






# Lianas associated with continued forest biomass losses following large-scale disturbances

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## Abstract

Lianas are important to rainforest ecosystems but often impede tree growth and increase tree mortality and stem damage after disturbances that favor their growth. Understanding how lianas affect biomass recovery and rates of carbon sequestration following disturbance is therefore of crucial importance. In this study, we determine how a tropical forest recovers biomass following a large-scale disturbance, and test how this varies with liana dominance and stem damage. We use remote sensing methods to develop a model, validated by field data from 40 20×20m vegetation plots, to measure the change in tree aboveground biomass 8 years after Tropical Cyclone Yasi damaged logged forests in the Australian Wet Tropics. We related tree biomass changes to field measures of current liana dominance over trees, expressed as liana: tree basal area ratio, and assessed how these measures related to tree stem damage. Biomass declined in 34 of the 40 plots during the 8 years post-disturbance, with loss rates and proportions of damaged tree stems increasing with the liana: tree ratio. From spatial upscaling, we found a net loss in biomass across the study landscape over the same period. Our results show that, following disturbances, lianas not only limit tree biomass recovery but also are associated with further biomass declines, most likely through their contribution to stem damage and delayed mortality. Furthermore, our finding of net biomass loss across the landscape since the cyclone shows that, post-disturbance, rainforests can act as a carbon source with consequences for the global carbon sink.

## KEYWORDS

arrested succession, Australian Wet Tropics, carbon sink, random forest, rattans, remote sensing, tropical cyclones, vines

## 1 | INTRODUCTION

Lianas (i.e., woody vines and climbing monocots) are a conspicuous component of tropical forests with substantial influences on ecological processes (van der Heijden et al., 2013). Lianas are increasing in many tropical forests (e.g., Phillips et al., 2002; Schnitzer &

Bongers, 2011), most likely due to increased disturbance (Ngute et al., 2024; Schnitzer et al., 2021) and climate change (Vogado et al., 2022). These increases in lianas may affect forest functions, including post-disturbance recovery, with potential ramifications for ecosystem services such as carbon sequestration (Marshall et al., 2020; van der Heijden et al., 2015).

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Lianas often proliferate after tropical forests are disturbed. For example, rates of liana recruitment and growth are often greater in secondary than primary forests (Barry et al., 2015; Benítez-Malvido & Martínez-Ramos, 2003; Martin et al., 2004) and lianas proliferate following treefalls (Dalling et al., 2012; Putz, 1984), in forest fragments, and along forest edges (Campbell et al., 2018; Ofosu-Bamfo et al., 2022). Lianas compete with trees for resources, both above and belowground (Meunier et al., 2020; Schnitzer et al., 2005) with a greater competitive effect than trees of similar biomass (Tobin et al., 2012). Furthermore, because lianas use trees as a structural support to climb and access the canopy, they cause mechanical stresses that can lead to branch and stem breakages (Kainer et al., 2006; Stevens, 1987). Accordingly, lianas can reduce tree performance (Estrada-Villegas et al., 2022), including rates of biomass accumulation (César et al., 2016; di Porcia e Brugnera et al., 2019; Lai et al., 2017), survival (Ingwell et al., 2010; McDowell et al., 2018), reproduction (García León et al., 2018), and recruitment (Dupuy & Chazdon, 2008; Martínez-Izquierdo et al., 2016).

The detrimental effects of lianas on trees, combined with their positive responses to disturbance, make them highly influential in post-disturbance forest recovery. Lianas are important to forest succession (Capers et al., 2005; Dewalt et al., 2000) but where prolific can also outcompete or overload small trees, creating a positive feedback loop between disturbance and liana proliferation (e.g., Griscom & Ashton, 2006; Marshall et al., 2020). When lianas suppress tree regeneration, the canopy does not close, thus maintaining the high light levels associated with disturbance, which promotes further liana proliferation. The outcome is an alternative successional pathway of liana-dominated suppressed recovery, with limited tree biomass recovery (e.g., Schnitzer et al., 2000; Schnitzer & Carson, 2010) that can persist for decades (Tymen et al., 2016). Arrested succession due to liana proliferation has been documented in Latin America (e.g., Schnitzer et al., 2000; Foster et al., 2008; Sánchez-Azofeifa et al., 2015; Tymen et al., 2016), Africa (Babaasa et al., 2004; Marshall et al., 2017), Southeast Asia (Takeshige et al., 2023), and Australia (e.g., Metcalfe et al., 2008; Turton, 2012; Webb, 1958) (Figure 1) suggesting it is a consistent phenomenon across the tropics. However, we lack empirical data relating long-term forest biomass recovery to measures of liana abundance that would allow quantification of this effect (Marshall et al., 2020).

