



## Mechanical vulnerability and resistance to snapping and uprooting for Central Amazon tree species



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### ARTICLE INFO

#### Article history:

Received 14 March 2016

Received in revised form 23 August 2016

Accepted 24 August 2016

Available online 28 August 2016

#### Keywords:

Tree static winching

Critical turning moment

Tree allometry

Functional traits

Blowdown

Wind-disturbance

### ABSTRACT

High descending winds generated by convective storms are a frequent and a major source of tree mortality disturbance events in the Amazon, affecting forest structure and diversity across a variety of scales, and more frequently observed in western and central portions of the basin. Soil texture in the Central Amazon also varies significantly with elevation along a topographic gradient, with decreasing clay content on plateaus, slopes and valleys respectively. In this study we investigated the critical turning moments ( $M_{crit}$  - rotational force at the moment of tree failure, an indicator of tree stability or wind resistance) of 60 trees, ranging from 19.0 to 41.1 cm in diameter at breast height (DBH) and located in different topographic positions, and for different species, using a cable-winch load-cell system. Our approach used torque as a measure of tree failure to the point of snapping or uprooting. This approach provides a better understanding of the mechanical forces required to topple trees in tropical forests, and will inform models of wind throw disturbance. Across the topographic positions, size controlled variation in  $M_{crit}$  was quantified for *cardeiro* (*Scleronema mincranthum* (Ducke) Ducke), *mata-matá* (*Eschweilera* spp.), and a random selection of trees from 19 other species. Our analysis of  $M_{crit}$  revealed that tree resistance to failure increased with size (DBH and ABG) and differed among species. No effects of topography or failure mode were found for the species either separately or pooled. For the random species, total variance in  $M_{crit}$  explained by tree size metrics increased from an  $R^2$  of 0.49 for DBH alone, to 0.68 when both DBH and stem fresh wood density (SWD) were included in a multiple regression model. This mechanistic approach allows the comparison of tree vulnerability induced by wind damage across ecosystems, and facilitates the use of forest structural information in ecosystem models that include variable resistance of trees to mortality inducing factors. Our results indicate that observed topographic differences in wind-throw vulnerability are likely due to elevational differences in wind velocities, rather than by differences in soil-related factors that might effect  $M_{crit}$ .

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### 1. Introduction

The stability of the erect habit of plant stems is primarily compromised by bending movements in response to wind and gravity (Almérás and Fournier, 2009). Wind is indicated as the primary abiotic agent damaging forests (Sellier and Fourcaud, 2009). Strong winds may cause deflection that may exceed critical thresholds of

tree stability, and thus wind interaction with forests causes a large fraction of tree mortality worldwide (Chambers et al., 2007; Dale et al., 2001; Esprito-Santo et al., 2010; Negrón-Juárez et al., 2010; Schelhaas et al., 2003). Wind disturbance also affects forest structure and functioning (Peltola et al., 2010), influencing tree species assembly processes (Denslow, 1980; Marra et al., 2014; Turner et al., 1998), regeneration patterns (Putz et al., 1983) and shifts in forest composition (Trumbore et al., 2015).

High wind events create tree fall gaps at varying spatial scales from stands to landscapes (Asner, 2013; Chambers et al., 2013;

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Espírito-Santo et al., 2014; Mitchell, 2013). Although a portion of the carbon from decomposing, dead, and damaged trees can be incorporated into the soil (dos Santos et al., 2015) rather than respired to the atmosphere, downed trees represent committed future CO<sub>2</sub> emissions (Chambers et al., 2004). Recruitment and enhanced growth of surviving trees following disturbance can offset some of those emissions (Chambers et al., 2004). Forest carbon stocks are also subject to temporal fluctuations, and decline with increased disturbance event frequency (Chambers et al., 2013). Thus, increasing global temperature can reduce forest carbon balance if more frequent storms or higher peak wind speeds occur under a warming climate (IPCC, 2013).

Variation in vulnerability to tree mortality generated by wind in Amazon forests is a complex phenomenon, involving a suite of biotic and abiotic variables (Chambers et al., 2009; Garstang et al., 1998; Nelson et al., 1994). Explanations for why some trees uproot (Garstang et al., 1998), while others do not, include differences in the forces exerted on tree crowns (from above and below), and the influence of rooting or soil depth. A recent study (Marra et al., 2014) reported that tree uprooting and snapping were more common on slopes and plateaus in the Central Amazon, with fewer uprooted or snapped trees in valleys. A previous study using wind tunnel measurements reported that wind speeds on hilltops were nearly twice that as observed for valley formations, with a larger variation in wind speed for valleys depending on the direction of the gusts (Ruel et al., 2001). It is also known that small increments in wind speed can result in substantial differences in mode and scale of forest wind disturbance. Wind speed frequently increases with elevation and the pattern of disturbance may be strongly influenced by topography (Quine and Gardiner, 2007).

Soil characteristics might have a strong influence on a tree's ability to withstand high wind events, yet there are few quantitative data linking soils and wind throw vulnerability for Amazon forests (Marra et al., 2014; Toledo et al., 2012). Soil and topography, in the context of tropical forests, has been studied to determine their influence on tree diversity (Baldeck et al., 2012; Laurance et al., 2010; Quesada et al., 2010). Soil texture, organic matter content, soil moisture, soil pH and soil C and N concentrations vary significantly with elevation along topographic gradient in the Central Amazon (Luizão et al., 2004). At regional scales, soil conditions such as fertility (Quesada et al., 2009), and the capacity of trees to develop effective anchorage (Mitchell, 2013) have been linked to variation in tree turnover rates.

Soil depth, soil physical properties, structure and other factors that vary with topography have a strong relationship with tree turnover rates (Chao et al., 2008; Quesada et al., 2009). And have been suggested as factors that control variability in wind-throw rates (Chao et al., 2009; Quesada et al., 2009). The present study was conducted in a region consisting of plateaus with clay-rich soils (with 65–75% of clay in the first 30 cm, increasing to 80–90% clay at 2–4 m of depth) and valleys with sand content approaching 100% near perennial streams (Chauvel et al., 1987). Slopes connecting plateaus to valleys exhibit a gradual decrease in clay content, and increase in sand content, with elevation (Chauvel et al., 1987). Clay soils are more likely to reduce root growth (Gerard et al., 1982), and this may explain previous results of lower uprooting rates in valley positions (Lenart et al., 2010; Marra et al., 2014).

