

Factors Affecting Tropical Tree Damage and Survival after Catastrophic Wind Disturbance

Edward L. Webb^{1,5}, Martin van de Bult², Siafoi Fa'aumu³, Rachel C. Webb⁴, Ailao Tualualelei³, and Luis R. Carrasco¹

¹ Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, 117543 Singapore

² Doi Tung Development Project, Social Development Department, 920 M 7 Mae Fah Luang, A. Mae Fah Luang, Chiang Rai, 57240 Thailand

³ Department of Marine and Wildlife Resources, Government of American Samoa, P.O. Box 3730 Pago Pago, 96799 American Samoa

⁴ 117 Clementi Road, 129800 Singapore

ABSTRACT

The structure and dynamics of cyclone-prone tropical forests are driven in part by variation in tree species resistance to and survival after wind-induced structural damage. We determined the factors associated with tree damage and 3-yr survival following Category 5 Cyclone Olaf on the Polynesian island of Ta'u, American Samoa. Despite sustaining a high rate of severe damage (34.6% of all trees snapped, 23.0% uprooted), system resilience was high with 74.3 percent stem survival overall and an annual mortality rate of 7.9 percent compared with 2.1 percent in nearby undisturbed late successional forest. Three-yr survival rate of trees sustaining severe damage was 63.1 percent, compared to about 89 percent for trees sustaining only branch loss or defoliation. Three-yr survival differed according to damage type, 78.5 percent after snapping vs. 38.4 percent after uprooting. Species differed widely in resistance to and survival after snapping and uprooting. Several species and individual traits were associated with the probability of snapping or uprooting; however, wood density was the only species trait consistently, and negatively, associated with the probability of sustaining either damage type. Survival after snapping was negatively associated with the proportion of the tree snapped off, which was determined by individual tree architecture. Species growth rate was negatively associated with survival after uprooting, indicating the importance of shade tolerance for survival after uprooting. Thus, whereas species traits seemed to exclusively underpin resistance to and survival after uprooting, they only partly accounted for snapping resistance, and did not determine the intensity of snap damage or survival after snapping. Our results highlight the importance of considering each damage type separately when considering ecological trade-offs.

Key words: cyclone; hurricane; life history; mortality; Polynesia; resilience; resistance; resprout; uproot.

CYCLONES HAVE IMPORTANT, IMMEDIATE, AND LONG-TERM EFFECTS on tropical forest structure, composition, and dynamics (Everham & Brokaw 1996, Burslem *et al.* 2000, Lugo 2008). Immediate structural impacts include minor damage such as defoliation and branch loss, and severe damage that includes stem breakage and uprooting. Previous studies have documented high variation in tree species damage and subsequent survival rates from cyclones and hurricanes (Everham & Brokaw 1996, Ostertag *et al.* 2005, Curran *et al.* 2008a). Such variation contributes to post-disturbance trajectories through the proportion of pre-cyclone trees surviving and resprouting; which in part determines the long-term trajectory of forest recovery (Pacala & Rees 1998, Uriarte *et al.* 2009) ultimately promoting species coexistence (Clark 1996, Loehle 2000).

Resistance is defined as the ability to avoid damage from natural disturbances (Holling 1973), and three principal dimensions of tropical tree species traits that may be associated with resistance to cyclones are wood characteristics, growth rate, and architecture. Studies suggest a trade-off between wood density and growth rate (King *et al.* 2005), such that fast growing, light

demanding species exhibit lower wood density than slow-growing, dense-wooded species, and therefore sustain greater levels of damage during cyclones (Putz *et al.* 1983, Bellingham *et al.* 1995, Ostertag *et al.* 2005, but see Read *et al.* 2011). Tree architecture (tree diameter, tree height, and canopy characteristics) may relate to damage susceptibility; however, the size–damage association has not been consistent across locations and storms. Several studies have found a positive association between tree diameter and damage (Ostertag *et al.* 2005, Van Bloem *et al.* 2005, Lewis & Bannar-Martin 2011). Other studies have reported tree height/diameter ratio positively associated with damage (Putz *et al.* 1983), both height and dbh positively associated with damage (Reilly 1991, Vandecar *et al.* 2011), intermediate size diameter trees sustaining more damage (Imbert *et al.* 1996), or little to no size–damage relationship (Bellingham 1991, Metcalfe *et al.* 2008, Canham *et al.* 2010).

After sustaining damage, survival may differ across species and be influenced by several factors, including the type of damage and species traits. Stem snapping and uprooting are the two most important damage types leading to mortality, and recovery from stem snapping may require different traits than recovering from uprooting. For example, uprooting effectively reduces tree height to ground level and exposes roots, limiting the ability to

Received 4 December 2012; revision accepted 4 July 2013.

⁵Corresponding author; e-mail: ted.webb@nus.edu.sg

access above- and belowground resources. Tree survival after uprooting may therefore depend upon shade tolerance and ability to access belowground resources. Snapped trees, on the other hand, retain an intact root system, and recovery may depend more upon species resprouting abilities along with shade tolerance (Bellingham *et al.* 1994, Curran *et al.* 2008b).

A general challenge associated with research on tropical tree responses to cyclones, is being able to separate the independent effects of species traits on resistance and survival, largely owing to the data requirements for analysis such as pre-disturbance surveys, repeated measures, and adequate sample size. Nevertheless, a few studies have been able to statistically separate out the effects of species or individual tree traits such as wood density, growth rate, architecture, and physical components such as forest type and topography, on variability in damage and survival; providing important insights into predictors of damage and survival across species in cyclone-disturbed tropical forests (*e.g.*, Putz *et al.* 1983, Ostertag *et al.* 2005, Canham *et al.* 2010). An understanding of these dimensions of damage resistance is improving further with long-term studies providing data to support multivariate models (*e.g.*, Uriarte *et al.* 2012).

The tropical South Pacific is a climatically dynamic region (Franklin *et al.* 2004, Keppel *et al.* 2010), and the Samoan archipelago has been hit by several cyclones in the last few decades (Elmqvist *et al.* 1994, Webb *et al.* 2011). On 16–17 February 2005, the eye of Cyclone Olaf passed 28 km to the east of the island of Ta'u, American Samoa, located at 169°28'W, 14°14'S (Figure S1). Olaf was classified as Category 5 on the Saffir-Simpson scale with barometric pressure of 915 h Pa, sustained winds of 260 km/h and gusts of 320 km/h (Joint Typhoon Warning Center 2005).

We studied the immediate and short-term impacts of Cyclone Olaf on tropical rain forest structure on Ta'u, American Samoa. We tested three hypotheses related to species traits, damage-resistance, and 3-yr post-cyclone survival. First, we hypothesized that species would differ in their resistances to snapping and uprooting damage (collectively, severe damage). The second hypothesis was that survival after sustaining severe damage would vary across species and damage types. Finally, we hypothesized that variation in damage resistance and post-damage survival would be associated with species traits including wood density, growth rate, and architecture.

