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The Impact of Cyclone Fanele on a Tropical Dry Forest in Madagascar

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ABSTRACT

Cyclones, which change tree communities and alter forest structure, are thought to have had a significant selective pressure on the flora and fauna of Madagascar. Very little information, however, is available on the actual impact of cyclones on Malagasy ecosystems. On 21 January 2009, Cyclone Fanele made landfall on the western coast of Madagascar with sustained winds of 185 km/h. We examined the immediate effects of the cyclone on tropical dry forest structure in the Kirindy Mitea National Park. In July and August 2009, we measured the height, diameter at breast height (dbh), and damage for 1361 trees in nine 25×25 m plots. We found that: (1) over 95 percent of trees experienced some sort of damage, including 8.8 percent mortality; (2) understory and emergent trees experienced significantly higher mortality than canopy trees; and (3) stem density was reduced 9.2 ± 4.5 percent and biomass was reduced 13.4 ± 8.1 percent after the cyclone. Dbh was the best predictor of trunk damage and mortality. This extensive alteration of forest structure will have a substantial short- and long-term impact on the biotic communities of western Madagascar.

Key words: damage; deciduous forest; forest structure; hurricane; Kirindy Mitea; mortality; natural disturbance.

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MAJOR DISTURBANCES, SUCH AS CYCLONES AND HURRICANES, CHANGE TREE COMMUNITIES (Vandermeer *et al.* 1996, Chazdon *et al.* 2007) and can have long-term effects on whole ecosystems (Ganzhorn 1995, de Gouvenain & Silander 2003, Lugo 2008). The high wind velocity of cyclones can cause substantial damage to tropical forests (Everham & Brokaw 1996) and has been an important selective factor shaping forests (Vandermeer *et al.* 1996, de Gouvenain & Silander 2003) by differentially affecting trees of different size classes. For example, Imbert *et al.* (1996) found that trees with intermediate girths experienced the most major damage while the largest trees experienced the most lethal damage, but these post-cyclone results varied by both forest type and tree species. Trees are often snapped or uprooted and can experience complete defoliation (Pavelka *et al.* 2003). Emergent and understory trees experience higher mortality than the rest of the canopy (Dittus 1985), leading to changes in canopy height, along with the density of both understory and emergent trees (Lugo 2008). In particular, forests that have experienced at least one cyclone or hurricane in the last 70 yr have shorter canopies than forests that have not been affected by a major climatic disturbance (de Gouvenain & Silander 2003).

The numerous treefalls associated with cyclones leads to the creation of abundant gaps in the canopy (Phillips & Gentry 1994). These gaps result in increased light intensity, higher soil temperatures, lower relative humidity, and changes in seedling and sapling communities (Zimmerman *et al.* 1994, Lugo 2008, Metcalfe *et al.* 2008). Thus, stem density can increase following a cyclone, especially for pioneer species (species which colonize from seed and whose saplings occur only in gaps, *sensu* Brokaw 1985) (Vandermeer *et al.* 1998). Additionally, basal area, stand composition, and species diversity can change (Vandermeer *et al.* 1998, Imbert & Portecop 2008, Lugo 2008).

While Madagascar's biodiversity is thought to have been strongly influenced by an evolutionary history of cyclonic activity (Wright 1999, Binggeli 2003), knowledge of the effects of cyclones on Malagasy ecosystems is limited (Birkinshaw & Randrianjanahary 2007). Because cyclones are stochastic events, researching the influence of cyclones on Madagascar's biodiversity is difficult and opportunities to study their impact on forests are rare. The few studies of cyclone impacts on Malagasy ecosystems (*e.g.*, Birkinshaw & Randrianjanahary 2007, Johnson *et al.* 2011) have been restricted to humid forests.

Dry forests represent approximately a quarter of the forest cover in Madagascar (Dufils 2003). They exhibit great floral diversity but have lower species richness than the Malagasy humid forests (Jenkins 1987). Moreover, the deciduous, dry forest is less dense and has a more open canopy than the humid forests (Jenkins 1987). Consequently, cyclones might impact dry forests differently than humid forests.

