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Floristic diversity and patch dynamics in hyper-disturbed tropical lowland rainforest fragments in north Queensland: no evidence for cyclone-disturbance and fragmentation driving species assemblages towards early-successional states

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Copyright statement

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ABSTRACT

Tropical cyclones reshape the structure, composition and successional trajectories of forest ecosystems. Climate warming is expected to increase the intensity and impact of these storms while habitat fragmentation further modifies trajectories of response. Many studies over the past decade suggest that tropical forest fragments are locked into a future dominated by edge-favoured pioneer species, dramatic loss of late-successional, large-fruited species, and invasion by exotic weeds. However, this study shows that severely storm-damaged and fragmented tropical forests are remarkably resilient, with a capacity for rebuilding and maintaining plant species composition and diversity.

My study followed two severe tropical cyclone events, Cyclones Larry (2006) and Yasi (2011) in the Australian Wet Tropics. To date, no comparable investigation has measured the effects of successive severe tropical cyclone events on different forest habitats in lowland rainforest. My study investigated: 1) immediate effects of a second severe cyclone on the structural characteristics of different forest habitat types; 2) family and species-level responses to damage and short-term survival rates; 3) plant community and species-level assemblages across different forest habitats; and 4) life-history successional characteristics of species for different habitat types.

My results showed all trees sustained some level of damage (i.e. minor to severe) due to the effects of these two severe cyclone events. About 75% of trees had their main stem snapped compared to 11% of trees with major breakage of branches and less than 4% were uprooted. 10% of all trees sustained only minor damage including partial defoliation, twig-snapping and minor branches snapped. Snapping of tree trunks was higher in fragmented forest compared to continuous forest whereas snapping of major branches was significantly higher in continuous forest and edges. Trees resprouted within weeks of the cyclone and 96% of standing stems continued to show vigourous growth after eighteen months.

Although there was a dramatic loss of large canopy and emergent trees during Cyclone Larry five years earlier, 83% of all stems in my plots were identified as belonging to mid-late and late successional species, while only 13% of stems were early-mid successional species. These stems are mainly saplings (≤ 10-20cm DBH) which have survived successive severe cyclone events within the understorey 'vine tangles.' I found no evidence for proliferation of early successional or pioneer species in any of the habitat types, including fragmented forest sites, within the time-frame of this study. No evidence was found for elevated levels of exotic weed invasion following these events with these species comprising less than 1% of total assemblages. All forest habitat types showed an unexpected capacity for resistance and resilience following the combined effects of fragmentation and two severe tropical cyclones. My data suggest that forest habitat types influence successional life-history characteristics but are not driving species assemblages in fragmented forests towards proliferation of short-lived, edge-favoured generalists (i.e. pioneer species).

Key words: tropical cyclones; Australian Wet Tropics; fragmented forest; life-history; successional species; resprouting; resistance; resilience.

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CHAPTER ONE:

The effects of tropical cyclones and fragmentation on forest structure and community assemblages

1-1 Introduction

Tropical cyclones (described as hurricanes or typhoons in the Northern Hemisphere) are significant disturbance agents disrupting function, structure and composition in forest ecosystems (Bellingham, 1991; Everham & Brokaw, 1996; Keppel et al., 2010; Lugo et al., 1983; Zimmerman et al., 1994). As powerful modifiers of ecosystems, tropical cyclones trigger immediate and long-term changes to vegetation heterogeneity at the landscape scale and variability in ecosystem processes, reorganising successional trajectories and providing new evolutionary pathways (Keppel et al., 2010; Lugo, 2008). Climate warming is expected to increase the intensity of tropical storms, including wind speeds and rainfall, during these events (GFDL & NOAA, 2017; Uriarte et al., 2019).

These natural disturbances impact forest ecosystems which are increasingly under chronic stress from human activities. It is widely acknowledged that habitat loss and fragmentation represent the most serious threats to tropical rainforest biodiversity (Laurance et al., 2002; Laurance et al., 2006; Wright & Muller-Landau, 2006) and relationships between ecosystem diversity and response to disturbance is a particular area of interest for future research (Tanner & Bellingham, 2006).

The frequency and intensity of tropical cyclones drive forest ecosystems such as those found in Mission Beach, northeast Queensland towards a more or less continuous cycle of disturbance, reorganization and successional responses (Lugo, 2008; Turton, 2008a; Webb, 1958), thus precluding any state of equilibrium or progression towards a stable and predictable endpoint (Attiwill, 1994). The relatively frequent occurrence of tropical cyclones (Grove et al., 2000) tends to perpetuate rainforest communities characterized by low, uneven canopies with scattered emergent trees and dominant vines (Webb, 1958). Described in the literature as ‘hyper-disturbed’ (Turton, 2008; Webb, 1958) these lowland tropical mesophyll rainforests are also increasingly subject to habitat fragmentation.

Following two Severe Tropical Cyclones, Larry (2006) and Yasi (2011), questions have remained over fragmented rainforests and the likelihood of declining trajectories for plant diversity, exclusion of forest-interior species, dramatic loss of large canopy and emergent trees and a compositional shift towards early successional species (Laurance & Curran, 2008; Metcalfe et al., 2008; Murphy & Metcalfe, 2016). Fragmented rainforest is widely considered to be more susceptible to strong wind damage (e.g. cyclones) (Laurance & Curran, 2008) and vulnerable to exotic weed invasion (Laurance, 1991; Laurance et al., 1998; Murphy et al., 2008; Turton & Siegenthaler, 2004), however some studies in the Australian Wet Tropics have failed to find these effects (Catterall et al., 2008; Grimbacher et al., 2008). Following Severe Tropical Cyclone Larry much of the literature focussed on the impacts of cyclones acting synergistically with fragmentation leading to disruption of key ecological processes, ecosystem simplification, impoverishment of tree assemblages, proliferation of edge-favoured generalists, weed invasion and local extinctions (Laurance & Curran, 2008; Metcalfe et al., 2008; Murphy & Metcalfe, 2016; Turton, 2008, 2012).

1-2 Tropical cyclones – crossing the threshold

1-2-1 Measuring the intensity of tropical wind-storms

Tropical cyclones (referred to as hurricanes and typhoons in the Northern Hemisphere) tend to develop pole-wards of about 10° latitude (i.e. equatorial rainforests of the Amazon and Congo basins and most of Malesia are unaffected by these systems) (Richards, 1996). These closed-circulation low-pressure systems vary in magnitude but by definition sustain surface wind speeds of at least ~ 61 km/h (17 ms^{-1}) (Richards, 1996). In Australia, tropical cyclones are categorised according to the Australian Tropical Cyclone Intensity Scale based on 10-minute maximum sustained winds (BOM Australian Government, 2017b). On this five-point scale, categories 3-5 are considered severe tropical cyclones and are defined by sustained winds of 118-157 km/h (~33–44 ms^{-1}) for Category 3; 158-198 km/h (~44–55 ms^{-1}) for Category 4; and >198 km/h (>55 ms^{-1}) for Category 5. By comparison, the Saffir–Simpson hurricane wind scale (SSHWS), formerly the Saffir-Simpson hurricane scale (SSHS), categorises western hemisphere tropical storms that exceed wind intensities of tropical depressions (National Hurricane Centre, 2017). On this scale, wind speed is divided into five categories of hurricanes: Category 1: 119–153 km/h (~33–42 ms^{-1}); Category 2: 154-177 km/h (~43–49 ms^{-1}); Category 3: 178-208 km/h (~49–58 ms^{-1}); Category 4: 209-251 km/h (~58–70 ms^{-1}); and Category 5: wind speeds exceeding 252 km/h (> 70 m/s) (National Hurricane Centre, 2017). All references to cyclone categories in this study are according to the Australian Tropical Cyclone Intensity Scale unless otherwise stated.