In addition to suppressing tree growth, lianas can reduce stand-level forest biomass by increasing tree mortality rates (McDowell et al., 2018). Data from the Neotropics suggest that trees with heavy liana infestation are two to three times more likely to die than liana-free trees (Ingwell et al., 2010; Phillips et al., 2005). When lianas cover multiple tree crowns, they can spread damage from lightning (Gora et al., 2023) and one treefall can bring down multiple trees (Putz, 1984). Overall, liana proliferation displaces tree biomass (van der Heijden et al., 2013) and may do so at scales sufficient to threaten the global carbon sink (Marshall et al., 2020). The reported increases in liana abundance make their effects on the global carbon sink even more profound (van der Heijden et al., 2015). In light of the



**FIGURE 1** Example of a liana-dominated area in the Australian Wet Tropics of northeast Queensland. There is minimal tree regeneration visible and the trees are heavily infested with lianas. Slow tree mortality and slow growth maintain the open canopy and promote further liana proliferation. Photograph by Andrew R. Marshall.

increased frequency with which forests are disturbed due to climate change and other factors, studies of the relationship between lianas and forest biomass recovery are important.

Changes in tree biomass can be used to monitor forest recovery over time after disturbances. Traditionally, this has involved manual measurement of aboveground biomass using forest inventory plots, which can be labour-intensive and not representative of inaccessible areas (Timothy et al., 2016). Advances in remote sensing increasingly allow us to predict tree biomass at improved spatial scales and with acceptable temporal resolution (Foody et al., 2001; Lechner et al., 2020; Lu, 2005). There is now a wide range of satellite data freely available at varying resolutions over multiple time intervals that can be used to estimate biomass and monitor it over time, retrospectively (Hansen et al., 2013; Nguyen et al., 2018; Pfeifer et al., 2016; Pflugmacher et al., 2014). Despite uncertainties in these satellite-derived biomass estimates at stand scales (Turton et al., 2022), remote sensing can provide useful estimates of forest recovery indicators in relation to lianas and has the potential to advance our understanding of liana ecology (e.g., van der Heijden et al., 2022; Waite et al., 2019) such as by estimating rates of forest biomass recovery after disturbances under varying degrees of liana infestation.

Here, we aim to determine how tropical forest landscapes recover their biomass following a large-scale disturbance and how this relates to liana dominance and stem damage in the Australian Wet Tropics. Our objectives were to: (a) use vegetation plots and remote sensing data to identify changes in plot-level forest aboveground biomass since a major tropical cyclone; (b) determine how this biomass change relates to present-day measures of liana dominance and stem damage; (c) use remote-sensing data to predict landscape level biomass change; and (d) infer consequences for forest recovery in disturbed tropical forest landscapes.

## 2 | METHODS

### 2.1 | Study site

The study took place in rainforests of the Wet Tropics World Heritage Area (WTWHA), northeast Queensland, Australia. The region is a biodiversity hotspot with a globally significant number of endemic species across several taxa (Le Saout et al., 2013). The study site is located within the WTWHA and spans an elevation gradient of 4–1320 m above sea level, from the Cassowary Coast lowlands to the Atherton Tablelands (17° 17'S–146° 0'E). The climate is tropical, with a mean annual rainfall of around 3000 mm in the lowlands and 1400 mm in the highlands, the majority of which falls during the pronounced December–April wet season (Bureau of Meteorology, 2023). The WTWHA is prone to tropical cyclones and the rainforests of the study area around the Cassowary Coast suffered severe damage from Tropical Cyclone Larry (Australian TC Category 4) in 2006 and Tropical Cyclone Yasi (Australian TC Category 5) in 2011 (Turton, 2019). Much of this rainforest was cleared for agriculture and urban development following European settlement in the early 20th Century (Winter et al., 1987) and was selectively logged until the area received World Heritage listing in 1988 (Goosem & Tucker, 2013). However, specific details on the location and extent of the logging are no longer available following the closure of the forestry industries in the region. Because of these human and natural disturbances, the landscape is heavily fragmented, consisting of many patches of disturbed forest in varying stages of recovery with characteristically low and uneven canopies and an abundance of lianas (Murphy & Metcalfe, 2016; Webb, 1958).