On 21 January 2009, cyclone Fanele made landfall on the western shore of Madagascar (Fig. 1), with sustained winds of 185 km/h and gusts up to 260 km/h (Réunion Météo-France). The cyclone, a category 3 storm (Saffir-Simpson Hurricane Scale), passed over the Kirindy Mitea National Park, which contains some of the largest contiguous tracts of protected tropical dry forest in Madagascar (Whitehurst *et al.* 2009). We report the immediate (*sensu* Lugo 2008) results of the storm's impact on the structure of this tropical dry forest. We hypothesized that tree damage and

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mortality vary with tree size (Dittus 1985, Lugo 2008). Specifically we predicted that girth and height influenced whether a tree experiences: (1) any damage; (2) particular types of trunk damage; and (3) the amount of delimbing; as well as (4) the probability of mortality. Additionally, we expected stem density and biomass to be reduced as a short-term consequence of this major stochastic event (Dittus 1985).

METHODS

STUDY SITE.—This study was conducted in the dry, deciduous forest of the Kirindy Mitea National Park (KMNP) in western Madagascar. The park is approximately 140,000 ha. The mean annual temperature is 25°C (range: 9–40°C). Rainfall data are not currently available but are probably similar to the nearby Kirindy Forest (CNFEREF) approximately 100 km to the north, which receives approximately 800 mm of rain per yr (Lewis & Kappeler 2005). A 1 km^2 trail system has been cut into a portion of the KMNP forest at 20°47′17″ S, 44°10′08″ E, approximately 21 km east of Belo-sur-Mer. Within this 1 km^2, a grid system of trails every 25 m creates vegetation plots of 25 m × 25 m. Altitude is 50–100 m within the grid system and 0–300 m within the park.

DAMAGE SAMPLING.—All trees ≥ 5 cm in diameter at breast height (dbh) in each of nine equidistant 0.06 ha vegetation plots (Fig. S1) were sampled during July and August 2009. Three variables were recorded for each tree. First, tree dbh was measured using dbh measuring tape to the nearest millimeter. Second, tree height was visually estimated to the nearest meter. Third, damage was scored using seven, nonmutually exclusive categories, following Pavelka and Behie (2005): no damage, minor delimbing, major delimbing, trunk leaning > 45°, trunk snapped, trunk uprooted, and dead. Note that trees could be scored as damaged due to delimbing but have no trunk damage. Because the data were collected approximately 7 mo after the cyclone, we did not attempt to determine the cause of a tree's death. Species identification was not possible in this study, but see Lewis and Bannar-Martin (unpubl. data) for an analysis of damage to a subset of trees in the forest. Two or three observers, including RJL, estimated height and scored tree damage simultaneously but independently. Data were only recorded once interobserver reliability was established.

ANALYSIS.—We used generalized linear mixed models (GLMM) to assess the effects of tree dbh and tree height (fixed effects) on cyclone-induced tree mortality and types of damage. GLMMs are a sophisticated extension of generalized linear models (McCullagh & Nelder 1989) that allow random effects to be fitted within the framework of regular logistic regressions (Schall 1991). The random effects included in this model were the nine sampled vegetation plots. The first two sets of models, mortality and damage, were evaluated with a binomial error structure and logit link functions were used to fit a probability curve to the data with fixed and random effects. Delimbing and trunk damage were evaluated separately with a multinomial error structure, and logit link functions were used. Thus, we were able to test (1) whether tree height and dbh were determinants of tree mortality and damage from Cyclone Fanele, and (2) whether the risk of certain types of damage (to the trunk or branches) was related to tree dbh and height. Multinomial tests only examined the subset of trees that were scored as damaged and hence are independent tests of forest damage.

To assess which models had the best fit we systematically simplified our four sets of models. The first model in each set included all interactions between the two dependent variables (dbh and height), the second model included dbh and height as separate fixed effects, and the final two models of each set included each independent variable (dbh and height) in isolation. In our binomial GLMMs, the response variable was defined as whether (1) a tree was damaged, or (2) it was killed. In our multinomial GLMMs, the response variable was the level and type of damage to either tree trunks or tree branches. Note that a tree considered damaged in the binomial analysis might be considered not damaged in the multinomial analysis because it might have only experienced one type of damage.