METHODS

STUDY SITE.—This study was conducted on the eastern portion of Ta'u island, in the Samoan archipelago of the South Pacific (Figure S1). Ta'u was formed approximately 300,000 yr BP (Nunn 1998) as a shield volcano. The eastern coast of the island has a narrow, flat bed of basaltic alluvium and coral rubble (an extremely cobbly and sandy Ngedbus variant, Natural Resources Conservation Service 2004) extending approximately 150 m inland, where a steep escarpment rises to approximately 170 m asl. Slopes above the escarpment average 12° (Webb *et al.* 2006), and soils are moderately deep, well-drained stony clay loams (Typic

Dystrandepts) formed in volcanic ash and underlain with lava (Natural Resources Conservation Service 2004).

Lowland rain forest of Ta'u is dominated by the large, long-lived tree species *Dysoxylum samoense* (Whistler 1992, Webb *et al.* 2006). In Ta'u coastal lowland forest, *Dysoxylum* is found in association with *Diospyros samoensis*, *Sterculia fanaibo*, and *Pisonia umbellifera*, whereas above the escarpment (to about 250 m asl) *Hibiscus tiliaceus*, *Syzygium inophylloides*, *Rhus taitensis*, and *Alphitonia zizyphoides* are important associates (Webb *et al.* 2006).

The Samoan archipelago has been inhabited for ca. 3000 yr (Kirch 2000), and much of the forest on Ta'u has been used for agroforestry to grow staple crops including banana (*Musa*), breadfruit (*Artocarpus altilis*), coconut (*Cocos nucifera*), and taro (*Colocasia esculenta*), as well as recent introductions such as papaya (*Carica papaya*) (Whistler 2002). On eastern Ta'u, agroforestry cultivation was present until about 1987, when most inhabitants abandoned cultivation after Cyclone Tusi, and any remaining cultivation ceased with the establishment of the Ta'u unit of the National Park of American Samoa in 1992 (Webb *et al.* 2006). Abandoned plantations contained naturalized populations of *A. altilis* and *C. nucifera* in the forest, along with other species common in disturbed forest and abandoned plantations, including *Dysoxylum samoense*, *Macaranga harveyana*, and *Ficus scabra* (Webb *et al.* 2006).

PLOT ESTABLISHMENT AND PRE-CYCLONE SURVEY.—Four permanent forest monitoring plots were established in late 2004, on the eastern aspect of Ta'u island (Webb *et al.* 2006, Figure S1). Plot locations were selected after reconnaissance hikes into the forest, combined with interviews with local village inhabitants familiar with locations of recent agroforestry prior to Cyclone Tusi in 1987 and the establishment of the National Park in 1992. Two 1-ha plots (50 × 200 m) were at sea level, and two 2-ha plots (100 × 200 m) were at about 200 m asl. At each elevation, one plot was established in approximately 20-yr old regenerating agroforestry ('secondary'), and a second was established in forest without evidence of recent cultivation ('primary'). Aside from elevation, there were no major topographical features such as ridges or stream valleys, either within or near the plots, which would vary plot exposure to cyclone winds.

For the two coastal plots, there was only one section of the coastline that did not have evidence of recent plantations, and so that location was chosen as the 'primary' site. This was the site described by Whistler (1995) as a representation of *Dysoxylum* coastal forest. For the coastal secondary forest plot location, there was only a small portion of the coastline remaining to the south of the primary forest plot in which we could lay out the plot given the required dimensions (50 × 200 m). So we first calculated the amount of available space to the south of the primary forest plot and then randomly chose a distance within the range of possible distances from the primary forest plot.

For two plots above the escarpment, a different selection technique was used owing to the fact that forest was difficult to access and thus limited the extent of forest we could survey efficiently. Through reconnaissance hikes, we evaluated forest accessibility and observed where uncultivated forest patches might be

located. Our hikes occurred below 300 m asl, where the forest begins to transition into Ta'u summit scrub (Whistler 2002). We explored forest that could be reached within a 1.5-h hike from the village of Fitiuta, accessed by a trail traditionally used by Samoans to access their agroforest areas, and to hunt wildlife (e.g., the Pacific Pigeon *Ducula pacifica* or fruit bats *Pteropus tonganus* and *P. samoensis*). We located a region that had no evidence of recent cultivation, was traditionally used for non-agricultural (hunting) purposes, dominated by native tree species, and with little or no representation of plantation species in the immediate vicinity (Webb *et al.* 2006). For the secondary forest site, we chose an area that had been utilized in the recent past for agroforestry, contained established and reproductive populations of *Artocarpus altilis* (breadfruit) and *Cocos nucifera* (coconut), had been terraced in places to facilitate taro cultivation, but exhibited prolific regeneration of native tree species, in particular *Dysoxylum samoense* and *Ficus scabra* (Webb *et al.* 2007).

In each plot, every woody tree stem ≥ 10 cm diameter at 1.4 m height above the base (dbh) was tagged, identified to species, measured for dbh and height (using a clinometers), and mapped using Cartesian coordinates (Webb *et al.* 2006).

POST-CYCLONE SURVEYS.—We conducted a post-cyclone damage assessment in April 2005, two mo after Cyclone Olaf (Figure S2). We relocated >99 percent of all trees and coded the damage sustained. Trees sustaining severe damage were uprooted (on the ground or leaning at least 45 degrees, and with the roots exposed), or snapped (stem fully or partially broken beneath the crown). Trees sustaining minor damage were leaning <45 degrees (without the roots exposed), or had sustained crown loss (leaf loss or single- or multiple-branch loss). The height at which a trunk snap occurred was calculated to the nearest meter using a clinometer for trunks snapped >4 m above the base, and estimated by eye for snaps less than 4 m.

We returned to the plots at 18 and 36 mo after the cyclone to assess survival. A tree was considered to be alive if it had living cambium under the bark, living branches, or coppices/sprouts anywhere along the stem (including basal sprouts).

DAMAGE AND SURVIVAL RATE CALCULATIONS.—Species damage rates were calculated for snapping and uprooting, collectively termed 'severe damage'. We ran a correlation on snap rate vs. uprooting rate. As more stems of a species were damaged in one manner, however, fewer were available to be damaged in the other manner. To control this effect, we calculated the 'adjusted damage rate', which was the percent of available stems (*i.e.*, not damaged otherwise) that sustained a particular damage type. Thus, the adjusted trunk snap rate was calculated as the percent of stems not uprooted that were snapped, and the adjusted uproot rate was the percent of stems not snapped that were uprooted. The association between adjusted damage rates was measured with a Pearson correlation on 31 species with at least 10 single-stemmed trees prior to the cyclone.

We ordered species according to total severe damage rate. Adapting a modification in the classification by [Comita *et al.*](#)

(2009), we considered a species as damage-resistant if ≤ 30 percent population sustained severe damage, or damage-susceptible if ≥ 70 percent of the population sustained severe damage. The cutoffs for susceptible and resistant classes in this study are different from Comita *et al.* (2009, who used 6% and 10% stem breakage as cutoffs for resistant and susceptible species, respectively) because there was a much greater range of damage rates in this study than theirs. For classifying species as resistant or susceptible to snapping or uprooting, we used a more relaxed cutoff of 40 percent and 60 percent of the population sustaining that damage type.

