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# High resilience of Pacific Island forests to a category- 5 cyclone

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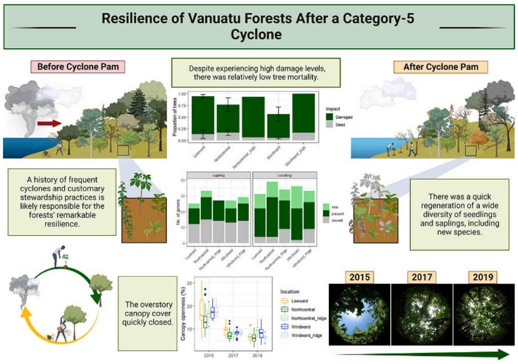
## HIGHLIGHTS

- High intensity cyclones expected to increase with climate change but impacts unknown.
- Effects of Category 5 cyclone examined on Pacific Island forests.
- Vegetation transects across 3 contrasting Vanuatu sites surveyed over 5 years.
- Forests showed high levels of both resistance and resilience.
- Cyclone frequency and customary stewardship practices likely foster resilience.

## GRAPHICAL ABSTRACT



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## ABSTRACT

Assessing how forests respond to, and recuperate from, cyclones is critical to understanding forest dynamics and planning for the impacts of climate change. Projected increases in the intensity and frequency of severe cyclones can threaten both forests and forest-dependent communities. The Pacific Islands are subject to frequent low-intensity cyclones, but there is little information on the effects of high intensity cyclones, or on how forest stewardship practices may affect outcomes. We assess the resistance and resilience of forests in three community-stewarded sites on the island of Tanna, Vanuatu, to the wind-related effects of 2015 Category-5 Cyclone Pam, one of the most intense cyclones to make landfall globally. Drawing on transect data established pre-and post-cyclone, we (1) test whether windspeed and tree structural traits predict survival and damage intensity, and whether this varies across sites; (2) assess post-cyclone regeneration of canopy, ground cover, seedlings, and saplings, and how community composition shifts over time and across sites. In sites that sustained a direct hit, 88 % of trees were defoliated, 34 % sustained severe damage, and immediate mortality was 13 %. Initial mortality,

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but not severe damage, was lower in areas that received an indirect hit and had lower windspeed. Larger trees and those with lighter wood had a higher probability of uprooting and snapping, respectively. Canopy and ground cover regenerated within three years and seedling and sapling regeneration was widespread across life histories, from pioneer to mature forest species. Three species of non-native vines recruited post-cyclone but within 5 years had largely declined or disappeared with canopy closure. Tanna's historical cyclone frequency, combined with customary stewardship practices that actively maintain a diversity of species and multiplicity of regeneration pathways, are likely responsible for the island's resistance and resilience to an intense tropical cyclone.

## 1. Introduction

Understanding how forests respond to, and recover from, cyclones is central to understanding current patterns of forest structure and function (Lin et al., 2020) and critical to informing and planning for the impacts of climate change. Cyclones can affect forests at multiple scales and in multiple ways, from the individual tree to the ecosystem, and from the short- to the long-term (e.g., Metcalfe et al., 2008, Tanner et al., 2014). For example, cyclones can cause immediate damage or mortality to individual trees; differential patterns of individual damage and mortality can in turn affect stand structure and composition, the distribution and intensity of understory light, and the quantity and composition of leaf litter. These processes can shape patterns of regeneration, eventually altering long-term species composition and diversity (Lin et al., 2020).

The response of forests to cyclones depends both on their ability to withstand damage induced by the cyclone, and on their ability to recover after the disturbance. The former is referred to as resistance, and for trees it is usually assessed through measures of damage severity, such as levels of canopy defoliation, stem snapping, uprooting and immediate tree mortality (e.g., Batista and Platt, 2003; Bellingham et al., 1995; Webb et al., 2014). The latter is often referred to as resilience, and it may be measured in multiple ways. For vegetation, it can include post-cyclone refoliation and resprouting of surviving trees, seeding regeneration, changes in growth and survival of juveniles and adult trees, and other measures of re-accumulation of biomass (e.g., Batista and Platt, 2003; Bellingham et al., 1995; Curran et al., 2008a; Paz et al., 2018).

The resistance of trees to wind damage can vary as a function of many factors, including cyclone intensity, size and duration; as well as topography, tree structural traits and ontogeny. For example, tree damage often increases with windspeed or proximity to cyclone track (Delaporte et al., 2022). The tree structural traits most frequently reported to affect individual resistance are wood density and tree size, but reports of these effects vary widely across studies. Tall trees or those with wide crowns are expected to be less resistant than smaller ones because, when exposed to lateral winds, taller trees may transmit higher tension to the bole or roots (Paz et al., 2018). Many studies have confirmed the expectation that larger trees suffer more severe damage than smaller ones (e.g., Paz et al., 2018; Tanner et al., 2014; Uriarte et al., 2019), but others have found no relationship (e.g., Curran et al., 2008b) or a variable effect (e.g., Webb et al., 2014). Wood density increases bole stiffness, potentially making a stem less likely to snap, but it also reduces flexibility, and therefore may reduce the capacity to avoid root fracture and uprooting (Paz et al., 2018). As with tree size, a number of studies have found that wood density increases resistance to severe damage (e.g. Curran et al., 2008b; Webb et al., 2014), but others have found the opposite (e.g. Paz et al., 2018) or no effect (e.g. Lin et al., 2018). These contrasting results highlight that the effects of tree structural traits are complex and depend on other variables. Indeed, the effect of structural traits on resistance have been demonstrated to vary as a function of windspeed (Curran et al., 2008a, 2008b; Vandecar et al., 2011; Uriarte et al., 2019) and of the type of damage sustained (Zimmerman et al., 1994; Webb et al., 2014).

In terms of resilience, revegetation can occur via refoliation and resprouting of damaged trees, recruitment of seedlings, growth of juveniles, or increased growth of non-damaged trees (e.g., Bellingham et al., 1995; Burslem et al., 2000; Batista and Platt, 2003). Resprouting ability is expected to be higher in faster growing species (Putz et al., 1983), while high-wood density, slow-growing species are expected to suffer less damage but resprout more slowly. This has been borne out by some studies (Curran et al., 2008b; Paz et al., 2018), but not others (Zimmerman et al., 1994).

Tree damage and mortality lead to changes in canopy cover and, along with other abiotic and biotic changes, can create differential opportunities for seedlings and saplings to recruit (Comita et al., 2009; Luke et al., 2014). For example, some species, including those with pioneer traits, respond to cyclones through large increases in recruitment (Bellingham et al., 1995; Batista and Platt, 2003; Iida et al., 2019). This can lead to shifts in community composition towards early successional species (Lin et al., 2020). In some places, disturbance from cyclones has led to large increases in non-native invasive species, including pioneer trees or shrubs, and vines (e.g., Camarero, 2019; Hjerpe et al., 2001; Iida et al., 2019). This is a special concern on oceanic islands, which have high levels of endemism and are especially susceptible to invasive species (Russell et al., 2017).

Both resistance and resilience to cyclones can be affected by forest management. For example, timber plantations and young agricultural fallows have been shown to have lowered resistance to wind (e.g., Franklin et al., 2004; Stas et al., 2023). However, the effects of lower-intensity practices typical of community-managed forests across the globe, such as selective harvest, planting, grazing, and caring for favored species and individuals, have not been explored. This suite of practices is commonly used by Indigenous and local communities to manage successional processes, both to reduce initial damage caused by disturbance and to speed up post-disturbance regeneration of useful resources. For example, this has been long documented in the context of disturbances caused by swidden agriculture (e.g., Alcorn, 1989; Balée and Gély, 1989; Berkes, 2017) and fire (Kimmerer and Lake, 2001; Trauernicht et al., 2015; Yibarbuk et al., 2001). Recent research suggests that ecological legacies of Indigenous forest management of the Amazon increase its' current capacity for resilience to fire and drought (McMichael et al., 2023). In the case of cyclones, given that different species have different capacities for resistance and resilience (Bellingham et al., 1995; Batista and Platt, 2003), the planting or favoring of certain tree species, for example though selective weeding of other species, could affect forest responses. Similarly, planting, scattering seeds, or aiding in the regeneration of specific species post-cyclone could increase resilience.