In order to assess the impact of the cyclone on the forest strata, we divided the continuous height data into three categories based upon natural breaks in the data for trees ≥ 5 cm: 2–4 m (understory), 5–7 m (canopy), and 8–18 m (emergents). We then reran the above GLMM analyses with the predictor height as a categorical (dummy) variable. Because the canopy had the lowest damage and the lowest mortality (Table S2), we examined the understory and emergents in relation to the canopy.

For all GLMM model fits, we used STATA v. 10.1 (StataCorp 2007). The GLMMs were fitted with the gllamm function to estimate the variance due to random effects (variance of random effect for damage = 0.321, mortality = 0.132, delimbing = 0.499, trunk damage=4.421e-12). Regression coefficients are presented with standard errors (SE). Model fit within each set of models was evaluated with Aikake (AIC) values, AIC differences (Δ_i), and Akaike weights (w_i). The best model in each set was the simplest model with the lowest AIC, Δ_i, and w_i . Odds ratios were calculated with the eform function, which reports the natural log of the GLMM 'estimate' or *y*-intercept for each variable.

Stem density and basal area were used to estimate biomass before and after the cyclone. Precyclone measures were estimated as the total number of trees found both alive and dead. For comparison with studies sampling trees of ≥ 10 dbh, we present these results in the online supplement. Means are presented with standard deviations.

RESULTS

A total of 1361 trees of ≥ 5 cm dbh (411 trees of ≥ 10 cm dbh) were found within the nine vegetation plots with a mean and standard deviation of 151 ± 65 trees (46 ± 13 trees of ≥ 10 cm dbh) trees per plot. Median dbh was 7.6 cm and ranged from 5 to 144 cm (Table S1). Baobobs (*Adansonia grandidieri*) were the trees with the largest dbh. Median tree height was 6 m and ranged from 2 to 18 m. Fifteen percent of trees were understory, 70 percent