Three-yr survival was calculated as the percentage of the 2004 trees still alive in 2008. From this we calculated the annual mortality rate (AMR) (Swaine & Lieberman 1987 [Condit *et al.*](#) 1995). Survival rates and AMR were calculated as follows: (1) for all trees in the plots; (2) for trees sustaining each damage type; and (3) for trees sustaining only minor damage (defoliation, branch loss, or leaning bole, *i.e.*, all other trees). Species survival rates after damage were compared between damage types (snap vs. uproot) and between each severe damage type and stems sustaining minor damage (*i.e.*, snap vs. minor, uproot vs. minor); all comparisons were made with a related samples Wilcoxon signed rank test.

DAMAGE AND SURVIVAL MODELS.—We developed generalized linear models (GLM) and generalized linear mixed-models (GLMM) with binomial errors to test for associations of various tree parameters with the probability of a tree sustaining damage, and secondly the probability of survival after sustaining damage. The models were analyzed using the package lme4 (Bates *et al.* 2010) in the R environment for statistical computing (R Development Core Team 2005).

Three damage models were run to test for variables associated with (1) tree snapping and (2) uprooting, with a binary dependent variable of damaged or not damaged. For these two damage models, the independent variables were forest type (primary or secondary), elevation (coastal or upper), species wood density, mean species growth rate, tree dbh, tree height, and tree crown:bole ratio (the ratio of crown height [height of first branch to top of tree] divided by the bole height [height from base to first branch]). A third damage model was applied only to trees that were snapped, with the dependent variable being the percent of the total tree height snapped off.

Two survival models were applied to trees that experienced severe damage, to test for variables associated with 3-yr survival after (1) snapping and (2) uprooting. For these two models, the dependent variable was binary, *i.e.*, dead or alive. The independent variables were the same as the damage model. For the tree snap survival model, two additional independent variables were the percent of the total tree height snapped off, and the number of stems alive for that tree after snapping (for multiple-stemmed trees).

Tree snap damage and snap survival models treated each stem independently, including those in multiple-stemmed trees (but accounting for possible non-independence, see below). This

is because each stem of a multi-stemmed tree could snap independently of others. For uproot damage and survival models, we consolidated stems of multi-stemmed trees into single records (11.5% of all trees were multi-stemmed, Webb *et al.* 2007) because either all or none of the stems of a multi-stemmed tree were uprooted (non-independence). When reporting the results, we use the term ‘tree’ to refer to both single- and multi-stemmed trees, to maintain terminological consistency.

To account for possible non-independence at the tree (for multiple-stemmed trees) and plot level, we evaluated three types of random effects structures: random intercept based on plot; random intercept based on tree; and random intercept and slope based on plot and tree, respectively. The Akaike Information Criterion (AIC) was compared among GLMMs, and with an equivalent GLM model without random effects. AIC was used for model simplification, where non-significant variables were removed stepwise from the model to obtain the lowest AIC (model outputs are available from the authors).

Wood density data were calculated from wood cores collected in the yr 2010 from at least five large, healthy trees of 30 species near to (but outside of) the long-term forest monitoring plots on Ta’u and Tutuila islands (Webb *et al.* 1999, 2011). Samples approximately 50 percent of the stem diameter, including the outer bark, were extracted with an increment borer of 4.3 mm diameter and 25 cm length (Webb *et al.* 2011). The dimensions of each core were taken, all samples were dried at 105 °C for 48 h, and dry mass was recorded to the nearest 0.001 g. Wood specific gravity (hereafter referred to as ‘wood density’) was calculated as the mass of dried wood divided by the volume of the fresh sample and reported as g/cm³ (Williamson & Wiemann 2010). Wood density values for species we were unable to sample were supplemented from the Global Wood Density Data base (Chave *et al.* 2009, Zanne *et al.* 2009).

Growth rate data were the 10-yr mean (or median) species growth rates in late successional forest monitoring plots on the nearby island of Tutuila, approximately 130 km away (Webb & Fa’aumu 1999, Webb *et al.* 2011). We utilized growth rate data for 21 common species, thus constraining the models to only those species. The Tutuila growth data were used in lieu of pre-cyclone Ta’u growth rate data, as the Ta’u plots were established only 2 mo prior to Cyclone Olaf. The lack of individual-level pre-cyclone growth data precludes an individual-based assessment of growth-damage or growth-survival tradeoffs (Ostertag *et al.* 2005, Clark 2010, Uriarte *et al.* 2012). However, species growth rates in closed forest may align along a continuum of shade tolerance, with shade tolerant species exhibiting slower growth rates than shade intolerant species (Denslow 1987, Kitajima 1994). In this manner, the species growth rate data are likely to be more indicative of species-level shade tolerance than of individual-level condition.

RESULTS

CYCLONE DAMAGE AND SPECIES RESISTANCE.—Severe damage from Cyclone Olaf was sustained by 57.7 percent of all trees; 34.6

percent were snapped and 23.0 percent were uprooted (Table 1). There was no significant difference in the rates of snapping vs. uprooting across species (paired samples *t*-test $N = 32$, $t = 0.926$, $df = 31$, $P = 0.36$). Every species with at least 10 stems prior to the cyclone had ≥ 20 percent severe damage (Fig. 1) and no trees escaped some form of damage. Trees that were not snapped or uprooted were leaning or sustained branch loss of varying degrees, and all trees were completely defoliated (Fig. S2).

Rates of severe damage across species ranged from 23 percent to 98.7 percent (Fig. 1). Damage-resistant species, *i.e.*, those sustaining ≤ 30 percent severe damage, were *Barringtonia samoensis*, *Garuga floribunda*, *Flacourtia rukam*, and *Syzygium inophylloides*. In contrast, nine damage-susceptible species sustained ≥ 70 percent severe damage, including *Pipturus argenteus*, *Macaranga harveyana*, *Barringtonia asiatica*, *Rhus taitensis*, *Trichospermum richii*, *Cocos nucifera*, *Artocarpus altilis*, *Hernandia nymphaeifolia*, and *Sterculia fanaibo* (Fig. 1). Four species tended to snap with more than 60 percent of the pre-cyclone population snapping (*A. altilis*, *H. nymphaeifolia*, *Pisonia grandis*, and *Sterculia fanaibo*), and three species tended to uproot with >60 percent of the pre-cyclone population uprooting (*M. harveyana*, *P. argenteus*, and *R. taitensis*) (Fig. 1). There was a significant positive correlation between adjusted damage rates ($N = 31$ species, Pearson $R = 0.52$, $P < 0.01$), indicating that susceptibility to one damage type was associated with susceptibility to the other damage type, and confirming that species could be generally classified as resistant or susceptible based on total damage rate.

The results from damage models (Table 2) indicate that wood density, growth rate, and tree architecture (height, diameter, crown:bole ratio) were associated with the probability of trunk snapping, and tree architecture was associated with the percent of height snapped. Wood density, growth rate, forest type and to a

TABLE 1. Damage and mortality from Cyclone Olaf, Ta’u, American Samoa. Damage type ‘Minor’ refers to the number of stems or individuals that sustained defoliation, partial crown removal or were leaning. AMR is the annual mortality rate. Undisturbed late successional forest AMR was calculated for 1998–2008 on the nearby island of Tutuila (Webb *et al.* 2011).

