Damage to tropical forests caused by cyclones is driven by wind speed but mediated by topographical exposure and tree characteristics

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RESEARCH ARTICLE

Damage to tropical forests caused by cyclones is driven by wind speed but mediated by topographical exposure and tree characteristics

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Abstract

Each year, an average of 45 tropical cyclones affect coastal areas and potentially impact forests. The proportion of the most intense cyclones has increased over the past four decades and is predicted to continue to do so. Yet, it remains uncertain how topographical exposure and tree characteristics can mediate the damage caused by increasing wind speed. Here, we compiled empirical data on the damage caused by 11 cyclones occurring over the past 40 years, from 74 forest plots representing tropical regions worldwide, encompassing field data for 22,176 trees and 815 species. We reconstructed the wind structure of those tropical cyclones to estimate the maximum sustained wind speed (MSW) and wind direction at the studied plots. Then, we used a causal inference framework combined with Bayesian generalised linear mixed models to understand and quantify the causal effects of MSW, topographical exposure to wind (EXP), tree size (DBH) and species wood density (ρ) on the proportion of damaged trees at the community level, and on the probability of snapping or uprooting at the tree level. The probability of snapping or uprooting at the tree level and, hence, the proportion of damaged trees at the community level, increased with increasing MSW, and with increasing EXP accentuating the damaging effects of cyclones, in particular at higher wind speeds. Higher ρ decreased the probability of snapping and to a lesser extent of uprooting. Larger trees tended to have lower probabilities of snapping but increased probabilities of uprooting. Importantly, the effect of ρ decreasing

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the probabilities of snapping was more marked for smaller than larger trees and was further accentuated at higher MSW. Our work emphasises how local topography, tree size and species wood density together mediate cyclone damage to tropical forests, facilitating better predictions of the impacts of such disturbances in an increasingly windier world.

KEYWORDS
hurricane, mechanical failure, snapping, storm, tree, tropical cyclones, tropics, typhoon, uprooting

1 | INTRODUCTION

Tropical cyclones (also known as hurricanes or typhoons) are large-scale disturbances that predominantly impact islands and coastal areas (Ibanez et al., 2022; Lin et al., 2020; Lugo, 2008). Globally, an average of almost 90 tropical cyclones per year occurred over the past four decades (Bourdin et al., 2022; Murakami et al., 2020), of which a half affected coastal areas (Wang & Toumi, 2021). The proportion of Categories 3–5 tropical cyclones (using the Saffir–Simpson hurricane wind scale; Simpson, 1974) has increased over the same period, likely because of global warming, and this trend has been predicted to continue (IPCC, 2021). Even if warming is limited to 1.5°C, which is now unlikely to occur (UNEP, 2023), a further increase of 10% is predicted in the proportion of the most intense tropical cyclones (Categories 4 and 5) (IPCC, 2021). In order to forecast the likely impacts of these changes, it is critical to understand how damage to forests caused by tropical cyclones varies as a function of wind intensity and the characteristics of trees.

The Saffir–Simpson hurricane wind scale (Simpson, 1974) is widely used to describe the strength of tropical cyclones and to anticipate potential damage. The scale is a function of the maximum sustained wind speed (MSW) generated by tropical cyclones and classifies them from Category 1 (MSW 33–42 $m\,s^{-1}$) to Category 5 (MSW ≥70 $m\,s^{-1}$). Given the increasing intensity of tropical cyclones, as exemplified by super-typhoon Haiyan (2013), an additional 'Category 6' has been proposed for tropical cyclones with MSW ≥80 $m\,s^{-1}$ (Lin et al., 2014) and more recently with MSW ≥86 $m\,s^{-1}$ (Wehner & Kossin, 2024). Higher MSW should increase mechanical wind loads on trees and result in higher proportions of trees that are either snapped (bole failure) or uprooted (root failure). As such, Category 1 cyclones are predicted to mostly damage foliage, while those in Category 5 are predicted to cause extensive tree snapping and/or uprooting.

Field data collected after tropical cyclones suggest that the proportion of damaged trees and the intensity of damage increase with wind speed. For example, in El Yunque National Forest (Puerto Rico), Category 4 tropical cyclone María (2017), tripled the proportion of snapped trees compared with Category 3 tropical cyclones Hugo (1989) and George (1998) (Uriarte et al., 2019). In Queensland (Australia), the level of damage was negatively correlated with the distance to trajectory of Category 4 tropical cyclone Larry (2006) (Metcalfe et al., 2008). However, the relationship between MSW and the proportion of damaged trees or the probability of snapping and uprooting remains poorly explored, as most studies reported the damage caused by a single tropical cyclone on one or few plots (e.g., Asner & Goldstein, 1997; Basnet et al., 1992; Herbert et al., 1999; Webb et al., 2014; Zimmerman et al., 1994). For a given MSW, damage is also expected to be mediated by the topographical exposure to wind (EXP) with areas located on windward slopes and on ridges sustaining more damage than forests located on leeward slopes and valleys (e.g., Basnet et al., 1992; Bellingham, 1991; Franklin et al., 2004; Lugo et al., 1983; Reilly, 1991; Walker, 1991).

Tree dimensions (e.g., trunk diameter, height and crown size), together with wood strength, are believed to be the most important biotic characteristics affecting vulnerability to wind damage (Gardiner, 2021). Tree-winching experiments support that a larger diameter at breast height (DBH) should provide more mechanical stability (e.g., Cannon et al., 2015; Ribeiro et al., 2016), but DBH is usually positively related to tree height, crown size and tree weight (e.g., Blanchard et al., 2016; Chave et al., 2005), which should result in greater exposure to wind and mechanical loads (Gardiner, 2021). Some studies have indeed reported that, overall, larger trees experience more severe damage than smaller ones during tropical cyclones (Franklin et al., 2004; Ostertag et al., 2005; Reilly, 1991). However, the nature and the strength of the association between DBH and cyclone-induced uprooting or snapping remain unclear. Some studies found no significant association between tree DBH and snapping (Asner & Goldstein, 1997; Bellingham, 1991; Curran, Brown, et al., 2008; Zimmerman et al., 1994), while others found significant positive (Taylor et al., 2023; Uriarte et al., 2019) or negative associations (Webb et al., 2014). Likewise, most studies found no significant association between tree DBH and uprooting (Asner & Goldstein, 1997; Bellingham, 1991; Curran, Brown, et al., 2008; Elmqvist et al., 1994), while others found significant positive (Franklin et al., 2004; Taylor et al., 2023; Uriarte et al., 2019; Walker et al., 1992; Webb et al., 2014) or negative associations (Elmqvist et al., 1994). Furthermore, the direction and significance of these associations may vary among species (Zimmerman et al., 1994).