In addition to abiotic factors including topography and soil, biotic factors such as individual or species characteristics may also influence tree stability (Negrón-Juárez et al., 2014; Niklas and Spatz, 2010). A decision support system approach to assess hazard due wind driven mortality for single trees and stands emphasizes the importance of larger tree taper, strength and depth of tap roots, and interlocking root systems as good predictors of low failure hazard (Mickovski et al., 2005). It is expected that trees with a longer

life cycle and slower growth rates produce stiffer, stronger stems with greater strength and longevity (Niklas and Spatz, 2010; Williamson and Wiemann, 2010). Inferences of tree stability based on wood density alone are potentially misleading for species with complex life histories (Nock et al., 2009), where the ability of wood to resist mechanical forces may decline with increasing moisture content (Niklas and Spatz, 2010). Large trees vary more than saplings in their wood densities, and are also likely to vary more in their mechanical properties, with potentially important consequences for architecture, growth and survival (van Gelder et al., 2006).

Trees resist their own mass and wind forces by an adequate mechanical design (Sterck and Bongers, 1998), where plant architecture itself can alter the magnitude and spatial distribution of wind loading (Sellier and Fourcaud, 2009). The dynamic behavior of trees and their response to mechanical loads in particular in response to wind loading varies with time (Brüchert and Gardiner, 2006). Critical turning moment ( $M_{crit}$ ) of a tree is the rotational force (Newton meters) at the moment of failure (snap or uprooting), and indicates tree stability or wind resistance (Cannon et al., 2015).  $M_{crit}$  generally increases with tree size and often does not differ significantly across species for similar sized trees, (Cannon et al., 2015; Nicoll et al., 2006; Peltola et al., 2000; Peterson and Claassen, 2013). The best predictors of  $M_{crit}$  vary among studies but include stem volume or above ground biomass (AGB) (Cucchi et al., 2004; Fredericksen et al., 1993; Lundström et al., 2007; Peterson and Claassen, 2013), DBH (Kamimura et al., 2012), and stem mass (Cannon et al., 2015).

To our knowledge, tree pulling experiments based on static load tests have not previously been carried out in Amazon forests. Here we examine relationships among tree stability, topography, mode of failure, species, and tree biometric parameters (i.e. DBH, stem mass, crown mass, AGB, stem volume, stem fresh wood density, and total height). We hypothesized that (1) trees in valleys are more resistant than trees on plateaus (due to lower observed rates of wind mortality in this topographic position, found by Marra et al., 2014); (2)  $M_{crit}$  increases with tree size (e.g. DBH, AGB tree taper or Slenderness, (TH:DBH ratio, dimensionless), Stem, Crown and Center), for all species groups; (3) tree resistance to failure increases with increasing SWD, given that higher wood density implies stiffer stems and stronger or greater strength and longevity (and tropical forests has a very large range in wood density among species); and (4) the total force required to snap or uproot a tree do not differ in relation to  $M_{crit}$  (similar number of dead trees by failure mode, found by Marra et al., 2014).

## 2. Methods

### 2.1. Study site

We conducted the experiment at the EEST (Experimental Station of Forest Management) operated by Brazil's National Institute of Amazonian Research (Instituto Nacional de Pesquisas da Amazônia-INPA). The EEST is located at (2.45°–2.66°S, 60.02°–60.32°W) 90 km north of Manaus, the capital of Amazonas State, Brazil (Silva et al., 2002) and encompasses an area of 21,000 ha (Andrade and Higuchi, 2009). Annual rainfall for the period 1980–2000 was 2610 ± 124 mm, using data from an EMBRAPA experimental station, located 50 km east from EEST (Silva et al., 2003). The study region has a dry season (≤100 mm precipitation) from July to September (Chambers et al., 2004). Topography at EEST is composed mostly of flat plateaus (90–105 m ASL) incised by a dense drainage network within broad and often swampy valleys (45–55 m ASL) (Rennó et al., 2008). In this region, forests are composed of a high diversity of tree species (Carneiro, 2004;

Guillaumet, 1987; Marra et al., 2014; Rankin de Mérona et al., 1992; Vieira et al., 2004). About 280 species can be found in a single hectare (Oliveira and Mori, 1999), with low frequency (around 4 per ha) of emergent trees that exceed 30 m (Prance et al., 1976) and dominant height of trees  $\sim 29$  m (Lima, 2010).

## 2.2. Species selection

To test our hypotheses, species were chosen based on the species' abundance along the typical local topographic gradient found at the EEST (Carneiro, 2004). Cardeiro (*Scleronema mincranthum* (Ducke) Ducke [Malvaceae]) and mata-matá (*Eschweilera* spp. [Lecythidaceae]) were selected. *Scleronema* and *Eschweilera* are among the most frequent genera in our study area (Guillaumet, 1987) and both are listed as "hyperdominant" in the entire Amazon basin, with *Eschweilera* represented by 52 species (ter Steege et al., 2013). *Scleronema* and *Eschweilera* have also been described as genera favored (higher abundance) in intermediate and heavily damaged patches, respectively, of a nearby forest disturbed by the 2005 convective storm (Marra et al., 2014). In addition to these two genera, a random selection of trees across 19 species (see Supplementary material, Table S1) representing the local species assembly was also sampled to seek trends not specific to the above-mentioned dominant genera.

## 2.3. Field methods

Trees that were selected for winching followed procedures consistent with previous studies (Cannon et al., 2015; Nicoll et al., 2006; Peterson and Claassen, 2013). We used essentially the same equipment employed in previous studies (Cannon et al., 2015; Peterson and Claassen, 2013) with minor modifications. First, all trees were hand winched without the use of a snatch block, and the load cell used in this study (Straightpoint model Radiolink Plus) had a smaller rated capacity of 11.8 metric tons that was not exceeded, see Supplementary video. To find the center of mass of each tree, we recorded trunk diameter at 1 m intervals (and DBH) after each tree fall and weighed every 1 m section of the tree with a 300 kg load capacity balance. Details are presented in Supplementary data (see Section 2).