### 2.2 | Stem measurement

Forty permanent vegetation plots (20 × 20 m) (Figure S1) were established between September 2020 and November 2021 across a gradient of disturbance intensity, with plots categorized as either “heavily” or “lightly” disturbed. “Heavily disturbed” plots were defined as having ≤25% canopy coverage by trees >5 m tall. “Lightly disturbed” plots were defined as having ≥75% canopy cover by trees >5 m tall. Canopy structure within plots was a result of both natural disturbances, including wind damage, and anthropogenic disturbances, mainly selective logging. Areas with obvious presence of invasive species were avoided, as the focus of this study was native lianas. Twenty plots were established in the lowlands and one “lightly disturbed” and one “heavily disturbed” plot was established approximately every 100 m along an elevational gradient (100–1320 m) to ensure plots were representative of the entire study area. Further information about the plots can be found in the Supporting Information (Table S1). The coordinates of the four corners of each plot were recorded with a Garmin GPSMAP 64sx (accuracy to within ±3.65 m).

In each plot, standardized protocols were used to measure all tree and liana stems ≥1 cm diameter at breast height (DBH; 1.3 m)

(Gerwing et al., 2006; Marthews et al., 2012; Schnitzer et al., 2008). Lianas included all woody vines (true lianas) and climbing monocots, which consisted of rattans (Arecaceae) and climbers in Flagellariaceae, Poaceae, and Smilacaceae. Tree height was also measured using a tape measure, pole, or laser rangefinder. Damage to trees was noted; a tree was considered damaged if the main stem was broken.

Aboveground biomass for each tree stem was calculated using a pan-tropical equation (Equation 1; Chave et al., 2014). This equation was previously applied in Australian rainforests, and like this earlier study, we used a default value for wood density in Australian tropical forests of 0.5 g cm<sup>-3</sup> (Campbell et al., 2018) as we did not have complete species data available for every plot.

Equation 1 shows the pan-tropical equation for calculating aboveground biomass

$$AGB_{est} = 0.0673 \times (\rho D^2 H)^{0.976} \quad (1)$$

where  $\rho$  = wood density,  $D$  = DBH, and  $H$  = height.

The relative dominance of lianas over trees is expressed as the liana: tree basal area ratio (LTR), calculated as liana basal area divided by tree basal area.

### 2.3 | Remote sensing

We used atmospherically corrected RapidEye Surface Reflectance Ortho Tile products acquired in September 2019 (passive sensor data at 5 m pixel resolution collecting data in the blue, green, red, red-edge, and near infrared spectral bands; Planet Team, 2017). This was the most suitable imagery collected closest to the date of our field surveys that was sufficiently cloud-free and of high enough spatial resolution to allow detection of canopy disturbances and to align with the scale of our field plots; errors can be introduced if pixels are larger than plots (Réjou-Méchain et al., 2019). The RapidEye tiles were merged using QGIS v 3.22 (QGIS Development Team, 2022) to create a single multiband raster that covered the entire study area. We repeated the same process using RapidEye Surface Reflectance Ortho Tile products acquired in September 2011, 7 months after Tropical Cyclone Yasi made landfall over Mission Beach on February 3, 2011 (Turton, 2019). The cyclone caused considerable damage to the region's forests (Negrón-Juárez et al., 2014) hence over the post-cyclone 2011–2019 period; the rainforests would be expected to be at a state of recovery.

We extracted the surface reflectance of each mosaic band using the “raster” package (Hijmans & van Etten, 2010) in R statistical software (R Core Team, 2022). We calculated standard spectral vegetation indices: (i) Normalized Difference Vegetation Index (NDVI) which has been commonly used in ecological studies (Tucker, 1979) but tends to saturate in highly productive environments; (ii) Enhanced Vegetation Index (EVI), which was developed to address NDVI's oversaturation problem while also reducing the impacts of aerosol contamination (Liu & Huete, 1995); (iii) two-band Enhanced Vegetation Index (EVI2),

which is comparable to EVI but calculated without the blue spectral band (Jiang et al., 2008); (iv) Modified Soil Adjusted Vegetation Index (MSAVI2), which was developed to reduce soil noise (Qi et al., 1994); and the (v) Greenness Index (GI) (Woebbecke et al., 1995), which reportedly correlates with liana infestations in primary and secondary forests in Sabah, Malaysia (Chandler et al., 2021).

