BIOTROPICA 42(1): 87–94 2010 10.1111/j.1744-7429.2009.00545.x

# Variation in Susceptibility to Hurricane Damage as a Function of Storm Intensity in Puerto Rican Tree Species

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## ABSTRACT

One of the most significant challenges in developing a predictive understanding of the long-term effects of hurricanes on tropical forests is the development of quantitative models of the relationships between variation in storm intensity and the resulting severity of tree damage and mortality. There have been many comparative studies of interspecific variation in resistance of trees to wind damage based on aggregate responses to individual storms. We use a new approach, based on ordinal logistic regression, to fit quantitative models of the susceptibility of a tree species to different levels of damage across an explicit range of hurricane intensity. Our approach simultaneously estimates both the local intensity of the storm within a plot and the susceptibility to storm damage of different tree species within plots. Using the spatial variation of storm intensity embedded in two hurricanes (Hugo in 1989 and Georges in 1998) that struck the 16 ha Luquillo Forest Dynamics Plot in eastern Puerto Rico, we show that variation in susceptibility to storm damage is an important aspect of life history differentiation. Pioneers such as *Cecropia schreberiana* are highly susceptible to stem damage, while the late successional species *Dacryodes excelsa* suffered very little stem damage but significant crown damage. There was a surprisingly weak relationship between tree diameter and the susceptibility to damage for most of the 12 species examined. This may be due to the effects of repeated storms and trade winds on the architecture of trees and forest stands in this Puerto Rican subtropical wet forest.

Abstract in Spanish is available at http://www.blackwell-synergy.com/loi/btp

*Key words*: Luquillo Forest; Puerto Rico; subtropical forest.

Patterns of wind damage to forests typically reflect interactions among the meteorology of the storm, topography, soil conditions, and the attributes of individual trees and aggregate stand structure (Boose *et al.* 1994, 2004; Everham & Brokaw 1996). Numerous studies of tree damage from individual storms have demonstrated that species differ in their ability to withstand winds of a given intensity, primarily as a function of structural attributes related to tree size (Lugo *et al.* 1983, King 1986, Bellingham *et al.* 1995) and biomechanical traits such as wood density (Zimmerman *et al.* 1994) or elastic modulus (Asner & Goldstein 1997). Despite the conspicuousness of spatial variation in damage embedded within the path of an individual storm, much of the literature on the ecological effects of severe storms has aggregated the storm damage by averaging across spatial variation in storm intensity (*e.g.*, Greenberg & McNab 1998, Peterson 2000, Platt *et al.* 2000, Franklin *et al.* 2004). It is clear, however, that understanding the effects of wind disturbance on the dynamics of temperate and tropical forests requires an analysis of both the spatial variation in the intensity of individual storms, and the aggregate effects of long-term disturbance regimes composed of multiple storms of varying average intensity (Canham *et al.* 2001, Papaik & Canham 2006).

The effects of hurricanes on Caribbean tropical forests have been widely documented (Lugo *et al.* 1983, Bellingham 1991, Brokaw & Walker 1991, Bellingham *et al.* 1992, Boucher *et al.* 1994), particularly from studies in Puerto Rico following Hurricane Hugo in 1989 and Hurricane Georges in 1998 (*e.g.*, Brokaw & Grear 1991, Walker 1991, Lugo & Waide 1993, Zimmerman *et al.* 1994, Weaver 2002, Ostertag *et al.* 2005). Hurricanes Hugo and Georges were catastrophic in human terms as they caused severe damage to property in Puerto Rico, but their effects on forests were less severe, as they caused a wide range of damage to tree-crowns and low rates of tree mortality (Yih *et al.* 1991, Zimmerman *et al.* 1994, Ostertag *et al.* 2005). Recovery of ecosystem structure and function in this subtropical forest after Hurricanes Hugo and Georges was remarkably swift, particularly when compared with forest recovery in temperate regions from storms of comparable intensity (Peterson & Pickett 1995, Scatena *et al.* 1996, Cooper-Ellis *et al.* 1999, Beard *et al.* 2005). A model of hurricane effects on productivity and nutrient cycling in Puerto Rican tropical wet forests (Wang & Hall 2004) predicts relatively brief (*ca* 5 yr) impacts of a storm such as Hurricane Hugo on productivity in low elevation forests. It is more difficult, however, to predict how interspecific

Received 30 April 2008; revision accepted 26 March 2009.

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variation in resistance to wind damage will interact with past forest disturbances, over a broad range of storm intensities or repeated disturbance events, to affect forest community dynamics.