1-2-2 Patterns of forest damage caused by tropical wind-storms

Severe cyclone events can kill and damage exceedingly large numbers of trees in a very short time span (Lugo & Scatena, 1996) but in the longer-term these events can drive diversity in these ecosystems (Keppel et al., 2010), redirecting successional trajectories and creating new evolutionary pathways (Lugo, 2008). Many studies have commented on the heterogeneous pattern of damage following cyclone events with some areas experiencing total devastation while neighbouring locations may be left virtually unscathed (Bellingham et al., 1992; Brokaw & Walker, 1991; Grove et al., 2000; Lugo et al., 1983; Lugo & Scatena, 1996; Turton, 2008; Walker et al., 1996; Webb, 1958).

In a review of the effects of hurricane damage on Caribbean forests, Brokaw and Walker (1991) noted some unexpected results for aspect and exposure for a number of studies. While forests on slopes facing hurricane winds (Bellingham, 1991; Walker et al., 1996) and level areas exposed to wind from all directions (Reilly, 1991) tended to show more damage, other research has found that damage can be highly variable even when there is no topographical difference (Putz & Sharitz, 1991). Abiotic factors (e.g. topography, disturbance history and soil conditions) and biotic factors (e.g. stand condition, age structure, stem size, species composition and pathogens) may all influence the severity of wind-storm or cyclone (hurricane) damage (Basnet et al., 1992; Boose et al., 1994; Everham & Brokaw, 1996).

Boose et al., (1994) describes how different patterns of wind damage across varying spatial scales arise from complex interactions between meteorological, physiographic and biotic factors. At the regional scale, the level of forest damage is dependent upon wind velocity gradients and proximity to the storm track, as well as broader topographic effects of wind shielding or shadowing. Vegetation patterns reflecting differences in geology, climate, and disturbance history are also important factors (Boose et al., 1994). These effects are further modified by landscape-scale variations including abrupt changes in surface friction as the cyclone crosses the coast or passes over different topography (Grove et al., 2000). For example, powerful winds may be channelled up along valleys before accelerating over steep ridges creating strong leeward-side turbulence (Boose et al., 1994). These changes in topographic relief create varying levels of exposure and protection at the landscape-scale, resulting in more severe damage on peaks and hills (Boose et al., 2004). In the Australian Wet Tropics, following Cyclone Larry (Category 4), the patchy nature of forest damage at the landscape-scale was described as “a spectrum of disturbance regimes across topographically-complex forested landscapes” (Turton, 2008). Following Cyclone Agnes, Webb (1958) attributed variability in forest damage (i.e. stripping of foliage, shattering of tall trees, wind-throws and gap formation) to topographic influences in the landscape whereby forests on sheltered valley floors were less damaged than exposed slopes. A complex and “very patchy” pattern of forest damage was also detected at the landscape- and stand-level scales following Cyclone Rona in the Daintree area, north-eastern Queensland (Grove et al., 2000). A recent study of Cyclone Yasi (Category 5), found terrain features to be important factors influencing the pattern and severity of forest damage (Negrón-Juárez et al., 2014). Forests with greater directional wind exposure sustained the highest levels of damage with slope and aspect playing important roles. Forest disturbance also increased with higher elevation suggesting that complex terrain and higher elevation have a combined effect to increase wind speeds and forest damage (Negrón-Juárez et al., 2014).

1-2-3 Cyclone disturbance triggers dramatic shifts in forest microclimate gradients

Severe cyclone disturbance has a dramatic impact on the size and extent of canopy gaps. Forest structure can change from continuous canopy cover with some gaps to large gaps and only occasional continuous canopy cover (e.g. closed canopy of 70-100% projective foliage cover can be reduced to a value approaching zero post-cyclone) (Brokaw & Walker, 1991). Microclimatic conditions across all structural layers of the rainforest, particularly understorey levels are altered significantly by these events (Everham & Brokaw, 1996). Typically, cyclone disturbance allows direct and unfiltered sunlight to reach understorey plants and the ground layer raising the potential for scorching exposed trunks and new soft growth, as well as reducing humidity and increasing temperature, exposure to wind and desiccation (Everham & Brokaw, 1996; Turton & Freiberger, 1997; Turton, 1992; Turton & Siegenthaler, 2004; Whitmore, 1998). In the immediate aftermath of a cyclone, these changes may shift rainforests towards a more 'arid' microclimate potentially increasing vulnerability to fire should drought follow this event (Laurance & Curran, 2008). Higher light levels reaching the ground and understorey may trigger early-to mid-successional seedling recruitment in the soil seedbank (Graham & Hopkins, 1990), promote resprouting of damaged stems, particularly mid-to late successional species as well as creating opportunities for suppressed mid-to late successional saplings (Comita et al., 2009; Uriarte et al., 2005; Zimmerman et al., 1994).

1-2-4 Community and stand-level responses to severe tropical cyclones

Following severe cyclone disturbance, tropical rainforests display a range of structural and stand-level damage including defoliation and reduction in crown areas, wind-throw and uprooting of trees, snapping of main stems and branches, breakage of robust lianas and vines and dislodgement of epiphytes (Bellingham et al., 1995; Boose et al., 1994; Brokaw & Walker, 1991; Everham & Brokaw, 1996; Lugo et al., 1983). Large trees were found to be more susceptible to direct damage than small trees due to their own weight and decaying roots (Brokaw & Walker, 1991; Ostertag et al., 2005) however smaller trees also sustain varying levels of damage by falling large trees (i.e. indirect wind damage) (Frangi & Lugo, 1991).

Previous damage from earlier tropical storms, although partially related to species and size characteristics, may also be a predictor of future damage (Ostertag et al., 2005). The frequent occurrence of hurricanes (or cyclones) will likely favour disturbance-resistant, slow-growing species resulting in forest communities with shorter canopies and higher stem densities (Ostertag et al., 2005). Similar results for lowered canopies and proliferation of smaller stems have been reported in the cyclone-disturbed forests of the Wet Tropics of north Queensland (Webb, 1958), western Pacific (Keppel et al., 2010), eastern Pacific (Webb et al., 2014) and Madagascar (Gouvenain & Silander, 2003).

These results are also consistent with observations of response in subtropical littoral rainforest to severe wind-shear effects on exposed coastal headlands. The dense canopies of these stunted vine forests or vine thickets develop a typical wind-pruned profile with gradually increasing height as distance increases landward from the exposed edge. These communities exhibit increasing structural complexity and floristic diversity across an environmental gradient with the greatest development occurring within the more protected sites where wind-shear effects are minimised by local topographic influences. Notably, the stunted vine forests or vine thickets (i.e. a closed-canopy of multi-stemmed shrub/ tree species up to 3-6 metres high with many wiry vines and some woody climbers) have a far greater density of small stems per hectare than protected taller rainforest (up to 6-25 metres) with fewer and larger stem diameters per hectare (Ruting, 1979). Floristic composition will vary from site to site due to varying environmental factors (e.g. soil type and latitudinal variation) but general structural characteristics remain relatively consistent (Floyd, 1978; Ruting, 1979). Severe storm events in subtropical littoral rainforest will increase the level of wind exposure and desiccation affecting these communities. In some instances, these impacts will lead to significant structural and floristic changes, including lowering of canopies and loss of some species, particularly interior shade-tolerant species (Floyd, 1978; Ruting, 1979).