Metrics capturing texture in the image data (Haralick et al., 1973) were included to capture forest canopy heterogeneity, which differs between more and less disturbed sites, and thus potentially indicates biomass variation in the landscape (e.g., Gallardo-Cruz et al., 2012; Pfeifer et al., 2016; Wood et al., 2012). To calculate texture, we computed a gray-level co-occurrence matrix (GLCM) with varying window sizes from  $3 \times 3$  to  $9 \times 9$  pixels. These window sizes were chosen because they would cover the dimensions of a typical tree crown, thus providing the most appropriate resolution for our dataset (Pfeifer et al., 2016). We computed mean, variance, contrast, and dissimilarity for each of the five RapidEye bands using the “glcm” package in R (Zvoleff, 2014).

The addition of topographic variables has been shown to improve model accuracy when predicting biomass (Baccini et al., 2012; Chave et al., 2019; Li et al., 2008). A digital elevation model (DEM) was downloaded from the Queensland Spatial Data Catalogue (State of Queensland, Department of Resources, 2005) with a resolution of 25 m. This was resampled to a 5 m resolution using the bilinear interpolation method with the “resample” function in the “raster” package in R.

## 2.4 | Statistical analyses

Mean spectral and texture metrics, vegetation indices, and elevation of pixels covering the area within the coordinates of the plot corners were extracted using the “raster” package in R. We subsequently used these as variables in our predictive biomass modeling and mapping. These remotely sensed predictor variables were correlated with field-based measures of aboveground tree biomass and tested for intercorrelations using a correlation matrix with the “corrplot” package in R (Wei & Simko, 2021). We excluded highly intercorrelated predictor variables ( $r > .7$ ), retaining the variable of the pair that showed a stronger correlation with aboveground biomass measured in the plots (Zuur et al., 2010).

We used random forest models as an alternative to linear regression to develop models predicting biomass (Dye et al., 2012; Karlson et al., 2015; Li et al., 2019) because they are insensitive to skew and able to describe complex, non-linear interactions (Breimen, 2001; Pflugmacher et al., 2014). The random forest model was trained using the “caret” package in R (Kuhn, 2008). Eighty percent of the data were used for training and the remaining 20% were used for testing. We conducted repeated 10-fold cross-validation three times. Random forest models have two key parameters, *mtry* and *ntree*. We tested *mtry* values of 1–4 and confirmed that *mtry*=2 produced the best model, based on the lowest Root Mean Squared Error (Table S2). We used *ntree*=500 as this is the default setting for the “caret” package; 95% confidence intervals were calculated by multiplying by 1.96 by the standard error around the mean of the biomass prediction for each plot.

The resulting model was applied to the 2019 raster mosaic and used to predict biomass at the plot-level and across the landscape using the “predict” function. Biomass was predicted only across areas of the map categorized as “rainforest” according to the Queensland Remnant Broad Vegetation Group Classification (Neldner et al., 2021). We used linear regression to test the relationship between the predicted biomass and the measured biomass from field surveys to assess model accuracy.

The random forest model was also applied to the September 2011 raster mosaic and predicted biomass was extracted for each plot location. Plot-level change in biomass was analyzed as absolute change and as percentage change to remove the effects of differences in initial plot biomass.

To quantify how changes in tree biomass varied with LTR, we constructed a linear model with plot-level changes in biomass as the response variable and LTR as the explanatory variable. Following visual inspection of model residuals, LTR was natural log-transformed. To understand how this biomass change could be attributed to damage to living stems and how this related to LTR, we also constructed linear models to assess the relationship between the logit-transformed proportion of damaged tree stems and (1) LTR, and (2) change in tree biomass.

Landscape level biomass change was calculated by subtracting the predicted biomass value for each pixel in 2019 from its predicted biomass value from 7 months after Tropical Cyclone Yasi in 2011, resulting in a map of predicted biomass change over the 8-year study period. We used an average wood carbon composition of 47.35% (Martin & Thomas, 2011) to convert biomass estimates into carbon.

