongly related to damage as measured in the field plots. It was most strongly correlated with the proportion of stems damaged in field plots (R² = 0.699, Figure 3), but the relationship held when damage was quantified in terms of total number of stems damaged (R² = 0.649), total AGB damaged (R² = 0.542), or proportion of AGB damaged (R² = 0.603, Figure S6). On average ΔNPV was low across the landscape: mean ΔNPV was 0.03, and standard deviation was 0.04 (Figure 4). Five percent of forest pixels, or 2058 ha, had ΔNPV higher than 0.1, corresponding to 20.7% stems damaged, or 31.5% of carbon lost (22.5 Mg C ha⁻¹, Table 2). ΔNPV was greater than 0.2 in 0.8% of forest pixels (348.5 ha), corresponding to 48.6% stems damaged, or 82.0% of carbon lost (59.1 Mg C ha⁻¹, Table 2). The total biomass lost as a result of the wind event in second-growth forests was 0.161 Tg C.
(95% CI = 0.026, 0.553, Table 2). When extrapolating across the whole study area, carbon lost was approximately 0.296 Tg C (95% CI = 0.05, 1.02), with 54 percent in second growth forest, and 46 percent in old growth (Table 2). Estimates for carbon lost in old-growth forest are based on extrapolation of data from second-growth forest, and therefore they are conservative estimates of total carbon lost.

Characterizing land cover and fragmentation: The land cover classification accurately distinguished between oil palm, old-growth forest, second-growth forest, and other classes (Table S3). Overall accuracy was 96.4%. Forty-four percent of the study area, 95,596 ha, was classified as forest. Forty percent of forest pixels were classified as old-growth forest, and 60% were classified as second-growth forest (Figure 1). There were 6110 forest patches in the study area, with a mean area of 42.1 ha (Figure S7). Mean edginess (shape index) was 1.3, and mean isolation (-1*proximity index) was -19688 (Figure S7).

Fragmentation in old- vs. second-growth forests

Degree of fragmentation varied across old-growth and second-growth forest pixels, with second-growth forests more fragmented along most measures (Figure 5). Second-growth forest pixels were closer to forest edges (t = 237.15, p < 0.001, Table S5), but in less edgy patches (t = 134.76, p < 0.0001, Table S5). Second-growth pixels were also located in smaller (t = 141.28, p < 0.001, Figure 5) and more isolated patches, (t = 47.658, p < 0.0001, Figure 5).
Wind damage model

Fragmentation and forest type were significantly associated with ΔNPV ($R^2 = 0.158$, 95% bootstrap CI = [0.143, 0.173]). Distance to edge had the strongest association with ΔNPV (Figure 6), which exponentially decreased with pixel distance from forest edge (Figure 7a). Patch edginess was positively associated with ΔNPV, with pixels in edgier patches suffering more severe wind damage (Figure 6, Figure 7c). Isolation also influenced damage: ΔNPV was higher in more isolated patches (Figure 6, Figure 7d). Patch area was negatively associated with damage, though this effect was weaker than that of the other fragmentation predictors (Figure 6, Figure 7b). Predicted ΔNPV was slightly higher for old-growth forest pixels, though the difference between second growth and old growth was small compared to the predicted variation in ΔNPV associated with fragmentation (Figure 6, Figure 7).

Discussion

Effects of fragmentation on wind damage

This study provides the first unequivocal empirical evidence that fragmentation increases risk of damage from extreme wind events in tropical forests. The severe convection event that occurred in our study region caused an overall loss of approximately 0.3 Tg C in the study area (0.14 in second-growth forest and 0.16 in old-growth). When averaged across the total forested area in the study area (95,596 ha), this amounts to 3.09 Mg C ha⁻¹ (2.79 Mg C ha⁻¹ in second-growth, and 3.55 in old-growth), more than sixty percent greater per hectare than figures from a recent study that estimated annual carbon loss from natural disturbances in the entire Amazon forest (Espírito-Santo et al., 2014). That study estimated
the total loss at 1.3 Pg C y\(^{-1}\), an average of 1.9 Mg C ha\(^{-1}\) across the \(\sim 6.8 \times 10^8\) ha of Amazon forest.