Hurricane or cyclone-prone tropical forests have been found to be remarkably resilient after frequent and severe wind disturbance (Ostertag et al., 2005). These events play an important role in re-structuring these forests, allowing opportunities for recruitment and renewal. Brokaw & Walker (1991) argue that the influence of severe tropical storms should not be viewed as "catastrophic" as affected forest ecosystems are not destroyed. In fact, they respond rapidly to new opportunities and usually with a very high level of resilience (Lugo, 2008). For many plant species in cyclone-prone tropical forests, disturbance is a necessary part of the life cycle providing opportunities for persistence of populations and floristic diversity (Attiwill, 1994; Keppel et al., 2010). Following large-scale disturbances, such as severe tropical storms, species composition and richness may remain the same (Yih et al., 1991), or increase (Lugo, 2008; Vandermeer et al., 2000). Some authors have suggested focussing on the effects and trajectories of response rather than negative impacts and recovery (Lugo, 2008) to better understand the dynamics of these ecosystems (Folke et al., 2004; Scheffer et al., 2001; Walker & Salt, 2006).

1-2-5 Strategies for resistance vs. resilience and life-history traits

Forest ecosystems and individual tree species respond to cyclone disturbance with varying strategies for avoiding damage (i.e. resistance), or promoting rapid recovery (i.e. resilience), or a combination of these options (Ostertag et al., 2005). These differences in resistance and resilience among individual trees will significantly influence future forest structure and composition (Lugo, 2008; Ostertag et al., 2005). Some studies have shown that resistance to severe wind damage is related to individual characteristics such as tree size, spatial position in the landscape and past disturbance history but have failed to find a relationship with wood density (Ostertag et al., 2005). In the Australian Wet Tropics, Metcalfe et al. (2008) also found no clear evidence that wood density was a predictor of damage across different forest types. Another study in this region found no association between damage levels and tree size or presence of buttressed roots but detected relationships with wood density and types of damage for a small number of species in a specific forest type (Curran et al., 2008a). Others have shown individual traits such as wood characteristics, growth rate and architecture influence different types of damage (e.g. snapping or uprooting) (Frangi & Lugo, 1991; Webb et al., 2014).

Broad trends are evident in the type of response shown by different species (Metcalfe et al., 2008) and trade-offs between species traits and susceptibility to damage (Curran et al., 2008b; Uriarte et al., 2012; Webb et al., 2014). Late successional, shade-tolerant species with slower growth rates and higher wood density tend to be more resistant to cyclone damage compared to early successional or pioneer species which are more susceptible to damage and more likely to die after these events following snapping of the main stem (Basnet et al., 1992; Brokaw & Walker, 1991; Zimmerman et al., 1994). In contrast to late successional species, wood densities of early to mid-successional species (i.e. light-demanding pioneer and secondary species) tend to be less dense, increasing their susceptibility to breakage (Canham et al., 2010; Zimmerman et al., 1994). Early successional species also tend to have low rates of resprouting after severe damage and rely on seed dispersal for recovery of populations (Uriarte et al., 2012; Zimmerman et al., 1994). However, one study examining just snapped individuals, found evidence for relatively high levels of resprouting in a single pioneer species (Curran et al., 2008b).

1-3 Tropical cyclones in the Australian Wet Tropics Bioregion

1-3-1 Historic context of cyclones in the Mission Beach area

Tropical cyclones are powerful agents of change in regional ecosytems of north Queensland (Turton, 2008a; Webb, 1958). Between 1887-2011, a total of 46 severe east coast tropical cyclones, having formed in the Coral Sea, crossed the Queensland coastline (Callaghan, 2011a). It is believed that between 1874-2004 the Innisfail sub-region was impacted by at least 22 tropical cyclones (i.e. prior to Severe Tropical Cyclones Larry (2006) and Yasi (2011) (Callaghan, 2004). A 1920 survey plan of the El Arish area to the west of Mission Beach noted the "dense tropical jungle" of the floodplain and described its condition as "badly cyclone wrecked" following the devastating cyclone which destroyed the township of Innisfail (Kemp et al., 2007). Damage from this cyclone on 10th March 1918 was widespread, seriously impacting coastal districts from as far north as Cairns to the Atherton Tablelands in the west. The eye-wall passed directly over Innisfail, approximately 33 km north of Garners Beach (northern boundary of the Mission Beach study area). Mourilyan Sugar Mill recorded a minimum central barometric pressure reading of 926 hPa. The cyclone generated a storm surge which swept through Bingil Bay and Mission Beach inundating lower lying areas up to a depth of 3.6 metres for hundreds of metres inland. Storm debris was deposited in trees up to 7 metres above ground level (Callaghan, 2011b)

In 1956, Cyclone Agnes caused significant forest damage in the Mission Beach study area. Webb (1958) described the shattering and defoliation of trees and how variations in topography affected the amount of damage. He commented that these forests "appeared from a distance to have been scorched by fire, or to have been ring-barked" (Webb, 1958, p. 222). Cyclone Agnes was an intense low-pressure system (lowest central pressure measured at 961 hPa) (BOM Australian Government, 2013), probably a high Category 2 or marginal Category

3 cyclone with maximum wind gusts peaking at 148 km/h (~41 ms^{-1}) (Webb, 1958). It appears that Cyclone Agnes and extensive logging operations throughout the study area may have initiated a transition to a mixed upper canopy of *Acacia mangium, A. celsa*, *A. cincinnata* and, to a lesser degree, *A. crassicarpa* across much of the lowland mesophyll vine forests. In 1982 Tam O'Shanter Range and Fenby Gap supported mesophyll rainforest with a distinctive upper canopy co-dominated by *Acacia celsa (*syn. *A. aulocarpa)* and *A. mangium* and *A. cincinnata* and *A. mangium* respectively (Tracey, 1982). These species are favoured by canopy-disturbance and can remain dominant within floristic assemblages for decades.

In 1986, Cyclone Winifred (Category 3) directly affected Mission Beach study area with the eye-wall crossing the coast at Cowley Beach (immediately north of the study area) with a maximum mean wind speed of 126 km/h (35 ms^{-1}) (BOM Australian Government, 2017c). It was another 20-years before Severe Tropical Cyclone Larry impacted this coastal area, once again, significantly modifying forest community structure and floristic composition. Most of the mature co-dominant *Acacia* spp. were snapped, or to a lesser degree uprooted initiating a new successional trajectory and opportunities for immature slow-growing, late-maturing species in the understorey. It was only five years later that Severe Tropical Cyclone Yasi removed almost all remaining *Acacia* spp. from the canopy layer initiating a new phase of renewal and recruitment.

The lowland tropical rainforests of Mission Beach located in the Wet Tropics of north Queensland sustained a catastrophic impact by Severe Tropical Cyclone Larry, a Category 4 cyclone (2006) (Turton & Dale, 2007). Severe Tropical Cyclone Yasi, a marginal Category 5 cyclone (2011) inflicted massive damage once again when it made landfall in the same area (BOM Australian Government, 2013). In the days following these two events, the rainforestclad hills looked remarkably like the description by Webb (1958, p. 222) after Cyclone Agnes "as appearing from a distance to have been scorched by fire or to have been ring-barked".

1-3-2 Severe Tropical Cyclone Larry (2006)

On the morning of 20th March 2006, Severe Tropical Cyclone Larry, a Category 4 cyclone (i.e. Category 2-3 Hurricane on the Saffir–Simpson hurricane wind scale) crossed the North Queensland coast near Etty Bay, south of Innisfail (BOM Australian Government, 2013). It was the first severe tropical cyclone to cross this part of the coast since Cyclone Winifred (Category 3) in February 1986 and the most devastating cyclone event in almost 90 years (Turton, 2008a). Described in the literature as a compact 'midget cyclone' with a radar eye diameter of only 20-25 km, this fast-moving system (Turton, 2008) delivered extremely destructive winds near its core, as well as heavy rain and flooding across a wide area extending from the coastal lowlands to the Atherton Tablelands and Queensland's Gulf country (Geoscience Australia, 2006). Larry's eye-wall at landfall was only 28 km north of Garners Beach (northern boundary of the Mission Beach study area).