## 3 | RESULTS

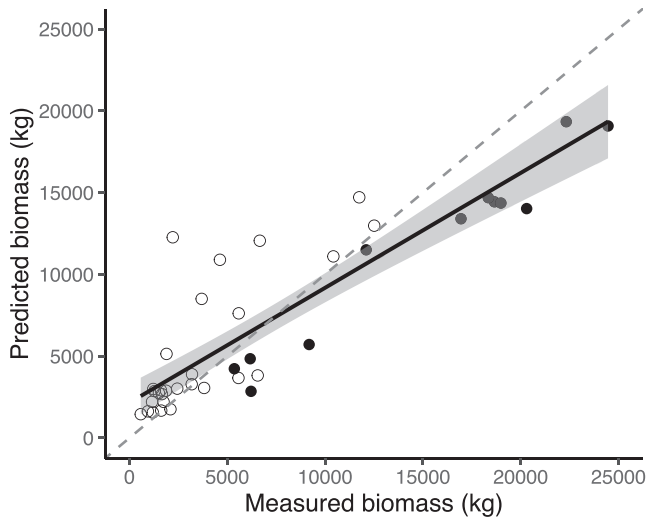
### 3.1 | Model performance

In the random forest model, elevation was the most important variable predicting biomass, followed by the variance of the B4 band at a moving window size of  $9 \times 9$  pixels, the contrast of the B4 band at a moving window size of  $3 \times 3$  pixels; the contrast of B5 band at a moving window size of  $3 \times 3$  pixels was the least important variable (see the Supplementary Information for more details on the final model; Figures S2 and S3). When predicted biomass values from the final random forest model were regressed against the field-measured biomass values, linear regression showed  $R^2 = .79$ ,  $p < .001$  (Figure 2). A full list of predicted biomass values with 95% confidence intervals can be found in the Supplementary Information (Table S3).

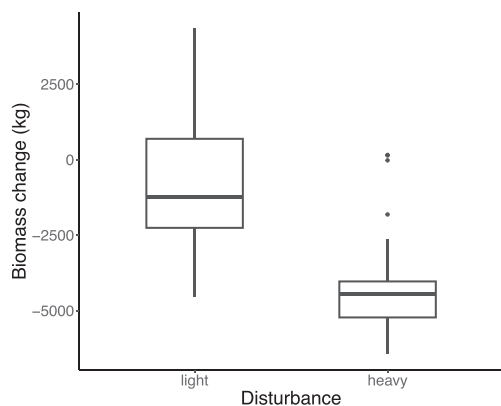
### 3.2 | Change in biomass

Over the 8 years after Tropical Cyclone Yasi, tree biomass declined in the majority of plots (34 out of 40), with greater losses in plots categorized as “heavily disturbed” (Figure 3). Across the 240,500-ha





**FIGURE 2** Field-measured tree above-ground tree biomass for 40 20×20m plots in northeast Queensland compared to biomass predicted by a random forest model based on remotely sensed metrics ( $R^2 = .79$ ,  $p < .001$ ) with fitted linear regression line (solid) with 95% confidence intervals and 1:1 line (dashed). Solid and open circles represent lightly and heavily disturbed plots, respectively.



**FIGURE 3** Boxplots show changes in predicted above-ground tree biomass (kg) between 2011 and 2019 from 20×20m vegetation plots in northeast Queensland, in lightly versus heavily disturbed plots.

landscape, total biomass decreased by 694,679 Mg (2.89 Mg/ha) over the 8-year period which is equivalent to a loss of 328,931 Mg of carbon (1.37 Mg/ha of carbon) (Supplementary Information, Figure S4).

Loss of tree biomass (2011–2019) increased with LTR, both as absolute values ( $R^2 = .56$ ,  $p < .001$ ; Figure 4a) and as percentage biomass ( $R^2 = .60$ ,  $p < .001$ ; Figure 4b).

### 3.3 | Stem damage

The proportion of stems with damage in 2019 increased with increasing LTR ( $R^2 = .27$ ,  $p < .001$ ; Figure 5a) while change in aboveground biomass (kg) decreased with increasing proportion of damaged tree

stems ( $R^2 = .16$ ,  $p = .01$ ) (Figure 5b). Heavily disturbed plots had a greater proportion of damaged stems compared to plots that were lightly disturbed (Figure 5c).