Understanding variation in the resistance and resilience of forests to high intensity cyclones is of growing interest because the intensity, frequency and distribution of high-intensity cyclones is expected to increase with climate change. The IPCC (2023) projects an increase in the intensity of tropical cyclones, including in the proportion of high-intensity cyclones and in peak windspeed. The geographic range of intense cyclones is also expected to expand, with peak wind intensities of western North Pacific cyclones shifting northward (Feng et al., 2021). Change in the intensity and frequency of cyclones can have strong impacts on forest responses because it can affect how much damage occurs and how much time there is for recovery (Lin et al., 2020). This in turn can have large impacts on forest-dependent communities.

Increased cyclone intensity is a growing concern in the Pacific

Islands, where much forest is stewarded by communities and large parts of the population remain dependent on forest resources. The Pacific Islands are subject to high cyclone frequency, but mostly of low-intensity cyclones, yet little information is available on the impacts on forests. Most cyclone research has focused on the Atlantic basin (Lin et al., 2020); only one study to date has evaluated the effects of a Category 5 cyclone in the Pacific Islands (Webb et al., 2014), and none have evaluated the effects of a direct hit.

We assess the response of Vanuatu forests to Category-5 Tropical Cyclone Pam (TC Pam), and explore the potential impacts of forest stewardship practices on outcomes. On March 2015, TC Pam directly crossed over the southern islands of Vanuatu as the strongest cyclone on record in the South Pacific. It exhibited maximum sustained winds of 278 km/h (https://coast.noaa.gov/hurricanes) and gusts estimated to be up to 320 km/h (World Metereological Organization, n.d.). Prior to TC Pam, we had established eight transects across three contrasting regions (leeward, windward, and north-central) on Tanna Island. The eye of the cyclone crossed over the leeward and north-central sites, but was just outside the windward site (Fig. 1). We monitored the transects post-TC Pam for nearly 5 years to ask:

1) How resistant were Tanna's forests to the wind-related effects of TC Pam? Specifically, a) What was the immediate damage to trees? b) Do differences in windspeed and tree structural traits (size, wood density) predict survival and intensity of damage, and does this vary across sites?
2) How resilient were Vanuatu's forests to TC Pam? Specifically, how did a) canopy cover b) ground cover, and c) seedling and sapling regeneration, d) invasive species and e) tree community composition shift over time, and did these vary across sites?

We then draw on interviews with forest stewards and our results to the questions above, to explore the potential role of forest stewardship in shaping forest resistance and resilience.

We expected that resistance, in terms of initial damage and mortality of trees, would be (i) lower in transects closer to the cyclone path and therefore subject to higher windspeeds and (ii) higher for larger trees and that (iii) the probability of snapping would increase as a function of wood density, but (iv) the effects of tree size and wood density would vary across sites. In terms of resilience, we expected (v) a shift in composition towards early pioneer species and (vi) an increase in the presence of invasive species across all sites.

## 2. Methods

Vanuatu is an archipelago of >80 islands located in the South Pacific (Fig. 1). It is considered part of the East Melanesian islands biodiversity hotspot (Mittermeier et al., 2005). The 'Vanuatu rainforest' vegetation type is recognized as a distinct terrestrial ecoregion because of its unique blend of species (Wikramanayake et al., 2002), and it has a threat status of Critical/Endangered (Aalbersberg et al., 2012). Tanna is a volcanic island located in the southernmost province of Tafea, which is the most biodiverse region in Vanuatu (Schmid, 1975). Climate in Tanna is seasonal, with a mean temperature of 24 °C, mean annual rainfall of 1263 mm, and a dry season that extends from April to October (http://www.vmgd.gov.vu). The trade winds blow from the east, bringing higher winds and associated moisture to the southeastern ("windward") side of the islands.

On Tanna, the majority of land is held under customary tenure and most of the population engages in traditional livelihood activities, which include subsistence agriculture, hunting, and fishing. Forests are subject to customary management, with resources regularly harvested for food, lodging, clothing, and medicines, as well as for traditional exchange and ceremonies. Ungulate grazing and selective logging are also practiced in some forest areas.

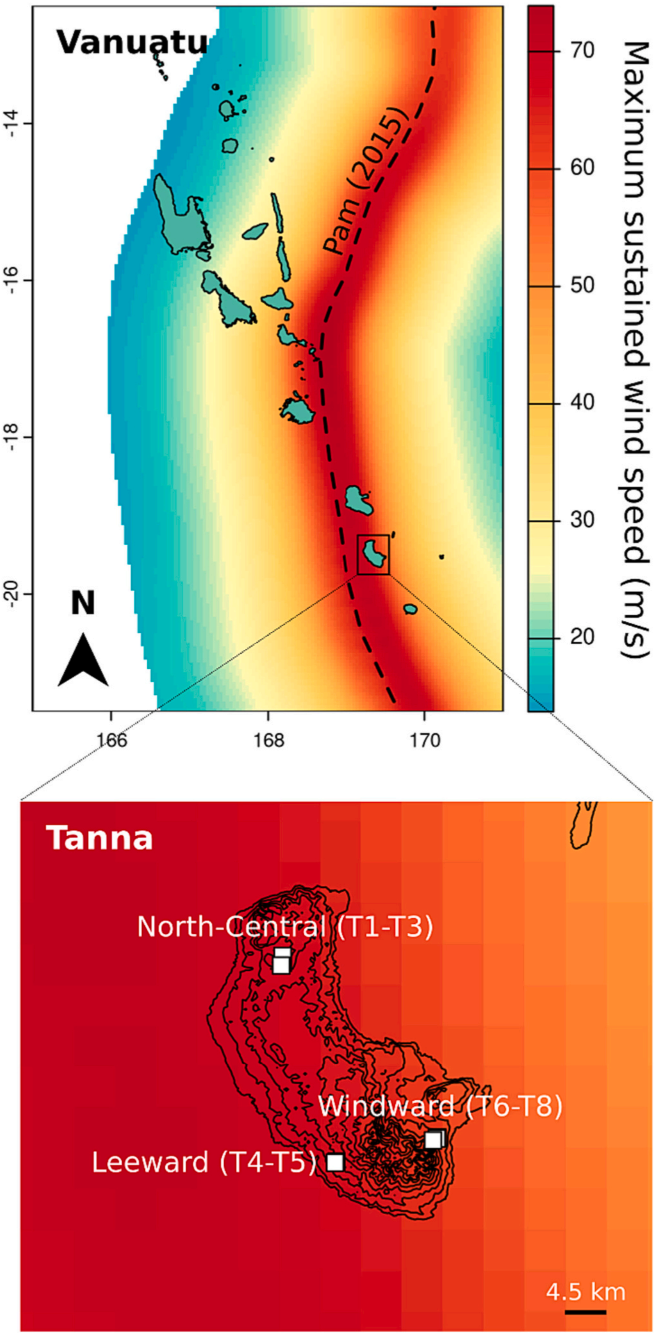

**Fig. 1.** Path and estimated maximum sustained windspeeds of 2015 Tropical Cyclone Pam (TC Pam), in relation to vegetation transects. Contour lines on Tanna are for each 100 m elevation band.

### 2.1. TC Pam

TC Pam formed in the Solomon Islands on March 6, 2015, and tracked slowly southward. It reached Tanna on March 13, and like most previous cyclones, approached the island from the northwest (Fig. 1). Data from the World Meteorological Organization's International Best Track Archive for Climate Stewardship (IBTrACS-WMO, version v03r09; Knapp et al., 2010) shows that during passage by Tanna, maximum sustained winds were 143 knots (265 km/h), pressure was 915 mb., forward direction speed was about 14 kts (25.9 km/h) and the width of the eye was estimated to be 15 nautical miles (28.8 km). Historically, cyclones that affect Tanna occur at decadal or slightly higher frequency, but with only one previously recorded high intensity (Category 4) cyclone (https://coast.noaa.gov/hurricanes). However, five additional high intensity TCs have passed through Vanuatu since TC Pam [Donna 2017 (Category 4), Harold 2020 (Category 5), Judy & Kevin 2023 (both Category 4, within 3 days of each other) and Lola 2023 (Category 5)].

### 2.2. Vegetation surveys

This research was carried out under a research agreement from the Vanuatu Department of Environmental Protection and Conservation, the Vanuatu Department of Forests, and the Vanuatu Kaljoral Senta. We set up eight, 80 × 10 m transects across three sites representing different regions of the island of Tanna: leeward, windward, and north-central (Fig. 1, Table 1). These sites were part of a study on the biodiversity of the island (Plunkett et al., 2022), and were chosen to span the broad variation in lowland tropical forests on the island. At each site, we established two transects in lowland forest. In the north-central and windward locations, we also established one ridge transect at a slightly higher elevation (Table 1). The lowland transects ranged from 245 to 279 m in elevation, with north-central and windward transects on east-facing slopes and the leeward transects on flat areas. The ridge transects were located on ridges 50–150 m higher than the lower elevation sites. Seven transects were established in November 2014, and the eighth was established in March 2015 (pre-TC Pam). In each transect, all trees $\geq 5$ cm diameter at breast height (dbh) were identified and measured.