Marked variations in wind gusts, particularly across elevated terrain, were observed leading to varying levels of damage across only relatively small distances. Initial estimates of maximum wind gusts were in the order of 55-65 ms^{-1} (~200-235 km/h) (Geoscience Australia, 2006) and up to 67 ms^{-1} (~240 km/h) (Turton, 2008) but have since been revised peaking at 56 ms^{-1} (~200 km/h) at 22:00hrs (1200 UTC) 19 March (BOM Australian Government, 2013). On approaching the coast from the Coral Sea, Severe Tropical Cyclone Larry had a minimum central barometric pressure reading of 940 hPa (20:00hrs 19 March 2006) and just before landfall recorded 980 hPa (06:00hrs 20 March 2006) (BOM Australian Government, 2013).

Turton (2008) noted that it was not surprising that Larry delivered a complex and patchy pattern of forest damage as it traversed topographically diverse terrain from coastal lowlands to Queensland's highest mountain peaks. A study of community and species-level cyclone damage in plots across north Queensland (10 affected to some degree by Larry), also commented on the 'patchy' nature of tree damage at the landscape and stand-level scales (Metcalfe et al., 2008). All affected plots were inland of the Mission Beach study area.

The most severe forest damage occurred ~30 km from the cyclone track with moderate to severe damage up to 50 km away (Turton, 2008). Satellite imagery confirmed that the most severe damage occurred within the immediate southern eye-wall of the cyclone near Clump Point, Mission Beach and this area experienced the largest storm surge (Callaghan & Otto, 2006). Although Severe Tropical Cyclone Larry's land-fall occurred at low tide, debris lines still measured 5.2 metres above mean high water mark at Bingil Bay, north of Clump Point.

The damage to rainforest communities within the study area (i.e. most severe impact zone) included multi-directional tree falls, almost complete defoliation of all canopy trees, most trees snapped, or uprooted or branches stripped from main stems and debris scattered across the forest floor (see Chapters 2 and 3). The most extensive damage was caused by south-east through to south-west and westerly winds (Callaghan & Otto, 2006). The level of damage to forests beyond the immediate eye-wall was significantly influenced by topography (e.g. exposure to upslope winds and leeward exposure to down-slope winds (Turton, 2008).

Larry generated significant interest in cyclone disturbance and response trajectories in the Australian Wet Tropics and the research which followed formed a special issue of *Austral*

Ecology in 2008 edited by Professor Steve Turton. In this issue Turton (2008a; 2008b) examined the landscape-scale impacts of this cyclone and compared them to earlier cyclone events (1858–2006).

1-3-3 Severe Tropical Cyclone Yasi (2011)

Almost five years after Larry, Severe Tropical Cyclone Yasi, a marginal Category 5 cyclone (i.e. Category 3-4 Hurricane on the Saffir–Simpson hurricane wind scale) made landfall near Mission Beach shortly after midnight on Thursday 3rd February 2011 (BOM Australian Government, 2013). The Bureau of Meteorology (BOM) identified Severe Tropical Cyclone Yasi as one of the most powerful cyclones to affect Queensland since records commenced, comparable to Cyclone Mahina (1899) and the two cyclones which devastated Mackay and Innisfail in 1918 (BOM Australian Government, 2017a). Yasi (2011) was a massive system in comparison to Larry (2006) (Turton, 2012). The eye wall crossed the coast directly over Dunk Island and Mission Beach (my study area) tracking west-southwest towards Tully and continued across north Queensland before weakening to a tropical low near Mount Isa two days later (BOM Australian Government, 2017a).

Although there are no verified observations of maximum wind gusts near the cyclone centre instrumentation at Tully Sugar Mill recorded a minimum central barometric pressure of 929 hPa as the eye passed over this location (west of Mission Beach) (BOM Australian Government, 2013). A minimum pressure of 930 hPa was recorded at Clump Point (Mission Beach) by the Department of Environment and Resource Management (DERM). By comparison, the 1918 cyclone which destroyed Innisfail, recorded a minimum pressure of 926 hPa at Mourilyan Sugar Mill (Callaghan, 2011b).

The Bureau of Meteorology (BOM) estimates Severe Tropical Cyclone Yasi had a sustained wind speed of 57 ms^{-1} (~205 km/h) with maximum wind gusts of 79 ms^{-1} (~285 km/h). Very destructive winds occurred over a very wide area from Innisfail to south of Cardwell. The meteorological station at South Mission Beach recorded 471mm of rainfall over a 24-hour period (BOM Australian Government, 2017a). A 5-metres tidal surge was observed at Cardwell (i.e. 2.3 metres above Highest Astronomical Tide HAT) at ~1:30am EST on a falling tide (BOM Australian Government, 2013). Estimates based on aerial surveys show that Cyclone Yasi affected, to some degree, approximately 55% of the Wet Tropics World Heritage Area (WTWHA) compared to about 30% of the same area for Cyclone Larry (Turton, 2012).

The immediate damage to rainforest communities within the study area (i.e. most severe impact zone) caused by Yasi was similar in many respects to Larry. Standing trees were almost completely defoliated. The main stems of trees were either snapped or branches stripped from the main stems with resulting debris scattered across the forest floor. Trees which were uprooted showed multi-directional tree falls. Forest disturbance was found to be highest along the path of the cyclone track, especially along the southern side, and levels of forest damage increased for sites with slopes facing the cyclone track and with increasing elevation and steepness (Negrón-Juárez et al., 2014).

Although many smaller cyclones occur frequently across this region, it is estimated that a return interval for severe tropical cyclones such as Larry and Yasi, is approximately 1 in 70 years (Turton, 2012). These two came together within five years. Notably, geomorphic evidence suggests that the frequency of severe tropical cyclone events may be seriously underestimated (Nott & Hayne, 2001; Nott, 2003) and a ‘super cyclone’ (i.e. never recorded in this region’s history) may have a return interval of about 200–300 years (Turton, 2012).

Cyclones of the magnitude and intensity of Larry and Yasi alter response trajectories, forest structure and floristic assemblages for at least many decades (Metcalfe et al., 2008) and likely much longer (Nott & Hayne, 2001; Nott, 2003; Webb, 1958). Cyclone Yasi triggered a repeat phase of chaotic release, uncertainty and reorganisation (Holling, 1973; Walker & Salt, 2006) raising questions over how these forests would respond after a second severe tropical cyclone in only a few years.

1-3-4 Future scenarios affecting tropical forests in the Wet Tropics Bioregion

Tropical cyclones in northern Australia’s Wet Tropics are likely to increase in intensity but decrease slightly in frequency (Turton, 2012). By the end of the 21st century anthropogenic warming will likely cause an increase in the intensity of tropical cyclones globally by 2-11% on average (according to model projections for an IPCC mid-range scenario) (GFDL & NOAA, 2017). Although the expected number of tropical cyclones is likely to decrease or have little change globally an increase in intense tropical storm occurrence is also projected with substantially higher average rainfall rates during these events (about 10-15% higher) than present-day tropical cyclones (GFDL & NOAA, 2017).