We suggest that one of the most significant challenges in understanding the long-term effects of hurricane disturbance regimes on tropical forests is the development of quantitative models of the relationships between variation in storm intensity and the resulting severity of damage to trees. Long-term studies using observations following a number of storms with different average intensity offer one approach. An alternative presented here takes advantage of the spatial variation in storm intensity embedded within each hurricane to assess the quantitative relationship between storm intensity and the patterns of damage to canopy trees. Specifically, we use the pattern of hurricane damage caused by Hurricanes Hugo and Georges to parameterize quantitative models of the degree of damage to trees as a function of species, tree size, and local storm severity. While there have been many comparative studies of interspecific variation in resistance to wind damage based on aggregate response to individual storms, our approach offers a quantitative assessment of the susceptibility of a given tree species to different levels of damage across an explicit range of storm intensity.

## METHODS

APPROACH.—This study uses an extension of the methods developed by Canham *et al.* (2001) for analysis of susceptibility to windthrow in temperate trees. The new method presented here is a form of ordinal logistic regression, in which the probability of different levels of damage during a severe windstorm is a function of (1) species, (2) individual tree size, and (3) local storm intensity (assessed using an index on an arbitrary but linear scale of 0–1). If an independent measure of local storm intensity (*e.g.*, wind speed) was available, standard logistic regression would suffice. In that case, the appropriate field methods would be to simply census the status of all trees in a series of subplots that varied in measured storm intensity, and then use a series of species-specific logistic regressions to predict damage to individual trees as a function of subplot-level storm intensity and individual tree attributes. Unfortunately, accurate, localized subplot-level measurements of wind speeds during severe storms are rarely available. Doppler radar systems can provide estimates of wind speeds aloft, but are not useful for estimating the spatial variation in surface wind speeds, particularly in complex topography. Another approach to assess storm severity would be to simply use the subplot-level degree of damage (as measured by total basal area or number of trees damaged) as an index of storm intensity, on a scale ranging from 0, when the storm was below the intensity required to produce any measurable degree of damage on any trees, to 1, when all canopy trees, regardless of size or species, would suffer catastrophic damage. This method would be quite reasonable if the subplots contained a very well-mixed sample of tree sizes and species. In the field, however, individual subplots may appear to have been subjected to particularly intense winds simply because they were dominated by sizes or species of trees that were particularly susceptible to wind damage even at relatively low storm intensities.

The new method we present here avoids the problem of not knowing whether the observed storm damage was the result of variation in storm intensity or tree susceptibility by simultaneously estimating both local (subplot) storm intensity and species susceptibility to wind damage (Canham *et al.* 2001). In effect, the analysis is a hierarchical model that estimates both subplot-level parameters (storm intensity) and species-level parameters that determine the responses of stems of a given species and size within subplots. The field methods are the same as those that would be used for a standard logistical model as described above: namely a damage assessment of trees in a series of subplots that varied widely in overall degree of damage. The subplots must be small enough to satisfy the assumption that local storm intensity was roughly uniform within the subplot, and also need to contain a mix of species and tree sizes. In practical terms, the subplots need to cover a large enough area to contain approximately 30–50 individual stems, in order to generate sample sizes sufficient for robust parameter estimates (Canham *et al.* 2001).

SITE AND STORM DESCRIPTIONS.—The research was conducted in the Luquillo Forest Dynamics Plot (LFDP), a 16-ha subtropical wet forest in the Luquillo Experimental Forest in Puerto Rico (see Thompson *et al.* 2002 for a detailed description of the site). Soils on the LFDP are clays formed from volcaniclastic sandstone (Soil Survey Staff 1995). Upper canopy height on the plot is 15–25 m (Brokaw *et al.* 2004). Basal area was estimated to average 36.7 $m^2$/ha and there were 89 species of self-supporting woody plants $\geq$10.0 cm dbh on the LFDP at the time of Hurricane Hugo (Thompson *et al.* 2002). Parts of the LFDP were subjected to a variety of human disturbance and agricultural use before 1934 (see Thompson *et al.* 2002 for details). After 57 yr without a major storm, two severe storms struck the plot: Hurricane Hugo in 1989 and Hurricane Georges in 1998. Hugo struck with maximum winds of 46 m/sec (Scatena & Larsen 1991), damaging about 25 percent and completely defoliating 56 percent of the trees in the LFDP (Zimmerman *et al.* 1994). The recovery of the Luquillo Experimental Forest from Hurricane Hugo has been extensively documented (Boose *et al.* 1994). As the forest was recovering from Hurricane Hugo, Hurricane Georges struck with winds up to 42 m/sec. Damage following both storms was highly variable across the Luquillo Experimental Forest (Boose *et al.* 2004), including the area of the LFDP (J. K. Zimmerman, pers. obs.).