Following TC Pam, we revisited each of the transects at two-year intervals (late November to early December of 2015, 2017 and 2019) and identified, measured and tagged all existing individuals and new recruits (individuals $\geq 5$ cm dbh). At each transect, we also systematically recorded, from within each of the eight 10 × 10m plots, the presence/absence of all species in the understory (seedlings, saplings, and herbs) and canopy (epiphytes and vines), and visually estimated the percent of ground covered by understory vegetation. All ground cover estimates, across transects and census years, were made by the same individual. During the November–December 2015 re-survey (ca. 8 months after the storm), we recorded the damage sustained by each individual tree using the following categories: uprooted, main-stem snapped ("snapped"), leaning, and defoliated (all or most leaves lost). At all censuses, we also recorded when damaged individuals were resprouting and/or re-leafing. Voucher specimens were deposited in the Vanuatu National Herbarium (PVNH) and the Steere Herbarium of the New York Botanical Garden (NY).

During the 2015 census, we also set up 16 1 × 1 m subplots in each of the transects to monitor seedling and sapling regeneration. These subplots were placed in two corners of each 10 × 10 plot of the transect, with the corner locations chosen randomly. In each 1 × 1 m subplot, and at each subsequent census, we identified, measured and tagged all woody seedlings and saplings (individuals $<5$ cm dbh), recording mortality and all new recruits. To quantify changes in canopy cover over time, we took canopy photos at the same location at each subplot in each census (2015, 2017, 2019). Photos were taken using a hemispheric lens and were analyzed using the software Gap Light Analyzer v2 (Frazer, 1999).

Maximum sustained windspeeds at each transect were estimated using the temporalBehaviour function of the R package StormR (Delaporte et al., 2023). We used the default setting, that is, the Willoughby et al. (2006) model with asymmetry following the Chen (1994) model. These models reconstruct the 2D idealized surface windspeed structure generated by tropical cyclones based on the latitudes of their centers, the maximum sustained windspeeds, and the radius of maximum sustained windspeed as provided by IBTrACS every six hours. We performed a linear interpolation of the original 6-h inputs from IBTrACS to reconstruct the 2D surface windspeed structure of each tropical cyclone every 1 h. Then, for each transect, we computed the maximum sustained windspeed as that observed along the passage of the cyclone at the transect location.

### 2.3. Interviews with forest stewards

To gain insight into the potential role of stewardship in affecting the resistance and resilience of Tanna forests to Cyclone Pam, we drew on three sources of information: 1) participation observation in daily activities of Tanna forest stewards over many years: our team includes residents of Tanna as well as foreign researchers with up to 20 years of experience working on the island; 2) a ten-year ethnobotanical study of plant uses (Balick et al., unpublished data), and 3) semi-structured interviews with the eight stewards of our forest plots, carried out between August and November 2023. For the latter, one of us asked each steward a series of standardized questions in Bislama (the creole language that serves as Vanuatu's lingua franca) about the stewardship activities they carried out in the forest plots; activities, if any, that stewards carry out after a cyclone; and information on trees used and harvested in the plot areas. We report the interview results and use our broader experience gained from the prior two methods to interpret them in the discussion.

### 2.4. Analyses

We assessed resistance to the wind effects of TC Pam using measures of tree damage severity and survival. To test whether the probability of damage type and survival varied as a function of site, individual attributes (size and wood density), and their interactions, we used binomial

**Table 1**

Vegetation transects established in forests on Tanna, Vanuatu in 2015, pre-Tropical Cyclone Pam (TC Pam). Across sites, customary stewardship includes selective harvest of both trees and herbaceous plants for subsistence and cultural uses; care and fostering of specific species; and hunting. Transects 3 and 4 also were subject to pre-cyclone ungulate (pigs or cattle) grazing.

| No. | Site | Forest type | Elevation (m) | Maximum sustained windspeed (MSW) m/s | Pre-cyclone tree density in transect | Dominant genera |
|---|---|---|---|---|---|---|
| 1 | North-Central | Mesic (ridge) | 404 | 67.49 | 267 | *Syzygium, Hedcarya, Ellatostachys, Myristica* |
| 2 | North-Central | Lowland | 249 | 67.296 | 125 | *Didymocheton, Syzgium, Elaeocarpus, Hedycarya* |
| 3 | North-Central | Lowland | 267 | 67.726 | 52 | *Dendrocnide, Ficus, Pisonia, Cryptocarya* |
| 4 | Leeward (southwest) | Lowland | 270 | 64.476 | 50 | *Didymocheton, Myristica, Cryptocarya, Ficus* |
| 5 | Leeward (southwest) | Lowland | 275 | 64.639 | 90 | *Didymocheton, Myristica, Cryptocarya, Ficus, Macaranga* |
| 6 | Windward (southeast) | Lowland | 273 | 56.499 | 98 | *Syzygium, Hedcarya, Maracanga, Ficus* |
| 7 | Windward (southeast) | Lowland | 252 | 56.559 | 88 | *Pleranda, Macaranga, Didymocheton, Ficus* |
| 8 | Windward (southeast) | Mesic (ridge) | 300 | 56.843 | 91 | *Syzygium, Myristica, Hedcarya, Didymocheton* |

generalized linear mixed models (GLMMs), where transect was a random factor (Zuur et al., 2009). We included genus as a random factor as well, to account for similarities among individuals of a given species and genus, which may not be related to wood density. The full models included interactions among all three predictors. We obtained values for wood density from the Global (Zanne et al., 2009) and World Agroforestry (http://db.worldagroforestry.org/databases) wood density databases. We were unable to obtain wood density values for 10 species, and in these cases, we used the mean values of species from the same genus in similar forest types in Oceania. Consistent with other studies (Uriarte et al., 2019), the results of the first post-cyclone census (November–December 2015 census, 8 months after TC Pam) are referred to as initial or immediate impacts. We refer to the 2017 and 2019 censuses as 3 and 5 years post-cyclone, even though they more precisely represent 2.75 and 4.75 years, respectively.

We assessed resilience to TC Pam using measures of change in canopy cover, ground cover, recruitment, and community composition. To test whether canopy openness, ground cover and new recruits varied as a function of site and time, we used GLMMs with a Gaussian distribution. For canopy openness, we used log values to improve model fit. For the canopy and ground cover models, transect/plot was included as a random factor since canopy openness was measured at the subplot level. For the recruitment model, transect was included as a random factor since recruitment was measured at the transect level. All analyses were carried out in R v.4.1.1. All models were run using the glmmTMB package v. 1.1.2.3 (Magnusson et al., 2017) and fit was assessed using the DHAMRa package (v. 0.4.6; Hartig, 2019). We fit the full model and then performed null hypothesis significance testing (Tredennick et al., 2021). To test if differences in windspeed affected our measures of resistance and resilience, we also conducted planned contrasts between north-central and leeward lowland transects versus the windward lowland transects. These were carried out with multivariate t-distribution adjustment using the emmeans package (v.1.8.4–1). To visualize differences in tree composition across sites and over time, we performed nonmetric multidimensional metric scaling (nMDS) (Minchin, 1987) using the vegan package (v.2.6–4). We used abundance data, and distances were calculated using the Bray-Curtis dissimilarity measure. We classified tree species life history as either early successional or late successional/mature forest species using both published descriptions (e.g., Franklin, 2003; Whistler, 1980) and expert opinion of AN and MT, based on their observations of life history over decades of work in Pacific Island forests. The Pacific Islands have few early successional species, with most late successional species continuing to exist as canopy trees in old growth forest (Mueller-Dombois, 2008).

## 3. Results

### 3.1. Resistance to TC Pam: Survival and damage

We measured a total of 887 trees ≥5 cm dbh across the 8 transects prior to TC Pam, representing 76 species in 63 genera (Fig. A.1, Table B.1). Across transects, pre-cyclone forest structure was dominated by trees <20 cm dbh (Fig. A.2a). In most transects, mean dbh ranged from 15 to 19 cm. The exceptions were one of the leeward transects, which had larger trees (mean dbh = 28 cm) and the north-central ridge transect, which had smaller trees (mean dbh = 9 cm). Transects included early successional species, but were dominated by mid-late successional tree species (Fig. A.2b).