Wood density (ρ) is a relatively easy-to-measure trait that is positively associated with mechanical stability (Chave et al., 2009; Niklas & Spatz, 2010) as supported by tree-winching experiments (Ribeiro et al., 2016). Yet, the relationship between ρ and resistance

to wind is not straightforward (Fournier et al., 2013). For instance, it has been argued that for a given DBH, higher ρ provides higher wind resistance, but for the same construction cost, higher ρ at the expense of smaller DBH decreases wind resistance (Larjavaara & Muller-Landau, 2010). Similar to DBH, no clear consensus on the nature and strength of the association between ρ and vulnerability to tropical cyclones has emerged. Wood density has been found to be negatively associated with snapping (Curran, Gersbach, et al., 2008; Taylor et al., 2023; Walker et al., 1992; Webb et al., 2014; Zimmerman et al., 1994) but not always significantly so (Asner & Goldstein, 1997; Bellingham et al., 1995; Uriarte et al., 2019; Walker et al., 1992). Most studies found that ρ was not significantly associated with uprooting (Asner & Goldstein, 1997; Bellingham et al., 1995; Curran, Gersbach, et al., 2008; Taylor et al., 2023; Zimmerman et al., 1994), while others found a significant negative association (Uriarte et al., 2019; Webb et al., 2014). Uprooting susceptibility should be primarily driven by soil and root properties, which determine tree anchorage, but for a given anchorage, heavier trees (larger DBH and/or ρ) should be more susceptible to uprooting (Gardiner, 2021).

Previous studies have been conducted mostly at single sites after one or two cyclones, and this approach has likely prevented the emergence of a consensus on the nature and strength of the relationships between tree characteristics and the damage trees experience. In this study, we analysed a consolidated dataset from 11 field-based studies conducted over a 40-year period to investigate the relationships among wind speed, tree size, wood density and cyclone-induced tree damage in forests. At the community level, we used reconstructed 2D surface wind speed and direction to test the relationships among MSW, topographical exposure to wind (EXP), and the proportion of snapped or uprooted trees. We then used the relationship between the proportion of damaged trees, MSW and EXP to forecast how tropical forests would be affected by higher intensity winds, including MSW ≥86 $m\,s^{-1}$. At the tree level, we explored whether tree size (DBH) and wood density (ρ) explained observed snapping and uprooting probabilities.

2 | MATERIALS AND METHODS

2.1 | Damage and tree characteristics

The categorisation of tree damage caused by tropical cyclones varies considerably across the literature. Tree snapping and uprooting are the most severe damage caused by tropical cyclones and are easy to identify in the field and are visible long after the passage of cyclones, and therefore are the most commonly quantified metrics of damage. Uprooting and, to a lesser extent, snapping increase tree mortality rates (Taylor et al., 2023; Webb et al., 2014) and result in structural changes to the forest by creating canopy gaps, which have important implications for regeneration and local diversity. Therefore, in this study we focus on tree snapping and uprooting damage.

We compiled published and unpublished data on tree snapping and uprooting resulting from tropical cyclones (Table 1) in the Atlantic, Indian and Pacific Ocean basins. We avoided data where damage could not be clearly attributed to a specific cyclone. Data were available for damage caused by 11 cyclones occurring between 1988 and 2021, which affected plots surveyed in islands from nine archipelagos and in Australia (Figure 1). All plots were located in tropical rainforests except two, which were located in subtropical rainforests in Luquillo (Puerto Rico, 18.2° N) and Yakushima (Japan, 30.2° N). We prioritised data with pre- and post-cyclone forest data to prevent bias in plot location regarding the intensity of damage. For instance, we excluded the data set from Curran, Gersbach, et al. (2008), because they located their plots after the cyclone in the most severely damaged areas while in the same general area, plots before were set up before the cyclone by Metcalfe et al. (2008). However, we included data from Birkinshaw and Randrianjanahary (2007) and Zimmerman et al. (1994), which did not have pre-cyclone survey data. Damage was assessed 2–17 months after the cyclones.

We focused on woody trees, that is, we excluded monocots (palms), tree ferns and cycads, and only considered individuals with a DBH ≥ 10 cm. Our final dataset consisted of 22,176 trees belonging to 815 species, 408 genera and 105 families. Data for each tree included its species name, DBH, and whether it had been uprooted (0/1) or snapped (0/1). The definitions of uprooting and snapping were fairly consistent across the different data sets. Uprooting is characterised by the leaning of the main bole an exposure of roots and snapping is characterised by the breakage of the main bole between the ground and the first branches of the crown. Species wood density (ρ) was taken directly from the primary studies when available, or from the getWoodDensity function of the BIOMASS R package (Réjou-Méchain et al., 2017). When species ρ was not available from either of these two sources, we used the averaged ρ from species of the genus or family, which generally explains ~75% and ~35%, respectively, of the species-level variation in ρ (Chave et al., 2006). Wood density (ρ) ranged from 0.10 to 1.03 $g\,cm^{-3}$ (58%, 36% and 6% inferred at the species, genus and family level, respectively).

2.2 | Wind speed and exposure

For each plot, we reconstructed the 1-min MSW generated by tropical cyclones using the temporalBehaviour function of the R package StormR (Delaporte et al., 2023, 2024). This function allows reconstruction of wind speed and direction using a set of cyclone models and tropical cyclone characteristics from the International Best Track Archive for Climate Stewardship (IBTrACS) database (Knapp et al., 2010). We used the default setting, that is, the Willoughby et al. (2006) model with asymmetry following Chen (1994). These models reconstruct the 2D idealised surface wind speed structure generated by tropical cyclones based on the latitudes of their centres, the MSWs and the radius of MSW speed as provided by IBTrACS every 6 h for each tropical cyclone. We performed a linear interpolation of the original 6-h inputs from IBTrACS to reconstruct the 2D surface wind speed structure of each tropical cyclone every

TABLE 1 Studies reporting damage by tropical cyclones in tropical and subtropical wet forests (Cat. is the maximum Saffir–Simpson hurricane wind scale category reached by the cyclone over its duration, species are the three most abundant species, maximum sustained wind speed (MSW) is the reconstructed maximum sustained wind speed at plot locations).

Cyclone (year)	Cat.	Reference	Location (elevation)	Forest type (species)	No. of plots	MSW ($m\,s^{-1}$)	Plot size (ha)	No. of trees
Cook (2017)	2	This study	New Caledonia (80 m)	Lowland tropical rainforest (*Xylopia vieillardii*, Annonaceae; *Crossostylis grandiflora*, Rhizophoraceae; *Tabernaemontana cerifera*, Apocynaceae)	1	38.2	1	896
Gilbert (1988)	5	Tanner and Bellingham (2006)	Jamaica (1560–1610 m)	Montane tropical rainforest (*Clethra occidentalis*, Clethraceae; *Podocarpus urbanii*, Podocarpaceae; *Cyrilla racemiflora*, Cyrillaceae)	4	62.2–62.2	0.07–0.20	750
Hudah (2000)	4	Birkinshaw and Randrianjanahary (2007)	Madagascar (0–350 m)	Lowland tropical rainforest (*Brochoneura voru*, Myristicaceae; *Anthostema madagascariense*, Euphorbiaceae; *Uapaca louvelii*, Phyllanthaceae)	15	65.9–71.0	0.1	1353
Hugo (1989)	5	Zimmerman et al. (1994)	Puerto Rico (300 m)	Lowland subtropical rainforest (*Casearia arborea*, Salicaceae; *Dacryodes excelsa*, Burseraceae; *Manilkara bidentata*, Sapotaceae)	1	55.9	16	8848
Larry (2006)	4	Metcalfe et al. (2008)	Australia (50–1100 m)	Lowland to montane tropical rainforest (*Franciscodendron laurifolium*, Malvaceae; *Backhousia bancroftii*, Myrtaceae; *Myristica insipida*, Myristicaceae)	9	29.9–45.9	0.5	1779
Maria (2017)	5	Taylor et al. (2023)	Dominica (250–800 m)	Lower montane tropical rainforest (*Amanoa caribaea*, Phyllanthaceae; *Sterculia caribaea*, Malvaceae; *Tapura latifolia*, Dichapetalaceae)	9	37.1–42.5	0.25	1647
Niran (2021)	5	This study	New Caledonia (290 m)	Lowland tropical rainforest (*Sparattosyce dioica*, Moraceae; *Deplanchea speciosa*, Bignoniaceae; *Pleurocalyptus pancheri*, Myrtaceae)	1	30.5	1	1225
Olaf (2005)	5	Webb et al. (2014)	American Samoa (20–260 m)	Lowland tropical rainforest (*Dysoxylum samoense*, Meliaceae; *Hibiscus tiliaceus*, Malvaceae; *Artocarpus altilis*, Moraceae)	4	72.4–72.8	1.00–2.00	3672
Pam (2015)	5	Ticktin et al. (2024)	Vanuatu (260–370 m)	Lowland tropical rainforest (*Myristica inutilis*, Myristicaceae *Syzygium myriadenum*, Myrtaceae; *Macaranga dioica*, Euphorbiaceae)	8	56.5–67.7	0.08	509