DAMAGE ASSESSMENT.—Following Hurricane Hugo (September 1989) and after the establishment of the plot in 1990, damage to all woody stems $\geq$10 cm dbh (diam at 130 cm from the ground) was assessed over the entire LFDP during the period from September 1990 to February 1991 to prevent loss of data due to tree decomposition of trees killed or damaged by the hurricane (Zimmerman *et al.* 1994). The concurrent assessment of live undamaged stems of trees ($\geq$10 cm dbh) started in September 1990 and continued until February 1992. While there had been significant growth of new branches on damaged trees by the end of the

TABLE 1. *Successional status, sample size (N), and mean and maximum dbh (in cm) of the 12 species selected for analysis.*

| Species | Family | Successional status | *N* | Mean dbh | Maximum dbh |
|---|---|---|---|---|---|
| *Cecropia schreberiana* | Cecropiaceae | Pioneer | 370 | 18.6 | 48 |
| *Schefflera morototoni* | Araliaceae | Pioneer | 246 | 18.1 | 93.3 |
| *Alchornea latifolia* | Euphorbiaceae | Secondary | 232 | 24.8 | 66 |
| *Casearia arborea* | Salicaceae | Secondary | 1251 | 16.5 | 48.7 |
| *Inga laurina* | Fabaceae | Secondary | 642 | 25.9 | 87 |
| *Prestoea acuminata* var *montana* | Arecaceae | Secondary | 1183 | 14.8 | 22.2 |
| *Tabebuia heterophylla* | Bignoniaceae | Secondary | 399 | 21.9 | 69.2 |
| *Buchenavia tetraphylla* | Combretaceae | Late | 223 | 50.4 | 150.8 |
| *Dacryodes excelsa* | Burseraceae | Late | 1236 | 27.1 | 82.2 |
| *Guarea guidonia* | Meliaceae | Late | 350 | 32.5 | 96.3 |
| *Manilkara bidentata* | Sapotaceae | Late | 828 | 22.6 | 78 |
| *Sloanea berteriana* | Elaeocarpaceae | Late | 647 | 23.9 | 75 |

TABLE 2. *Percentages of stems showing no damage, partial damage, or complete crown loss following Hurricane Georges as a function of damage for the 2007 trees in the no and partial damage classes following Hurricane Hugo.*

| | Hugo damage | | |
|---|---|---|---|
| Georges damage | None | Partial | *N* |
| None | 63.6 | 64.2 | 1279 |
| Partial | 26.4 | 25.2 | 525 |
| Complete | 10.0 | 10.6 | 203 |
| *N* | 1677 | 330 | 2007 |

damage assessment period, the overall level of damage from Hugo was still clearly visible. Trees that had died as a result of hurricane damage were identified from bark and stem form. For the analyses presented here, we treated the data from the damage assessment following Hugo for the total LFDP as a set of 96 contiguous $40 \times 40$ m subplots, starting at the southwest corner. This provided a manageable number of subplots, each containing sufficient numbers of individuals for the analysis. Following Hurricane Georges, damage to woody stems $\geq 10$ cm dbh was assessed using similar methodology, but in a subset of the 16-ha plot consisting of 40 subplots ($30 \times 30$ m in size) in a grid pattern (with 60 m spacing between centers of subplots) located regularly across the LFDP. Note that our analysis (described below) does not require identical subplot sizes during the two damage censuses. The post-Hurricane Georges (September 1998) assessment was completed in 6 mo soon after the storm (November 1998–April 1999). These data were combined with the 96 subplots assessed after Hurricane Hugo, for a full dataset of 136 subplots and 11,197 observations (Table 1). The vast majority of the observations (8023) represent a tree that was censused in only one of the two storms.

The damage assessments after both hurricanes contained of a variety of detailed information on the type and degree of damage, but for our purposes the critical data were the visual assessments of the proportion of the crown volume lost and damage to the stem that occurred during the storm. For this paper the field assessments of crown loss were grouped into a simple ordinal scale of damage with just three levels: (1) none or light damage (< 25% of crown volume lost), (2) partial crown damage (> 25% but < 100% of crown volume lost), and (3) complete loss of the crown (either due to stem snap, root break or tip-up). Percentage crown damage to the palm *Prestoea acuminata* var *montana* (hereafter *P. montana*) could not be assessed after Hurricane Hugo because of the rapid re-growth of palm fronds. So although *P. montana* stem break and tip up were recorded after Hugo we had to omit this species (as missing values) from the Hugo portion of the combined dataset. Our statistical analyses (described below) estimate susceptibility to hurricane damage for 12 canopy species selected to represent a range of life history characteristics and having sufficient sample sizes (Table 1).