During TC Pam, maximum sustained windspeeds ranged from about 65–67 m/s in the northwest and leeward parts of the island, which received a direct hit, and 56–57 m/s in the windward side, which did not (Table 1, Fig. 1). The proportion of trees that experienced damage of any kind (uprooting, main stem snapping, leaning or defoliation) ranged from 98 % in one leeward transect to 47 % in one windward transect. Initial (eight-months post-cyclone) mortality, however, was comparatively low. Initial mortality in the leeward and north-central sites was 13.8 % and there was no difference in the probability of survival of trees between these two sites (Table 2). However, initial mortality in the windward sites was about half as high (5.9 %) and this difference was significant (planned contrast, $p = 0.01$). Neither size (dbh) nor wood density were predictors of initial survival (Table 2).

Across transects, 3.5 % of trees were uprooted, with an initial mortality of 19.4 %. Larger trees had a higher probability of uprooting than smaller ones (Table 2, Fig. 2a). For example, the probability of uprooting was about 4 % for a tree of 30 cm dbh and 10 % for one of 60 cm dbh. There was no difference in the probability of uprooting across sites. Five-year survival after uprooting did not differ across sites or as a function of wood density or dbh.

Over one-quarter of trees (31 %) in the leeward and north-central lowland transects had their main stem snapped, and the probability of snapping was not significantly different in the windward sites (Table 2). The probability of snapping decreased with increasing wood density (Fig. 2b, Fig. A.3). For example, in the leeward transects, the probability of snapping was 44 % for the least dense trees (0.2 g/cm$^3$) versus 17 % for the most-dense trees (80 g/cm$^3$). Size (dbh) had no effect. Initial mortality of snapped trees was 8.8 %. Over 5 years, the probability of survival of snapped trees was lower in the lowland windward sites than in the leeward sites ($p < 0.01$, Table A.1). Neither wood density nor dbh had an effect on the 5-yr probability of survival of snapped trees, except in the windward region, where survival decreased with increasing dbh (site:dbh interaction, $p < 0.01$, Table A.1).

The probability of leaning ranged from 4 to 15 % per transect, and was similar across sites. Larger trees had a lower probability of leaning than smaller trees (Table 2). Wood density had no effect on leaning in all sites except for the windward upland site, where the probability of leaning decreased with increasing wood density (Fig. 2c).

The most common damage was defoliation, which was especially high in the leeward transects, where 88 % of trees were completely defoliated. Overall, defoliation was lower for trees in the two sites with higher windspeed (planned contrast, $p < 0.001$) than in the windward transects, (39.9 %; Table 2). The probability of defoliation increased as a function of tree size in the leeward and lowland north-central transects, but decreased as a function of size in the lowland windward transects (Table 2; Fig. 2d). For example, in the leeward transects, the probability of defoliation was 92 % for a tree of 30 cm dbh, versus 98 % for one of 60 cm dbh, while in the windward transects these values were 28 % and 12 %, respectively.

### 3.2. Resilience: Increase in canopy and ground cover

We did not measure pre-cyclone canopy openness. However, 8 months post-cyclone, median canopy openness varied from about 15–20 % across sites, except for the north-central lowland transects, where it was slightly, but significantly ($p < 0.001$) lower (Fig. 3a, Table A.2). There was large variation within the leeward and north-central lowland transects due to tree fall gaps. By 2017, canopy openness decreased significantly ($p < 0.001$) to about half 2015 levels. Variation within transects was also much lower. From 2017 to 2019, the canopy continued to close across most sites. By 2019, variation in canopy cover within the windward sites increased.

Pre-cyclone, ground cover composition was diverse in all sites, encompassing a wide range of woody seedlings, understory herbs, and ferns. However, percent ground cover ranged widely across sites, from a median of <25 % in the leeward and lowland north-central sites to >70 % in the windward and north-central ridge sites (Fig. 3b). The response of ground cover over time varied significantly across sites (Table A.2). Eight-months post TC Pam, ground cover had increased significantly ($p < 0.001$), but the increase was much steeper in the leeward and north-central lowland sites (rising from means of <25 % to >90 %) than in the windward sites which remained relatively stable. Species diversity remained high but *Macaranga dioica* initially dominated the seedling layer across sites. By 2019 ground cover decreased in the leeward and

**Table 2**

Coefficients of best fit models for the probability of trees sustaining damage from TC Pam on Tanna, Vanuatu. Full models included site, wood density, size (dbh) and their interactions as predictors. All models include transect and genus as random factors.

| | Initial survival | Uprooted | Snapped | Leaning | Defoliated |
|---|---|---|---|---|---|
| N | 887 | 862 | 765[a] | 764 | 597 |
| Intercept | 2.01*** | −4.28*** | 0.18 | −1.01 | 1.2* |
| Site:North-central | −0.3 | | 0.11 | −0.70 | −1.81** |
| Site:North-central high | 0.65 | | −0.97*** | −0.72 | 1.35 |
| Site:Windward | 0.79* | | −0.52† | −5.52† | −1.09 |
| Site: Windward high | 0.30 | | −0.004 | 6.19† | −0.22 |
| DBH | | 0.03** | | −0.04* | 0.03 |
| Wood density | | | −2.15** | −0.78 | |
| North-central:wood density | | | | −0.05 | |
| North-central high:wood density | | | | −4.78 | |
| Windward:wood density | | | | 7.47 | |
| Windward high: wood density | | | | −13.3* | |
| North-central:dbh | | | | | −0.01 |
| North-central_high:dbh | | | | | −0.07 |
| Windward:dbh | | | | | −0.08* |
| Windward high:dbh | | | | | −0.16** |

[a] Sample sizes for models that include wood density are lower since we did not have wood density values for all individuals. Sample size was lower for the defoliation model, since it excluded trees that were snapped or uprooted.

† $p < 0.1$.

* $p < 0.05$.

** $p < 0.01$.

*** $p < 0.001$.

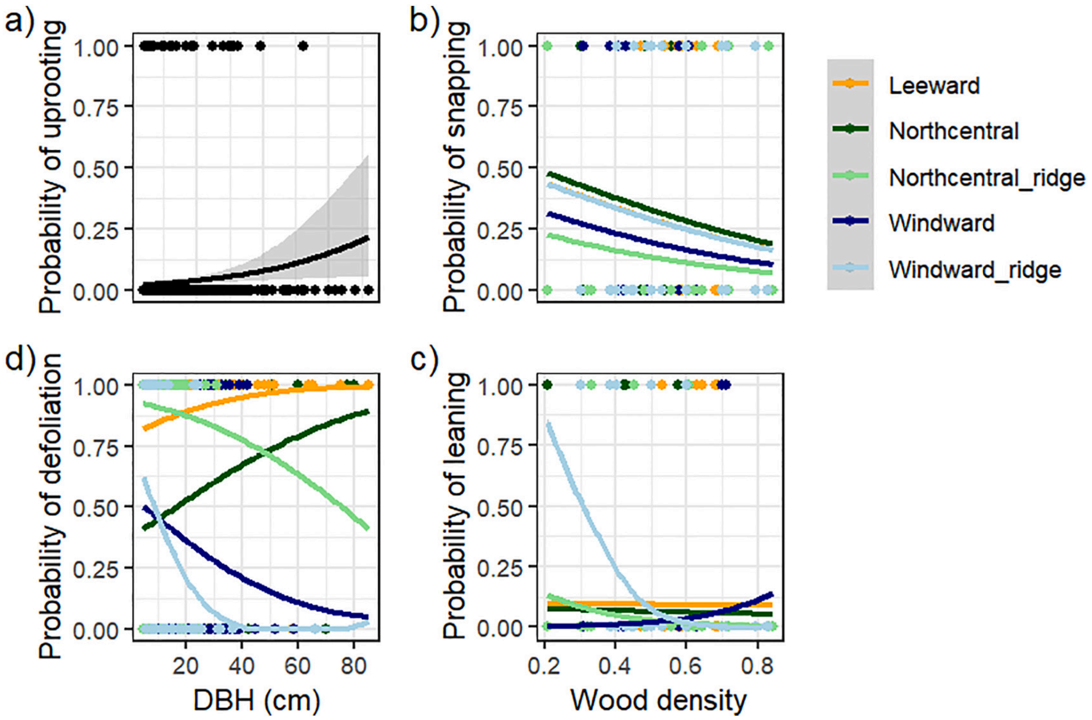

**Fig. 2.** Probability of damage by site, as a function of size (dbh) or wood density for a) uprooted, b) snapped, c) leaning and d) defoliated (excluding those counted in a-c) trees, 8 months after TC Pam.

north-central sites, but remained significantly higher ($p < 0.001$; means of 41 % and 50 % respectively) than pre-cyclone levels.