	N 2004	Damage		3-yr survival		AMR %	
		Type	N	%	N		%
Stems	3726	Trunk snap	1288	34.6	1011	78.5	6.5
		Minor	1587		1406	88.6	3.2
Individuals	3220	Uproot	739	23.0	284	38.4	25.5
		Minor	1362		1218	89.4	3.0
		Severe damage combined	1858	57.7	1173	63.1	12.3
All individuals	3220		3220		2391	74.3	7.9
Undisturbed late successional forest							2.1

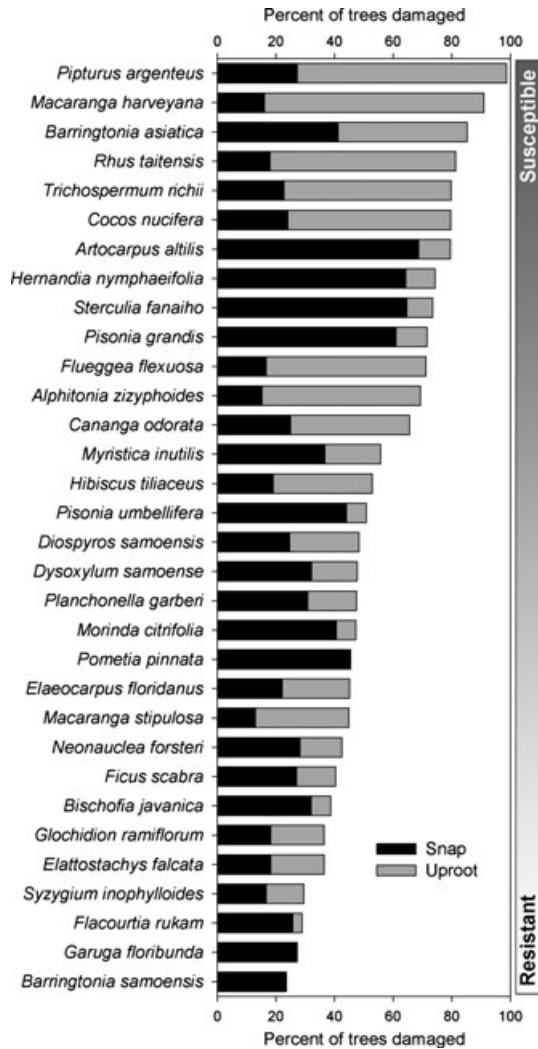


FIGURE 1. Damage rates and susceptibility to Cyclone Olaf for 32 common (pre-cyclone $N \geq 10$) tree species on Ta'u, American Samoa. The resistance-susceptibility gradient was based on total damage rates.

lesser extent dbh were associated with uprooting. Wood density was consistently, and negatively, associated with the probability of both damage types, and was strongly and negatively correlated with total severe damage (Fig. 2). Growth rate was negatively associated with the probability of snapping, but positively associated with the probability of uprooting. The probability of snapping, and the percent of the tree height snapped, increased for taller trees with smaller diameters. The crown:bole ratio was positively associated with the likelihood of snapping, but negatively associated with the percent of the tree snapped. Trees in secondary forest uprooted less than those in primary forest.

POST-CYCLONE SURVIVAL.—The three-yr survival rate of all pre-cyclone trees was 74.3 percent, equivalent to an AMR of 7.9 percent (Table 1). This AMR is nearly four times the AMR of 2.1 percent for undisturbed late successional forest on Tutuila

TABLE 2. Output from general linear mixed-models (GLMM) and generalized linear models (GLM), testing for association between life history variables, cyclone damage, and 3 yr post-damage survival. Sample size for each test is denoted as number of species and the number of trees (stems or individuals). Cells marked 'ns' were not included in the final model.

Variable	Damage [†]			Survival [‡]	
	Trunk Snap	Percent height snapped	Uproot	Trunk Snap	Uproot
Sample size (species, trees)	22, 1823	22, 540	20, 539	22, 1663	19, 416
Intercept	0.26	-0.17	0.19	3.29***	-0.25
Forest type (secondary)	Ns	Ns	-1.20***	Ns	0.55*
Elevation (upper)	Ns	Ns	Ns	Ns	Ns
Wood density	-2.93***	Ns	-3.93**	1.97	0.67
Growth rate	-0.99***	0.29	1.11***	Ns	-1.63**
Height	0.08***	0.10***	Ns	Ns	Ns
Crown:bole ratio	0.13**	-0.21***	-0.02	0.22*	0.01
Diameter (dbh)	-0.03***	-0.02***	0.01*	-0.02*	-0.01
Percent of tree height snapped				-0.05***	
Number of stems alive (after snap)				0.80*	

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

[†]Results from a GLMM

[‡]Results from a GLM

(Table 1). Survival of trees sustaining severe damage was 63.1 percent, (AMR = 12.3%). Snapped stems had 78.5 percent survival (AMR = 6.5%), while uprooted trees had 38.4 percent survival (AMR = 25.5%), compared to ~89 percent survival (AMR ~ 3.0) for trees sustaining minor damage (Table 1). Survival after snapping was significantly higher than survival after uprooting ($N = 11$ species, related samples Wilcoxon signed rank test, $P < 0.05$). Survival after either snapping or uprooting was lower than survival after minor damage (snap vs. minor, $n = 15$ species, related samples Wilcoxon signed rank test, $P < 0.05$; uproot vs. minor, $n = 11$ species, related samples Wilcoxon signed rank test, $P < 0.05$).

Species varied widely in survival after snapping and uprooting (Table 3). Survival models indicated that for snapped trees, 3-yr survival was strongly and negatively associated with the percent of total height snapped (Table 2); post-snap mortality increased significantly with the percentage of pre-cyclone height snapped off (Fig. 3, one-way ANOVA $df = 4$, $F = 243.4$, $P < 0.0001$). Post-snap survival was to a lesser extent related to

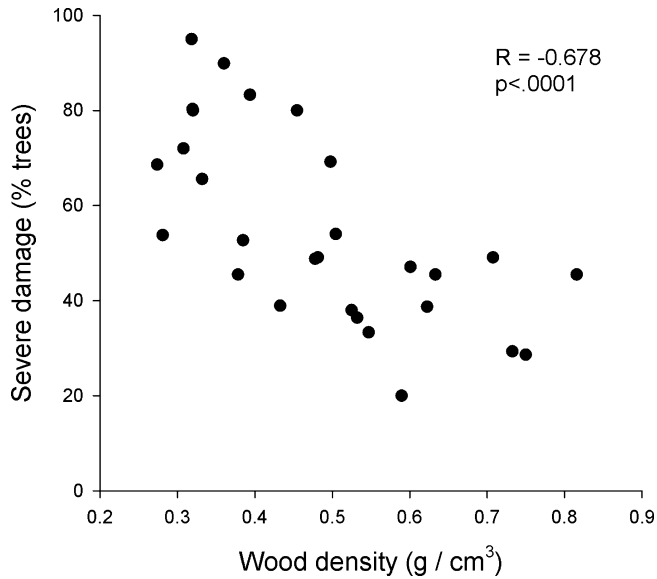


FIGURE 2. Scatterplot of wood density and severe damage rates (snapping + uprooting) for 28 common tree species on Ta'u, American Samoa. Results from a Pearson correlation are shown.

crown:bole ratio (positive), dbh (negative) and the number of living stems (positive) (Table 2). Wood density was positively, but not significantly, associated with survival after snapping.