EFFECT OF DAMAGE DURING HUGO ON SUBSEQUENT DAMAGE DURING GEORGES.—Slightly over 16 percent of the trees in the combined dataset (1587 of 9610 separate individuals) were censused in both storms. We first investigated whether we needed to incorporate terms in our model to account for an association between the damage to a given tree by Hurricane Hugo and subsequent damage to that tree by Hurricane Georges (Putz & Sharitz 1991, Ostertag *et al.* 2005) for trees in Puerto Rico. Specifically, we looked for evidence of any relationship between the level of damage to an individual tree as a result of Hurricane Hugo and the level of damage to the same tree from Hurricane Georges, using contingency table analyses of the proportion of trees in the three damage classes following Georges as a function of whether the trees were either undamaged or partially damaged following Hugo. Trees that suffered complete damage during Hugo were omitted because many of those trees were on the ground or had died as a result of Hugo storm damage and were, therefore, not subjected to Hurricane Georges. The analysis for all species showed a striking lack of relationship between damage during Hugo and damage during Georges (Table 2; $\chi^2 = 0.26$, df = 2, $P = 0.88$). We also tested independence of damage in the two storms at the individual species level, and there were no cases of individual species with a significant association between damage during Hugo and damage as a result of Georges (Table S1). These results allowed us to treat the damage from the two storm events as independent, and to combine the observations from both storms into a single analysis.

ORDINAL LOGISTIC REGRESSION ANALYSIS.—Ordinal logistic regression estimates the probability that an observation (in this case, degree of damage to a tree) will fall into one of *n* ordinal classes, as a function of a set of explanatory variables. The procedure is an extension of traditional logistic regression, in which the log of the odds ratio (the logit) of an event is assumed to be a linear function of a set of explanatory variables ($x_i$):

$$\mathrm{logit}(p) = \log(p/(1-p)) = a + b_1x_1 + b_2x_2 + \ldots \quad (1)$$

The most common approach for extending this method to an ordinal scale (*i.e.*, a range of damage levels) is often called 'parallel slopes logistic regression,' because it assumes that the coefficients $b_i$ do not change for different levels of the ordinal scale. Instead, additional intercept terms ($a_j$) are added to the model, so that the logits for the cumulative probability of a given ordinal level are a set of parallel lines with different intercepts. Thus, if $p_j = \Pr(y \le Y_j|X)$, *i.e.*, the probability that an observation $y$ will be less than or equal to ordinal level $Y_j$ ($j = 1, \ldots, n-1$ levels), given a vector ($X$) of explanatory variables, then the probability that an event will fall into a single class $j$ (rather than the cumulative probability) is

$$p_{j-1\to j} = \Pr(y \le Y_j|X) - \Pr(y \le Y_{j-1}|X) \quad (2)$$

Since the probabilities are cumulative, $p_3 = 1$ (*i.e.*, the probability that damage will be less than or equal to complete crown loss $= 1$). The probability of complete canopy loss (damage class 3) by itself is simply

$$p_{2\to 3} = 1 - \Pr(y \le Y_2|X). \quad (3)$$

As in Canham *et al.* (2001) we assume that the degree of damage to an individual tree varies as a function of (1) species, (2) tree size (dbh), and (3) local storm intensity. Storm intensity is assumed to vary between subplots, but to be uniform for all trees within a subplot. Our analysis then estimates storm intensity as a parameter of the model. In effect, our analysis is hierarchical, with trees nested within subplots, and storm intensity as a subplot factor that is estimated as a parameter in our analysis. The basic model for the cumulative probability of damage level $j = 1$ or $j = 2$ is then:

$$\mathrm{logit}(p_{isj}) = a_{js} + c_s S_k DBH_i^{b_s} \quad (4)$$

where $dbh_i$ is the dbh of the $i$th individual of species $s$, $a_{js}$, $c_s$, and $b_s$ are species-specific parameters (for $s = 1, \ldots, m$ species), and $S_k$ are the estimated storm intensities for the $k = 1, \ldots, n$ subplots. Thus, the procedure estimates four parameters (two intercepts [$a_{js}$], plus $b_s$ and $c_s$) for each of the 12 species. It also estimates the $S$ parameter (*i.e.*, storm intensity) for each of the 136 subplots, giving a total of 184 parameters to be estimated simultaneously.