### *3.3. Resilience: Recovery of damaged trees*

The probability of survival for trees that did not die immediately (i.e, by the first census, at eight months post-cyclone) depended on the damage sustained and the site. The mean probability of surviving to 2019, an additional four years, was 95 % (mean annual mortality of about 1.02 %) for undamaged, defoliated, and leaning trees, with no differences among these groups (Fig. 4a; Table A.3). Survival was lower for snapped ($p = 0.02$) and uprooted ($p < 0.001$) trees than for undamaged trees. Nonetheless, the vast majority of trees whose main stems snapped, and that did not die within the first eight months, resprouted and survived (80.6 %; mean annual mortality 5.2 %). In contrast, for uprooted trees that survived the first eight months, only 39.1 % were alive at the last census (mean annual mortality 20.9 %). Across all damage types (including undamaged trees), mortality over the four years post-cyclone was 1.5 times higher in windward lowland sites than in the leeward and north-central sites ($p < 0.05$, Fig. A.4).

### 3.4. Resilience: Post-cyclone recruitment

We recorded a total of 666 new recruits – individuals that were < 5 cm dbh pre-TC Pam, but that grew to ≥5 cm dbh post-cyclone. Recruitment into the ≥5 cm size-class occurred in all transects, and the number of recruits did not differ across years (~3 vs 5 years post cyclone) or as a function of initial tree density in the transects (Table A.2). However, annual recruitment varied widely across and within transects and was not correlated with annual mortality (Fig. 4b).

Across the lowland transects, the proportion of early successional species increased post-cyclone. Prior to TC Pam, the percentage of early successional species ranged from 0 to 11 %, with the exception of one windward transect, where this value was 17 %. (Fig. A.2b). The leeward transects had no *Homalanthus nutens* and few *Macaranga dioica*, but post TC Pam there was massive recruitment of these two species in those transects (Fig. A.1). This was especially true in the leeward transect which had no early successional species present before TC Pam, but had 107 new *H. nutans* individuals recruited by 2017. By 2019, these two species represented 88 % and 37 % of trees in the leeward and north-central transects, respectively. In the north-central site post-cyclone recruitment was dominated by *M. dioica*, but also included fast-growing species that persist in mature forests, such as *Dendrocnide latifolia* and *Ceodes umbellifera*. By 2019, early successional species represented 22–25 % of trees. In the lowland windward transects, *M. dioica* was the most abundant recruiter, and *Hedycarya dorstenioides* and *Melicope* sp. also showed high recruitment. In both ridge transects, the proportion of early successional species remained stable over time but the richness increased.

Across all sites, 41–48 % of tree genera present pre-cyclone produced new recruits into the overstory (trees ≥5 cm dbh) (Fig. 5, Fig. A.5). Recruits of almost all species initially present in the canopy were from advance regeneration (existing saplings); recruits from only a few early successional species in the canopy, such as *Macaranga dioica* and *Alphitonia zizyphoides* were from seed. All transects, except the north-central ridge, also recruited species not previously in the transect; these were largely early successional species that recruited from seed. Four years post-cyclone, seedlings (individuals <25 cm high) were observed for over 90 % of tree genera that were present pre-cyclone, despite the fact that *M. dioica* had initially dominated the seedling (< 25 cm high) community across sites in 2015. Since 87 % of the pre-cyclone tree genera are represented by single species, this also includes most species. Seedlings from genera not present in the canopy pre-TC Pam were also present, including both pioneer and late successional species.

Two non-native individual trees were recorded pre-cyclone (*Graptophyllum pictum* and *Carica papaya*) but both died during the cyclone. One individual of a non-native shrub was recorded post-cyclone (*Moeroris imbricata*). Three species of non-native vines were recorded post-cyclone (*Mikania micrantha*, *Ipomoea indica*, and *Passiflora maliformis*) (Fig. A.6). Peak abundances were recorded from 2015 to 2017 depending on the site and species, but across all transects, species presence declined or disappeared by 2019. The one exception was one of the leeward transects, where *P. maliformis* remained stable, but at low frequency (Fig. A.6).

The NMDS (stress = 0.13) shows that prior to TC Pam, tree composition was distinct across the three sites and that, nearly 5 years post-cyclone, composition shifted for all transects, largely towards pioneer as well as fast growing species that colonize gaps but remain as late successional trees (Fig. 6). For most transects, the dissimilarity index between years ranged from 0.09 to 0.33, with the exception of the leeward transect that showed massive recruitment of *H. nutens* and *M. dioica* which had a value of 0.71 (Table A4). Overall dissimilarity over time was highest in the leeward and north-central lowland transects.

### 3.5. Forest stewardship

All of the stewards we interviewed discussed using tree species in the forest plots for multiple uses, including for food, medicine and housing materials. Most mentioned that they cut down trees, especially small trees, for housing posts. One steward mentioned that he also regularly cut small trees for food for cattle. Another discussed branch cutting to hunt bats. Most stewards also described selective weeding in the form of clearing vegetation around trees to access foods or medicine.

The interviewees also described actions that they take after a cyclone. All mentioned removing some downed trees to use the wood for house building or firewood. They also discussed selectively clearing vegetation around trees to harvest resources and help those trees grow,

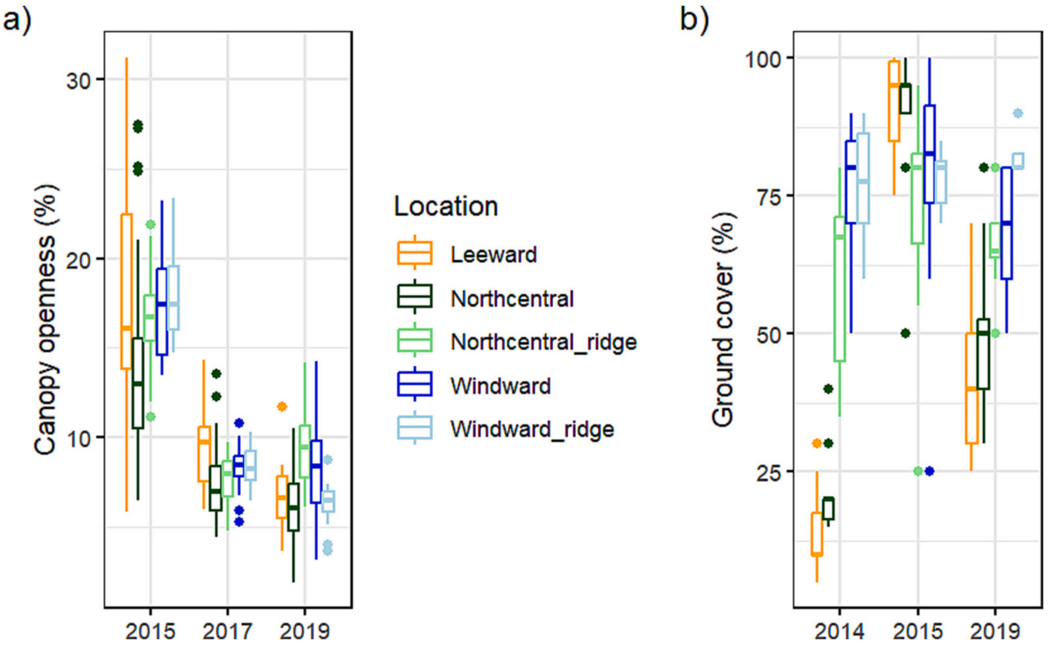

**Fig. 3.** Change in canopy (a) and ground (b) cover over time and across sites on Tanna, Vanuatu. The 2015 measurements were taken 8 months after TC Pam. There are no pre-TC (2014) measurements of canopy cover.