For uprooted trees, survival was strongly and negatively associated with species growth rate (Table 2). Trees in secondary forest tended to survive more after uprooting than trees in primary forest, but the significance of the association was weaker than the growth rate – survival association.

DISCUSSION

CYCLONE OLAF IN CONTEXT.—With sustained wind speeds of 260 km/h and gusts of up to 310 km/h, Cyclone Olaf was one of the strongest cyclones for which tropical forest damage and mortality has been investigated. Yet despite high severe damage rates overall (57.7%), the Ta'u forest exhibited high overall 3-yr survival rates (74.3% survival, AMR = 7.9%), indicating high system resilience (Gunderson 2000) and suggesting that direct succession will proceed, with early successional species temporarily outperforming late successional species. Whereas the AMR of 7.9 percent after Cyclone Olaf is 3.8 times the rate of undisturbed late successional forest in American Samoa (2.1%, Webb *et al.*

TABLE 3. Wood density, growth rates, and 3-yr survival rates for 21 tree species on Ta'u, American Samoa, following Cyclone Olaf. Survival rates are given only for $N \geq 10$ trees for each damage category. The number of pre-cyclone trees is the total number of stems, with the number of individuals in parentheses (*i.e.* multi-stemmed trees counted only once). Survival after snapping was calculated with stems and survival after uprooting with individuals.

Species	Pre-cyclone trees	Wood density (g/cm ³)	Growth rate (cm/yr)	3-yr survival		
				Snap (%)	Uproot (%)	Minor
<i>Alphitonia zizyphoides</i>	112 (109)	0.50	0.49		11.9	81.8
<i>Artocarpus altilis</i>	611 (532)	0.32		91.7	31.0	91.5
<i>Barringtonia asiatica</i>	34 (25)	0.39	0.40	78.6	63.6	
<i>Bischofia javanica</i>	150 (119)	0.52	0.25	91.7		98.9
<i>Cananga odorata</i>	32 (32)	0.33	1.09		15.4	54.5
<i>Cocos nucifera</i>	54 (54)			0.0	6.7	81.8
<i>Diospyros samoensis</i>	61 (59)	0.71	0.11	66.7	28.6	81.0
<i>Dysoxylum samoense</i>	753 (688)	0.48	0.81	74.0	22.4	93.4
<i>Ficus scabra</i>	178 (166)	0.43		83.3	40.9	84.7
<i>Hibiscus tiliaceus</i>	670 (457)	0.38	0.37	81.1	87.1	86.7
<i>Macaranga barveyana</i>	81 (80)	0.36	0.93	7.7	23.3	
<i>Morinda citrifolia</i>	101 (90)	0.48		53.7		70.4
<i>Myristica inutilis</i>	147 (142)	0.50	0.18	83.3	40.7	90.9
<i>Neonauclaea forsteri</i>	39 (35)	0.62	0.38	90.9		100.0
<i>Pipturus argenteus</i>	22 (21)	0.32	0.39		20.0	
<i>Pisonia grandis</i>	41 (38)	0.27		88.0		91.7
<i>Pisonia umbellifera</i>	34 (30)	0.28 [†]		93.3		76.5
<i>Rhus taitensis</i>	117 (101)	0.45	0.87	33.3	10.9	58.6
<i>Sterculia fanaibo</i>	85 (80)	0.31	0.20	74.5		86.4
<i>Syzygium inophylloides</i>	108 (94)	0.73	0.14	72.2	41.7	100.0
<i>Trichospermum richii</i>	22 (21)	0.32 [†]			0.0	
Total	3726 (3220)			78.5	38.4	89.0

[†]Wood density value from the Global Wood Density Data base (Chave *et al.* 2009, Zanne *et al.* 2009).

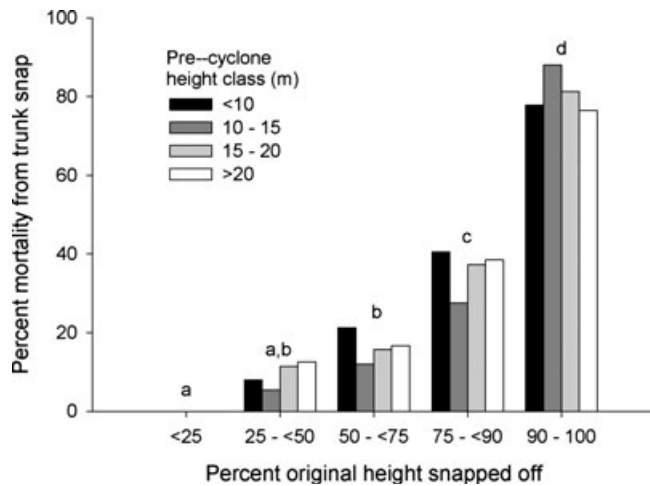


FIGURE 3. Mortality rates at 36-mo post-cyclone as a function of percent original height snapped off and pre-cyclone height, for single-stemmed trees on Ta'u, American Samoa ($N = 910$). Letters represent groupings based on a one-way ANOVA with a Bonferroni post-hoc multiple-comparison test across damage intensity groups (one-way ANOVA $df = 4$, $F = 243.4$, $P < 0.0001$).

2011), this is smaller than the sevenfold difference reported by Ostertag *et al.* (2005) for rehabilitated subtropical forest in Puerto Rico. High damage rates but relatively low mortality rates have been found in other studies: for example, Hurricane Joan resulted in severe damage to 73–82 percent of all tree in SE Nicaragua but resulted in only 17–23 percent mortality (Boucher *et al.* 1990, Yih *et al.* 1991). Thus, high-intensity cyclones might not always cause major forest reorganization, but rather they fall along a disturbance gradient that supports coexistence and temporal changes in relative abundances of species with variable life history traits (Pacala & Rees 1998, Vandermeer *et al.* 2000). However, when a cyclone is followed closely by another cyclone, or by anthropogenic disturbances such as fire, more significant and longer term structural and compositional changes can occur (Hjerpe *et al.* 2001, Franklin 2007).

SPECIES RESISTANCE TO CYCLONES—Species-wise damage was highly variable, thus supporting our first hypothesis. Variation in damage rates across species is well documented in the literature (Everham & Brokaw 1996, Ostertag *et al.* 2005, Curran *et al.* 2008a). The damage estimates on Ta'u ranged from 23–99 percent, a very wide range (cf. Zimmerman *et al.* 1994, Ostertag *et al.* 2005) that may elucidate trade-offs between species traits and susceptibility to damage.