Parameter estimation and model evaluation.—Equations 2 through 4 allow us to calculate the likelihood of observing that tree $i$ of a given species $s$ and size ($dbh_i$) suffered damage level $j$, given a particular set of parameter values ($a_1$, $a_2$, $b_s$, $c_s$, and $S_k$). We used simulated annealing (a global optimization algorithm) to determine the maximum likelihood estimates for the 184 parameters (see Canham *et al.* 2001 for further details). We also calculated asymptotic two-unit support intervals (roughly analogous to 95% CIs) for each parameter estimate.

To assess the goodness of fit of the logistic regression model we used the approach taken by Canham *et al.* (2001). For each tree in the data set (regardless of species), we calculated the predicted probability for each of the three damage classes given the maximum likelihood parameter values. We then divided the predicted probabilities of damage (for each damage class) into intervals (0–10%, 10–20%, etc.) and compared these with the observed percentage of trees that actually had that level of damage. Any interval with $< 15$ observations was lumped into an adjacent interval. We then plotted the observed proportion of trees with that level of damage vs. the predicted probability of damage for each of the three damage classes. The benefit of this approach is that it is easy to see if the model fits equally well across the entire range of predicted probabilities, or whether it falls apart within some particular range.

## RESULTS

The overall model produced a very good fit to the data (Fig. 1). There was a slight tendency for the model to over-predict complete damage, and under-predict partial damage at the upper levels of probability of damage for these two damage classes (Fig. 1).

Storm severity.—Our method scales the computed range of storm intensity ($S$) calculated from the dataset over a range from 0 to 1. As expected from the meteorological records of hurricane wind speed for these storms, our analysis of the tree damage showed that Hurricanes Hugo and Georges differed slightly in estimated mean storm intensity across the plot (Hugo = 0.70, Georges = 0.65; Fig. 2; separate variance $t$-test $t = 2.54$, df = 106.9, $P = 0.012$). However, the range of storm intensity across the plot varied from 0.28 to 0.99 as a result of Hurricane Hugo, and ranged from 0.41 to 0.84 for Hurricane Georges (Fig. 2). By simultaneously estimating storm intensity and the parameters that reflect an individual stem's susceptibility to damage as a result of the species-specific characteristics

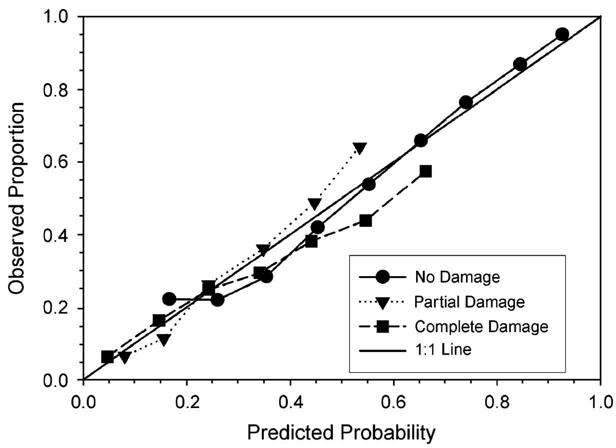


FIGURE 1. Goodness of fit of the ordinal logistic regression model. For each of the three damage classes (no damage, partial damage, and complete damage) the observations (all stems of all species and all plots) were grouped by the predicted probability of a given damage level, and then that probability was plotted against the observed proportion of stems that had that level of damage. Also shown is a 1:1 line for reference.

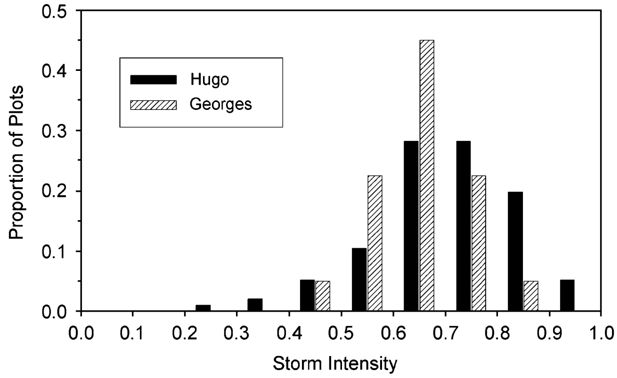


FIGURE 2. Estimated storm severity ($S$, Equation 4) for the 96 subplots sampled after Hurricane Hugo and the 40 subplots sampled after Hurricane Georges. All subplots were located within the 16-ha Luquillo Forest Dynamics Plot (LFDP). Mean storm severities were 0.7 for plots following Hurricane Hugo, and 0.65 following Hurricane Georges ($t$ = 2.54, df = 106.9, $P$ = 0.012).

and stem size, our estimates of local storm intensity are independent of the combination of species and stem sizes within a subplot.