TABLE 1 (Continued)

Cyclone (year)	Cat.	Reference	Location (elevation)	Forest type (species)	No. of plots	MSW ($m\,s^{-1}$)	Plot size (ha)	No. of trees
Waka (2001)	3	Franklin et al. (2004)	Tonga (10–180 m)	Lowland tropical rainforest (*Manilkara grandiflora*, Fabaceae; *Zanthoxylum pinnatum*, Rutaceae; *Cryptocarya turbinata*; Lauraceae)	21	44.5–51.3	0.06	996
Yancy (1993)	4	Bellingham et al. (1996)	Japan (530 m)	Lowland subtropical rainforest (*Distylium racemosum*, Hamamelidaceae; *Actinodaphne acuminata*, Lauraceae; *Camellia oleifera*, Theaceae)	1	60.1	0.62	501

1 h. Then, for each plot and cyclone, we computed MSW as the largest value of the MSW observed along the passage of the cyclone at the plot location (see Figure 2a). MSW ranged from 29.9 to 72.8 $m\,s^{-1}$ (with mean of 52.8 $m\,s^{-1}$ and standard deviation of 12.7 $m\,s^{-1}$).

Topographical exposure to wind (EXP) was computed using the hillShade function of the raster R package (Hijmans, 2023) and the Copernicus 30-m spatial resolution global digital elevation model (GLO-30 Copernicus DEM, https://doi.org/10.5270/ESA-c5d3d65). We set the wind inflexion angle to 6° as suggested by Boose et al. (1994). Given that wind direction changes along the movement of the cyclone, we computed EXP every 1 h. We then extracted the maximum EXP value (EXP) over the duration of the cyclone when the centre of the cyclone was located ≤300 km away from the plot. Negative EXP values represent areas sheltered from the wind, while positive values represent areas exposed to the wind (e.g., see Figure 2b). For the site reporting impacts from Hurricane Hugo (1989) in Puerto Rico (Luquillo Experimental Forest), because the plot is large with a varying topography (e.g., elevation ranges from 330 to 430 m), we used the average value within the extent of the 16-ha plot. The maximum topographical exposure to wind (EXP) across the full dataset ranged from 0.04 to 0.85 (with a mean of 0.29 and standard deviation of 0.17).

2.3 | Data analysis

We used a causal inference analytical framework (Structural Causal Modelling, Pearl, 2009) to understand the causal effects of MSW, wood density and tree size (further referred to as 'predictors of interest') on the outcomes of interest (see below) from these models. We first defined a causal diagram of the studied system—one at the community level and a second at the tree level—using directed acyclic graphs (DAGs; see Figure 3). For each predictor of interest (i.e., predictors whose total causal effect we aim to quantify), we then applied the 'backdoor criterion' to the DAG. This criterion allowed us to define the minimum set of covariates to condition on, to close non-causal paths and allow a causal interpretation of the slope of the predictor of interest (conditional on the DAG's assumptions being true, while avoiding common interpretational problems such as confounding, overcontrol or collider biases, Arif & MacNeil, 2023; McElreath, 2020).

We used Bayesian generalised linear mixed models to test the effects of the predictors of interest on the different response variables. In the first model, we aimed to quantify the causal effect of MSW on the total proportion of snapped or uprooted trees by a cyclone at the community (or plot) level. We also investigated how this effect may be mediated by the topographical exposure to wind (EXP)—that is, the interaction effect of MSW and EXP. Given that topography also affects forest structure and composition (e.g., Blanchard et al., 2019; Webb et al., 1999), which in turn can affect the proportion of damaged trees, we controlled for different forest structures by adding the plot's mean DBH and wood density (ρ) of the trees as predictors. We expect that forests with larger trees and

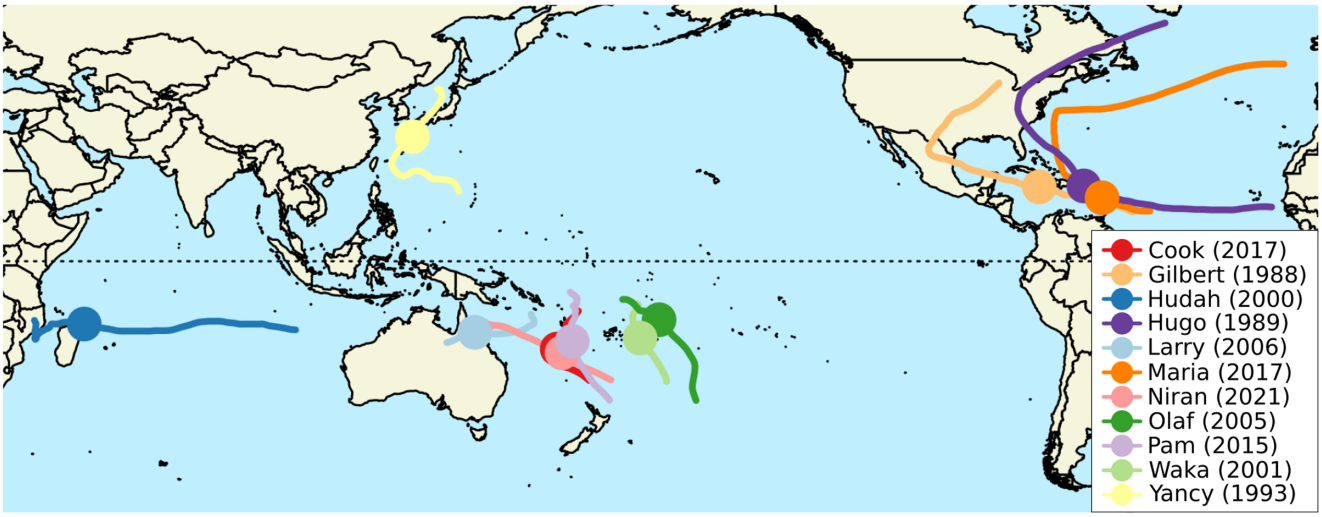

FIGURE 1 Location of the study sites (points) and trajectories of studied cyclones (lines). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

lower wood density would suffer more damage than forests with smaller trees and higher wood density. We used a binomial distribution with a logit link function and a varying intercept for the study identity, a variable that gathers plots from the same study (i.e., same region, cyclone and survey team; detailed model described in the Supplementary Material S1). We performed Pareto-smoothed importance sampling leave-one-out cross-validation (PSIS-LOO) with the *loo* function from the *loo* R package (Vehtari et al., 2017, 2023) to assess the predictive performance of our models. The *loo* function returns a summary table of Pareto *k* diagnostic; prediction are very well when $k \leq 0.5$, well when $0.5 > k \leq 0.7$, poor when $0.7 > k \leq 1$, very poorly $k > 1$.