The data further support the hypothesis that resistance varied according to species and individual traits. One widely debated trade-off is the growth-safety trade-off, whereby species with faster growth rates exhibit less shade tolerance and lower wood densities, thus incurring higher damage rates. Some previous studies have found a negative relationship between wood density and damage rates (Putz *et al.* 1983, Zimmerman *et al.* 1994, Curran *et al.* 2008b, Vandecar *et al.* 2011), but others have failed to find such

an association (Bellingham *et al.* 1995, Ostertag *et al.* 2005). Our results agree with studies finding higher wood density confers greater resistance to mechanical damage from cyclones. Furthermore, in fast growing, light-demanding species, carbon may be preferentially allocated to aboveground structures (Paz 2003), meaning that root systems of fast growing, light-demanding species may be unable to withstand cyclone-force wind stress. This could have underpinned the growth-uproot trade-off we observed.

Previous studies in tropical cyclone-disturbed forests have not found a consistent size–damage relationship (see Introduction). We found that taller trees with thinner diameters were more likely to snap, a result explained by the longer lever arm for taller trees and less stem diameter to resist breakage; this effect is most pronounced for species with low wood density (Table 2). In contrast, we found that architecture was not associated with uprooting, highlighting the result that wood density and growth rate were the principle factors associated with species susceptibility to uprooting. This emphasizes the need to separate damage type when assessing life history trade-offs in a disturbance-prone environment.

SURVIVAL AFTER CYCLONE DAMAGE.—We hypothesized that survival after damage would vary across species and damage types. Consistent with the hypothesis, we found that species exhibited substantial variation in post-damage survival rates. We further hypothesized that survival of damaged trees would be a function of species and individual traits. Support for this hypothesis varied according to damage type.

Sprouting is a common response to damage (Bellingham & Sparrow 2000, Bond & Midgley 2001) and is necessary for damaged and defoliated trees to survive. Studies have found variable rates in resprouting across species (Bellingham *et al.* 1994, Zimmerman *et al.* 1994, Curran *et al.* 2008b). Some authors have suggested that early successional (light-wooded, fast growing) species may use rapid resprouting as a compensatory mechanism for sustaining higher damage rates from cyclones (Putz *et al.* 1983, Curran *et al.* 2008b). However, others have suggested that pioneers species sustain high damage rates, exhibit low resprouting ability, and rely more on seed dispersal for post-cyclone population recovery (Uriarte *et al.* 2012). Vandecar *et al.* (2011) found that wood density was not associated with resprouting after damage. Thus, there remains substantial debate on whether species traits associated with successional status may be associated with resprouting and survival after damage.

Our results suggest that factors conferring survival after damage varied according to the type of damage sustained. Principally, survival tended to be greater after snapping (78.5%) than after uprooting (38.5%), and for each damage type survival varied widely across species. Indeed, annual mortality rate after sustaining minor damage (3%) and snapping (6.5%) were substantially lower than for uprooted trees (25.5%) clearly indicating the importance of damage type on survival. Our finding that snapped trees survived better than uprooted trees deviates from several previous studies (Yih *et al.* 1991, Bellingham *et al.* 1992, Zimmerman *et al.* 1994). Further, we found no evidence for an association between species traits of wood density or growth rate with post-snap sur-

vival. Rather, the probability of survival after snapping was strongly associated with the intensity of damage, as well as individual status, including the number of surviving stems (multi-stemmed trees had greater survival rates), diameter (larger trees fared poorer after snapping) and crown:bole ratio (trees with shorter boles survived less, presumably because they were shorter than trees with taller boles after snapping the same proportion). In light of our results that height, diameter and crown:bole ratio were associated with the percent of height snapped off, our results indicate a cascading effect of: (1) species traits (wood density, growth rate) that determine whether a tree is snapped; followed by (2) individual architectural traits (height, dbh, crown:bole ratio) that determine the severity of, and ultimately survival after, stem breakage. Beyond the species-specific traits, then, ontogenetic factors affecting the morphology of individual trees play a role in trunk snap severity and ultimately mortality caused by cyclones.

In contrast, species growth rate—associated with shade tolerance and a key dimension of successional status (Denslow 1987, Kitajima 1994)—was negatively associated with post-uprooting survival. Fast growing, light-demanding species with low tolerance for low light environments, could survive uprooting in the short-term, owing to favorable light conditions associated with high post-cyclone canopy openness (Walker *et al.* 1992, Grove *et al.* 2000, Turton & Siegenthaler 2004). However, as canopy closure proceeds and ruderal species overtop uprooted trees, higher long-term survival rates for uprooted trees would be achieved by species that can persist in lower light levels. Furthermore, light demanding species may have poorly developed root structures unable to access sufficient resources for survival after uprooting, particularly when the majority of the roots are exposed.

In summary, despite nearly 60 percent of trees sustaining severe structural damage and elevated mortality rates, the Ta'u forest exhibited resilience to a single, high-intensity storm event. The present study lends further evidence to the argument that cyclones are not necessarily catastrophic (Bellingham 1991). Cyclones are important disturbances that promote species coexistence through differential damage and mortality rates. Species responses to cyclones—through resistance, resprouting, or through seed dispersal and seed bank regeneration (not considered in this study)—interact with the cyclone periodicity and land use to determine long-term trajectories of tropical forest composition (Franklin 2007, Uriarte *et al.* 2009). In evaluating resistance and survival to damage types separately, we found only partial evidence for successional status driving species resistance and mortality; whereas species traits seemed to exclusively underpin resistance and survival to uprooting, it only partly accounted for snapping resistance, and did not determine the intensity of snap damage or survival after snapping. Our results highlight the importance of considering each damage type separately when considering ecological trade-offs.

ACKNOWLEDGMENTS

This research was conducted under permit NPSA-2006-SCI-0007 from the National Park of American Samoa, with funding from

the National Park of American Samoa and the Wildlife Restoration Grant (series W-1-R, FY 2004-2008) to the Department of Marine and Wildlife Resources, Government of American Samoa. R. Corlett, J. Phelps and J. Seamon provided useful comments on the manuscript. The authors greatly benefitted from the assistance of many people during post-cyclone damage surveys: Tualagi Gatoote Jr., Stephen Kostelnik, Taga'i Masaniai, Peter Siale, and Visa Vaivai. Logistical support was provided by the National Park of American Samoa, and the Department of Marine and Wildlife Resources. The authors received kind assistance from Ufagafa Ray Tulafono, Ruth Utzurum, Joshua Seamon and the support staff of the Department of Marine and Wildlife Resources. The authors thank the Moliga family in Ta'u Village, and James and Meleagi Chapman for their hospitality and support in Fitiuta.

SUPPORTING INFORMATION

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

FIGURE S1. Location of the Samoan archipelago and topographic map of Ta'u island indicating the locations of the four permanent forest monitoring plots.

FIGURE S2. Coastal forest on Ta'u island, American Samoa, 2 mo before and 2 mo after Cyclone Olaf.