## 2.4. Biometric parameters influencing tree stability

For each tree we measured the stump diameter ( $D_{\text{stump}}$ ), diameter at breast height (DBH), stem volume (Vol), stem mass (Stem), crown mass (Crown), above ground biomass (AGB), stem wood density (SWD), tree center of mass (Center) and tree height (TH). Descriptive analyses for each species group versus topographic position are shown in the Supplementary material (Tables S2–S4, for *Eschweilera* spp., a random set of tree species and *Scleronema mincranthum*, respectively). The measure for linear association between the variables using Pearson product-moment correlation and Bonferroni probabilities are shown respectively for *Eschweilera* spp. (Tables S5 and S6), for a random set of tree species (Tables S7 and S8), for *Scleronema mincranthum* (Tables S9 and S10) and for all species groups pooled together (Tables S11 and S12). To compare our results with previous studies, we ran simple (linear and non-linear) and multiple regressions between  $M_{\text{crit}}$  versus tree biometric parameters, such as DBH, total tree height (TH), above ground biomass (AGB), stem volume (Vol), fresh stem wood density (SWD), for *Eschweilera* spp., a random set of tree species, *Scleronema mincranthum*, and species groups pooled, respectively (Tables S13–S16).

$M_{\text{crit}}$  was calculated at the base of each pulled tree (Fig. S2). We winched 20 trees for each group (*Scleronema mincranthum*, *Eschweilera* spp., and a random selection of tree species), 10 in each

topographic position (plateau and valley), totaling 60 trees ranging from 19 cm to 41.1 cm DBH. Trees larger than 41.1 cm DBH were not winched in this study as a safety precaution. This is a reasonable maximum size since 93% of trees in a nearby 18 ha plot had DBH values between 10 and 40 cm (Higuchi et al., 2012), and the mean DBH of trees with DBH  $\geq 10$  cm in Central Amazon undisturbed forest in the region is about 22 cm (Lima, 2010). The mean DBH of dead trees (i.e. snapped and uprooted) found in a contiguous wind-disturbed forest was approximately  $27.5 \pm 2.3$  cm (mean  $\pm$  95%CI) (Marra et al., 2014). Thus the tree size range sampled in this study is representative of forests of the Central Amazon.

## 2.5. Tree stability

To check the first hypothesis (trees in valleys are more resistant than trees on plateaus), we compared  $M_{\text{crit}}$  of species groups versus topographic position (as a factor) by means of one-way ANOVA. Subsequently, we ran an ANOVA including topographic position as a predictor of  $M_{\text{crit}}$  with DBH as an independent variable. After checking for differences among each species group, individuals from all species were pooled for the same analysis. To check the second hypothesis (evaluate whether  $M_{\text{crit}}$  increases with tree size), the effects of species group (as a factor), DBH, AGB, tree taper or Slenderness (TH:DBH ratio, dimensionless), Stem, Crown and Center as independent variables, we used analysis of covariance (ANCOVAs), one for each independent variable. Tree height was not a good predictor of  $M_{\text{crit}}$  in previous studies (Cannon et al., 2015; Peterson and Claassen, 2013). To check the third hypothesis (evaluate if  $M_{\text{crit}}$  increases with SWD), the effects of species group, tree mode of failure (both as factors), and fresh stem wood density (as independent variable) on  $M_{\text{crit}}$  were tested using analysis of covariance (ANCOVA). To check the fourth hypothesis ( $M_{\text{crit}}$  varies among tree mode of failure), individuals of all species groups were pooled, and the effects of tree mode of failure (categorical variable) and DBH (independent variable) on  $M_{\text{crit}}$  were tested using simple ANCOVA. To test which tree biometric parameter better predict  $M_{\text{crit}}$ , simple and multiple linear and nonlinear regressions were carried out separately for each species groups and for species groups pooled together.

## 3. Results

A total of 60 trees ranging from 19 cm to 41.1 cm in DBH were winched from August 2014 to April 2015 totaling 76,229 kg of above ground biomass. The mode of failure (snapping and uprooting) differed significantly between the species groups. All *Scleronema mincranthum* trees snapped in both topographic positions. For *Eschweilera* spp., equal number of trees in the valleys were snapped and uprooted, while in the plateau 60% failed by snapping and 40% by uprooting. The random set of trees had equal numbers of failures in both modes in the valley, but 40% snapped versus 60% uprooted on the plateau. Topographic position was not a significant predictor of Critical turning moment ( $M_{\text{crit}}$ ) of trees in our study for any species groups tested, even when all species were pooled. According to One-way ANOVAs, topography had not effect on  $M_{\text{crit}}$  for random species ( $p = 0.45$ ), for *S. mincranthum* ( $p = 0.70$ ), for *Eschweilera* spp. ( $p = 0.73$ ), or for all species groups pooled ( $p = 0.72$ ). Results from subsequent ANOVAs with DBH are presented in Fig. 1.

$M_{\text{crit}}$  varied among species groups when measures of tree size (e.g. DBH, AGB and Slenderness) were used as independent variables in an ANCOVA analysis. The interaction terms between species group with DBH, AGB and Slenderness were not significant ( $p = 0.72, 0.12, 0.07$  respectively) with no evidence of different