Future scenarios for increasing intensity of tropical cyclones globally suggest that long-term sustainability of ecosystems in the Wet Tropics may be threatened, potentially leading to dramatic shifts in regional vegetation types, structure and composition (Turton, 2012). Many potential successional trajectories exist after a cyclone event including repetition of the previous cycle or initiation of a new and novel pattern of succession (Lugo, 2008; Lugo, 2009), or collapse into a degraded state (Walker & Salt, 2006). Ecosystem collapse, particularly within fragmented tropical forests in the Wet Tropics, is a trajectory that has been extensively discussed in the post-Cyclone Larry literature (Laurance & Curran, 2008; Metcalfe et al., 2008; Turton, 2008). Debate continues over future resilience of storm-damaged fragmented tropical forests and whether these communities are locked into declining successional trajectories with a proliferation of edge-favoured pioneer species, loss of late-successional, large-fruited species, weed invasion and local extinctions (Murphy & Metcalfe, 2016; Turton, 2012).

1-4 Fragmentation in the Australian Wet Tropics Bioregion

In addition to an evolutionary history of natural cyclonic disturbance, the region's tropical rainforests continue to be impacted by habitat loss and fragmentation for agriculture and urban development. These impacts across varying spatial scales have given rise to a severely fragmented landscape across the Wet Tropics Bioregion. The Mission Beach coastal area conserves a rich mosaic of vegetation communities dominated by lowland rainforest (including complex mesophyll and notophyll vine forest). The protected area estate includes Djiru National Park (part of the Wet Tropics World Heritage Area) and Clump Mountain National Park (comprised of a series of small, unconnected and fragmented habitat). Additional rainforest fragments occur in public reserves and private land holdings and are often surrounded by an inhospitable landscape matrix of sugar-cane and banana plantations, cleared areas for cattle grazing and/or coastal urban development.

Small fragmented and isolated forests occurring within an increasingly human-modified matrix, are particularly susceptible to further degradation, loss of biomass and species extinctions (Laurance, 1991; Laurance et al., 1998) and proliferation of early successional species (Laurance et al., 2006). The process of fragmentation is marked by a progressive shift in floristic assemblages from long-lived, large-fruited forest-interior tree species with high wood density to disturbance-favoured pioneer and secondary tree species with relatively low wood density and low carbon storage (Laurance & Curran, 2008; Laurance et al., 2002; Laurance et al., 2006). Laurance et al. (2002, p. 614) describes a shift in forest fragments towards "matrix-tolerant generalists, disturbance-adapted opportunists and species with small area requirements". The structure and floristic composition is inevitably altered over time leading to mass recruitment of light-demanding species (Metcalfe et al., 2008) and hyper-abundance of edge-favoured generalists (i.e. pioneer and secondary species) and exclusion of forest-interior species (Laurance & Curran, 2008). Fragmented rainforest patches display a dramatic loss of large canopy and emergent trees (Laurance et al., 2000).

Edge effects alter physical gradients and microclimatic characteristics. For example, forest edges have higher light levels, greater variability in temperatures, reduced humidity, lower soil moisture levels and elevated leaf fall and leaf litter (Laurance et al., 1998; Laurance et al., 2002). In combination, these effects increase levels of desiccation and leaf fall and may expose the rainforest to fire hazard (Briant et al., 2010; Cochrane & Laurance, 2008; Laurance & Curran, 2008). Altered edge conditions also promote the growth and proliferation of lianas (i.e. robust woody vines), described as "important structural parasites" (Laurance et al., 2000, p.836), and development of "climber towers" (Webb, 1958) dominated by common liana species (e.g. *Merremia peltata, Entada phaseoloides* and *Faradaya splendida*). These robust lianas, together with climbing rattan-palms (e.g. *Calamus* spp.), may suppress regeneration and recruitment of tree seedlings. However, the role of lianas in terms of their successional pathways and different life-histories continue to be debated (Campbell et al., 2018; Laurance & Curran, 2008; Letcher & Chazdon, 2012; Schnitzer et al., 2012). Recent studies in the Australian Wet Tropics have failed to find an expected hyper-abundance of lianas (≥2.5cm diameter) in cyclone-impacted lowland rainforest, based on understorey measurements (Cox et al., 2019). Although lianas respond to disturbance with rapid growth, no evidence was found for outcompeting trees during dry periods of stress (Buckton et al., 2019).

Fragmented tropical forests appear to be inherently vulnerable to wind damage (Laurance et al., 1998). When forest edges are struck by strong winds, increased levels of turbulence can exacerbate windshear effects. In cyclone-disturbed fragmented forests these effects can penetrate several hundred meters from the forest edge (Laurance, 1991). Laurance et al. (2002) suggested that the proliferation of lianas along forest edges may further predispose trees to wind-shear damage and increased mortality. Long-term studies in Amazonian forests have shown a corresponding increase in the rates of stand-level tree mortality and damage due to edge effects (Laurance et al., 2000; Laurance et al., 1998). Tree mortality in fragments is unlikely to decline over time due to probable increases in downwind turbulence as edge permeability declines (Laurance, 2004). Reville et al. (1990) described how higher wind speeds result in more persistent eddies and that fragmented forest with broken canopies tend to generate gusts which are more frequent and erratic than over continuous forest (i.e. unbroken canopy) resulting in downward transfer of wind energy. Laurance (1997) suggested that these wind-generated impacts lead to increased structural damage up to 80-400 m from the forest edge. These effects can be further exacerbated by local topography, particularly in locations of topographic prominence such as hill-tops and ridgelines (Turton, 2008).

Notably, three studies located in the Australian Wet Tropics within the severe damage zone of Severe Tropical Cyclone Larry (2006), found no evidence to support the notion that edge effects increase the susceptibility of rainforest fragments to cyclone damage (Catterall et al., 2008; Grimbacher et al., 2008; Pohlman et al., 2008). First, the study by Grimbacher et al., (2008) on the Atherton Tablelands found that there were large effects across many components of forest structure but sites even within 30 m of forest edges in small and large remnants were not impacted more than the interiors of large remnants. Grimbacher et al., (2008) concluded that the high wind intensity from severe tropical cyclones likely overrides the modest wind protection provided by surrounding forest. A second study on the Tablelands found that sites 30–50 metres from the edge of rainforest fragments (5–40 ha in size) were no more vulnerable to cyclone damage than sites 80–260 metres from the edge of continuous forest (Catterall et al., 2008). A third study, located in the adjacent lowlands, also noted that distance to forest edge was not associated with the degree of cyclone damage for several different rainforest edge types (Pohlman et al., 2008).

Although Catterall et al. (2008) could not find evidence for wind-damage protection by a continuous forest canopy, they detected an interaction between fragmentation and disturbance on seedling recruitment during the period of post-cyclone recovery. Seedling communities were found to contain a higher diversity of exotic or alien species in fragments independent of the extent of cyclone damage (Catterall et al., 2008). Weed invasion interactions vary from one site to another and likely involve complex relationships between species assemblages, gap dynamics, disturbance history and successional life-history traits of individual species (Baret et al., 2008; Graham & Hopkins, 1990; Murphy et al., 2008; Rejmanek & Richardson, 1996; Whitmore, 1998).