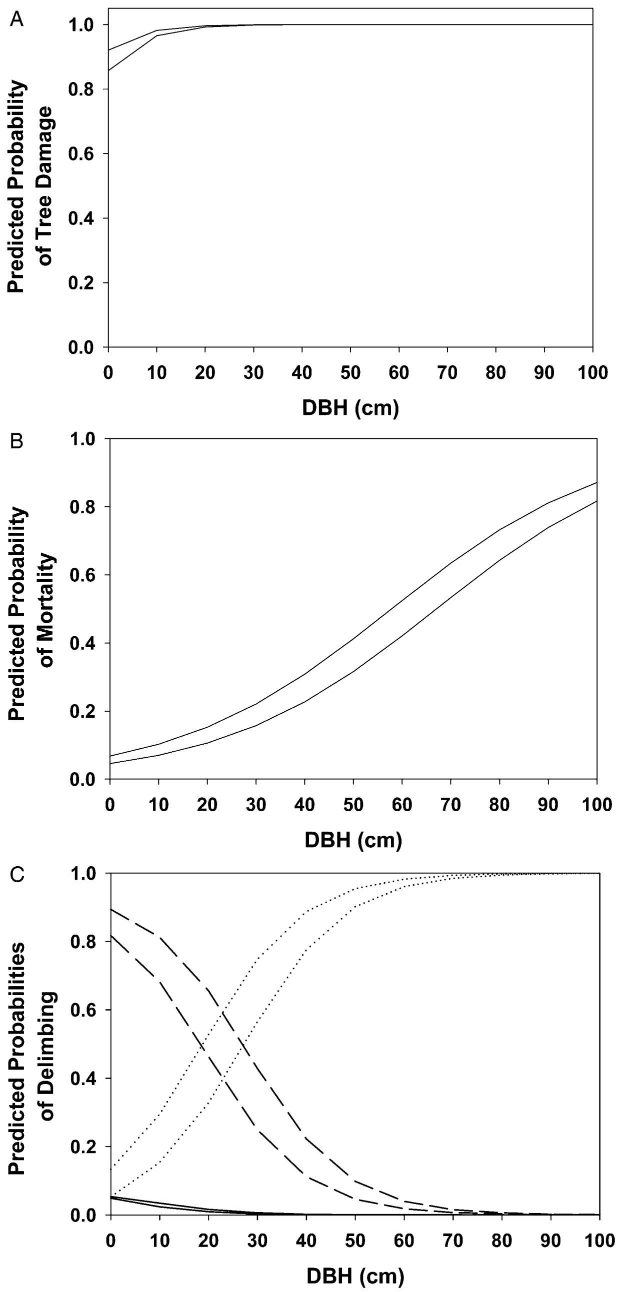

FIGURE 1. Predicted probabilities of (A) tree damage and (B) tree mortality based on the binomial generalized linear mixed models (GLMMs) with logit link functions, and (C) delimbing based on the multinomial GLMMs with logit link functions for trees in a tropical dry forest of Madagascar 7–8 mo following Cyclone Fanele. The two lines represent the predicted probabilities for trees with height one standard deviation greater than the mean and for trees with height one standard deviation less than the mean. In (C), solid lines indicate probabilities for whether a tree experienced no delimbing after the cyclone. Dashed lines indicate probabilities that a tree experienced minor delimbing and dotted lines indicate major delimbing. Dbh, diameter at breast height.

canopy, and 15 percent emergents. Dbh and height were significantly correlated (Pearson: $r = 0.590$, $N = 1361$, $P < 0.001$).

Over 95 percent of trees sampled sustained some type of damage (Table S2). One hundred percent of trees between 15 and 25 cm dbh and greater than 30 cm dbh experienced damage. A third (33 percent) of trees experienced severe damage (major delimbing or trunk damage). Approximately 74 percent of trees only experienced minor delimbing. Understory and emergent trees experienced more damage to their trunks or branches than canopy trees. Nearly nine percent of the trees ≥ 10 cm were found dead after the cyclone. Of the trees that were dead, 82.5 percent had major delimbing, 49.2 percent had trunks that were snapped, 16.7 percent were uprooted, 11.7 percent were leaning, and 22.5 percent had no trunk damage.

HEIGHT.—Height was not a significant predictor of whether a tree died (coef. $\pm$ SE = $-$ 0.117 $\pm$ 0.069, $z = -1.69$, $P = 0.091$) and only approached significance as a predictor of damage in the binomial analyses (coefficient $\pm$ SE = $-$ 0.185 $\pm$ 0.097, $z = -1.91$, $P = 0.056$). Taller trees tended to be more likely to survive the cyclone (odds ratio = 0.890). However, our multinomial analyses examining particular types of damage (trunk damage or delimbing) found slightly different results. Height was a significant predictor of a tree experiencing major delimbing (coefficient $\pm$ SE = $-$ 0.287 $\pm$ 0.105, $z = -2.72$, $P = 0.006$). The probability of a tree experiencing minor delimbing was not dependent upon its height (coefficient $\pm$ SE = $-$ 0.057 $\pm$ 0.096, $z = -0.59$, $P = 0.556$). However, a tree was more likely to have no delimbing than major delimbing as height increased. The odds ratio of a tree experiencing major delimbing with increasing height was 0.751/m. Trunk damage was not dependent on height. While trees tended to be more likely to be uprooted than to have no trunk damage as height increased, this result did not reach statistical significance (coefficient $\pm$ SE = 0.172 $\pm$ 0.089, $z = 1.94$, $P = 0.053$; Table S3).

Mortality was not distributed evenly among the height categories. In comparison to the canopy, understory (coefficient $\pm$ SE = 0.857 $\pm$ 0.248, $z = 3.46$, $P = 0.001$) and emergent (coefficient $\pm$ SE = 0.838 $\pm$ 0.245, $z = 3.42$, $P = 0.001$) trees were significantly more likely to be dead, with odds ratios of 2.355 and 2.313 respectively for understory and emergents. Our binomial analysis of tree damage, however, found that this relationship was only significant for understory trees (coefficient $\pm$ SE = 1.627 $\pm$ 0.731, $z = 2.23$, $P = 0.026$) and not significant for emergent trees (coefficient $\pm$ SE = 0.560 $\pm$ 0.448, $z = 1.25$, $P = 0.211$).

DBH.—Dbh was a significant predictor of whether a tree was damaged (coefficient $\pm$ SE = 0.154 $\pm$ 0.050, $z = 3.05$, $P = 0.002$) or dead (coefficient $\pm$ SE = 0.045 $\pm$ 0.015, $z = 3.07$, $P = 0.002$). Trees with larger girths had a greater probability of being damaged and dead (Fig. 1; Table S1). As tree dbh increased, the odds of damage was 1.166/cm ($z = 3.05$, $P = 0.002$) and the odds of mortality was 1.046/cm ($z = 3.07$, $P = 0.002$).