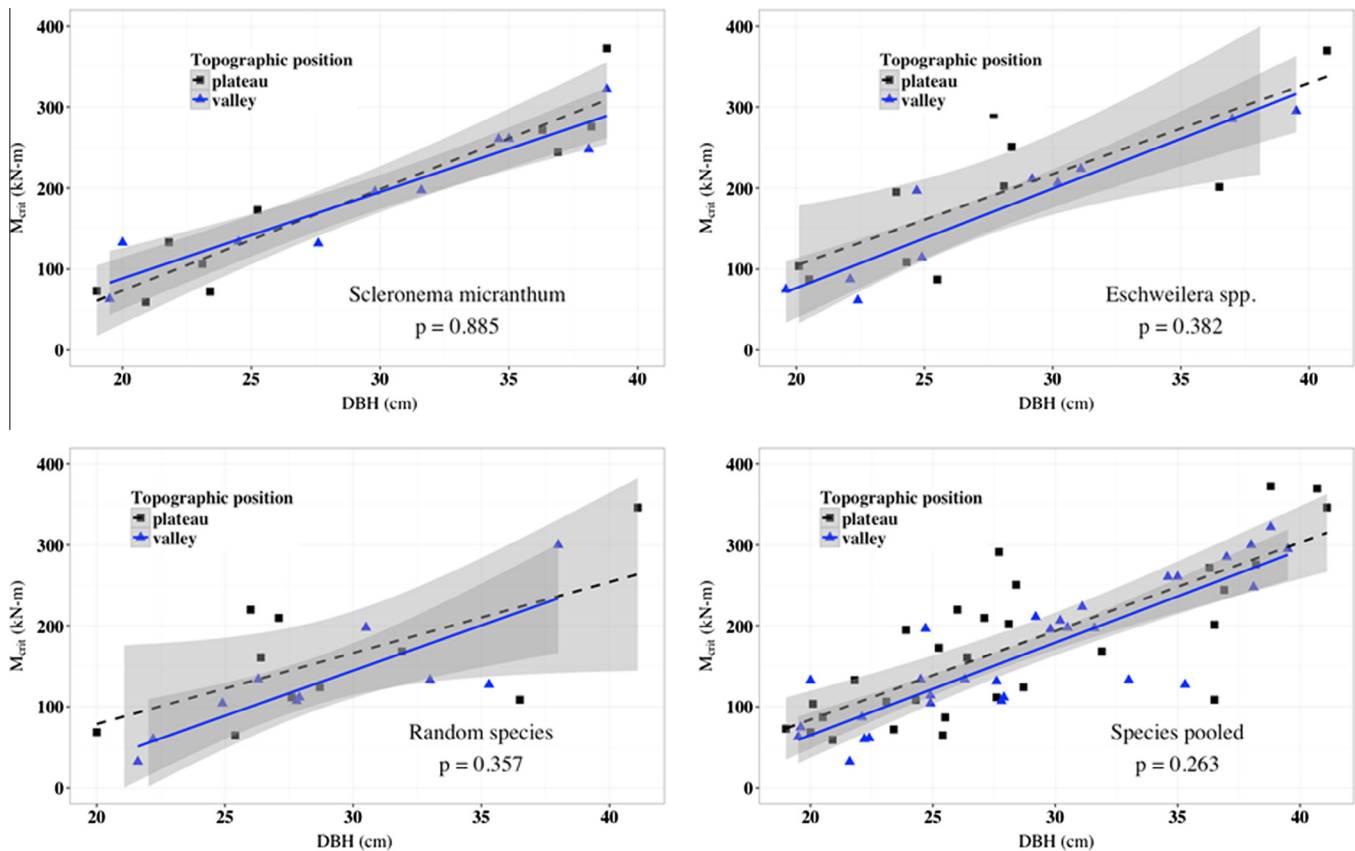


Fig. 1. Analysis of variance (ANOVA) using topographic position as factor and DBH as independent variable on critical turning moments for species groups and for species pooled together with regression lines and 95% confidence envelopes.

slopes. Nonetheless, the intercepts differ among groups, DBH, AGB and Slenderness showed significant increases in  $M_{crit}$  ( $p < 0.005$ ). For a given DBH *Eschweilera* spp. was the most resistant group followed by *S. micranthum* and random species. When increasing AGB, *Eschweilera* spp. became more prone to failure (Fig. 2). The AGB distribution behavior for *Eschweilera* spp. together with tree Slenderness can be explained by differences in allometry among the other tested groups in relation to tree center of mass, stem and crown biomass. The interaction terms between species group with Stem and Center were non-significant ( $p = 0.871$ ,  $0.2511$  respectively) with no evidence of different slopes. Nonetheless, the intercepts differ among groups, Stem, Crown and Center showed significant increases in  $M_{crit}$  ( $p < 0.005$ ) (Fig. 3). This difference in allometry, changes the tree center of mass of *Eschweilera* spp. to a higher point from the ground mainly by differences in crown mass, and wind loading is expected to occur at a higher effective height (Hale et al., 2012).

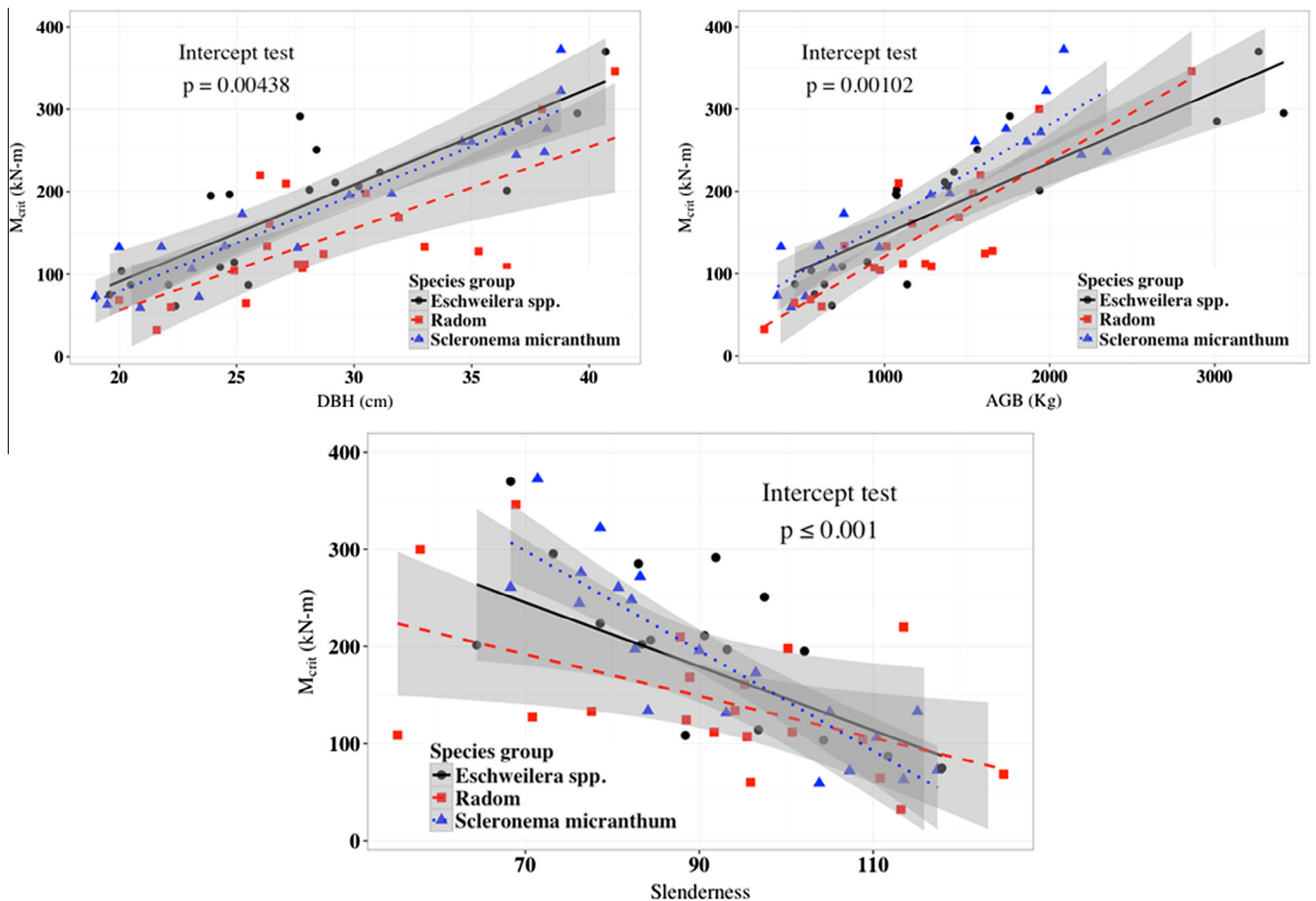
Pos-hoc Tukey tests were performed to evaluate differences among species groups (Table 1). Variance inflation factors (VIF) were assessed to check multicollinearity among the previous mentioned size attributes with species groups. VIF values were 4.83, 2.44, 4.24, 2.88, 1.70 and 2.37 for DBH, AGB, Slenderness, Stem, Crown and Center. Note that DBH values were fixed around values between 20 cm to 40 cm for all sampled species groups as mentioned in Section 2.4.