In the second and third models, we aimed to understand the causal effects of tree size (DBH) and the species' wood density (ρ) on the probability of individual tree snapping (Model 2) or uprooting (Model 3), and how these effects are mediated by MSW. We also accounted for the interaction between tree DBH and species ρ (the effect of ρ is expected to decrease with increasing DBH). We kept the effect of EXP (and its interaction with MSW) and added the study, plot and species identities as three varying intercepts to capture residual variation related to these grouping variables. Using the backdoor criterion, the defined set of necessary covariates was MSW, EXP, DBH and ρ. For Models 2 and 3, we used a Bernoulli family distribution with a logit link function (detailed model descriptions in the Supplementary Material S1). For all models, predictors were centred and scaled before fitting the model to facilitate prior assignment and exploration of the posterior distribution by the sampler.

We used the joint posterior distributions to generate posterior predictions of the response variables of Models 1, 2 and 3, to visualise the expected causal effects of interest and their uncertainty at different combinations of predictor values. For Model 1, we generated predictions of the proportion of damaged trees at 100 values of MSW equally spaced within the range of observed MSW and extrapolated wind speed values to 95 $m.s^{-1}$, the record MSW for tropical cyclones in the IBTrACS database (see Rogers et al., 2017). We

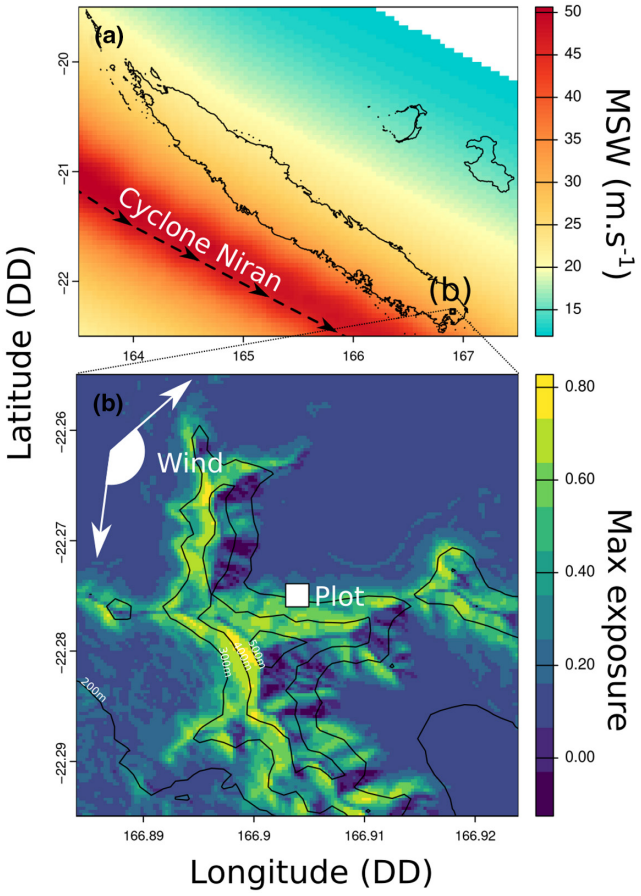

FIGURE 2 Example of (a) maximum sustained wind speed (MSW) generated by cyclone Niran (2021) over New Caledonia, including the location of the sample plot and surrounding area shown in (b), and (b) Maximum topographical exposure in the area around the example plot. Spatial resolutions are 1 km and 30 m, respectively ($MSW = 25.0\,m\,s^{-1}$ and $EXP = 0.26$ at the plot location). In (b), white arrows represent wind direction blowing from North to South at the beginning of the cyclone and from South–West to North–East at the end of the cyclone.

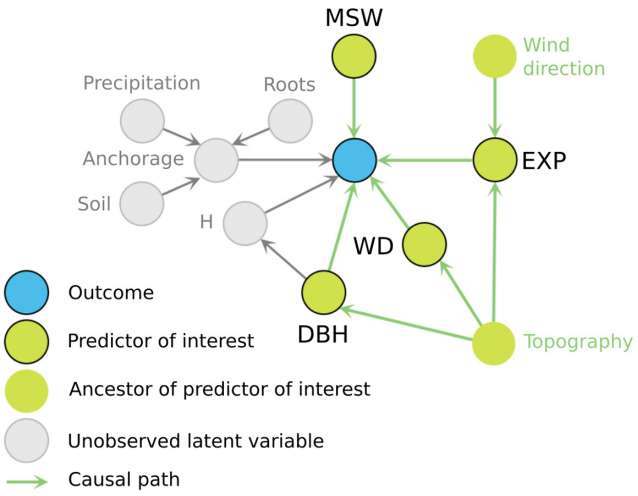

FIGURE 3 Directed acyclic graph (DAG) at the tree level. Outcomes are the probabilities of tree snapping or uprooting (DBH, diameter at breast height; EXP, topographical exposure to wind; H, tree height; MSW, maximum sustained wind speed; WD, wood density). At the community level, outcomes are the proportion of snapped or uprooted trees and averaged values were used as predictors.

also compared the predicted posterior probability distributions of these proportions at the five threshold values of the Saffir–Simpson hurricane wind scale, namely 33, 43, 50, 58 and 70 $m\,s^{-1}$, and at the suggested threshold for 'Category 6' cyclones (86 $m\,s^{-1}$). These predictions were made at maximum EXP values of 0 (low), 0.3 (medium) and 0.6 (high) to visualise the implications of the interaction effect on the scale of the outcome variable. We used a mean DBH value of 20 cm (i.e., close to the median value, 21.3 cm) and a mean wood density of 0.60 $g\,cm^{-3}$ (i.e., close to the median value, 0.61 $g.cm^{-3}$). For Models 2 and 3, we followed the same approach as for Model 1, but replaced EXP by ρ (low, $\rho = 0.35\,g\,cm^{-3}$, medium $\rho = 0.60\,g\,cm^{-3}$ and high-density $\rho = 0.85\,g\,cm^{-3}$), and used the three values of DBH (small, DBH = 10 cm, medium, DBH = 45 cm and large DBH = 80 cm), to visualise the predicted individual probabilities of being snapped or uprooted as MSW increases, depending on species ρ and at different DBHs, and at the same threshold wind values based on the Saffir–Simpson scale as for Model 1. Finally, we compared predicted individual probabilities of being snapped or uprooted for four different types of trees when exposed to high wind speed (70 $m\,s^{-1}$): small trees with low wood density, small trees with high wood density, large trees with low wood density and large trees with high wood density.