EFFECTS OF TREE SIZE ON SUSCEPTIBILITY TO HURRICANE DAMAGE.—Parameters $a_1$, $a_2$, and $c$ in Equation (4) control the shape of the response to variation in storm intensity, while the exponent $b$ controls the shape of the effect of tree size (dbh) on susceptibility to damage. With the exception of *Sloanea berteriana*, all of the estimated $b$ exponents were much $< 1.0$ (Table S2). Thus, damage (or more precisely, the log of the odds ratio of damage) increases as an asymptotic function of tree size. Note that for *S. berteriana*, the support limit for $b$ was extremely wide, showing only weak evidence for an effect of tree size on risk of damage (Table S2). This was in marked contrast to the tight support limits for the $b$ parameter estimates for all other species (Table S2). For the palm (*P. montana*) the parameter estimate was actually negative, indicating that the probability of damage was lower for palms with a larger stem diameter. The $b$ exponents for all species in this analysis were substantially lower than were obtained for complete canopy windthrow of northern temperate species (which were in the range of 0.5–1.3) (Canham *et al.* 2001).

SPECIES-SPECIFIC VARIATION IN SUSCEPTIBILITY TO HURRICANE DAMAGE.—The 12 species showed a wide range of variation in susceptibility to crown damage for a given storm intensity (Fig. 3; damage calculated relative to a standardized 30 cm dbh stem, except for the palm *P. montana*, for which calculations were done for a 15 cm dbh stem). Note that since the functional form of a logistic regression is asymptotic at predicted probabilities of 0 and 1, the predicted probability of no damage is not exactly zero at zero estimated storm intensity. This simply reflects the combined effects of limitations in the functional form of Equation 4 and uncertainty in parameter estimation. The probability of complete loss of the crown when exposed to the most extreme storm intensity (0.99) varied from a high of 0.74 in *Casearia arborea* to a low of 0.24 for *P. montana*. Four of the 12 species were characterized by high risk of complete crown loss (probability $> 0.66$ under the most intense winds; Fig. 3). These included the pioneer *Cecropia schreberiana*

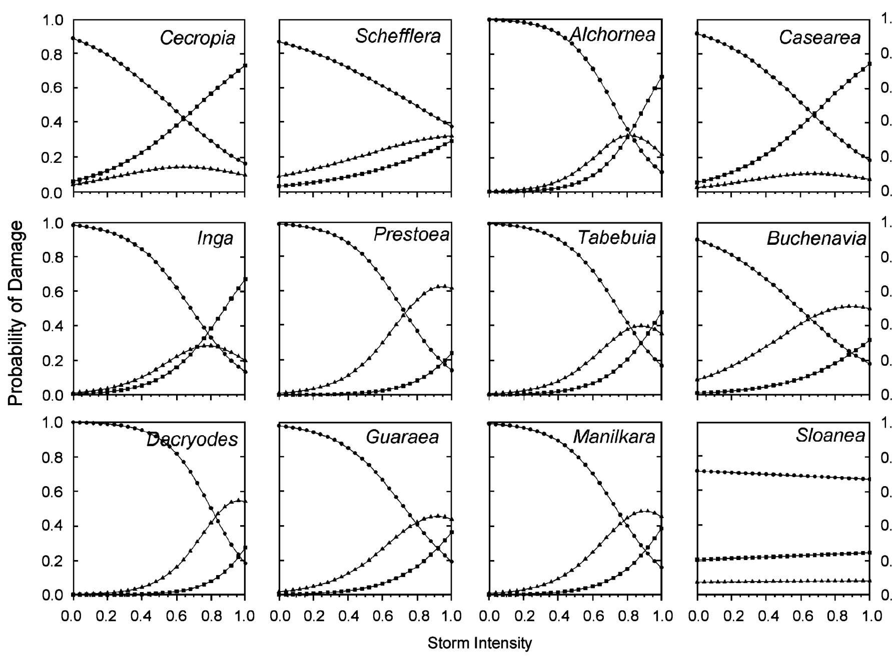


FIGURE 3. Predicted probability of (1) no or light crown damage (circles), (2) partial crown damage (triangles), or (3) complete crown loss (squares) for the 12 study species as a function of storm intensity, using Equation 4 and the parameters in Table S2. Calculations were done for 30 cm dbh stems, except for the palm *P. montana*, for which calculations were done for a 15 cm dbh stem.