In the multinomial models of trunk damage and delimbing, dbh was a better predictor of trunk and branch damage than tree height. Minor delimbing was not dependent on dbh (coefficient $\pm$

SE = 0.055 ± 0.038, z = 1.43, P = 0.153). By contrast, major delimbing was significantly related to dbh (coefficient ± SE = 0.152 ± 0.040, z = 3.82, P = 0.000). As dbh increased, the odds of a tree experiencing major delimbing (1.164, z = 3.82, P = 0.000) was greater than the odds of minor delimbing (1.056, z = 1.53, P = 0.153) (Fig. 1).

Trunk damage was dependent on dbh but not height (Table S3). Frequencies of trunk damage by dbh are shown in Fig. 2. A tree was significantly more likely to have no trunk damage than to be leaning as dbh increased. By contrast, as dbh increased, the odds of a trunk being snapped or a tree being uprooted was significantly greater than the odds of having no trunk damage (Fig. 3) As dbh increased, the odds of a trunk leaning was 0.938/cm (z = − 2.44, P = 0.015), 1.038/cm for snapped trunks (z = 2.61, P = 0.009), and 1.044/cm for uprooted trunks (z = 2.58, P = 0.010).

MODEL FIT.—The simplest model with the most explanatory power for the mortality of trees included dbh and height as separate fixed effects even though dbh and height were correlated (AIC = 805.97, Δ_i = 0, w_i = 0.574). The best model for damage included only dbh as a fixed effect (AIC = 446.59, Δ_i = 0, w_i = 0.647). The best models for the multinomial GLMM of delimbing (AIC = 1839.67, Δ_i = 0, w_i = 0.999) and trunk damage (AIC = 2028.39, Δ_i = 0, w_i = 0.579) included dbh, height, and the interaction between dbh and height.

STEM DENSITY AND BIOMASS.—Forest biomass decreased substantially. Basal area of trees ≥ 5 cm per vegetation plot before the cyclone was reduced from 1.8 ± 1.1 m^2 to 1.6 ± 1.1 m^2, a reduction of 13.4 ± 8.1 percent. Stem density of trees ≥ 5 cm decreased from 2420 ± 1039 stems/ha before the cyclone to 2206 ± 970 stems/ha, a reduction of 9.2 ± 4.5 percent.

DISCUSSION

Cyclone Fanele significantly impacted the structure of the tropical dry forest in the KMNP, with few of the trees escaping damage. However, only a third of the trees ≥ 5 cm experienced severe damage, a result much lower than some humid tropical forests (*e.g.*, Johnson *et al.* 2011). Dbh was better than tree height at predicting tree damage and mortality. Taller trees were significantly more likely to avoid major delimbing, but contrary to expectations, tree height only had a weak relationship with mortality. Stem density and biomass experienced reductions of 13 percent as a consequence of the cyclone. Our study demonstrates that cyclone damage can be assessed even without precyclone data. Knowledge of the ecological effects of large-scale tropical disturbances, such as cyclones, on terrestrial ecosystems is critical because cyclonic activity is expected to increase globally, including in Madagascar