Parameter or predicted outcome posterior distributions were shown in their entirety or were summarised using the median as the central point and a 90%-highest posterior density interval (90%-highest posterior density interval, HPDI), that is, the narrowest interval capturing 90% of the probability mass. All models were run in the R statistical environment (version 4.3.2, R Core Team, 2023) and were fitted using the No-U-Turn (NUTS) sampler of stan (Carpenter et al., 2017) through the *brms* R package (Bürkner, 2017). Models were run on four chains, for 1500 iterations, with 500 warm-ups. Chain mixing was checked visually using trace plots and model convergence was verified using Rhats (all were <1.01, as required). Posterior draws were extracted using the *tidybayes* R package (Kay, 2023).

3 | RESULTS

At the plot scale, the proportion of uprooted or snapped trees increased with MSW and to a lesser extent with the maximum topographical exposure to wind (EXP) (Figure 4a; Figure S2). We also found a positive interaction between MSW and EXP (in 97.6% of iterations) showing that the proportion of damaged trees increased more quickly with increasing MSW on topographically exposed areas compared with topographically sheltered areas (Figure 4). The proportion of damaged trees also increased with increasing mean DBH and to a lesser extent with decreasing mean wood density (in 83.2% of iterations). The uncertainty in the predicted proportion of damaged trees also increased with MSW. For an MSW of 33 $m\,s^{-1}$ (Category 1 cyclones, Figure 4b), a mean DBH of 20 cm and a mean wood density of 0.60 $g\,cm^{-3}$, the predicted median proportion of damaged trees was low regardless of EXP (median = 0.03%) with low uncertainty (90%-HPDI between 0.01% and 0.06%). For a MSW of 70 $m\,s^{-1}$ (Category 5 cyclones, Figure 4f) the predicted proportion of damaged trees increased with increasing EXP but with large uncertainty around the median prediction, 0.36% (90%-HPDI between 0.22% and 0.51%), 0.41% (90%-HPDI between 0.27% and 0.57%), 0.45% (90%-HPDI between 0.31% and 0.63%), for EXP = 0, 0.3 and 0.6, respectively. For extreme MSW of 86 $m\,s^{-1}$ ('Category 6' cyclones, Figure 4g) the uncertainty in the predicted damage remained large, but the distribution of probabilities of predicted damage were skewed towards greater damage, especially in topographically exposed areas (median = 0.78%, 90%-HPDI between 0.65% and 0.91% when EXP = 0.6). Leave-one-out cross-validation indicated that our model was able to predict very well the observed proportion of damaged trees (Pareto's $k \leq 0.5$) for 68.9% of the plots, well for 8.1% of the plots ($0.5 >$ Pareto's $k \leq 0.7$), poorly for 17.6% of the plots ($0.7 >$ Pareto's $k \leq 1$) and very poorly for only 5.4% of the plots (Pareto's $k > 1$).

At the tree level, the probabilities of snapping and uprooting decreased with increasing wood density (ρ), which had a negative slope estimate in 100% and 96.0% of the iterations in Models 2 and 3, respectively (Figure 5; Figure S3). The DBH of the trees had a lesser effect on the probability of snapping than ρ, with smaller trees tending to be more prone to snapping than large trees (DBH having a negative slope in 61.1% of the iterations). The negative effect of DBH on the probability of snapping increased with increasing MSW (starting to be noticeable for winds generated by Category 4 or higher tropical cyclones). The effect of DBH was more important for uprooting, with large trees being more likely to uproot than small trees (DBH having a positive slope in 100% of the iterations). This positive effect of DBH on the probability of

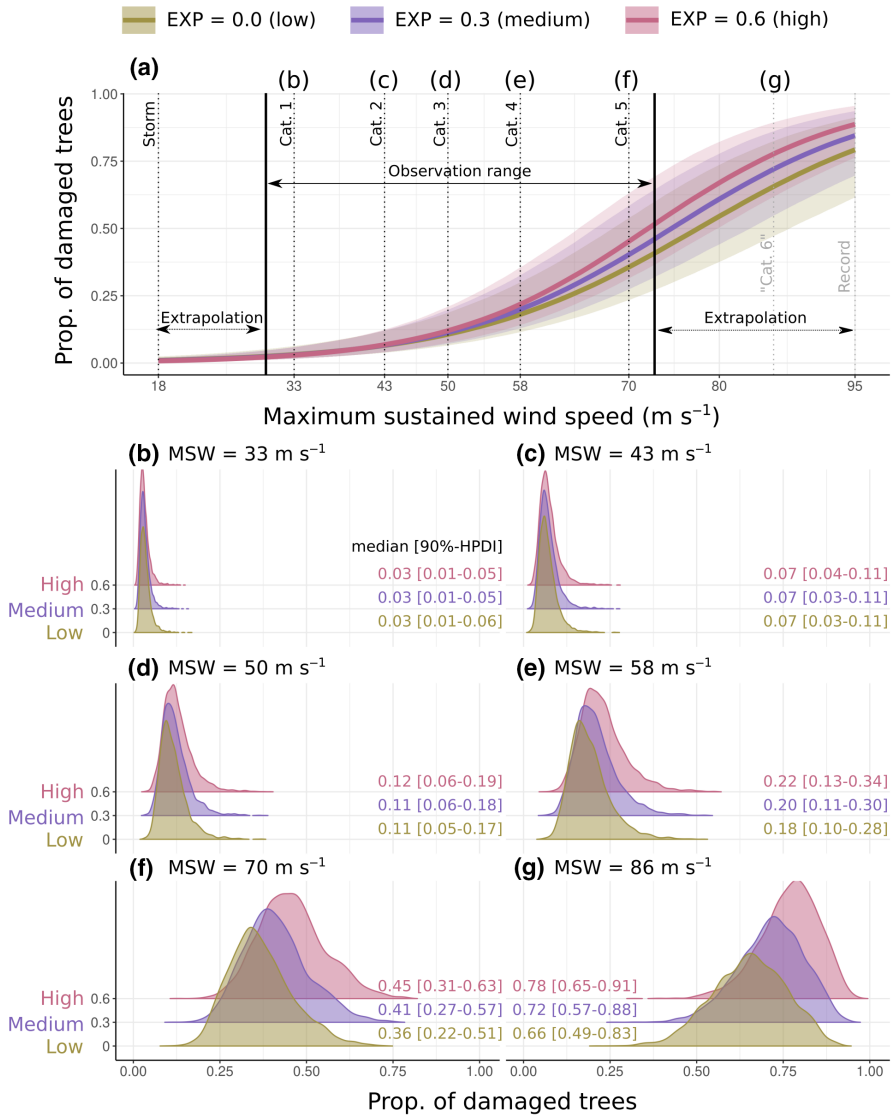

FIGURE 4 Predicted proportion of damaged (snapped or uprooted) trees by Model 1 ($N = 74$ plots), (a) median prediction (lines) and 90%-highest posterior density interval along the extended range of observed maximum sustained wind speed (MSW) for three different values of maximum topographical exposure to wind (EXP, 0.0, 0.3 and 0.6), (b–g) predicted posterior distribution of the proportion of damaged trees for different combinations of MSW (33, 43, 50, 58, 70 and 86 m s^{-1}) and EXP (0.0, 0.3 and 0.6). Predictions were made for an 'average Study Identity' (i.e., we ignored the varying Study Identity intercept to generate predictions), a mean DBH of 20 cm and a mean wood density of 0.60 g cm^{-3}.

uprooting was modulated by species' ρ, such that large trees with low wood density were more likely to be uprooted than large trees with high wood density (Figure 5d).