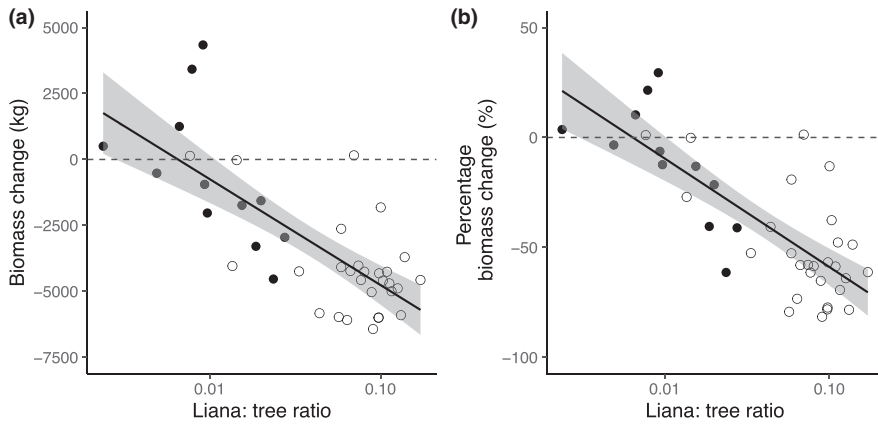
## 4 | DISCUSSION

Our study provides evidence that forests may not follow a trajectory towards biomass recovery following severe disturbances, which has implications for the functions of forests as carbon sinks. Advances in remote sensing, including the availability of spectral data covering multiple time periods, allowed estimation of changes in above-ground biomass over time with reasonable accuracy. In our study landscape in the Australian Wet Tropics, biomass declined rather than recovered, and these decreases were associated with increased LTR and tree stem damage.

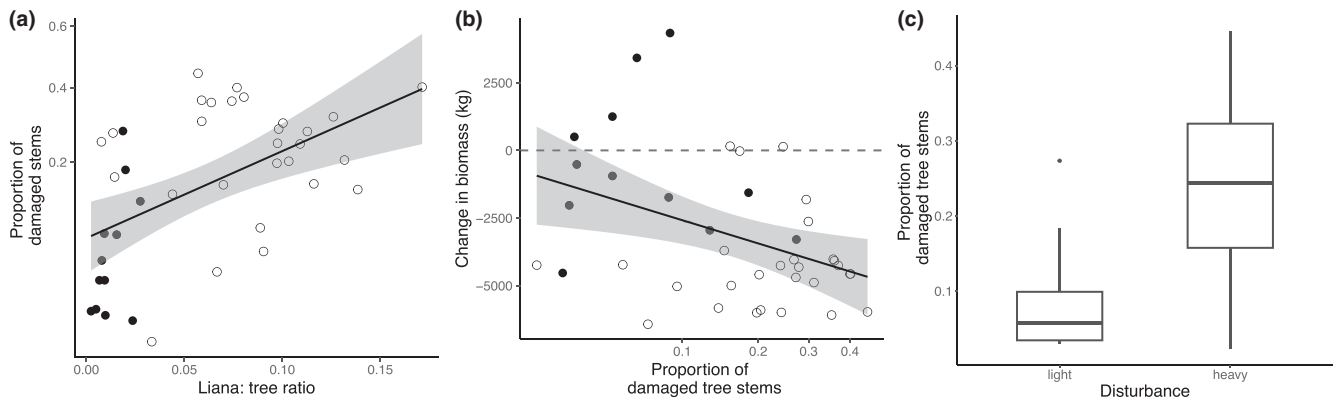
Previous studies have found slow, or even a lack of, biomass recovery after disturbances (e.g., Nunes et al., 2021; Wigneron et al., 2020). This can often be attributed to delayed mortality, with reports of increased tree mortality in the years following the disturbance, presumably because the damage that the trees suffered rendered them vulnerable. Delayed mortality has been found to occur following drought (Aleixo et al., 2019), logging (Shenkin et al., 2015), fire (Barlow et al., 2003), and hurricanes (Lugo, 2008; Uriarte et al., 2019; Walker, 1995). We put these findings in the context of liana proliferation.

The finding that tree biomass continued to decline following a disturbance and that the rate of decline increased with LTR aligns with expectations that liana infestations increase tree mortality rates (Ingwell et al., 2010; McDowell et al., 2018; Phillips et al., 2005). Our findings are also consistent with literature from other tropical regions that show lianas reduce tree growth and recruitment (Estrada-Villegas et al., 2022; Mills et al., 2019; Putz, 1984; Reis et al., 2020) and may prevent biomass recovery (e.g., Schnitzer et al., 2000; Foster et al., 2008; Murphy & Metcalfe, 2016; Tymen et al., 2016).

There is likely a reciprocal relationship between liana dominance and the observed tree biomass decline. First, lianas that proliferate after disturbances may damage or kill trees that initially survived (Ingwell et al., 2010; McDowell et al., 2018; Phillips et al., 2002), thereby reducing existing biomass and limiting new biomass growth. Mortality can be exacerbated further when a tree falls that is connected to other trees with lianas, as this can pull down multiple trees (Putz, 1984). Second, following disturbances, delayed mortality can occur (Aleixo et al., 2019; Everham & Brokaw, 1996; Lugo, 2008; Shenkin et al., 2015). The subsequent treefalls can create more trellises for lianas as well as increase canopy openness (Schnitzer & Bongers, 2011), leading to liana proliferation and resulting in the high LTR values we observed 8 years after Tropical Cyclone Yasi. It is likely both of these scenarios occur and result in a positive feedback loop that involves liana proliferation, tree mortality and disturbance that drives biomass loss (Laurance et al., 2001).