The surrounding matrix strongly influences fragment dynamics, microclimatic gradients, tree mortality, species assemblages and connectivity (Laurance et al., 1998). Matrix “harshness” is defined as the ability of the matrix to degrade the primary forest (Gascon et al., 2000). Forest fragments embedded within landscapes of high matrix harshness (e.g. sugar-cane plantations where clearing, burning and/ or herbicides are routine operations) will be subject to greater edge effects. These will include changes in biomass, higher tree mortality rates than recruitment, promotion of weedy vegetation, impoverishment and potential collapse of interior forest within fragments (Gascon et al., 2000; Laurance et al., 2002). Matrix harshness and distance effects are also likely to affect vital pollinators and seed dispersers, potentially leading to local extinctions (Williams & Adam, 2010). Frugivore-mediated seed dispersal is vital to regeneration and seedling recruitment (Catterall et al., 2008). The iconic keystone species, *Casuarius casuarius johnsonii* (southern cassowary) is a key dispersal agent for large-fruited, late-maturing, shade-tolerant tree species in the Wet Tropics. In Mission Beach this species freely moves between varying habitats (including many small fragmented patches) and across the cleared matrix. The conservation management of this threatened species is a key requirement for continued resilience of these forests, particularly fragments.

Long-term studies based on Amazonian and Atlantic rainforests suggest that current conservation policy will fail to protect forest fragments from dramatic impoverishment of their structural and floristic assemblages (Oliveira et al., 2008; Pütz et al., 2011; Santos et al., 2008; Tabarelli et al., 2008; Tabarelli et al., 2012). Highly fragmented landscapes face a severe threat of biodiversity loss, a fact which clearly limits their status as conservation priorities (Oliveira et al., 2008). Even global hotspots of biodiversity are affected by these processes, raising issues of economic opportunity and potential value of ecosystem services (Myers et al., 2000).

Lugo (2009) argues that this focus on the negative aspects of declining trajectories ignores the vital role of secondary growth or fragmented forests in providing opportunities for successional trajectories towards mature forests (or successional cycles in cyclone-disturbed landscapes). This process of devaluing fragmented habitat gives the impression that the biota is incapable of adjusting, adapting or coping with the modified environmental conditions (Lugo, 2009). In the Australian Wet Tropics, similar arguments apply to hyper-disturbed and fragmented habitat, particularly remnant parcels located on private land and/ or mapped as secondary regrowth. Ultimately, forest fragments occurring within the coastal landscape of Mission Beach are valued low on a sliding scale of declining habitat quality (i.e. forest fragments are considered to have lesser value compared to neighbouring blocks of continuous rainforest) and therefore become expendable. As such, this focus on declining trajectories for fragmented habitat may perversely undermine arguments for avoiding further clearing in an already severely fragmented and highly contested landscape.

Lugo (2009) draws attention to the fact that without secondary forest regrowth, mature systems would have no opportunity to develop in modified landscapes. These forests are now an important part of human-modified tropical landscapes and increasingly they are composed of novel combinations of species not found in the original systems (Folke et al., 2004; Scheffer et al., 2001). This concept of valuing the ‘potential’ of fragments in terms of their successional trajectories and opportunities for renewal has important consequences for conservation outcomes. It is particularly pressing within the context of managing a mosaic of forest fragments within a largely cleared and rapidly urbanising landscape matrix.

1-5 Thesis objectives and structure

My study followed two severe tropical cyclone events, Cyclones Larry (2006) and Yasi (2011) in the Australian Wet Tropics. To date, no comparable investigation has measured the effects of successive severe tropical cyclone events on different forest habitats in lowland rainforest. Notably, a single study in the Yucatan Peninsula, Mexico, investigated the effects of two successive hurricanes but compared different successional stages (post-clearing) of seasonally-dry tropical forest, over a very short return interval (only 3 months apart) (Bonilla-Moheno, 2012). My study of lowland rainforest habitats followed a second severe tropical cyclone after a five-year return interval and includes no secondary regrowth sites.

The three following chapters of my thesis include two empirical chapters and a discussion paper as my final chapter. In Chapter 2, I examined the immediate effects of a second severe cyclone on the structural characteristics of different forest habitat types and compared family and species-level responses to damage and short-term survival rates. In Chapter 3, I investigated plant community and species-level assemblages across different forest habitat types and compared life-history successional characteristics of species for different habitat types. In Chapter 4, I synthesised the results of this study drawing conclusions about the influence of different forest habitat types on post-cyclone structure and composition and life-history successional characteristics. This chapter also examined evidence for an unexpected capacity for resistance and resilience in fragmented forests following the combined effects of two severe tropical cyclones and continuing fragmentation.

CHAPTER TWO

Immediate and short-term effects of Severe Tropical Cyclone Yasi on the structure and community-level characteristics of lowland rainforest

2-1 Introduction

Tropical cyclones are powerful modifiers of forest ecosystems generating immediate and long-term changes to forest structure and community composition (Keppel et al., 2010; Lugo, 2008). Severe tropical cyclones can kill and damage huge numbers of trees in a very short time span (Lugo & Scatena, 1996) but in the longer-term they drive diversity (Keppel et al., 2010), alter successional trajectories and create new evolutionary pathways (Lugo, 2008).

Patterns of forest damage immediately following cyclone events can be highly variable with some areas experiencing total devastation while neighbouring locations can be left virtually unscathed (Bellingham et al., 1992; Brokaw & Walker, 1991; Grove et al., 2000; Lugo et al., 1983; Lugo & Scatena, 1996; Turton, 2008; Walker et al., 1996; Webb, 1958). At the regional scale, forest damage is dependent upon wind velocity gradients and proximity to the storm track, as well as broader topographic effects of wind shielding or shadowing (Boose et al., 1994). At the landscape-scale, changes in topographic relief create varying levels of exposure and protection resulting in more severe forest damage on peaks and hills (Boose et al., 2004), especially on steeper slopes directly facing the cyclone track (Bellingham, 1991; Negrón-Juárez et al., 2014; Walker et al., 1996). These landscape-scale effects can create a complex and “very patchy” pattern of forest damage (Grove et al., 2000; Turton, 2008). At the stand-level scale, disturbance history and soil conditions, forest age structure, stem size, species composition and presence of pathogens can all influence the severity of cyclone damage (Basnet et al., 1992; Boose et al., 1994; Everham & Brokaw, 1996)

Typical cyclone damage to a tropical rainforest includes defoliation and reduction in crown areas, wind-throw and uprooting of trees, snapping of main stems and branches, breakage of robust lianas and smaller vines, dislodgement of epiphytes and scattering of broken debris (Bellingham et al., 1995; Boose et al., 1994; Brokaw & Walker, 1991; Everham & Brokaw, 1996; Lugo et al., 1983). Large trees are more susceptible to direct damage than small trees due to their own weight and decaying roots (Brokaw & Walker, 1991; Ostertag et al., 2005), but smaller trees are frequently damaged by falling large trees (Frangi & Lugo, 1991). Tropical cyclones have a dramatic impact on the size and extent of canopy gaps, changing forest structure from a continuous canopy cover with some gaps to a forest with large gaps and only occasional continuous canopy cover (Brokaw & Walker, 1991).

Tree species affected by frequent cyclones display life-history strategies which focus on resistance (i.e. slow-growing, late-maturing, shade-tolerant species with high wood density) or alternatively, resilience (typically early to mid-successional species with fast growth rates and low wood density) (Curran et al., 2008a; Curran et al., 2008b; Ostertag et al., 2005; Zimmerman et al., 1994). Ostertag et al. (2005) found that species with rapid growth rates sustained greater damage, reflecting these life-history strategies or trade-offs. Rapid recovery involving resprouting from snapped and leaning stems or damaged crowns typically occurs in species with low resistance, but high resilience to severe cyclone disturbance, within the first few weeks after these events. For tropical forests, this life-history strategy is the most common response after cyclone disturbance followed by sapling regrowth (Bellingham et al., 1994; Burslem et al., 2000; Zimmerman et al., 1994). By contrast, early successional species tend to have low rates of resprouting, but not always (Curran et al., 2008b), and depend on seed dispersal following severe cyclone damage (Uriarte et al., 2005). They are also more likely to die following snapping of the main stem (Basnet et al., 1992; Brokaw & Walker, 1991; Zimmerman et al., 1994). However, not all pioneer species share these traits. A study examining species responses to Severe Tropical Cyclone Larry in Mabi rainforest fragments on the Atherton Tablelands, Australian Wet Tropics, found evidence that one pioneer species, *Dendrocnide photinophylla,* had the highest rate of resprouting amongst six taxa (five identified to species level and one to generic level only – *Argyrodendron* spp.). Notably, *D. photinophylla,* recorded the lowest wood density whereas *Argyrodendron* spp. had the highest wood density, but lowest rates of resprouting (Curran et al., 2008b). This is an interesting result, as *Argyrodendron actinophyllum*, shows vigorous resprouting after disturbance, including severe storm damage (Ruting, 1979).