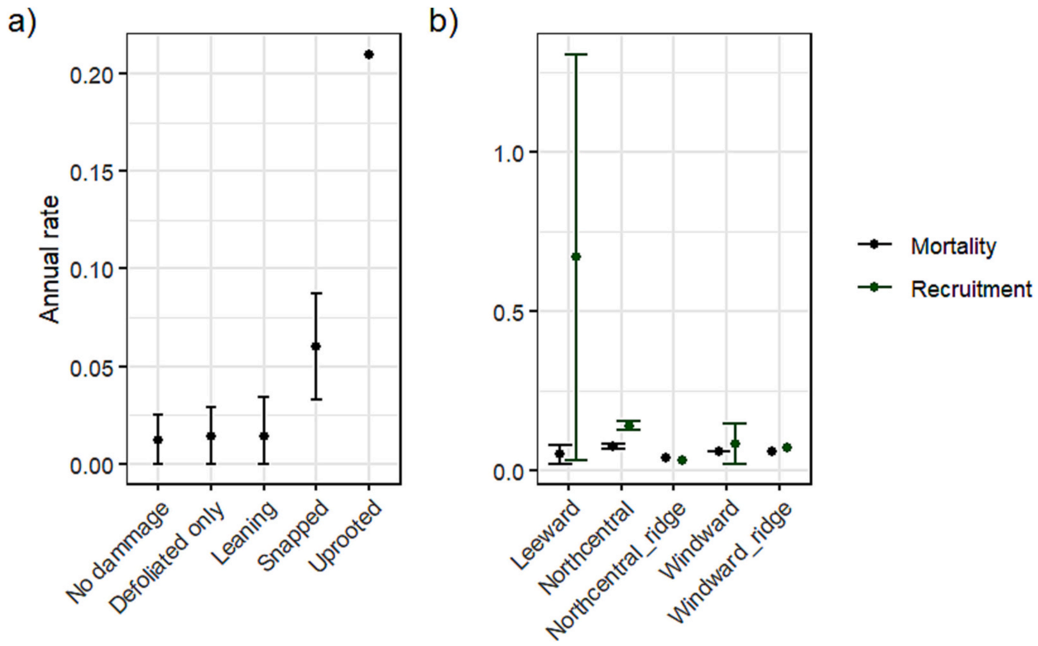

**Fig. 4.** a) Post-cyclone annual mortality of trees by damage type and b) total annual mortality and recruitment, by site on Tanna, Vanuatu. Post-cyclone rates, calculated 2015–2019, exclude trees that died immediately after TC Pam to illustrate longer-term recovery potential. Total rates, calculated 2014–2019, include the impact of the cyclone. Note the difference in scales on the Y axis. The number of uprooted trees was very low, therefore the rate was calculated by combining all transects.

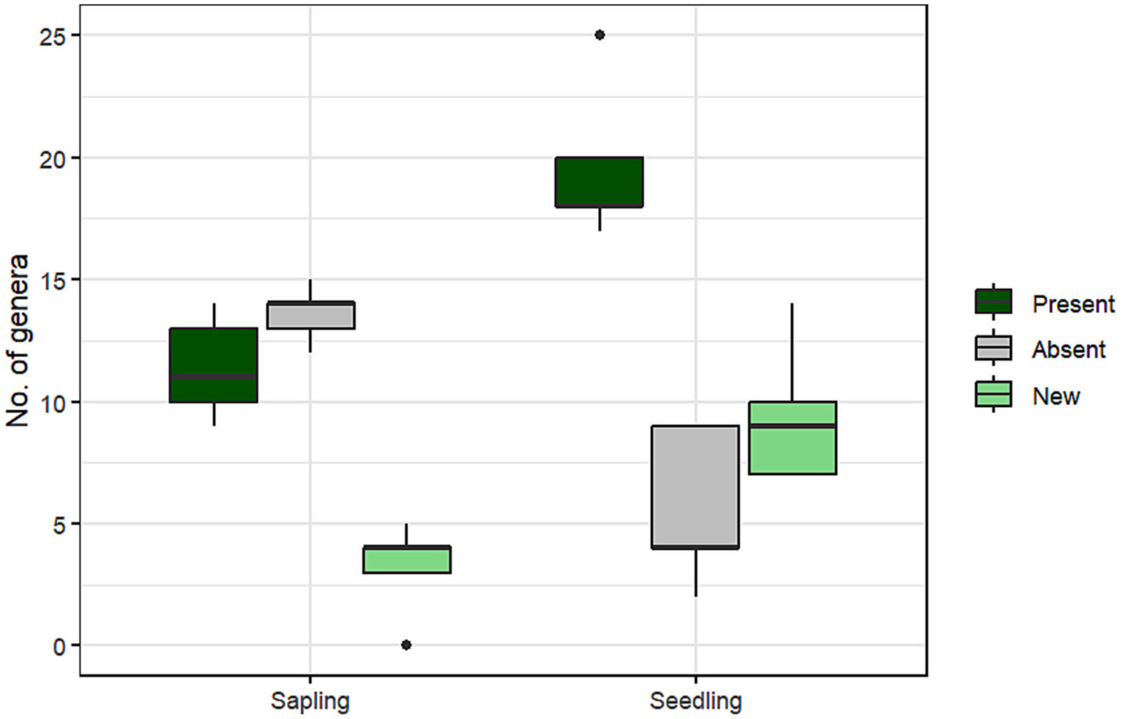

**Fig. 5.** Number of tree genera per transect represented by post-cyclone recruits a) into the canopy (“saplings” ≥ 5 cm dbh) and b) seedling layer (< 15 cm high). ‘Present’, ‘Absent’, and ‘New’ refer to pre-cyclone status in the canopy.

as well as to encourage post-cyclone regeneration of seedlings and saplings. In the words of one steward, “*We need to clear near the stem of trees so that younger trees can grow*”. Finally, all stewards explained that the forest regenerates on its own after a cyclone, but five of the eight also mentioned planting some trees. For example, one steward explained, “*The forest plants itself, [but] I just plant some native species*.”

## 4. Discussion

We assessed the resistance and resilience of forests on Tanna, Vanuatu, to the highest-intensity cyclone recorded in the South Pacific at that time, the 2015 Category-5 Tropical Cyclone Pam. Our results show that levels and predictors of damage and resilience varied across sites, but that overall, Tanna’s forests were both highly resistant and

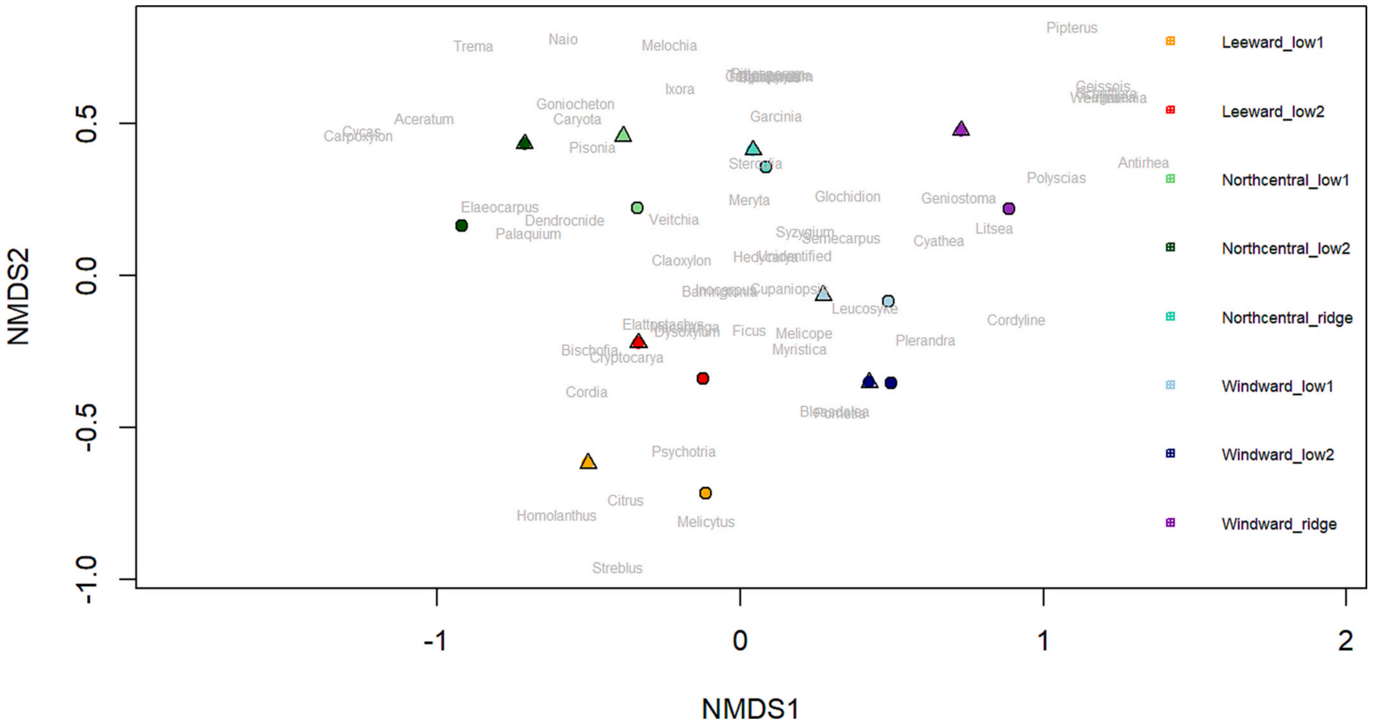

**Fig. 6.** Non-metric multidimensional scaling of genus-level tree composition in 2014, pre- TC Pam (circle) and close to five years later, in 2019 (triangle). Each point represents a transect.

resilient to TC Pam.