**FIGURE 4** Changes in (a) tree above-ground biomass (kg) and (b) percentage tree above-ground biomass (%) over an 8-year post-cyclone period in 20×20m plots as a function of natural-log transformed liana: tree ratio basal area (LTR) (a)  $R^2 = .56$ ,  $p < .001$ ; (b)  $R^2 = .60$ ,  $p < .001$ ). Closed circles represent lightly disturbed plots and open circles represent heavily disturbed plots. The x-axes show natural log scales.



**FIGURE 5** Relationships between the proportion of damaged tree stems in 20×20m plots and (a) liana: tree basal area ratio (LTR) ( $R^2 = .27$ ,  $p < .001$ ) and (b) change in tree biomass (kg) ( $R^2 = .16$ ,  $p = .01$ ) over an 8-year post-cyclone period. Closed circles represent lightly disturbed plots and open circles represent heavily disturbed plots. The x-axes have a logit scale. Boxplot (c) shows the proportion of damaged tree stems in heavily versus lightly disturbed plots.

Our finding that the proportion of damaged tree stems in each plot increases with LTR and with the change in biomass over the 8-year period suggests that biomass losses could result from lianas breaking trees. Past findings from Peru reported that plots dominated by climbers had up to a nine-fold increase in the percentage of trees with physical damage compared to control plots (Griscom & Ashton, 2006) so it is feasible that lianas contribute substantially to this stem damage where they are abundant. It was recently documented that damage to living trees contributes to a substantial amount of biomass loss in the tropics (Zuleta et al., 2023); our study suggests this could be partly attributed to liana infestations. However, the trees may have already been damaged by the tropical cyclones (Turton, 2019) and the opening of the canopy as a result contributed to the increase in LTR. Hence, in this study we cannot distinguish between cause and effect—mechanisms are complex and need further study. Nevertheless, the abundance of broken stems in this study highlights the importance of measuring the height of every tree stem directly and using an allometric equation that incorporates height (Feldpausch et al., 2012; Marshall et al., 2012). Measuring diameter alone and using allometric equations that assume height based on DBH would result in an overestimation of the biomass of broken stems.

Our finding that biomass was lost across the wider study landscape, equating to a carbon loss of 1.37Mg/ha over the 8 years

after Tropical Cyclone Yasi, shows that these forests acted as carbon sources rather than carbon sinks over that period. At the time, Tropical Cyclone Yasi was found to cause an important release of carbon from the carbon sink of Australian forests (Negrón-Juárez et al., 2014) and these findings show this effect continues even 8 years later. This finding has important implications considering that forest carbon sinks are a key component in Queensland's strategy to meet its targets for reduced carbon emissions (WTMA, 2022). Previous studies of carbon density across other tropical regions also reported these ecosystems might be net carbon sources due to degradation and disturbance (Baccini et al., 2017). Given that forests are expected to play a key role in mitigating climate change through carbon sequestration at both global (Chazdon et al., 2016; Grassi et al., 2017; Heinrich et al., 2023) and national scales (DCCEW, 2022), yet they continue to suffer from ongoing disturbances Curtis et al. (2018), is concerning and warrants further study.

Our observation on decreasing forest biomass over time after a tropical cyclone also supports findings from past long-term studies of vegetation plots in the Australian Wet Tropics. One study in the region reported that from 2001 to 2012, tree growth rates decreased and mortality rates consistently exceeded recruitment rates (Murphy et al., 2013), while another reported that stand-level basal area decreased across plots between 1971 and 2019 and that tree mortality risk doubled over this time period (Bauman et al., 2022).

These patterns were ascribed to the effects of cyclones, droughts, and climate change. For example, decreased growth may be due to increased forest respiration rates caused by higher temperatures (Feeley et al., 2007). It is possible that lianas and their interactions with these variables also contributed to the increased mortality and reduced growth rates. The inclusion of liana data in future studies would allow further investigation into the role of lianas in explaining forest biomass losses.