In a study of the impact of Hurricane Georges on a rehabilitated subtropical moist forest in Puerto Rico, Ostertag et al. (2005) found that frequent occurrence of wind-storms favoured disturbance-resistant, slower-growing species resulting in forest communities with shorter canopies and higher stem densities. Lowered, uneven canopies with scattered emergent trees and proliferation of smaller stems and vines are typical of cyclone-disturbed forests of the Wet Tropics of north Queensland (Webb, 1958), western Pacific (Keppel et al., 2010), eastern Pacific (Webb et al., 2014) and Madagascar (Gouvenain & Silander, 2003). Tropical forest ecosystems are increasingly under chronic stress from human activities. Frequent cyclone disturbance in conjunction with habitat fragmentation are likely to have complex effects on community structure and floristic assemblages (Houseman et al., 2008; Laurance & Curran, 2008; Lugo, 2008). Studies have found fragmented forests to be particularly susceptible to windstorm damage (Laurance & Curran, 2008), further degradation and species extinctions (Laurance, 1991; Laurance et al., 1998), proliferation of early successional species (Laurance et al., 2006), exclusion of forest-interior species and dramatic losses of large canopy and emergent trees (Laurance & Curran, 2008) and exotic weed invasion (Laurance, 1991; Laurance et al., 1998; Murphy & Metcalfe, 2016; Murphy et al., 2008; Turton & Siegenthaler, 2004).

In 2006, the lowland tropical rainforests of Mission Beach located in the Wet Tropics of north-eastern Queensland sustained a catastrophic impact by Severe Tropical Cyclone Larry, a Category 4 cyclone (Turton & Dale, 2007). Within less than five years, Severe Tropical Cyclone Yasi, a marginal Category 5 cyclone, again inflicted massive damage when it made landfall in the same area (BOM Australian Government, 2013). Yasi was a much larger system in comparison to Larry (Turton, 2012), and believed to be one of the most powerful cyclones to affect north Queensland since records commenced (BOM Australian Government, 2013, 2017a). This cyclone event was preceeded by more than double the average rainfall over six out of the seven previous months, recording 2,587mm compared to 1,182mm mean rainfall for this period (BOM Australian Government, 2018). Cyclone Yasi delivered a further 471mm of rainfall over a 24-hour period (BOM Australian Government, 2017a).

I investigated the effects of cyclone disturbance on forest structure across three different habitat types in Mission Beach, north Queensland immediately following Severe Tropical Cyclone Yasi. My research focussed on three questions: (1) Does forest structure (i.e. stem frequency, tree stem size (DBH) and basal area) differ across habitat types immediately following cyclone damage? (2) Does the type of cyclone damage affecting trees (e.g. minor defoliation, branch snapping, main stem (bole) snapping and/ or uprooting) vary across habitat types? (3) Are there different family and species responses to severe cyclone damage?

I hypothesized that the damage to forest structure caused by Severe Tropical Cyclone Yasi would be influenced by different habitat types and have varying impacts on different tree families and species. Specifically, I predicted that (1) continuous forest will retain larger trees with fewer small stems and less severe canopy damage compared to fragmented forest and forest edges; (2) higher rates of severe damage will be found in fragmented forests and forest edges compared to continuous forest; and (3) different tree families and species will show different types of cyclone damage.

2-2 Methods

2-2-1 Study area

The study area is the lowland rainforests of Mission Beach in the Australian Wet Tropics Bioregion of northern Queensland (17°49′–17°56′S, 146°04′–146°07′E) (Figure 2.1). The region experiences a tropical climate moderated by sea breezes with mean annual rainfall of 3,090 mm/yr and average monthly temperatures range from 19 - 26°C. Rainfall is strongly seasonal with a wet season from December to May. The study area covers the coastal lowlands and adjacent foothills. The village of Mission Beach lies roughly at the centre of the study area. The western foothills and southern wetlands form part of the Wet Tropics World Heritage Area (WTWHA). This protected area estate known as Djiru National Park (formerly Tam O'Shanter and Licuala State Forests) and Hull River National Park conserves a contiguous mosaic of natural habitat largely dominated by lowland tropical rainforest (i.e. regional ecosystems including simple to complex mesophyll and notophyll vine forest on a mix of substrates – granites, rhyolites, basalts and alluvium) (Kemp et al., 2007; Stanton & Stanton, 2005; Tracey, 1982; Tracey & Webb, 1975).

Lowland rainforests define the broad landscape context and visual character of Mission Beach. They conserve vital habitat and provide a varying level of connectivity with the immediate hinterland (Goosem et al., 2010). Apart from this corridor of remnant vegetation most of the surrounding western and northern lowlands have been cleared for sugar cane growing, banana plantations and cattle grazing. To the east along the coastal strip the protected area estate extends to a patch-work of small forest fragments including Clump Mountain National Park. This is a highly contested coastal environment, recognised internationally for its exceptional natural heritage values and scenic qualities, but also subject to significant development pressures, often leading to conflict over conservation outcomes. The coastal strip is comprised of a mix of forest fragments, agricultural land-uses and increasing urban development and network of road corridors (Laurance, 1997; Turton, 2012). Notably, most of the fragmented rainforest habitat within this coastal zone lies outside the protected area estate (Goosem et al., 2010). Private land-holdings conserve both continuous and fragmented patches of rainforest. The Mission Beach area retains only 14.5% of the original lowland tropical forest mosaic (<40m a.s.l.), habitat which is considered essential to conservation of a key frugivore disperser, the Southern Cassowary *(Casuarius casuarius johnsonii)* (Buosi & Burnett, 2006; Crome & Bentrupperbaumer, 1993; DEWHA, 2009; Hill et al., 2010; Latch, 2007; Moore, 2007; Westcott et al., 2005).

2-2-2 Vegetation communities

The study area supports a mosaic of natural vegetation communities rather than just a single rainforest ecosystem and these communities have considerable significance within the context of the Australian Wet Tropics Bioregion (Kemp et al., 2007; Metcalfe & Ford, 2009). The foothills and slopes of the study area are dominated by dense cyclone-disturbed, simple to complex-statured rainforests (locally classified as mesophyll and notophyll vine forests). In seasonally waterlogged areas, fan palms *(Licuala ramsayi* var. *ramsayi)* are conspicuous (Kemp et al., 2007; Stanton & Stanton, 2005; Tracey, 1982; Tracey & Webb, 1975). Cyclone disturbance is a key variable shaping the structure of these tropical forests, favouring disturbance-resistant, slow-growing species and resulting in forest communities with shorter canopies and higher stem densities (Ostertag et al., 2005). Even forests with little evidence of anthropogenic disturbance display these characteristics. Observing the scrub-like appearance of certain north Queensland lowland and foothill forests with low uneven canopies and dense vine tangles and taller rainforests with dense vine understoreys, Webb (1958) suggested that these forest structural features were related to past cyclone damage.