and three secondary forest species (*Alchornea latifolia*, *C. arborea* and *Inga laurina*; Fig. 3). The architecture of *C. arborea* appears to make it susceptible to either complete damage or no significant damage, with very few stems showing partial damage at any level of storm severity (Fig. 3). Four of the species (*Tabebuia heterophylla*, *Manilkara bidentata*, *Guarea guidonia*, and *Buchenavia tetraphylla*) had intermediate susceptibility to damage ($0.33 < P < 0.5$ for complete canopy loss under the most intense winds). *Tabebuia heterophylla* is a secondary forest species with relatively low density wood, and *B. tetraphylla* has large, horizontally spreading branches, characterisitics that may increase their susceptibility to wind damage, while *M. bidentata* has high density wood and together with *G. guidonia* is found mainly in late successional stands. The remaining four species (*Schefflera morototoni*, *Dacryodes excelsa*, *S. berteriana*, and *P. montana*) all had low probabilities of complete canopy loss even under the most severe conditions estimated for the two storms (Fig. 3). This last group contains a wide range of successional status, from the pioneer *S. morototoni* to the secondary forest palm *P. montana* and the late successional *D. excelsa* and *S. berteriana*. Given the very low values estimated for the *b* exponents (Table S2), both the rankings and the absolute values of the probabilities of damage do not vary dramatically as a function of tree size. *Sloanea berteriana* is an exception: the relatively flat response of 30 cm dbh stems to variation in storm intensity (Fig. 3) does not hold true for larger stems of this species. For example, the probability of complete canopy loss rises to 0.60 under the most intense winds for a 75 cm dbh stem (the largest *S. berteriana* in the dataset).

## DISCUSSION

Our analyses provide a predictive model of variation in species susceptibility to hurricane damage as an explicit function of variation in the local intensity of the storm. The model is far simpler than many biomechanically based models for wind damage to trees (*e.g.*, Niklas 2000, Ancelin *et al.* 2004). The only attributes of the trees incorporated in our model are species identity and a measure of tree size. These two simple variables, however, encapsulate much of the variation in individual tree attributes (*i.e.*, allometric relationships with crown diameter and tree height, and species-specific differences in crown architecture, wood density, and rooting patterns) that are the proximate cause of the damage to an individual, given the local intensity of a storm.

Our results lend further support to the belief that species-specific responses to wind disturbance represent an important axis of differentiation in the life histories of tropical trees. Overall, late successional species with high wood density such as *M. bidentata* and *S. berteriana*, tend to be more resistant to stem damage but more likely to lose branches (Zimmerman *et al.* 1994). In contrast, the wood of pioneer and secondary successional species, such as *A. latifolia* and *C. shreberiana*, tends to be less dense and more susceptible to breakage. *Dacryodes excelsa* and *Casearia arborea* have similar mid-range wood densities but respond differently to hurricane damage. *Casearia arborea*, which prefers a higher light environment and establishes in secondary forest, tends to tip-up in hurricane force wind, possibly due to a shallow root system. *Dacryodes excelsa* may suffer considerable branch damage during hurricanes (J. Thompson, pers. obs.) but rarely suffers stem breaks and does not tip-up because of its extensive root grafts and root anchorage to bedrock and subsurface rocks that provide resistance to windthrow (Basnet *et al.* 1993). The highly resistant species *S. berteriana* has buttresses that may confer some stability during wind storms, but the size of the buttresses are not reflected in the stem diameter measurements as diameters are conventionally measured above the buttresses.

The overall patterns of damage from the two different hurricanes are similar to those reported by Zimmerman *et al.* (1994) following Hurricane Hugo. A notable exception was the pioneer *S. morototoni*, which displayed low susceptibility to wind damage in the combined analysis of both hurricanes presented here, while patterns of damage following Hurricane Hugo suggested that *S. morototoni* had a response similar to the other common pioneer, *C. schreberiana* (Zimmerman *et al.* 1994). Possible explanations for the difference might be that *S. morototoni* was slow to recover from Hurricane Hugo and had not re-grown large branches that could be subsequently damaged by Hurricane Georges and these smaller crowns made the trees less vulnerable to being snapped or broken. There was also a dramatic increase in the number of *C. schrebriana* across the LFDP after Hurricane Hugo so many more medium-sized *C. schreberiana* were available in the forest to be damaged at the time of Hurricane Georges.