Cyclones are a natural part of forest dynamics in the study region (Webb, 1958), so it might be expected that the ecosystem should recover biomass rapidly following disturbance (Cole et al., 2014). For example, in a rainforest in Puerto Rico that was hit by a hurricane, biomass reportedly recovered to 86% of pre-disturbance levels after only 5 years (Scatena et al., 1996). Our results contrast with this expectation, at least within the timeframe of our study. Anthropogenic pressures, such as fragmentation and logging, may increase the susceptibility of forests to damage and reduce their ability to recover without human intervention (Laurance & Curran, 2008; Lugo, 2008; Silvério et al., 2019; Turton, 2019). The Australian Wet Tropics are heavily fragmented, particularly in the coastal lowlands (Metcalfe & Lawson, 2015), which may reduce their resilience. Additionally, tropical cyclones are projected to increase in intensity as a result of climate change (Negrón-Juárez et al., 2014), putting forests in cyclone-prone regions under even more pressure. Other human impacts are also likely to increase with increasing population pressures in the future, so interactions between anthropogenic factors and rainforest recovery are of utmost concern.

The finding that lianas are linked to biomass loss suggests that liana cutting has potential as a restoration management tool. Numerous studies show liana cutting is a cost-effective method to restore degraded forests and sequester carbon (e.g., Estrada-Villegas et al., 2022; Finlayson et al., 2022; Putz et al., 2023). However, native lianas do play key roles in ecosystem functioning. For example, lianas contribute disproportionately to leaf litter turnover, facilitating nutrient cycling and distribution (Hegarty, 1991; Tang et al., 2012), contribute to biodiversity (Campbell et al., 2015; Tng et al., 2016), and provide resources and connectivity for arboreal wildlife (e.g., Arroyo-Rodríguez et al., 2015; Yanoviak & Schnitzer, 2013). Complete liana removal at large scales could have adverse effects, hence further research is needed before this treatment should be widely implemented.

Australia has been often left out of meta-analyses on both lianas and rainforest recovery (e.g., Cole et al., 2014; Estrada-Villegas et al., 2022; Finlayson et al., 2022; Poorter et al., 2021). Given its high levels of endemism, with little species overlap with Latin America (Chave et al., 2019; Corlett & Primack, 2006), differences in the effects of lianas on recovery might be expected but were not found in our study. This is an important finding because it supports predictions that lianas slow forest recovery and deplete biomass and thus carbon sequestration at a global scale (e.g., di Porcia e Brugnera et al., 2019; Marshall et al., 2020; van der Heijden et al., 2015).

Possible future studies should be conducted over longer time scales with interim measures to assess the shape of any trends.

A limitation of our study is the lack of historic liana and tree data, which means that we can only infer that liana dominance increased and that trees died over the 8-year period of the study. Supporting these inferences are the well-established findings that lianas recruit rapidly after disturbance (e.g., Putz, 1984; Schnitzer et al., 2000; Schnitzer & Bongers, 2002; Webb, 1958; Whitmore, 1989) and can exceed pre-disturbance levels (Allen et al., 2005). Nevertheless, future studies that include pre-disturbance vegetation data and interim measures could clarify the extent to which continued losses in forest biomass after disturbances are due to liana proliferation. Additionally, the inclusion of species data would improve the accuracy of plot-level biomass estimations (Chave et al., 2014) resulting in increased model accuracy (Réjou-Méchain et al., 2019). Wood density can be highly variable among tree species (Chave et al., 2009). In particular, species found in heavily disturbed sites tend to have lower wood density compared to those from the less disturbed sites (Berenguer et al., 2018), which means using a standard wood density value across all plots in this study may have introduced error.

This study not only adds to the increasing body of evidence that lianas can stall forest biomass recovery but also presents new evidence that lianas may contribute to further biomass loss following disturbances. Scaling up from plots to landscapes, our results also indicate that after disturbances, forests may continue to act as carbon sources rather than sinks. These findings have implications for forest carbon storage estimates and could inform management at both global and regional scales. At a regional scale, it highlights the need for studies exploring liana cutting as a management tool for preventing further biomass loss and promoting biomass recovery. At a global scale, if tropical forests are unable to recover biomass after disturbances, this will have serious consequences for the global carbon sink.

#### AUTHOR CONTRIBUTIONS

Emma J. Mackintosh: Data curation, investigation, formal analysis, methodology, validation, project administration, resources, visualization, writing—original draft. Catherine E. Waite: Conceptualization, formal analysis, methodology, validation, writing—review and editing, supervision. Francis E. Putz: Validation, writing—review and editing, supervision. Sophie Brennan: Investigation, data curation, resources, project administration, writing—review and editing. Marion Pfeifer: Conceptualization, methodology, validation, supervision, writing—review and editing, funding acquisition. Andrew R. Marshall: Conceptualization, methodology, validation, supervision, writing—review and editing, project administration, resources, funding acquisition.

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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 openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.prr4xgvvh>.

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