The interaction terms between species group and mode of failure (both categorical variables) with fresh stem wood density were non-significant ( $p = 0.63$  and  $0.77$ , respectively) but SWD showed effects on critical turning moment ( $p = 0.036$ ) for species groups (mainly by large differences in the random set of trees, see Table S2) but no effect for mode of failure ( $p = 0.08$ ). Multiple

regression combining DBH and SWD showed an increase of about 40% in explained variance ( $R^2$ ) related to the simple regression for the random set of trees (Table S15), but no increases were found for *Eschweilera* spp. (Table S13), nor were increases found for *Scleronema micranthum* (Table S14). Because the higher variance in SWD for the random set of tree species, this group was analyzed separately from the others so the effect of SWD was not confounded with species groups. The graphical relationship among  $M_{crit}$ , SWD and the random set of tree species did not show a linear trend, but show increases in  $M_{crit}$  while increasing SWD values (Fig. 4).

The presence of decay and rot in tree parts can change SWD values. For two similar sized trees in DBH of *Eperua glabriflora*, presented SWD values of  $1.02 \text{ g cm}^{-3}$  (38 cm in DBH) and  $0.594 \text{ g cm}^{-3}$  (35.3 cm in DBH). For the second tree, decay and rot could be noted over 6 m from the stem base. Among the architectural attributes related to tree resistance to wind, the measure of slenderness; quotient of height and diameter (total tree height divided by DBH, both variables in meters) have been used as a indices of tree stability for Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) stands (Jelonek et al., 2013; Mickovski et al., 2005; Slodickac and Novak, 2006). Information's about Stem, Crown and Slenderness, to further explore other tree architecture attributes, were included in graphical relationships among  $M_{crit}$ , SWD and the random species (Fig. 5). Trees can have different above ground biomass allocation patterns. Thus the Slenderness factor can be influenced by the relationship among crown biomass and stem biomass and consequently affect tree stability to with stand strong winds.

Critical turning moments were influenced by tree mode of failure with DBH as independent variable. The interaction term



**Fig. 2.** Analysis of covariance (ANCOVA) using species group as factor and DBH (left panel), AGB (right panel) and slenderness (lower panel) as independent variable on critical turning moments with regression lines and 95% confidence envelopes.

between species group with DBH was not significant ( $p = 0.823$ ) with no evidence of different slopes. The intercepts differ among mode of failure, and DBH was positively related to  $M_{crit}$  ( $p < 0.001$ ). For different trees with the same DBH, more force is required to cause stem breakage (Fig. 6).