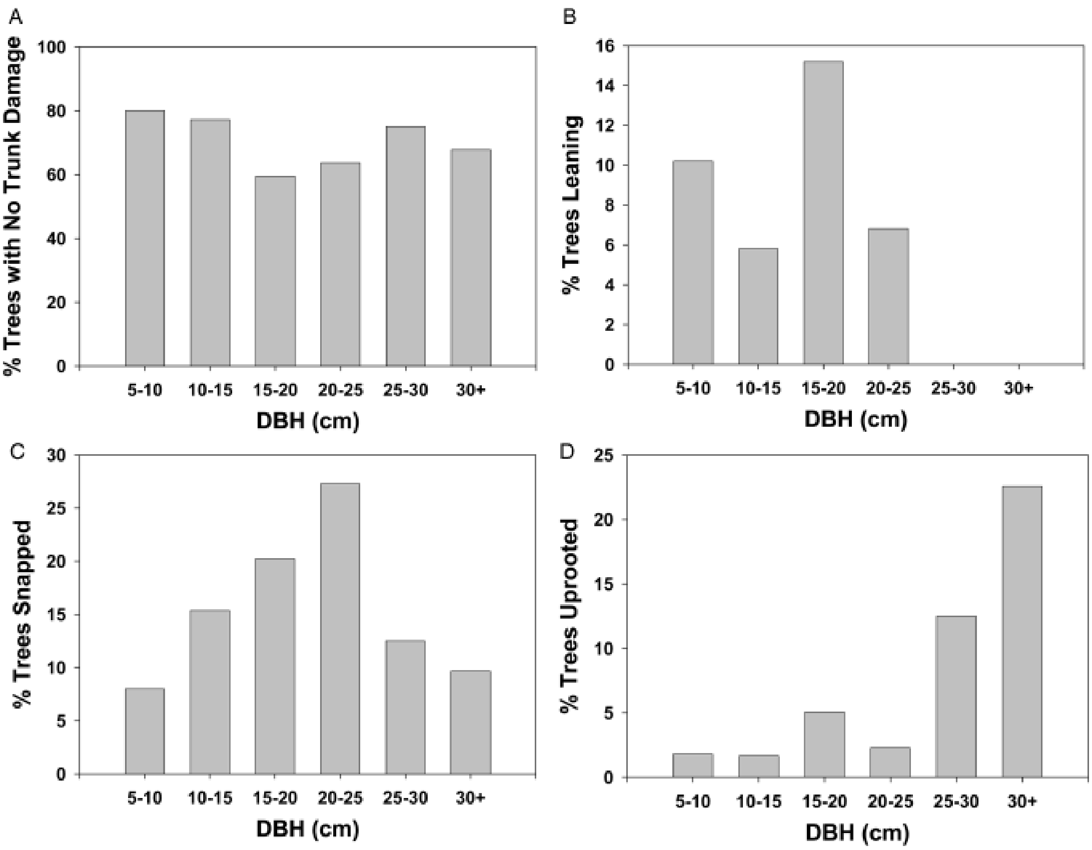

FIGURE 2. The relationship between diameter at breast height (dbh) and damage to tree trunks in a dry forest in western Madagascar after a cyclone: (A) no trunk damage, (B) leaning, (C) snapped, (D) uprooted; $N_{5-10\,cm}$ = 950, $N_{10-15\,cm}$ = 241, $N_{15-20\,cm}$ = 79, $N_{20-25\,cm}$ = 44, $N_{25-30\,cm}$ = 16, $N_{30+\,cm}$ = 31. Percentages refer to the number of trees with this type of damage out of the total number of trees in this size category.

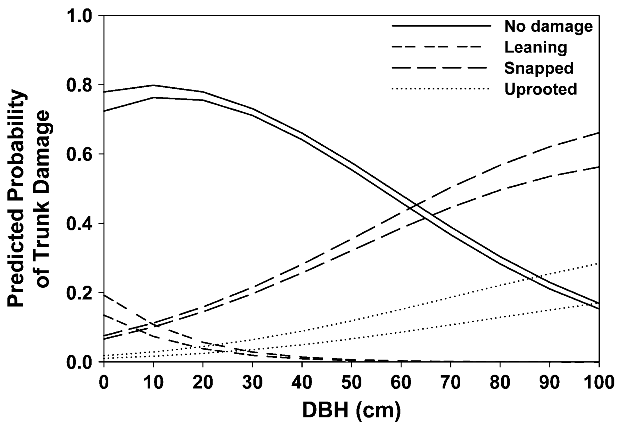

FIGURE 3. Predicted probabilities of trunk damage based on the multinomial generalized linear mixed models (GLMMs) with logit link functions for trees in a tropical dry forest of Madagascar 7–8 mo following Cyclone Fanele. Two lines are presented for each category of probabilities, representing the predicted probabilities for trees with height 1 SD greater than the mean and for trees with height 1 SD less than the mean. Dbh, diameter at breast height.

(Metcalfe *et al.* 2008). Hence, knowledge of the impacts of cyclones on Malagasy forests is a critical goal for understanding Malagasy forest ecology.