A number of differences between their study and ours could explain the discrepancy. The Espírito-Santo et al. study mapped disturbances across a study area many times the size of ours, and developed a disturbance size-frequency distribution for the entire Amazon. The disturbances captured in our far smaller study are likely on the intermediate-to-large end of their disturbance size-frequency distribution. However, the discrepancy might also reflect differences in landscape structure in the two studies. Espírito-Santo et al. focused on contiguous forest, where, based on our results, wind damage is likely to be less severe than in the fragmented landscapes of our study region. These findings illustrate the importance of considering fragmented landscapes when assessing disturbance regimes in tropical forests. Studies that do not consider the effects of landscape configuration may underestimate the importance of wind disturbance for quantifying the tropical forest carbon sink. Recent estimates suggest 70% of the world’s forests are within 1 km of a forest edge (Haddad et al., 2015), and that 19% of tropical forests are less than 100 m from an edge (Brinck et al. 2017). Brinck et al. (2017) estimate that edge effects result in 0.34 Gt additional carbon emissions from tropical forests per year, though this estimate does not explicitly take into account effects of extreme winds. Considering the impacts of extreme winds in fragmented landscapes would likely affect estimates of the effects of fragmentation on forest carbon balance, and would influence our understanding of the importance of extreme wind events for driving carbon cycling in the Amazon.

Though many studies suggest that fragmented forests should have heightened vulnerability to wind damage (Saunders et al., 1991; Laurance & Curran, 2008), evidence for this phenomenon has been lacking. For example, a number of studies that set out to
measure effects of fragmentation on wind damage after Cyclone Larry, a category 5 tropical cyclone, found little difference in wind damage between fragments and continuous forest (Catterall et al., 2008; Grimbacher et al., 2008; Pohlman et al., 2008). Our study may have detected an effect where former studies did not for several reasons. First, the storm we considered was not as intense as a Cyclone Larry, and continuous forest cover may provide a protective benefit only up to a certain degree of storm intensity (Catterall et al. 2008). We do not have precise wind speed measurements from the date of the storm, but the presence and intensity of overshooting tops indicates that winds were probably ≥ 93 km/h (Bedka and Khlopenkov, 2016). In contrast, Category 5 tropical storms are associated with sustained winds > 200 km/h. Lending support to this threshold hypothesis, a study after Hurricane Hugo in South Carolina found that in areas struck by the most intense part of the hurricane, species differences in wind resistance were not apparent (Hook et al., 1991). Differences in rates of damage across species were only observed in areas where wind speeds were lower. Variation in exposure and vulnerability to extreme winds due to species composition and landscape configuration may come into play only when winds are not so severe that they cause widespread damage regardless.

Second, previous studies of fragmentation and wind damage were based on field data from a relatively small number of plots. Heterogeneity in damage and wind speeds may have affected the statistical ability to detect underlying patterns related to fragmentation (Grimbacher et al., 2008). This patchiness and unmodeled variation in wind speeds is likely the reason for the substantial unexplained variance in our statistical models. However, because our remote sensing approach allows us to consider a broad landscape with a large sample size we are able to detect an effect of fragmentation despite the noise, demonstrating, as many other studies have, the usefulness of remote sensing for understanding ecosystems at landscape to regional scales (Chambers et al. 2007).
Fragmented forests may be more prone to wind damage via two main mechanisms: because they are exposed to stronger winds than continuous forest, or because they are more vulnerable to strong winds due to differences in species composition or forest structure (Laurance and Curran 2008). We found effects of all three axes of fragmentation – isolation, edge, and area – on wind damage, which suggest possible support for both mechanisms. The effects of isolation are probably due to exposure to stronger winds. Forest slows wind down; rougher surfaces exert more drag leading to slower wind speeds (Davies-Colley et al., 2000). Wind picks up more speed over smoother vegetation types, like pasture. Because isolated fragments are surrounded by larger expanses of open areas and non-forest land cover types, they likely are subject to stronger winds. However, species composition may also differ depending on patch isolation. Because we do not have measurements of species composition in relation to isolation, we cannot rule out that differences in composition also contribute to the observed effect of isolation.