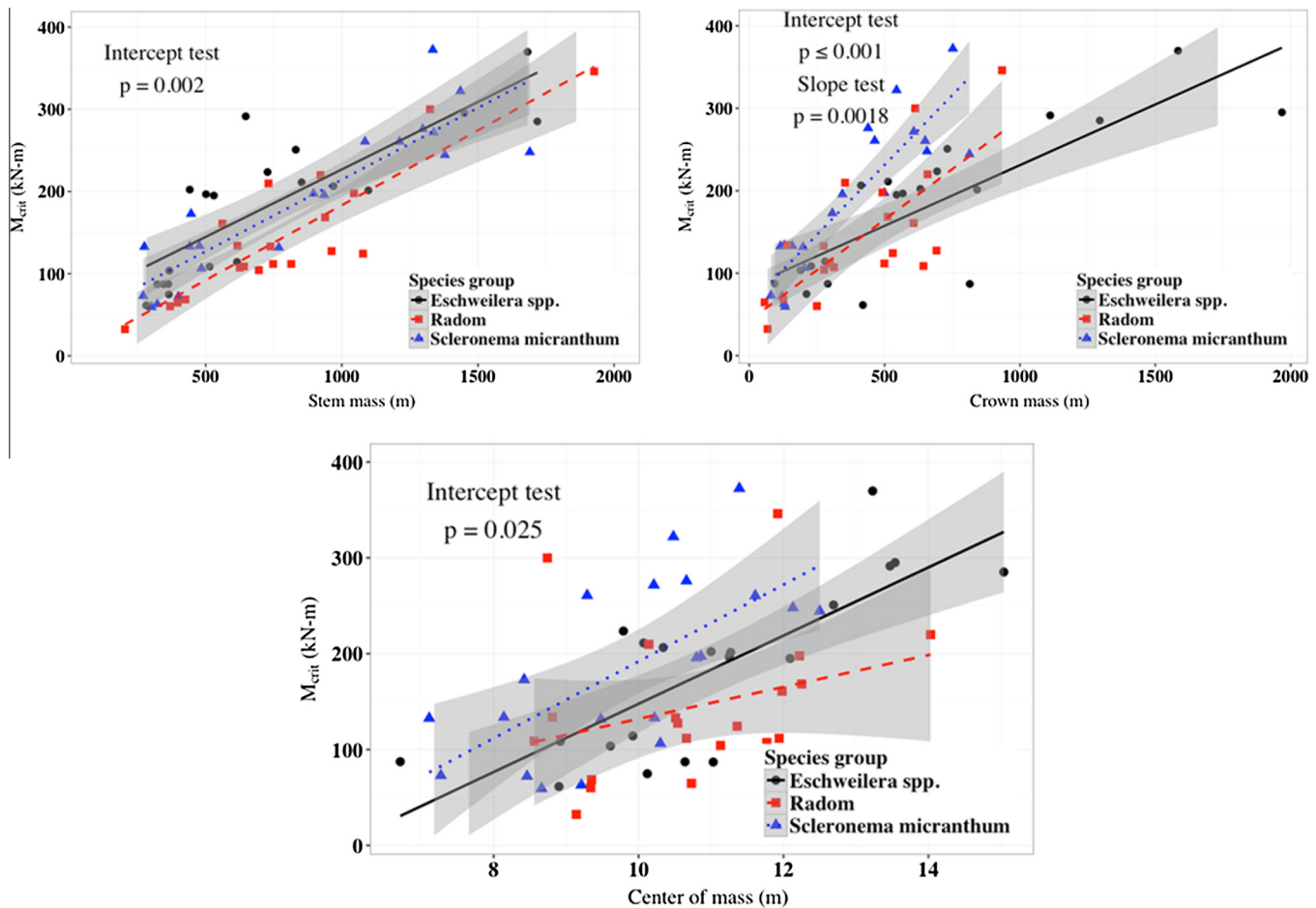
Values of  $M_{crit}$  were best predicted by different biometric parameters according to the species groups. For *Scleronema micranthum*, DBH was the best individual predictor (Table S14). For *Eschweilera* spp., the random set of species and species groups pooled, the best individual predictor was AGB (Tables S13, S15 and S16 respectively).

#### 4. Discussion

Although the tree wind-damage was assessed in different studies, the correlation between topographic exposure and intensity of damage is unclear (Zhu et al., 2004). Direction of slope aspect and orientation of valleys with respect to the prevailing wind direction can have a considerable influence on the magnitude of wind speed experienced at a location, and in many storms, the highest wind speeds were found on ridge tops and on gentle slopes facing the wind (Quine and Gardiner, 2007). In our study, there was no overall difference in  $M_{crit}$  of trees on plateaus and valleys, independent of whether species groups were analyzed separately or pooled. We have evidence to reject our first hypothesis, as we found no differences in tree stability between valleys and plateaus. Other factors such as higher wind-exposure and differences in wind speed and

direction in plateaus (upland) areas (Negrón-Juárez et al., 2014; Quine and Gardiner, 2007; Ruel et al., 2001) may explain the higher wind-related mortality reported for plateaus and top of slopes (Marra et al., 2014). Regressions of  $M_{crit}$  with tree size descriptors (i.e. DBH and AGB) showed that the topographic position did not influence tree resistance to failure, and therefore differences in soil texture between valleys and plateaus (Chauvel et al., 1987; Luizão et al., 2004) do not influence tree resistance to failure. In same soil condition, when the influence of slope in anchorage was analyzed for 40-year-old Sitka spruce (*Picea sitchensis*), more force was needed to pull trees upslope than downslope. However no overall difference in anchorage was found between trees grown on the horizontal and sloping parts of the site (Nicoll et al., 2005). Studies that used crown architecture improve the understanding of dynamic response of standing trees to wind (Hale et al., 2012), but in Central Amazon forests calculating the average crown width based on measurements of maximum crown radius in eight directions was not possible due to difficulties defining neighbors for each sampled tree. Our winching experiment confirmed the effect of tree size on  $M_{crit}$  suggested by previous studies carried out in different forest types (i.e. structure and species composition), where tree stability increases substantially with increases in tree size (Cannon et al., 2015; Nicoll et al., 2006; Peltola, 2006). The same pattern was not confirmed for slenderness, for which values below 80 indicated higher stability against wind damage (Slodick and Novak, 2006).

The different species groups investigated in this study suggest that there is a relation between mode of failure and tree biometric



**Fig. 3.** Analysis of covariance (ANCOVA) using species group as factor and Stem (left panel), Crown (right panel) and Center (lower panel) as independent variable on critical turning moments with regression lines and 95% confidence envelopes.

**Table 1**  
Pos-hoc Tukey tests for species groups using DBH, AGB, Slenderness, Stem, Crown and Center.

Tukey multiple comparisons of means	DBH p	AGB p	Slenderness p	Stem p	Crown p	Center p
Random and <i>Eschweilera</i> spp.	0.0034	0.3758	0.1923	0.0200	0.0865	0.1998
<i>S. micranthum</i> and <i>Eschweilera</i> spp.	0.7251	0.1951	0.9840	0.9611	0.9760	0.9844
<i>S. micranthum</i> and Random	0.0286	0.0084	0.1394	0.0101	0.0541	0.1459

parameters. All individuals of *S. micranthum* snapped independent of topographic position and corresponding soil texture. This pattern suggests that tap root systems, typical of *S. micranthum*, partly influence tree mode of failure (see Fig. S1, Supplementary material). In contrast, this pattern was not observed for *Eschweilera* spp. The lack of pattern in *Eschweilera* spp. can be attributed to the higher variation on biometric attributes from this genus, including the presence or absence of buttress depending on the species (Ribeiro et al., 1999). Failure mode was closely linked to soil type for *Pinus radiata* in a range of New Zealand soils were 92% of trees uprooted in non-cohesive soils (Moore, 2000). In our study the same pattern was not observed, 40% of Random trees and 60% *Eschweilera* spp. uprooted on cohesive plateau soil. In some cases, uprooting one tree can additionally uproot four surrounding trees when roots are interlocked (Coutts, 1983). Despite recent advances in the understanding of the relative roles of root components (lateral, superficial or tap roots) in tree anchorage strength (Fourcaud et al., 2008), general knowledge about roots