The uncertainty in the predicted probability of snapping or uprooting increased with increasing MSW and with increasing DBH and also tended to be higher for uprooting than for snapping (Figure S4). Trees with light wood ($\rho = 0.35$ g cm^{-3}) showed very different responses when exposed to high wind speed (MSW = 70 m s^{-1}) depending on their size (Figure 6). Small trees with light wood (DBH = 10 cm) were 2.3 times as likely to be snapped than uprooted (median values, Figure 6a), while large trees (DBH = 80 cm), were 1.7 times as likely to be uprooted than snapped (median values, Figure 6d). Differences were less pronounced for trees with dense wood ($\rho = 0.85$ g cm^{-3}). Small, dense-wooded trees were 1.9 times as likely to be snapped than to be uprooted (median values, Figure 6b) but large dense-wooded trees were 1.3 times as likely to be uprooted than to be snapped with probability distribution skewed towards small probabilities of damage (Figure 6d).

4 | DISCUSSION

We show that reconstructed MSW is a good predictor of observed cyclone-induced damage in the studied forests. We also demonstrate that modelled tree damage impacts broadly correspond with the predictions made based on the Saffir–Simpson hurricane wind scale (Simpson, 1974). Our community-level model predicts that for a forest with median average tree size (20 cm) and wood density (0.6 g cm^{-3}), for Category 1 tropical cyclones (MSW = 33–43 m s^{-1}), <15% of trees could be snapped or uprooted, while for MSW of 70 m s^{-1} (Category 5 tropical cyclones threshold value) ~25%–65% of trees could be snapped or uprooted, depending on topographical exposure to wind. Based on our models, these proportions can reach ~45%–90% for MSW of 86 m s^{-1} (the proposed 'Category 6' tropical cyclone threshold value suggested by Wehner & Kossin, 2024). Our model indicates a sharp increase in damage when wind speeds reach Category 3 intensity or higher (≥50 m s^{-1}); similar patterns were found using a remote sensing vegetation index in the southwest Pacific

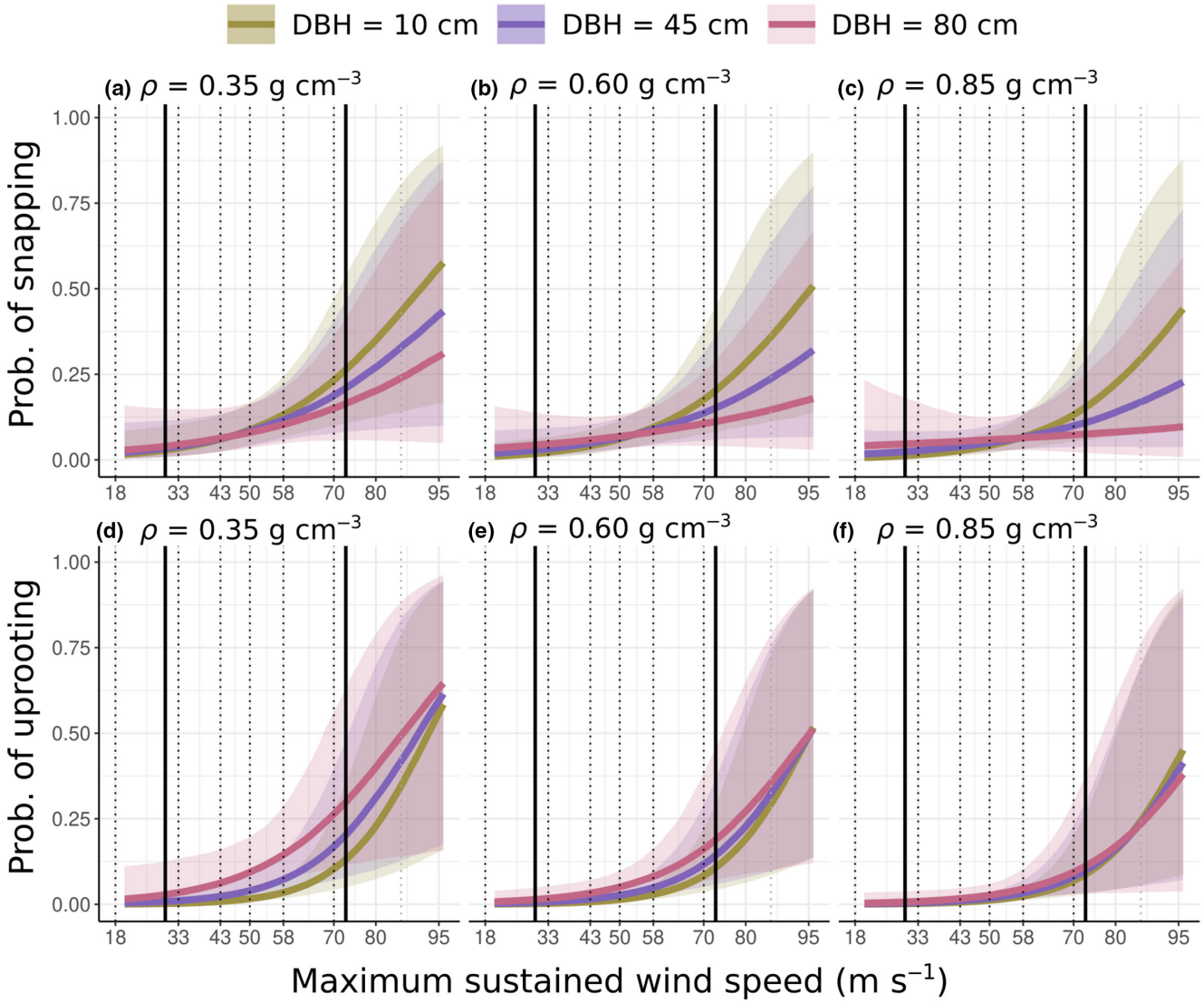

FIGURE 5 Predicted probabilities of snapping by Model 2 (a–c) and uprooting by Model 3 (d–f). Median prediction (lines) and 90%-highest posterior density interval along the extended range of observed maximum sustained wind speed (MSW) for three different values of diameter at breast height (DBH, 10, 45 and 80 cm) and three different values of wood density (ρ, 0.35, 0.60 and 0.85 g cm^{-3}). Predictions were made for a medium topographical exposure to wind (EXP = 0.3) and ignore the varying intercept between the identities of studies, plots and species.

