Factors Affecting Tropical Tree Damage and Survival after Catastrophic Wind Disturbance

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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.

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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, Oster tag 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 hPa, 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 Diatryma samoensis, Sterculia fanaloba, and Pisonia umbellifera, whereas above the escarpment (to about 250 m asl) Hibiscus tilicua, Syzygium inophyloides, Rhis laitensis, and Alphitonia zigyphodes 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 agro-forest (‘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 Dypsisium 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). A second damage type, called minor damage (defoliation, 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 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 samanensis, Gauriga floribunda, Flacourtia rukam, and Syzygium implexifolium. In contrast, nine damage-susceptible species sustained ≥70 percent severe damage, including Pipturus argenteus, Maturaanga barreyana, Barringtonia asiatica, Rhox taitensis, Trichoperaumum richii, Coix nejera, Arboecarpus allii, Hernandia nymphaefolia, and Sterculia fanaiho (Fig. 1). Four species tended to snap with more than 60 percent of the pre-cyclone population snapping (A. allii, H. nymphaefolia, Pisonia grandi, and S. fanaiho) (Fig. 1). 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). |
|-----------------------------------|--------|------|------|------|
| Damage                            | Type   | N    | %    | N    | %    |
|-----------------------------------|--------|------|------|------|
| Damage                            | Type   | N    | %    | N    | %    |
|-----------------------------------|--------|------|------|------|
| Stems                             | Trunk snap | 1288 | 34.6  | 1011 | 78.5 |
| Minor                            | 1587   | 1406 | 88.6 |
| Individuals                       | Uproot | 739  | 23.0  | 284  | 38.4 |
| Minor                            | 1362   | 1218 | 88.6 |
| Severe damage                    |        | 1858 | 57.7  | 1173 | 63.1 |
| combined                         |        |      |      |      |
| All individuals                  |        | 3220 | 2391 | 74.3 |
| Undisturbed late successional forest |        | 3220 |      | 74.3 |
| AMR                              |        |      |      |      |
|                                  |        |      |      | 2.1  |
|                                  |        |      |      | 2.1  |
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 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

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.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Damage†</th>
<th>Survival‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample size (species, trees)</td>
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<td>22, 540</td>
</tr>
<tr>
<td>Intercept</td>
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<td>-0.17</td>
</tr>
<tr>
<td>Forest type (secondary)</td>
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<td>Ns</td>
</tr>
<tr>
<td>Elevation (upper)</td>
<td>Ns</td>
<td>Ns</td>
</tr>
<tr>
<td>Wood density</td>
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<td>-3.93</td>
</tr>
<tr>
<td>Growth rate</td>
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<td>1.11</td>
</tr>
<tr>
<td>Height</td>
<td>0.08</td>
<td>-0.21</td>
</tr>
<tr>
<td>Crown:bole ratio</td>
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<td>-0.02</td>
</tr>
<tr>
<td>Diameter (dbh)</td>
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<td>0.01</td>
</tr>
<tr>
<td>Percent of tree height snapped</td>
<td>0.02</td>
<td>-0.03</td>
</tr>
<tr>
<td>Number of stems alive (after snap)</td>
<td>0.80</td>
<td></td>
</tr>
</tbody>
</table>

*P < 0.05; **P < 0.01; ***P < 0.001.
†Results from a GLMM
‡Results from a GLM

FIGURE 1. Damage rates and susceptibility to Cyclone Olaf for 32 common (pre-cyclone N ≥ 10) tree species on Tā’u, American Samoa. The resistance-susceptibility gradient was based on total damage rates.
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. 2009).
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-

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**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).
sival. 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 better 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 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.

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**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**