architecture in tropical species is still scarce. Although this is the first study to describe  $M_{crit}$  for Amazonian tree species, our results (Tables S2–S4) are in accord with previous studies (Peterson and Claassen, 2013; Cannon et al., 2015) for similar-sized hardwood and coniferous species of the United States. As in other static winching studies,  $M_{crit}$  of trees from this study also increased with tree size, supporting our second hypothesis.  $M_{crit}$  differs among Amazonian tree species, depending on the tree size (i.e., DBH, AGB, Slenderness, Stem, Crown, Center), and some species are simply more resistant than others (see Figs. 2 and 3). For instance, for a given DBH, *Eschweilera* spp. are more resistant than the other tested species. However, *Eschweilera* spp. trees with an AGB >~2000 kg are more susceptible to failure than similar AGB *S. micranthum*, probably due to the large contribution of crown biomass observed for this genus (see Fig. 2 left panel and Fig. 3 left panel). This result does not corroborate previous studies (Cannon et al., 2015; Nicoll et al., 2006; Peltola, 2006; Peterson and Claassen, 2013), in which no differences in  $M_{crit}$  between species

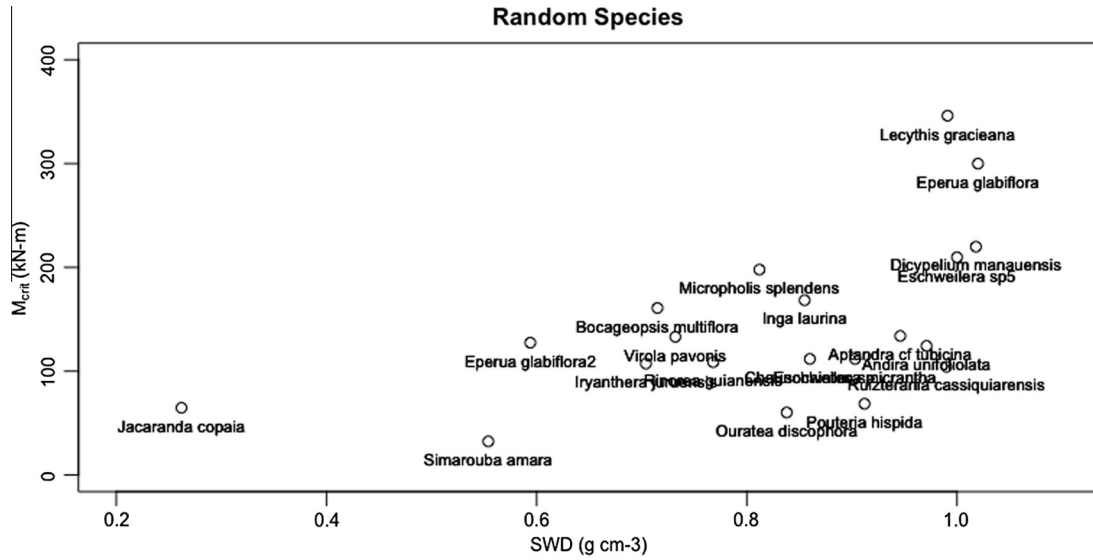


Fig. 4. Scatter plot of  $M_{crit}$  and SWD for the random species.

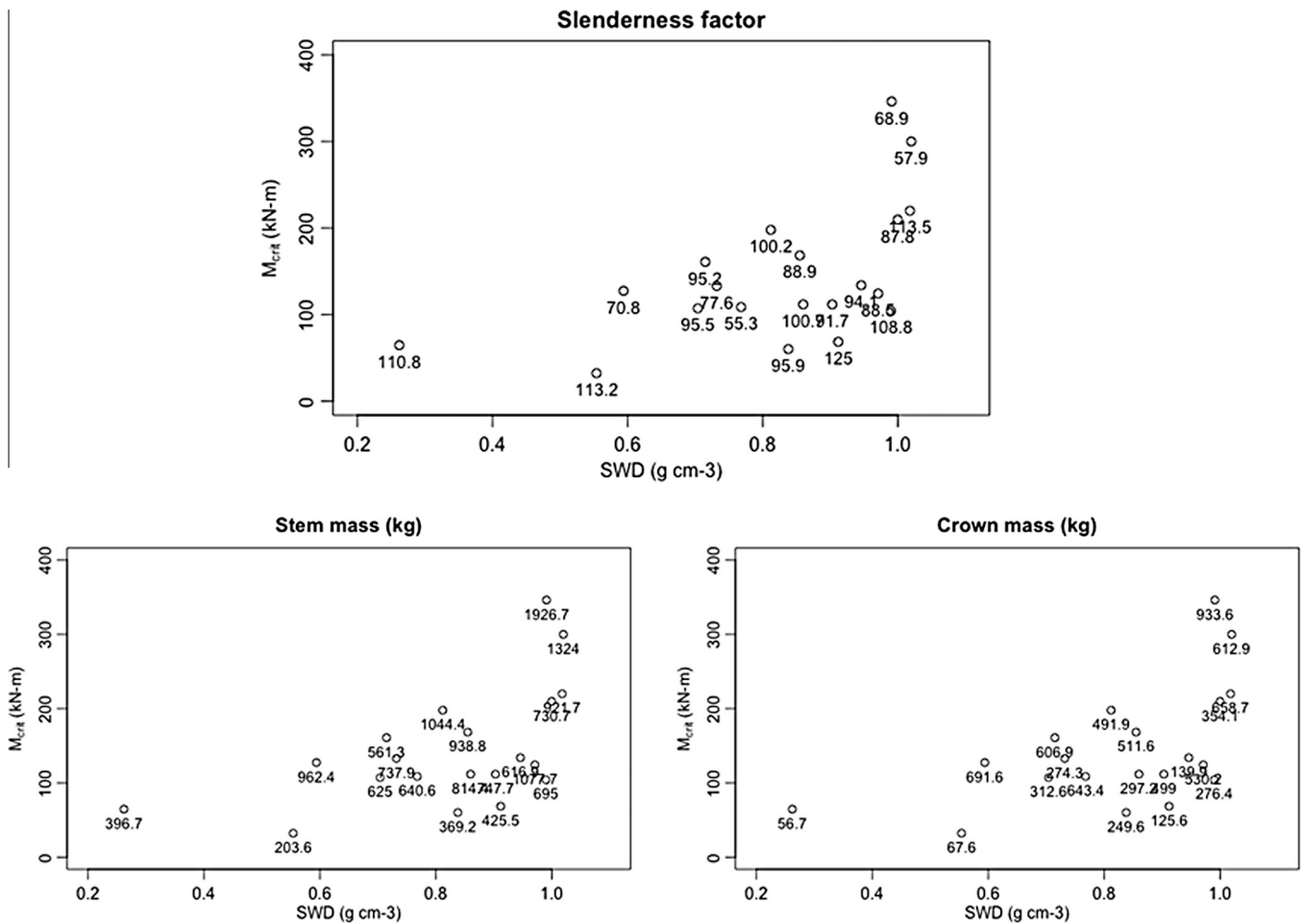
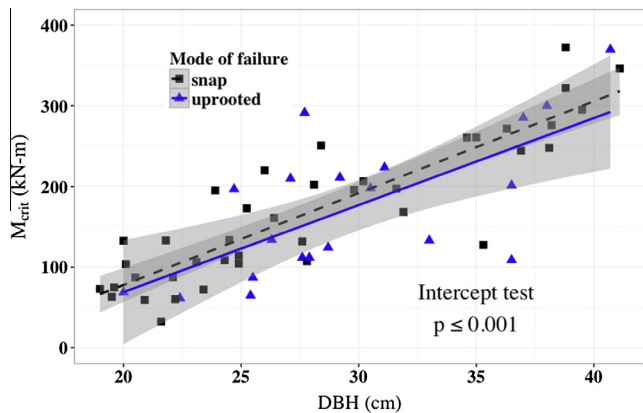