(Delaporte et al., 2022). This nonlinear increase in tree damage with greater wind speed is due to the geometric scaling of wind effects on trees, which is proportional to the square of the horizontal wind speed (Ancelin et al., 2004; Gardiner et al., 2000; Mayhead, 1973). Such non-linearity has critical implications for forests in the context of climate change, because the proportion of the most intense tropical cyclones (Categories 3–5) has increased over the past four decades and is predicted to further increase in the future (IPCC, 2021), which will lead to more snapped and uprooted trees.

A large amount of uncertainty remained in the predictions of the damaged tree proportion for a given MSW, which increased with greater MSW. As suggested by previous observations (e.g., Basnet et al., 1992; Bellingham, 1991; Franklin et al., 2004; Lugo et al., 1983; Reilly, 1991; Walker, 1991), we found that the effect of MSW was mediated by the topographical exposure to wind (EXP) and that the mediating effect of topography increased with increasing wind speed. Forests located on windward slopes and on ridges sustained more damage than forests located on leeward slopes and valleys. However, our results support the conclusion of an analysis of remotely sensed damage caused by the major tropical cyclone María (2017) in Puerto Rico suggesting that the effects of EXP are negligible compared with that of MSW (Hall et al., 2020). The relatively small effect of topography in our model and in the earlier study by Hall et al. (2020) could be partially explained by how the effect of topography on winds was integrated, where wind is treated analogously to light (e.g., Boose et al., 1994). Indeed, unlike light, topography does not only act as a barrier to wind, sheltering some parts of the landscape, but also changes its direction and speed (e.g., Ruel et al., 1998). Rainfall, before and during tropical cyclones, has also been suggested to be a better predictor

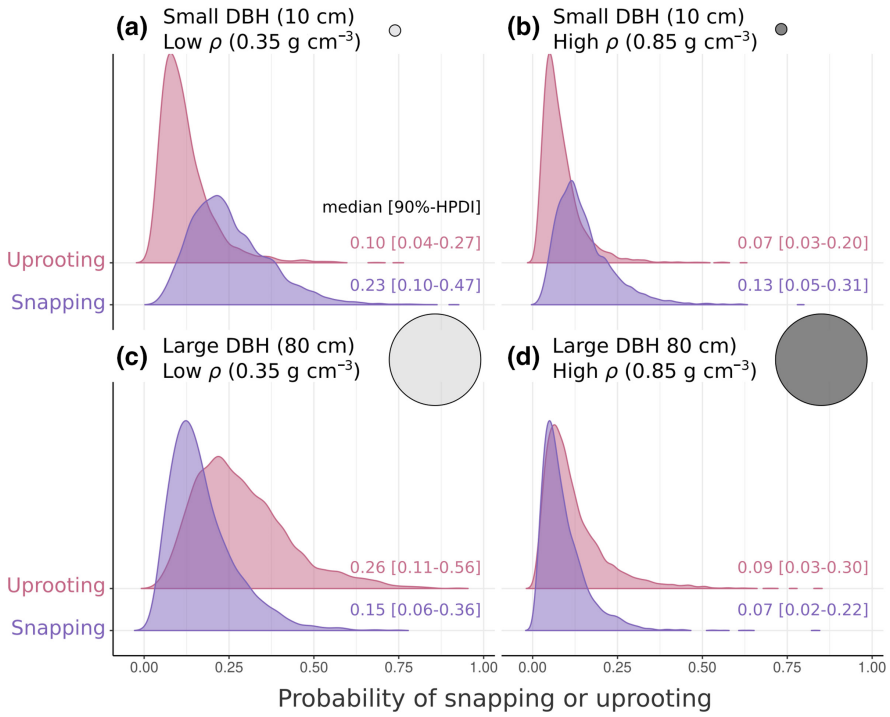

FIGURE 6 Predicted posterior distribution of the probability of snapping by Model 2 and uprooting by Model 3 for different combinations of tree size (diameter at breast height, DBH = 10 cm in (a) and (b), and DBH = 80 cm in (c) and (d)) and wood density ($\rho = 0.35\ g\,cm^{-3}$ in (a) and (c), and $\rho = 0.85\ g\,cm^{-3}$ in (b) and (d)), as illustrated by the grey circles. Predictions were made for a maximum sustained wind speed (MSW) of $70\ m\,s^{-1}$, a medium topographical exposure to wind (EXP = 0.3) and generalised across the identities of studies, plots and species (i.e., used the grand effects, ignoring the varying intercept parameters).

of cyclone-induced damages than MSW (Hall et al., 2020). Heavy rainfall can decrease the resistance of trees to uprooting by saturating soils with water, reducing soil strength (Gardiner, 2021) and also by increasing the weight of trees, and thus mechanical stress, because of large amount of water intercepted and stored by the canopy (e.g., in the bark, leaves or epiphytes) (e.g., Herwitz, 1985). However, we suggest that wind is the main factor causing the mechanical stress while rainfall mediates its effect.

We also found that tree communities with larger DBH experience more damage than communities with smaller DBH. This is likely due to the positive relationship between DBH and tree height with taller trees being more exposed to wind and experiencing greater mechanical stress due to longer lever arm (Gardiner, 2021). We lack reliable tree height data from our sites to directly test the relationship between tree height and the damage experienced by forests during cyclones. However, forests exposed to frequent cyclones have lower canopy heights than other areas at equivalent latitudes where cyclones are absent or infrequent (Ankori-Karlinsky et al., 2024; Ibanez et al., 2019; Quigley & Platt, 2003) and trees in forests exposed to frequent cyclones invest more in secondary (diameter) than primary (height) growth which increases their mechanical stability (Blanchard et al., 2016; Thomas et al., 2015). Canopy height is also driven by environmental factors such that, in drier areas or at higher elevations, canopy heights are lower and forests may be less damaged by cyclones (Boose et al., 1994).

Our results support studies concluding that species with higher wood density (ρ) have a lower snapping probability than species with lower ρ (Curran, Gersbach, et al., 2008; Taylor et al., 2023; Walker et al., 1992; Webb et al., 2014; Zimmerman et al., 1994). We also found that species with higher wood density (ρ) tend to be less likely to uproot than species with lower ρ, but this effect was smaller than for snapping, as had been suggested in previous studies (Asner & Goldstein, 1997; Bellingham et al., 1995; Curran, Gersbach, et al., 2008; Taylor et al., 2023; Zimmerman et al., 1994). This is not surprising because uprooting should involve complex interactions between roots and soils (Gardiner, 2021). To our knowledge, few studies have explored the effect of soils (e.g., Franklin et al., 2004) or root characteristics (e.g., Basnet et al., 1993) on cyclone-induced damage in tropical wet forests. For instance, uprooting is likely to be more frequent on poorly drained soils than on well-drained soils because trees have shallower rooting depth the poorer the drainage (Rutledge et al., 2021; Wang & Xu, 2009). Root dimensions (e.g., the root branching organisation, the diameter of lateral roots or the rooting depth) were identified as key parameters to better explain uprooting (Freschet et al., 2021; Gardiner, 2021; Stokes, 2002) and need to be validated in a tropical context.