### 4.1. *High resistance to TC Pam*

Tanna's forests showed high levels of damage to trees, but relatively low mortality. This pattern is consistent with other studies of high intensity cyclones in the Pacific Islands (e.g., Franklin et al., 2004; Webb et al., 2014), and some studies in the Atlantic basin (e.g., Walker, 1991; Yih et al., 1991). High damage levels are consistent with TC Pam's high windspeeds, as reductions in cover increase linearly with increasing windspeed above 50 m/s (Delaporte et al., 2022).

However, Tanna's forests suffered less severe damage (main stem snapping, uprooting) than recorded for high intensity cyclones elsewhere in the Pacific Islands. For example, only one-quarter and one-third (25–34 %) of trees were severely damaged in sites that were indirectly or directly hit in Tanna, respectively, compared to nearly double that (58 %) in Ta'u, Samoa, by Cyclone Olaf (February 2005; Webb et al., 2014), the only other study to document the effects of a Category 5 cyclone in the Pacific Islands. Other severe (Category 4) cyclones in the Pacific resulted in >70 % severe damage in Samoa (TC Ofa, February 1990; Elmqvist et al., 1994) and 25 % damage in Tonga (TC Waka, December 2001; Franklin et al., 2004).

Variation in community-level resistance to severe damage can depend on multiple factors apart from windspeed. One key factor is the historical frequency of cyclones - areas subject to more frequent cyclones often have lower damage because only resilient and resistant species can survive, and because of acclimation or adaptation of trees to smaller sizes (Lin et al., 2020; Monoy et al., 2016). However, given that Tanna's cyclone frequency is not highly different from Samoa and Tonga (https://coast.noaa.gov/hurricanes), cyclone frequency is not likely the main explanation here. Nonetheless, variation in wind patterns and cyclone forward speed may play important roles and deserve further attention (Delaporte et al., 2022).

Forest management can also affect resistance to wind and likely played a role on Tanna. Other studies have indicated that early successional forests (agricultural fallows) dominated by pioneer species are more susceptible to wind damage than mature forests (Franklin et al., 2004), as are single-species timber plantations (Stas et al., 2023), which typically support even-aged stands. In contrast, Tanna's forests contain a diverse mix of early and mature/late successional life histories across a range of sizes (Figs. S2 & S3). Given that trees of different species, sizes and growth rates can confer different types of resistance to cyclone pressures (e.g., Curran et al., 2008b, Iida et al., 2023, Paz et al., 2018, Webb et al., 2014, and see Section 4.3), a diversity of species, life histories and ontogenetic stages likely allows for greater community resistance (see Section 4.5).

### 4.2. *Predictors of resistance across sites*

Within Tanna, patterns of resistance across sites were consistent with some, but not all of our expectations, highlighting the importance of multiple interacting factors in determining damage levels. First, as expected, initial mortality of trees was higher in sites closer to the cyclone's central path and subject to higher windspeeds, as was the probability of defoliation. However, contrary to expectations, we found no significant differences in the probability of severe damage between these sites. Since full models for all our analyses included size and wood density, any differences in these variables across sites were accounted for. Forest type may be a confounding factor here, since the windward site, which was further from the cyclone central path, is generally also wetter.

### 4.3. *Effect of tree structural traits on resistance*

Consistent with other studies (e.g., Zimmerman et al., 1994; Paz et al., 2018; Webb et al., 2014), we found that the effects of structural traits on the resistance of individual trees depended on the type of damage sustained. Our finding that larger trees had a higher probability of uprooting than smaller ones is consistent with theory that lateral wind tension faced by taller trees may transmit higher tension to the bole or roots (Gardiner, 2021; Paz et al., 2018), and with the empirical findings of many other studies (e.g., Lewis and Bannar-Martin, 2012; Paz et al., 2018; Tanner et al., 2014; Uriarte et al., 2019). In contrast to Webb et al. (2014), in our study, tree size, as measured by dbh, had no effect on the probability of snapping. However, other measures of tree architecture, such as slenderness (crown:dbh or crown:bole ratio) might yield different results (Paz et al., 2018; Webb et al., 2014).

The negative relationship we found between wood density and the probability of stem snapping is consistent with findings elsewhere in the Southwest Pacific basin (Curran et al., 2008a; Webb et al., 2014). This is likely because wood density increases bole stiffness. However, other traits may also have strong effects. For example, *Myristica inutilis* subsp. *platyphylla* was the only species in our plots to have stilt roots and, despite its high wood density, it had disproportionally high probability of snapping (Fig. A.3). In addition, under extreme conditions, high wood density may no longer provide resistance (Uriarte et al., 2019). Contrary to other studies (e.g., Curran et al., 2008a), but consistent with Vandecar et al. (2011), wood density had no effect on the resprouting ability of snapped trees in our study.

We had expected that the effects of structural traits on measures of resistance would depend on the site (trait × site interaction), but we found this to be true in only three instances. First, the five-year probability of survival after snapping decreased with increasing dbh, but only in the transects at the windward site. This could be a result of heavier stress suffered by trees on the windward side due to more consistent winds, since repeated stresses after cyclones can lead to increased mortality (Burslem et al., 2000; Hjerpe et al., 2001). Webb et al. (2014) also found that on windward coast sites, larger trees had a lower probability of survival after snapping than smaller ones, but they did not have sites in other locations. Second, trees with low-wood densities had a higher chance of leaning, but only in the ridge transect at the windward site. This may be due to potentially shallower soils and lower rooting depth, although this effect was not observed in the north-central ridge transect. Third, larger trees had a higher probability of defoliation in the two sites that suffered a direct hit (leeward and north-central), but the reverse was true at the windward site. This finding is more difficult to interpret. Leaf traits can influence the probability of defoliation (Curran et al., 2008b) and could play a confounding role here. Overall, these results highlight the need to consider the interacting effects of traits and environmental conditions (Paz et al., 2018).

### 4.4. High resilience to TC Pam

Our results demonstrate variation in patterns of regeneration across sites, but overall, there was a rapid regeneration of canopy and ground cover, and recruitment of a diversity of species.

The rate of canopy closure we documented is consistent with studies elsewhere, which have shown that post-cyclone canopy closure can occur within about three years (Bellingham et al., 2009; Comita et al., 2009; Herbert et al., 1999). Although we do not have pre-cyclone data on canopy openness, the lack of change in canopy cover we observed from about 3 to 5 years post cyclone suggests it had likely filled out by 3 years.

Rapid canopy regeneration reflects several aspects of resistance and resilience in our plots. First, it is a consequence of the relatively low rates of severe damage discussed above, combined with high resprouting of snapped trees, which appeared to be largely through epicormic sprouts. Other studies have also shown high resprouting after intense cyclones (e.g., Walker, 1991, Bellingham et al., 1994, Vandermeer et al., 1995).

Second, it reflects the quick re-leafing of defoliated trees, which showed no difference in mortality rates from trees that were undamaged. The mortality rates we documented are similar or lower than background rates documented in other lowland Pacific Island forests (Burslem et al., 2000; Franklin et al., 2004; Webb et al., 2014). However, rates of mortality of severely damaged trees may be elevated for many years following a severe cyclone (Burslem et al., 2000; Tanner et al., 2014), and our data includes only just under 5 years post-cyclone.

Third, the rapidly closing canopy also reflects high rates of recruitment into the canopy layer. The rates we recorded are higher than those reported after other cyclones in the Pacific Islands (Burslem et al., 2000; Franklin et al., 2004). High recruitment into the canopy resulted from the high pre-cyclone abundance of advanced regeneration (saplings) of mature forest species, as well as the growth of pioneer species not previously recorded in the transects, which then germinated post-cyclone and grew quickly under the new canopy gaps.

The abundance of saplings of mature forest species is at least in part a consequence of Tanna's historical cyclone frequency. Tanna's approximately decadal return interval for cyclones allows for canopy closure and the regeneration of late successional species. Throughout the Pacific Islands, many late successional species recruit into gaps but remain dominant elements of mature forests (Mueller-Dombois, 2008). The last cyclone to make landfall on Tanna occurred 20 years prior to TC Pam, as a Category 1 storm. Across transects, the relative abundance of late-successional or mature forest species in the canopy and the low percentage of multi-stemmed trees (<2 %) indicate the absence of recent cyclone disturbances.