Fig. 5. Scatter plot of  $M_{crit}$  and SWD for the random species with correspondent slenderness factor (top panel), stem mass in kg (left panel) and crown mass in kg (right panel).

were reported. One hectare in Amazon forest can hold more tree species than in all of Canada and the continental US (Coley and Kursar, 2014), thus there is a much larger range in interspecific differences.

In contrast with wood engineering studies, cell walls in living trees are fully water-saturated (Fournier et al., 2013), reducing the ability of wood to resist mechanical forces (Niklas and Spatz, 2010). Due to low variance in wood density within species, there



**Fig. 6.** Analysis of covariance (ANCOVA) using tree mode of failure as factor, DBH as independent variable on critical turning moments, with regression lines and 95% confidence envelopes.

was no significant difference in  $M_{crit}$  with wood density for *S. micranthum* and *Eschweilera* spp. (see Tables S2 and S4). However, among the random set of tree species explained variance with single entry models, one linear and one non-linear, explained 0.28 and 0.31, respectively. But total explained variance increased from an  $R^2$  of 0.49 for DBH alone, to 0.68 when including both DBH and SWD in a multiple regression model (model 12 and model 17, respectively, from Table S15). As previously suggested (Niklas and Spatz, 2010, 2012), SWD has a strong effect on  $M_{crit}$ . Further work is needed to explore a larger range of wood density and its effect on the variation of  $M_{crit}$  together with tree architectural attributes. In this study, considering the random set of tree species, a non-linear relationship was found, and species with higher SWD tends to exhibit higher values of  $M_{crit}$ . Other studies indicate that species with high wood density have more slender stems, but larger crowns than similar sized trees of low wood density species (Iida et al., 2012). Theoretical studies, in which the experiments have been conducted from the wood technological or timber use perspective (focusing on properties of dry wood), limit's the understanding of the biomechanics of living plants (Niklas and Spatz, 2010) and the understanding of wood characteristics from an ecological or evolutionary perspective (Larjavaara and Muller-Landau, 2012).

We found differences in  $M_{crit}$  related with tree mode of failure as a factor and DBH as independent variable. Based on these findings, we have strong evidence to reject our fourth hypothesis that  $M_{crit}$  does not vary with mode of failure. For a given DBH, more force is required to snap the stem than to uproot the tree. This result is in contrast with Peltola et al. (2000), but similar to Cannon et al. (2015). In the later study, tree modes of failure were reported with stem mass as independent variable of  $M_{crit}$ . This result suggests that tree mode of death in wind throw areas in Amazon forests depends on tree biometric parameters (e.g. root architecture, root: shoot ratio, crown architecture) and should be analyzed at the species level in future studies.

## 5. Conclusion

This mechanistic approach allows the comparison of tree vulnerability and resistance to snapping and uprooting across tropical and temperate forests and facilitates the use of current findings in the context of ecosystem models. Higher wind-induced tree mortality observed on plateaus and top of slopes may be explained by different wind speeds and gusts direction (valleys have different aspects and the wind can blow parallel or perpendicular), rather than by differences in soil-related factors that might effect  $M_{crit}$ .

Further studies on root architecture can enhance our understanding about the vulnerability of Amazonian tree species to wind disturbance and consequent changes in tree species communities with greater storm intensity with a warming climate. In this study, values of  $M_{crit}$  were governed by species-specific size attributes and vary among Amazonian tree species.

## Conflict of interest

The authors declare no conflict of interest.

## Acknowledgements

The authors gratefully thank the staff of EEST. This study was financed by the Brazilian Council for Scientific and Technological Development (CNPq) within the projects Succession After Wind-throws (SAWI) (Chamada Universal MCTI/No14/2012, Proc. 473357/2012-7), INCT - Madeiras da Amazônia, and the Next Generation Ecosystem Experiment (NGEE) Tropics at Lawrence Berkeley National Laboratory, and also supported by the Max-Planck-Institute for Biogeochemistry within the Tree Assimilation and Carbon Allocation Physiology Experiment (TACAPE). Robinson Negrón-Juárez was supported by the Director, Office of Science, Office of Biological and Environmental Research of the U.S. Department of Energy under Contract No. DE-AC02-05CH11231 as part of Next-Generation Ecosystems Experiments (NGEE Tropics) and the Regional and Global Climate Modeling (RGCM) and Programs.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2016.08.039>. These data include Google maps of the most important areas described in this article.

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