The failure to see a strong relationship between stem diameter and probability of crown damage may be a distinctive characteristic of the Luquillo forest that has suffered repeated hurricane damage throughout the life of many of these long-lived trees. Hurricanes are estimated to strike the Luquillo experimental forest every 50–60 yr (Scatena & Larsen 1991) so it is likely that the trees that are currently in the forest have experienced several hurricanes and survived. The trade winds and repeated hurricanes have also trimmed the crowns on these trees so that their crown dimensions are smaller than their diameter would predict, and thus their wind exposure and vulnerability would be lower than trees with comparative diameters in regions without comparable hurricane frequency.

Our analysis confirms that the average intensity of Hurricane Hugo was greater than the average intensity of Hurricane Georges within the LFDP, but the differences in average storm intensity are much smaller than would be suggested by simple examination of the total amount and nature of damage to trees during the two storms. For example, before Hurricane Hugo, the site had not suffered a severe hurricane since 1932 (57 yr earlier). This allowed the accumulation of stems of species with high susceptibility to complete canopy loss. In contrast to assessments of storm severity based on observed patterns of damage, our estimates of storm intensity are not confounded by differences in the makeup of the forest at the times of the two storms.

Previous studies have found both positive and negative correlations between damage to individual trees in one storm and damage to the trees in a subsequent storm (Putz & Sharitz 1991, Ostertag *et al.* 2005). Ostertag *et al.* (2005) showed that trees that were undamaged in Hurricane Hugo were more likely to receive damage 9 yr later during Hurricane Georges, while trees with intermediate levels of damage during Hugo were least likely to be damaged during Georges. In contrast, there was no relationship between damage to trees within the LFDP during Hurricane Hugo and the degree of damage to the same trees during Hurricane George. Part of the explanation for the differences between our results and the study by Ostertag *et al.* (2005) may be that their study involved primarily exotic or plantation species that have not evolved in hurricane exposed environments. In addition, the Ostertag *et al.* (2005) research site is on the south side of the Luquillo Mountains and is likely to have experienced much higher winds during Hurricane Georges (whose eye passed to the south side of the Mountains) than did the LFDP, which is on the north side.

Land-use history has a greater effect on present-day forest composition in the LFDP than do marked differences in topography, soil, and hurricane damage (Thompson *et al.* 2002). Land-use history also influences the spatial distribution of hurricane damage within the plot, since the species that colonized abandoned agricultural portions of the plot tend to be more vulnerable to hurricane damage than those from undisturbed habitats (current results, Zimmerman *et al.* 1994, Thompson *et al.* 2002, Boose *et al.* 2004). Typically, greater exposure to winds at higher elevations generates more severe damage patterns on topographic peaks and hills (Boose *et al.* 1994). Contrary to this expectation, damage in the Luquillo Experimental forest was greater at the lower elevations, which are dominated by the more susceptible secondary species that became established on land disturbed by human land use and agriculture (Everham 1996). The elevational range across the LFDP is only 95 m and probably not large enough to show an elevation effect. Repeated hurricane disturbance may reinforce land use legacies in this forest by repeatedly damaging the more vulnerable secondary species and generating large gaps that favor the subsequent re-establishment of pioneer and secondary species.

## ACKNOWLEDGMENTS

We thank the founders of the LFDP: R. B. Waide, D. J. Lodge, C. M. Taylor, and E. M. Everham III. J. Thomlinson helped to prepare the tree maps. This work was supported by an NSF Postdoctoral Fellowship to M.U., NSF DEB-0087214 to C.D.C. and J.T., and grants from NSF to the Institute for Tropical Ecosystem Studies, University of Puerto Rico, working with the International Institute of Tropical Forestry (USDA Forest Service) for the Luquillo Long-Term Ecological Research Program. The US Forest Service and the University of Puerto Rico provided additional support. This study is a contribution to the program of the Cary Institute of Ecosystem Studies.

## SUPPORTING INFORMATION

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

TABLE S1. *Contingency table results for tests of association between level of damage to stems during Hurricane Hugo, and level of damage observed on those stems following Hurricane Georges.*

TABLE S2. *Maximum likelihood parameter estimates for variation in susceptibility to hurricane damage for the 12 dominant tree species as a function of size and storm intensity.*



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