The shift in relative abundance of early-versus late- successional species in the lowland transects is consistent with our expectations and typical of this cyclone return frequency (Lin et al., 2020). Even in forests subject to much higher cyclone return frequency, an intense cyclone can shift a community towards species with pioneer traits (Monoy et al., 2016). Within sites, the leeward and north-central transects that showed larger shifts in community had lower pre-cyclone tree density, higher mortality, and larger canopy gaps.

The high diversity of seedlings and saplings that we documented four years post-cyclone was fostered by the large variation in canopy cover. The latter creates variability in understory light environments and allows for the germination and survival of seedlings with a wide range of light requirements (Lin et al., 2020). Indeed, we documented the presence of all pre-cyclone tree taxa, plus many additional species (both pioneer and later successional species). Other studies have similarly shown recruitment of both pioneer and old growth species after cyclones, with the latter emerging from advance regeneration (Bellingham et al., 1994, Yih et al., 1991, Vandermeer et al., 1995). Species found in the sapling stage that were not previously present in our transects were early successional species such as *Trema cannabina* and *Pipturus argenteus*, that grew from seeds that had likely been present in the soil seedbank. These species may have been previously present in the transects as a result of prior disturbance, including small gaps created by tree falls, stewardship activities, or the last cyclone; or they may have been in nearby areas outside of our transects. The high diversity of seedlings and saplings suggests the maintenance of a high-diversity canopy over the longer-term.

Rapid canopy closure and high rates of regeneration are also likely responsible for the remarkably limited spread of invasive species we observed post-cyclone in Tanna. In contrast to our expectations and to the findings of other post-cyclone studies of oceanic islands (Bellingham et al., 2005), including in the South Pacific (Hjerpe et al., 2001, Iida et al., 2019, Murphy and Metcalfe, 2016), we did not document the recruitment of any invasive tree species. While we did observe an initial spread of invasive vines, as has been reported elsewhere in the Pacific (Murphy and Metcalfe, 2016; Camarero, 2019), these declined with canopy closure. The fact that *Mikania micrantha* largely disappeared from the leeward and north-central sites, but was still present in the windward sites is likely due to the elevated tree mortality there and associated gaps, but our data do show that this invasive species is continuing to decline there.

### 4.5. Role of forest stewardship

Forest stewardship practices also appear to have played an important role in shaping the resistance and resilience of Tanna forests to TC Pam. While Tanna's historical cyclone frequency likely fostered the abundance of resistant and resilient species, Tanna's customary stewardship practices appear to augment this by actively promoting a diversity of species, life histories and ontogenetic stages, and by supporting a multiplicity of pathways for regeneration. These pathways include the ability to resprout, a diverse advance regeneration layer, and a range of conditions for germination and growth of new seedlings.

For example, Tanna's stewards value a wide range of species, and by actively caring for them, increase their probability of survival, growth and regeneration. Our interviews and broader ethnobotanical research (Balick et al., unpublished data) revealed that most of the tree species continue to be used for food, medicine, arts and other uses; moreover, stewards increase the persistence of some of these species through supportive practices such as selective weeding around trees. Selective weeding can also reduce the abundance of dominant species in the understory, and thereby support a wider diversity of seedlings and saplings – i.e. a diverse advance regeneration layer that can regenerate post-cyclone. Stewardship activities that enhance the demographic success of wild useful species are common in many Indigenous communities (Alcorn, 1981; Berkes, 2017; Turner et al., 2013).

The range of species for which Tanna stewards care supports a diversity of traits that can confer different types of resistance and resilience. For example, small trees with dense woods - traits that we found to increase resistance to wind - are favored in Tanna for certain construction purposes. Fast growing weedy species with low wood densities – those that can often regenerate quickly after disturbance - tend to be favored for medicine (Gaoue et al., 2017). All of the early successional species in our transects are used in Tanna for medicine (in addition to other uses, Balick et al., unpublished data). Similarly, woody species with the ability to resprout after harvest tend to be maintained for uses such as firewood or fencing, and this trait also confers the ability of resprout after cyclone damage.

Customary harvesting practices can also help sustain a range of conditions available for germination and growth of new seedlings, and can help maintain species assemblages with a variety of life histories and ontogenetic stages. For example, rapid canopy closure after a cyclone can inhibit growth and survival of seedlings and saplings (Monoy et al., 2016). However, the felling of individual trees, and patches of trees, for building materials, as reported in our interviews, continually creates small forest gaps. These supplement natural tree falls, leading to forests with a range of gaps sizes and ages that can support the germination, growth, and survival of seedlings and saplings with a range of life histories.

Finally, after a cyclone, Tanna stewards actively promote multiple regeneration pathways. As discussed in our interviews, these include clearing vegetation around specific trees (which can enhance both resprouting and regeneration by seed), selectively weeding the understory (which can prevent dominance of single species), and even planting native trees (which jumpstarts their regeneration). The practices are consistent with those that many Indigenous communities globally use to enhance resilience to other types of disturbance (e.g., Alcorn, 1989; Berkes, 2017; Turner et al., 2013).

The high levels of seedling regeneration we documented also point to sustainable hunting practices. Pacific Island trees are largely dispersed by frugivorous birds and bats (Carlquist, 1996; Scanlon et al., 2014), both of which are hunted for food in Tanna. In Pacific Islands where seed dispersers have declined, seedling regeneration represents a major demographic bottleneck (e.g., Nerfa et al., 2022; Ticktin et al., 2023; Wotton and Kelly, 2011). Robust seedling regeneration suggests that seed disperser populations are present in adequate levels to perform this function and support recovery.

At the same time, our results indicate that some forest management practices clearly had negative impacts. In particular, the two transects subject to pre-cyclone ungulate (pigs, cattle) grazing showed lower resilience than the other transects within the same sites. For example, the leeward transect that had been grazed had sparse pre-cyclone understory cover and limited advance regeneration. This led to very large post-cyclone canopy gaps, and to a shift in community composition to near total domination of the two early pioneer species, *Homalanthus nutens* and *Macaranga dioica*. Post-cyclone recovery in Samoa was similarly heavily dominated by the pioneer species *Macaranga harveyana,* which germinated in large gaps (Hjerpe et al., 2001). The persistent dominance of *H. nutens* and *M. dioica* may also be exacerbated by the continuation of grazing post-cyclone, and indicates that succession will proceed more slowly in this area. In addition, even-aged stands of these two species, which have low wood densities, may also be less resistant to the next cyclone. Nonetheless, the decision of stewards to prohibit grazing post-cyclone at the north-central site appears to have led to both higher levels of ground cover and seedling richness, indicating both the potential for long-term regeneration and the importance of adaptive management.

Overall, our results suggest that forests such as those on Tanna, which maintain a wide range of tree species, sizes, and life histories and support a multiplicity of healthy regeneration pathways, can be capable of resisting and recuperating quickly from even a highly intense cyclone. Fijian agroforests, which maintain very high levels of species and functional trait diversity of native and introduced trees (Ticktin et al., 2018), similarly showed high resistance after Category 5 TC Winston (February 2016; McGuigan et al., 2024). Further research is needed to better understand the relationships between Indigenous forest stewardship and resistance and resilience to cyclones, including the role that stewardship may play in the context of increasing cyclone frequency or intensity.

Social and ecological resilience are linked in multiple ways (Ticktin et al., 2018), and so it is not surprising that Tanna's human communities were also remarkably resilient to TC Pam. However, socioeconomic shifts that also lead to changes in forest management such as increased grazing, clear-cut logging, shorter fallow times, and abandonment of customary forest stewardship, may increase vulnerability to intense cyclones. Finding alternatives to these practices while supporting the resilience of Tanna's communities should be a focus of efforts to build resilience to climate change.

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## CRediT authorship contribution statement

**Tamara Ticktin:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ashley McGuigan:** Writing – review & editing, Visualization, Investigation. **Frazer Alo:** Investigation. **Michael J. Balick:** Writing – review & editing, Funding acquisition, Conceptualization. **Andre Boraks:** Writing – review & editing, Investigation. **Chanel Sam:** Investigation. **Thomas Doro:** Investigation. **Presley Dovo:** Project administration. **Thomas Ibanez:** Writing – review & editing, Visualization, Formal analysis. **Alivereti Naikatini:** Investigation. **Tom A. Ranker:** Writing – review & editing, Investigation, Funding acquisition. **Marika V. Tuiwawa:** Methodology, Investigation. **Jean-Pascal Wahe:** Investigation. **Gregory M. Plunkett:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data will be made available on request.

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