Forest damage did not exhibit a linear relationship with tree height because understory (2–3 m) and emergent (8–18 m) trees experienced significantly greater mortality than the canopy. The pattern of higher mortality rates of tall and understory trees has been reported for other cyclone-affected forests and may result from smaller trees being damaged by falling emergent trees or their branches (Sherman *et al.* 2001, Metcalfe *et al.* 2008). In fact, the probability of major delimbing was greater for shorter trees in the KMNP but we did not attempt to assess whether a tree's damage was caused by another tree. Additionally, tall, emergent trees lack the relative protection afforded by the canopy and are subjected to stronger winds and increased biomechanical stresses (Lugo 2008).

Tree dbh was a better predictor of forest damage than tree height, although the inclusion of height often improved the models. Trees with larger dbh were more resistant to the strong forces of the wind but experienced increased snapping and uprooting. Trees with larger girths also had a greater probability of major delimbing, perhaps because dbh is a good predictor of crown volume (Chapman *et al.* 1992). Some studies have found that the relationship between dbh and damage is dependent upon species (*e.g.*, Sherman *et al.* 2001). Species identification was not possible for many trees in this study but a companion study of damage to lemur food supply in the research area found that some species did indeed experience greater damage than others (R. J. Lewis & K. H. Bannar-Martin unpubl. data). Trees that could be identified and were found dead, however, included *Baudouinia fluggeiformis* (Cesalpiniaceae), *Bauhinia porosa* (Meliaceae), *Cedrelopsis grevei* (Meliaceae), *Commiphora guillaumini* (Burseraceae), and *Dalbergia spp*. (Fabaceae).

Stem density and biomass were both markedly reduced approximately 7 mo following the cyclone. These findings are similar to reports from other forests (for a review see Lugo 2008). For example, a tropical dry forest in the Caribbean exhibited reductions in stem density and biomass within the first year following Hurricane Hugo similar to those found in this study (Imbert *et al.* 1996) but these reductions doubled over time (Whigham *et al.* 1991, Imbert & Potercop 2008). Because immediate and delayed mortality can differ substantially, the immediate 8.8 percent mortality in the KMNP almost certainly underestimates the stem mortality caused by Cyclone Fanele.

Our results represent the first study of the impact of a cyclone on a Malagasy dry, deciduous forest. The dry forest of KMNP did not experience the severe damage reported in previous studies of Malagasy lowland humid forests. Birkinshaw and Randrianjanahary (2007) found nearly 50 percent mortality 1 mo after cyclone Hudah hit the Masoala Peninsula, and Johnson *et al.* (2011) found that over 60 percent of trees were severely damaged 5 mo after Cyclone Gretelle hit the Manombo forest. The dry forest of KMNP experienced substantially lower damage and mortality rates than these eastern humid forests, even though it has a similar stem density and Cyclone Fanele was a stronger storm (*e.g.*, Manombo: ~850 trees ≥ 10 cm dbh/ha, Cyclone Gratelle sustained winds = 140 km/h, Johnson *et al.* 2011).

By changing the forest structure, biomass, and composition, major climatic events, such as cyclones, heavily influence forest dynamics (Sherman *et al.* 2001, Lugo 2008) and result in a restructuring and reorganization of species assemblages (Holling *et al.* 1995). The immediate changes in abiotic and biotic factors as a result of Cyclone Fanele will likely have substantial long-term impacts on both the flora and fauna of KMNP. For instance, the post-disturbance succession that results from the large number of light gaps created simultaneously by the death of 14 percent of the emergent trees in the KMNP differs from the typical gap ecology (*cf.* Vandermeer *et al.* 1998, Lugo 2008). Vertebrate frugivores and remnant trees will be key organisms in the reorganization phase of the forest. Post-disturbance adaptive management should focus on maintaining the ecosystem's capacity to buffer and reorganize (Elmqvist *et al.* 2001). The full impact of Cyclone Fanele, however, can only be determined with long-term monitoring.

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SUPPORTING INFORMATION

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

TABLE S1. *Distribution of tree girth and post-cyclone damage and mortality.*

TABLE S2. *Tree damage and mortality frequencies 7–8 mo after Cyclone Fanele.*

TABLE S3. *Results of the multinomial generalized linear mixed models with logit link functions comparing each trunk damage category with no trunk damage after a cyclone*.

FIGURE S1. Location of Kirindy Mitea National Park in Madagascar.

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