Edge and area effects on wind damage are more difficult to attribute to exposure versus vulnerability, and could be due to either or both mechanisms. We found that pixels close to forest edges and pixels in edgier patches were more likely to be severely damaged. We also found a weak effect of patch size, likely because pixels in smaller patches are closer to edges. Forest edges are exposed to stronger winds (Somerville, 1980; Morse et al., 2002), but there are also well-documented edge effects on species composition that could increase vulnerability to wind damage (Oosterhoorn & Kappelle, 2000; Laurance et al., 2006). The degree to which differences in exposure or vulnerability explain the relationship between fragmentation and wind damage has implications for management actions to minimize impacts of strong winds. Future research could focus on disentangling the mechanisms responsible for these patterns.
Wind damage in old- vs. second-growth forest

The results from the model predicting wind damage (ΔNPV) indicate that when controlling for fragmentation, second-growth forests suffer slightly lower damage (have lower ΔNPV) than old-growth forests, counter to our initial hypothesis. Because trees with lower wood density are more prone to wind damage and community mean wood density tends to increase over succession in wet tropical forests (Bazzaz & Pickett, 1980; Lohbeck et al., 2013), we hypothesized that wind damage would be more severe in second-growth forests. Our finding to the contrary may be due to differences in tree stature between old-growth and second-growth forests. Larger trees and more slender trees are more susceptible to wind damage, in particular to uprooting (Putz et al., 1983; Zimmerman et al., 1994; Everham & Brokaw, 1996; Canham et al., 2010, Slodicak and Novak 2006, Ribeiro et al. 2016), which translates into differences in damage across sites with different forest structure. For example, Uriarte et al. (2004) found that damage after Hurricane Georges in the Dominican Republic was higher in sites with higher basal area and that young forests with low basal area were not severely affected by hurricane. Similarly, McGroddy et al. (2013) found that forest stands in the southern Yucatan with taller canopies and higher basal area suffered more severe hurricane damage, and that these structural differences were associated with past land use. Furthermore, because of the high levels of anthropogenic disturbance in the study area, we do not necessarily expect the successional shifts in species composition that are predicted for relatively undisturbed forests. Old-growth forests in the study area have never been completely cleared, but they have still been subject to anthropogenic disturbance, such as selective logging and fire. Selective logging tends to target timber species with higher wood density (Verburg & van Eijk-Bos, 2003), so the largest remaining trees in selectively logged forests may be species with low wood density. Large stature and low-density wood would make these forest fragments

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especially prone to wind damage, perhaps explaining the higher damage we observed in old-growth forests. Alternatively, it is possible that large, high wood-density trees are more vulnerable to wind, or that when they do fall, they result in larger blowdowns due to a domino effect of large, heavy trees causing more damage than trees with lighter wood. In future studies, additional field plot data, with information on forest stature, species identification and wood density from damaged vs. undamaged trees could help further elucidate which of these mechanisms drives the observed pattern.

In our model, however, fragmentation had a much stronger influence on damage than forest type (Figure 6, 8). Second-growth forests in the study area are more fragmented than old-growth forests, which ultimately might result in more severe wind impacts in these forests. Elsewhere, studies have found that second growth tends to happen along forest margins and in small fragments surrounded by non-forest land use (Helmer, 2000; Asner et al., 2009; Sloan et al., 2015). Wind is not the only disturbance for which risk is higher along edges: fire in the Amazon tends to be concentrated along forest edges (Cochrane & Laurance, 2002; Alencar et al., 2004; Armenteras et al., 2013). There is potential for wind and fire to interact and amplify the other’s impacts: studies in temperate ecosystems have found that an earlier fire can increase the severity of subsequent blow downs, and wind damage can increase the risk of fire by adding fuels and opening up the forest canopy (Myers & van Lear, 1998; Kulakowski & Veblen, 2002; Kulakowski & Veblen, 2007). These interactions might occur in the Amazon, and could exacerbate disturbance effects on forest carbon balance.