We also showed that the effect of ρ on snapping or uprooting probabilities was mediated by both the size of the trees and the strength of the wind they had been exposed to. This could explain why other studies did not find that increasing ρ noticeably decreases the probability of snapping (Asner & Goldstein, 1997; Bellingham et al., 1995; Uriarte et al., 2019; Walker et al., 1992). This is also supported by a study in the dry forests of the Yucatán Peninsula, where ρ only had a significant effect in areas affected by winds $\geq 58\ m\,s^{-1}$ (Vandecar et al., 2011). The differences between studies in the effects of ρ on wind-induced damage might also reflect differences in the ranges of ρ studied. For instance, ρ tends to be higher in dry forests (e.g., 0.30 to $1.10\ g\,cm^{-3}$ in Vandecar et al., 2011) than in wet forests (e.g., 0.10 to $1.03\ g\,cm^{-3}$ in our dataset), potentially due to adaptations to other factors, such as drought (O'Brien et al., 2017).

The negative effect of ρ on the probability of snapping accords with ρ being well correlated with many other physical properties of

wood (Niklas & Spatz, 2010). However, the relatively large effect of ρ compared with DBH in determining snapping probabilities contradicts physics-based modelling of tree resistance to wind. In these models, tree DBH (together with tree height) is the most important factor determining the resistance of trees, with the probability of snapping and uprooting being proportional to DBH^3 and DBH^2, respectively (Gardiner, 2021). The discrepancy between the physics and our findings might stem from the fact that those models have been developed using properties of wooden beams and have been mostly applied in forestry to monospecific stands (often conifers) (e.g., Ancelin et al., 2004; Virot et al., 2016). Indeed, in addition to its effect on the mechanical properties of wood (e.g., Young's modulus, modulus of rupture and modulus of elasticity), ρ is very likely to capture other architectural features in species-rich tropical forests (e.g., Poorter et al., 2006) that can also affect tree resistance to wind. Higher ρ is also associated with better resistance to pathogens and wood decay, which allows trees to better maintain wood mechanical properties (Chave et al., 2009; Larjavaara & Muller-Landau, 2010).

Most studies used in our analysis covered the damage caused by major tropical cyclones that reached Category 4 or 5 at their maximum intensity, but only half reported damage in areas affected by winds ≥58 $m\,s^{-1}$ (Bellingham et al., 1996; Birkinshaw & Randrianjanahary, 2007; Tanner & Bellingham, 2006; Ticktin et al., 2024; Webb et al., 2014) and only two in areas affected by winds ≥70 $m\,s^{-1}$ (Birkinshaw & Randrianjanahary, 2007; Webb et al., 2014). This likely contributed to uncertainty in our model predictions for high wind speeds. This is important because the most severe damage occurs at these extreme speeds and because of the predicted increasing frequency of the most extreme tropical cyclones. Finally, as noted in recent reviews (e.g., Heartsill-Scalley & López-Marrero, 2021; Lin et al., 2020), available data is highly biased towards the North Atlantic Basin or individual cyclone events. Notable in our dataset, we only have one site in each of the Indian Ocean and the North Pacific.

A network of permanent plots with standardised post-cyclone damage assessment survey protocols across the main tropical cyclone basins that had a greater focus on tree biomechanical traits and on measuring actual wind speeds (and rainfalls) would help to further understand how tropical cyclones are shaping forest ecosystems. Integrating a combination of traits that are more directly linked to the biomechanical properties of trees than ρ (e.g., modulus of rupture and elasticity) and additional dimensional (e.g., tree height and crown size) or architectural (e.g., growth and branching patterns, root architecture and rooting depth) tree characteristics, may provide a more nuanced understanding of the responses of trees to tropical cyclones (Asner & Goldstein, 1997; Fournier et al., 2013; Laurans et al., 2024; Read et al., 2011). Conducting tree-winching experiments would also help in assessing the mechanical stability of tropical trees and their potential resistance to wind (e.g., Ribeiro et al., 2016); so far, tree-winching experiments have mostly been conducted in temperate forests (e.g., Peltola, 2006). This knowledge will be critical for understanding tropical forest resistance and resilience to increasing frequency of intense cyclones in the coming decades resulting from global warming.

Our finding that greater wood density reduces the likelihood of cyclone damage has implications for large-scale extrapolation of the future effects of more intense tropical cyclones and as their tracks move more poleward (Studholme et al., 2022). Since community-level variation in wood density declines as latitude increases (Swenson & Enquist, 2007), forests at higher latitudes may have less resistance to cyclones, especially when community-level mean wood density that is lower than that required to withstand high wind speeds. This is manifest when tropical cyclones affect cool temperate and boreal forests dominated by conifers of low wood density, especially Pinaceae, causing very high levels of damage (e.g., Foster, 1988; Korznikov et al., 2022), and a lack of resilience in forests such as these to the effect of high wind speeds could turn them from being carbon sinks to carbon sources (e.g., Zeng et al., 2009). Moreover, a changing cyclone disturbance regime as high-intensity cyclones become more prevalent and move to higher latitudes could alter selection pressures (e.g. Cannon et al., 2023). If cyclones of proposed Category-6 intensity became recurrent in a region, it may become impossible to maintain populations of tree species of low wood density if they cannot grow to maturity fast enough to set seed between cyclones or cannot be maintained by resprouting (Batista & Platt, 2003; Bellingham et al., 1995). This would result in chronic loss of forest diversity and, potentially, reduced resilience to other disturbances that interact with cyclones, such as pathogens, drought or fire (Ibanez et al., 2022; Seidl et al., 2017).

AUTHOR CONTRIBUTIONS

Thomas Ibanez: Conceptualization; formal analysis; investigation; writing – original draft; writing – review and editing. **David Bauman:** Formal analysis; writing – review and editing. **Shin-ichiro Aiba:** Investigation; writing – review and editing. **Thomas Arsouze:** Methodology; writing – review and editing. **Peter J. Bellingham:** Investigation; writing – review and editing. **Chris Birkinshaw:** Investigation; writing – review and editing. **Philippe Birnbaum:** Investigation; writing – review and editing. **Timothy J. Curran:** Writing – review and editing. **Saara J. DeWalt:** Investigation; writing – review and editing. **John Dwyer:** Writing – review and editing. **Thierry Fourcaud:** Writing – review and editing. **Janet Franklin:** Investigation; writing – review and editing. **Takashi S. Kohyama:** Investigation; writing – review and editing. **Christophe Menkes:** Methodology; writing – review and editing. **Dan J. Metcalfe:** Investigation; writing – review and editing. **Helen Murphy:** Investigation; writing – review and editing. **Robert Muscarella:** Investigation; writing – review and editing. **Gregory M. Plunkett:** Investigation; writing – review and editing. **Chanel Sam:** Investigation; writing – review and editing. **Edmund Tanner:** Investigation; writing – review and editing. **Benton N. Taylor:** Investigation; writing – review and editing. **Jill Thompson:** Investigation; writing – review and editing. **Tamara Ticktin:** Investigation; writing – review and editing. **Marika V. Tuiwawa:** Investigation; writing – review and editing. **Maria Uriarte:**

Investigation; writing – review and editing. **Edward L. Webb:** Investigation; writing – review and editing. **Jess K. Zimmerman:** Investigation; writing – review and editing. **Gunnar Keppel:** Conceptualization; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are archived and publicly available on Zenodo (https://doi.org/10.5281/zenodo.11062523). Tree-level data for forests of Dominica after the hurricane Maria (2017) are only available on request.

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