LITERATURE CITED

- BATES, D., M. MAECHLER, AND B. DAI. 2010. lme4: Linear Mixed-Effects Models Using Eigen and S4 Classes. R package version 0.999375-33. R Foundation for Statistical Computing, Vienna, Austria. CRAN R-project org/packageplme4.
- BELLINGHAM, P. J. 1991. Landforms influence patterns of hurricane damage: Evidence from Jamaican montane forests. *Biotropica* 24: 427–433.
- BELLINGHAM, P. J., V. KAPOV, N. VARTY, J. R. HEALEY, E. V. J. TANNER, D. L. KELLY, J. W. DALLING, L. S. BURNS, D. LEE, AND G. SIDRAK. 1992. Hurricanes need not cause high mortality: The effects of Hurricane Gilbert on forests in Jamaica. *J. Trop. Ecol.* 8: 217–223.
- BELLINGHAM, P. J., AND A. D. SPARROW. 2000. Resprouting as a life history strategy in woody plant communities. *Oikos* 89: 409–416.
- BELLINGHAM, P. J., E. V. J. TANNER, AND J. R. HEALEY. 1994. Sprouting of trees in Jamaican montane forests, after a hurricane. *J. Ecol.* 82: 747–758.
- BELLINGHAM, P. J., E. V. J. TANNER, AND J. R. HEALEY. 1995. Damage and responsiveness of Jamaican montane tree species after disturbance by a hurricane. *Ecology* 76: 2562–2580.
- BOND, W. J., AND J. J. MIDGLEY. 2001. Ecology of sprouting in woody plants: The persistence niche. *Trends Ecol. Evol.* 16: 45–51.
- BOUCHER, D. H., J. H. VANDERMEER, K. YIH, AND N. ZAMORA. 1990. Contrasting hurricane damage in tropical rain forest and pine forest. *Ecology* 71: 2022–2024.
- BURSLEM, D. F. R. P., T. C. WHITMORE, AND G. C. BROWN. 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *J. Ecol.* 88: 1063–1078.
- CANHAM, C. D., J. THOMPSON, J. K. ZIMMERMAN, AND M. URIARTE. 2010. Variation in susceptibility to hurricane damage as a function of storm intensity in Puerto Rican tree species. *Biotropica* 42: 87–94.
- CHAVE, J., D. COOMES, S. JANSEN, S. L. LEWIS, N. G. SWENSON, AND A. E. ZANNE. 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12: 351–366.

- CLARK, J. S. 1996. Testing disturbance theory with long-term data: Alternative life-history solutions to the distribution of events. *Am. Nat.* 148: 976–996.
- CLARK, J. S. 2010. Individuals and the variation needed for high species diversity in forest trees. *Science* 327: 1129–1132.
- COMITA, L. S., M. URIARTE, J. THOMPSON, I. JONCKHEERE, C. D. CANHAM, AND J. K. ZIMMERMAN. 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *J. Ecol.* 97: 1346–1359.
- CONDIT, R., S. P. HUBBELL, AND R. B. FOSTER. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecol. Monogr.* 65: 419–439.
- CURRAN, T. J., R. L. BROWN, E. EDWARDS, K. HOPKINS, C. KELLEY, E. MCCARTHY, E. POUNDS, R. SOLAN, AND J. WOLF. 2008a. Plant functional traits explain interspecific differences in immediate cyclone damage to trees of an endangered rainforest community in north Queensland. *Austral Ecol.* 33: 451–461.
- CURRAN, T. J., L. N. GERSBACH, W. EDWARDS, AND A. K. KRICKENBERGER. 2008b. Wood density predicts plant damage and vegetative recovery rates caused by cyclone disturbance in tropical rainforest tree species of North Queensland, Australia. *Austral Ecol.* 33: 442–450.
- DENSILOW, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annu. Rev. Ecol. Syst.* 18: 431–451.
- ELMQVIST, T., W. E. RAINEY, E. D. PIERSON, AND P. A. COX. 1994. Effects of tropical cyclones Ofa and Val on the structure of a Samoan lowland rain forest. *Biotropica* 26: 384–391.
- EVERHAM, E. M., III, AND N. V. L. BROKAW. 1996. Forest damage and recovery from catastrophic wind. *Bot. Rev.* 62: 113–185.
- FRANKLIN, J. 2007. Recovery from clearing, cyclone and fire in rain forests of Tonga, South Pacific: Vegetation dynamics 1995–2005. *Austral. Ecol.* 32: 789–797.
- FRANKLIN, J., D. R. DRAKE, K. R. MCCONKEY, F. TONGA, AND L. B. SMITH. 2004. The effects of Cyclone Waka on the structure of lowland rain forest in Vava'u, Tonga. *J. Trop. Ecol.* 20: 409–420.
- GROVE, S. J., S. M. TURTON, AND D. T. SIEGENTHALER. 2000. Mosaics of canopy openness induced by tropical cyclones in lowland rain forests with contrasting management histories in northeastern Australia. *J. Trop. Ecol.* 16: 883–894.
- GUNDERSON, L. H. 2000. Ecological resilience—in theory and application. *Annu. Rev. Ecol. Syst.* 31: 425–439.
- HJERPE, J., H. HEDENÅS, AND T. ELMQVIST. 2001. Tropical rain forest recovery from cyclone damage and fire in Samoa. *Biotropica* 33: 249–259.
- HOLLING, C. S. 1973. Resilience and stability of ecological systems. *Ann. Rev. Ecol. Syst.* 4: 124.
- IMBERT, D., P. LABBÉ, AND A. ROUSTEAU. 1996. Hurricane damage and forest structure in Guadeloupe, French West Indies. *J. Trop. Ecol.* 12: 663–680.
- JOINT TYPHOON WARNING CENTER. 2005. Annual Tropical Cyclone Report. U.S. Naval Maritime Forecast Center, Pearl Harbor, Hawaii. Available at: <http://metocph.nmci.navy.mil/jtwc/atcr/2005atcr/2005atcr.pdf> (accessed 3 August 2009).
- KEPPEL, G., Y. M. BUCKLEY, AND H. P. POSSINGHAM. 2010. Drivers of lowland rain forest community assembly, species diversity and forest structure on islands in the tropical South Pacific. *J. Ecol.* 98: 87–95.
- KING, D. A., S. J. DAVIES, M. N. NUR SUPARTI, AND S. TAN. 2005. Tree growth is related to light interception and wood density in two mixed dipterocarp forests of Malaysia. *Funct. Ecol.* 19: 445–453.
- KIRCH, P. V. 2000. *On the Road of the Winds: An Archaeological History of the Pacific Islands Before European Contact*. University of California Press, Berkeley.
- KITAJIMA, K. 1994. Relative importance of photosynthetic and allocation traits as correlates of seedling shade tolerance of 15 tropical tree species. *Oecologia* 98: 419–428.
- LEWIS, R. J., AND K. H. BANNAR-MARTIN. 2011. The impact of cyclone Fanele on a tropical dry forest in Madagascar. *Biotropica* 44: 135–140.
- LOEHLE, C. 2000. Strategy space and the disturbance spectrum: A life-history model for tree species coexistence. *Am. Nat.* 156: 14–33.
- LUGO, A. E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: An international review. *Austral. Ecol.* 33: 368–398.
- METCALFE, D. J., M. G. BRADFORD, AND A. J. FORD. 2008. Cyclone damage to tropical rain forests: species- and community-level impacts. *Austral. Ecol.* 33: 432–441.
- Natural Resources Conservation Service. 2004. Soil Series Classification Database. U.S. Department of Agriculture. Available at: <http://soils.usda.gov> (accessed 1 July 2013).
- NUNN, P. D. 1998. *Pacific Island Landscapes*. Institute of Pacific Studies, University of the South Pacific, Suva.
- OSTERTAG, R., W. L. SILVER, AND A. E. LUGO. 2005. Factors affecting mortality and resistance to damage following hurricanes in a rehabilitated subtropical moist forest. *Biotropica* 37: 16–24.
- PACALA, S. W., AND M. REES. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. *Am. Nat.* 152: 729–737.
- PAZ, H. 2003. Root/shoot allocation and root architecture in seedlings: Variation among forest sites, microhabitats, and ecological groups. *Biotropica* 35: 318–332.
- PUTZ, F. E., P. D. COLEY, K. LU, A. MONTALVO, AND A. AIELLO. 1983. Uprooting and snapping of trees: Structural determinants and ecological consequences. *Can. J. For. Res.* 13: 1011–1020.
- R DEVELOPMENT CORE TEAM. 2005. R: A Language and Environment for Statistical Computing. Computing RfFS, (Ed.). R Foundation for Statistical Computing, Vienna, Austria.
- READ, J., R. EVANS, G. D. SANSON, S. KERR, AND T. JAFFRÉ. 2011. Wood properties and trunk allometry of co-occurring rainforest canopy trees in a cyclone-prone environment. *Am. J. Bot.* 98: 1762–1772.
- REILLY, A. E. 1991. The effects of Hurricane Hugo in three tropical forests in the U.S. Virgin Islands. *Biotropica* 23: 414–419.
- SWAINE, M. D., AND D. LIEBERMAN. 1987. The dynamics of tree populations in tropical forest. *J. Trop. Ecol.* 3: i–iii.
- TURTON, S. M., AND D. T. SIEGENTHALER. 2004. Immediate impacts of a severe tropical cyclone on the microclimate of a rain-forest canopy in north-east Australia. *J. Trop. Ecol.* 20: 583–586.
- URIARTE, M., C. D. CANHAM, J. THOMPSON, J. K. ZIMMERMAN, L. MURPHY, A. M. SABAT, N. FETCHER, AND B. L. HAINES. 2009. Natural disturbance and human land use as determinants of tropical forest dynamics: Results from a forest simulator. *Ecol. Monogr.* 79: 423–443.
- URIARTE, M., J. S. CLARK, J. K. ZIMMERMAN, L. S. COMITA, J. FORERO-MONTAÑA, AND J. THOMPSON. 2012. Multidimensional trade-offs in species responses to disturbance: Implications for diversity in a subtropical forest. *Ecology* 93: 191–205.
- VAN BLOEM, S. J., P. G. MURPHY, A. E. LUGO, R. OSTERTAG, M. R. COSTA, I. R. BERNARD, S. M. COLÓN, AND M. C. MORA. 2005. The influence of hurricane winds on Caribbean dry forest structure and nutrient pools. *Biotropica* 37: 571–583.
- VANDECAR, K. L., D. LAWRENCE, D. RICHARDS, L. SCHNEIDER, J. ROGEN, B. SCHMOOK, AND H. WILBUR. 2011. High mortality rate for rare species following hurricane disturbance in the southern Yucatán. *Biotropica* 43: 676–684.
- VANDERMEER, J., I. G. de la CERDA, D. BOUCHER, I. PERFECTO, AND J. RUIZ. 2000. Hurricane disturbance and tropical tree species diversity. *Science* 290: 788–791.
- WALKER, L. R., J. VOLTZOW, J. D. ACKERMAN, D. S. FERNANDEZ, AND N. FETCHER. 1992. Immediate impact of Hurricane Hugo on a Puerto Rican rain forest. *Ecology* 73: 691–694.
- WEBB, E. L., AND S. FA'AUMU. 1999. Diversity and structure of tropical rain forest of Tutuila, American Samoa: Effects of site age and substrate. *Plant Ecol.* 144: 257–274.
- WEBB, E. L., J. O. SEAMON, AND S. FA'AUMU. 2011. Frequent, low-amplitude disturbances drive high tree turnover rates on a remote, cyclone-prone Polynesian island. *J. Biogeogr.* 38: 1240–1252.