Wind and other disturbances can alter successional pathways in regrowing forests (Anderson-Teixeira et al., 2013; Uriarte et al. 2016). Variability in disturbance risk should thus be taken into account in spatial planning, management, and carbon accounting in
tropical second-growth forests where the goal is to promote carbon sequestration. Silviculture has long considered wind damage risk in site and species selection and planting configuration (Somerville, 1980; Savill, 1983; Talkkari et al., 2000). However, managing tropical second-growth forests for carbon is a relatively new endeavor and the way landscape configuration influences susceptibility to disturbance is not well understood for tropical forests (US DOE, 2012). However, where possible, and where risk of extreme winds is high, minimizing fragmentation and isolation could reduce risk of wind damage. Smallholders, too, get services such as timber or other forest products from forest fragments on their properties, and may wish to protect their forest fragments from the impacts of extreme winds. Promoting regrowth close to existing forests, maintaining less edgy patches, or planting wind-firm species in isolated fragments and close to forest edges are all steps that smallholders could take to reduce risk of wind damage in their forests.

Future research should attempt to disentangle the mechanisms behind the patterns observed in this study. Understanding the degree to which differences in vulnerability versus exposure underlie variation in wind impacts will clarify appropriate management actions to minimize risk of wind damage in second-growth or remnant forests. Fragmentation experiments such as the Biological Dynamics of Forest Fragments experiment in Brazil have shed light on how fragmentation affects forest composition, structure, and microclimate (Laurance et al., 2002). However, understanding what those changes mean for impacts of extreme winds is not straightforward, and doing so would require some “luck” in that a severe windstorm would have to strike the experiment. This limitation presents some challenges in studying mechanisms of wind damage in fragmented landscapes, but there are ways forward. Fragmentation experiments like the aforementioned, but located in landscapes that suffer frequent severe wind events, such as Caribbean forests, could be useful in that the likelihood of extreme winds striking an

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experiment would be higher. However, an experimental approach relying on random chance is not the only way to further investigate these mechanisms. Improvements in modeling and mapping wind speed and in our understanding of how wind interacts with complex landscapes will further shed light on how exposure varies with fragmentation. Advances in remote sensing technology, which are beginning to provide a more detailed picture of forest structure and composition, will be useful in understanding ecological mechanisms responsible for variability in disturbance impacts (Chambers et al., 2007). Finally, much of what we already know about variation in species and stand susceptibility to wind comes from opportunistic field sampling after extreme winds (e.g. Zimmerman et al., 1994; Uriarte et al., 2004; McGroddy et al., 2013), and there is a need for further opportunistic post-storm sampling in fragmented landscapes. Continued monitoring of forest disturbance in fragmented landscapes, such as with the remote sensing approach demonstrated in this paper, is essential so that such opportunities are not lost. An improved understanding of how and why fragmentation and landscape configuration influence disturbance regimes in tropical second-growth forests will help ensure that the carbon potential of tropical second-growth forests is better achieved.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data available from the Columbia Academic Commons:

https://doi.org/10.7916/D8VH5V6W
### Tables

Table 1: Model covariates, descriptions, and summary statistics.

<table>
<thead>
<tr>
<th>Variable name</th>
<th>Description</th>
<th>Landscape mean (SD)</th>
<th>Bootstrap sample mean (95% bootstrapped CI)</th>
<th>Bootstrap sample SD (95% bootstrapped CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Response</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ΔNPV</td>
<td>Change in non-photosynthetic vegetation fraction in pixel, i.e. wind damage (log transformed).</td>
<td>0.034 (0.039)</td>
<td>0.1560 [0.1556, 0.1565]</td>
<td>0.1318 [0.1312, 0.1322]</td>
</tr>
<tr>
<td><strong>Predictors</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Distance to edge</td>
<td>Pixel distance to forest edge (meters)</td>
<td>102.5 (2.5)</td>
<td>69.4 [68.0, 70.8]</td>
<td>2.39 [2.36, 2.44]</td>
</tr>
<tr>
<td>Secondary</td>
<td>Binary variable for second growth. 0 = old growth, 1 = second growth</td>
<td>0.53 (0.50)</td>
<td>0.59 [0.58, 0.60]</td>
<td>0.491 [0.490, 0.493]</td>
</tr>
<tr>
<td>Area</td>
<td>Patch size in which pixel is located (hectares).</td>
<td>33247.5 (28869.9)</td>
<td>33035.4 [32503.2, 33605.0]</td>
<td>30899.6 [30592.6, 31200.1]</td>
</tr>
<tr>
<td>Edginess (shape index)</td>
<td>Shape index for patch in which pixel is located.</td>
<td>24.4 (14.6)</td>
<td>24.9 [24.6, 25.2]</td>
<td>15.9 [15.7, 16.0]</td>
</tr>
<tr>
<td>Isolation (-1* proximity index)</td>
<td>Proximity index for patch in which pixel is located.</td>
<td>75887.7 (50523.7)</td>
<td>-71336.3 [-72230.3, -70415.9]</td>
<td>48734.9 [47999.9, 49327.5]</td>
</tr>
</tbody>
</table>

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Table 2: Summary of wind damage effects by forest type. 95% confidence intervals for lost carbon are in parenthesis.

<table>
<thead>
<tr>
<th></th>
<th>Old growth</th>
<th>Second growth</th>
<th>All forest</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total area (hectares)</td>
<td>38137</td>
<td>57459</td>
<td>95596</td>
</tr>
<tr>
<td>Mean ΔNPV</td>
<td>0.033</td>
<td>0.035</td>
<td>0.034</td>
</tr>
<tr>
<td>Proportion pixels with ΔNPV &gt; 0.1</td>
<td>0.04</td>
<td>0.05</td>
<td>0.05</td>
</tr>
<tr>
<td>Proportion pixels with ΔNPV &gt; 0.2</td>
<td>0.01</td>
<td>0.01</td>
<td>0.01</td>
</tr>
<tr>
<td>Carbon lost (Tg C)</td>
<td>0.135 (0.020, 0.470)</td>
<td>0.161 (0.026, 0.553)</td>
<td>0.296 (0.05, 1.02)</td>
</tr>
<tr>
<td>Biomass lost per ha (Mg C/ha)</td>
<td>3.55 (0.519, 12.32)</td>
<td>2.79 (0.460, 9.63)</td>
<td>3.09</td>
</tr>
</tbody>
</table>
Figure captions

Figure 1: Location of the study area, near Pucallpa, Ucayali, Peru. Inset depicts forest cover, and locations of field plots and roads.

Figure 2: Conceptual figure illustrating axes of fragmentation, and variables associated with fragmentation included in analyses. Green squares represent forest pixels, and adjacent pixels represent a patch. Orange outline indicates focal pixel/patch for distance to edge and isolation measures.

Figure 3: ΔNPV vs. proportion of stems > 5 cm DBH damaged in second growth forest field plots. Shaded areas indicate 95% confidence interval of regression line. Regression p-value < 0.001.

Figure 4: Map of wind damage (ΔNPV) in study area. Insets show two areas of interest where several field plots were located.

Figure 5: Comparison of the distribution of fragmentation variables between old-growth and second-growth forest pixels. Boxes show 25, 50, and 75% quantiles and whisker endpoints are 2.5 and 97.5% quantiles of observed data. Light grey points are outliers. Figures include data from all forest pixels in the study area. Fragmentation variables are a)

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distance to edge, b) area, c) edginess, and d) isolation.

Figure 6: Parameter estimates from wind damage model. Points show the median coefficient estimates from the 200 bootstrapped model fits, whiskers show bootstrapped 95% confidence interval.

Figure 7: Model predictions of ΔNPV and the fragmentation predictors. Solid lines depict predictions of the median coefficient estimates from bootstrapped model fits, dashed lines and shaded areas show predictions of 2.5 and 97.5% quantiles of coefficient estimates. a) distance from edge. b) patch area. c) edginess. d) isolation.
$y = 0.026 + 0.36 \cdot x, \quad R^2 = 0.699$
$r.m.s.e. = 0.036$
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