- WEBB, E. L., B. J. STANFIELD, AND M. JENSEN. 1999. Effects of topography on rainforest tree community structure and diversity in American Samoa, and implications for frugivore and nectarivore populations. *J. Biogeogr.* 26: 887–897.
- WEBB, E. L., M. van de BULT, W. CHUTIPONG, AND MD. E. KABIR.. 2006. Composition and structure of lowland rain-forest tree communities on Ta'u, American Samoa. *Pac. Sci.* 60: 333–354.
- WEBB, E. L., M. van de BULT, W. CHUTIPONG, AND MD. E. KABIR. 2007. Species composition and forest structure of tree communities in four permanent forest monitoring plots in the Ta'u unit of the National Park of American Samoa. Pacific Cooperative Studies Unit Technical Report 138. Available at: <http://manoa.hawaii.edu/hpicesu/techrep.htm> (accessed 1 July 2013).
- WHISTLER, W. A. 1992. Botanical inventory of the proposed Ta'u unit of the National Park of American Samoa. Technical Report 83, Pacific Cooperative Studies Unit, Honolulu, HI. Available at: <http://manoa.hawaii.edu/hpicesu/techrep.htm> (accessed 1 July 2013).
- WHISTLER, W. A. 1995. Permanent Forest Plot Data from the National Park of American Samoa. Technical Report 98, Pacific Cooperative Studies Unit, Honolulu, HI. Available at: <http://manoa.hawaii.edu/hpicesu/techrep.htm> (accessed 1 July 2013).
- WHISTLER, W. A. 2002. The Samoan Rainforest: A Guide to the Vegetation of the Samoan Archipelago. Isle Botanica, Honolulu.
- WILLIAMSON, G. B., AND M. C. WIEMANN. 2010. Measuring wood specific gravity...correctly. *Am. J. Bot.* 97: 519–524.
- YIH, K., D. H. BOUCHER, J. H. VANDERMEER, AND N. SAMORA. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. *Biotropica* 23: 106–113.
- ZANNE, A. E., G. LOPEZ-GONZALEZ, D. A. COOMES, J. ILIC, S. JANSEN, S. L. LEWIS, R. B. MILLER, N. G. SWENSON, M. C. WIEMANN, AND J. CHAVE. 2009. Data from: Towards a worldwide wood economics spectrum. Dryad Digital Repository. 82: 911–922. doi:10.5061/dryad.234.
- ZIMMERMAN, J. K., E. M. EVERHAM, III, R. B. WAIDE, D. J. LODGE, C. M. TAYLOR, AND N. V. L. BROKAW. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: Implications for tropical tree life histories. *J. Ecol.* 82: 911–922.