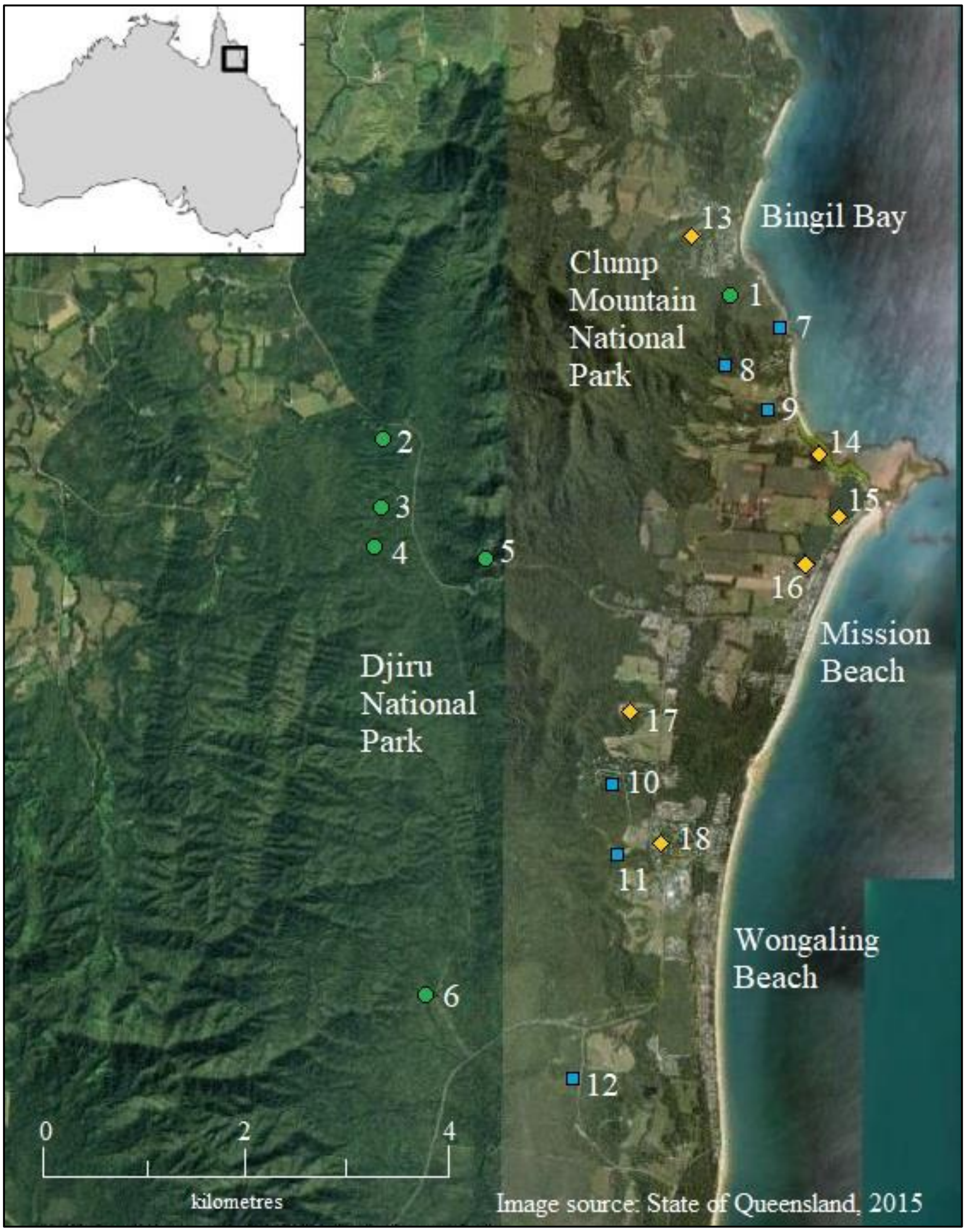

Figure 2.1. Mission Beach Study Area: Inset map shows location of study area in north-eastern Queensland, Australian Wet Tropics. Main map shows the location of sites: continuous forest sites shown as green circles (1-6); continuous forest edge as blue squares (7-12); and fragmented forest sites as yellow diamonds (13-18).

2-2-3 Historic fragmentation

Historically, almost all the study area has been logged since European settlement in the 1880s. Much of the lowland rainforest of the coastal strip and lower foothills was cleared by the early to mid-twentieth century (Hathaway, pers. comm., 2012) and selective logging continued until 1979 in some areas including in what is now the Djiru National Park. Notably, some small parcels of vegetation were specifically protected from logging or set aside in reserves including Clump Point National Park (O'Malley, pers. comm., 2016). Other areas were spared from clearing due to physical constraints, such as low soil fertility/ moisture holding capacity (e.g. Holocene sand deposits), seasonal water-logging (e.g. fan palm *(Licuala ramsayi)* swamps), coastal processes (e.g. North Hull River wetlands), or local topography, was too steep for logging or agriculture. For example, large tracts of rainforest within the former state forest lands (now Djiru National Park) remained unlogged due to either cyclone damage (described as "unproductive") or designated as "inaccessible" due to very steep topography (WTMA, 2013). Fragmented forests have also been retained along riparian corridors and within State lands along beaches, headlands and road reserves. Narrow, linear-shaped rainforest strips have also been retained as tall hedgerows or protective buffers in the rural landscape, particularly on the gently rolling basalt hill-slopes in response to prevailing south-easterly winds.

2-2-4 Study area sites and data collection

I sampled a total of 18 sites comprising six sites each in the following habitat categories: 1) Continuous forest sites; 2) Continuous forest edge sites; and 3) Fragmented forest sites. Continuous forest is defined as non-fragmented lowland rainforest covering >100 hectares (ha) in area. Sampling sites within this habitat were located a minimum distance of 100 metres to forest edges, in order to encounter forest habitat undisturbed from edges (Laurance et al., 2006). Continuous forest edge sites are located within 100 metres of the forest edge and perpendicular to the edge. Fragmented forest sites are located within fragmented rainforest blocks, patches and narrow riparian corridors (area < 10ha). These sites are separated from continuous forest by a cleared or modified land matrix (e.g. pasture, plantations, residential development and other infrastructure).

Fieldwork commenced after Cyclone Yasi in June 2011 and, completed 18 months later in November 2012. For each site, along a 50-metre transect I established three 10 x 10m plots (300 m^2 total) spaced 10m apart. Within each plot I identified to species and measured the stem diameters and heights of all damaged and resprouting (live) tree, shrub, palm and robust liana stems $\geq$ 5cm DBH at 1.3 m height above ground level. Uprooted or leaning live stems were measured 1.3 m along the stem length from the base. Standing dead trees (i.e. stags) were included in the data collection but I could not verify if mortality occurred pre-or post-Cyclone Yasi. Individual trees may have multiple stems (e.g. coppiced regrowth) and these were counted and measured (i.e. all stems $\geq$ 5cm DBH were recorded). These additional stems were included in total stem counts, DBH classes and basal area calculations for different habitat types.

Plant identifications were made on site, and where that was not possible, samples were taken for subsequent identification in the laboratory using the online interactive database and key of the Australian Tropical Rainforest Plants: Trees, Shrubs and Vines (Hyland et al., 2010) or the Australian Tropical Herbarium archival collection and Queensland Herbarium database. For this study, a robust liana is defined as a liana or climber capable of developing stems $\geq$ 5cm DBH and measured at 1.3 m height above ground level. Multiple stems of this size or larger arising from the same individual were shown with the diameter range (e.g. 5-10cm).

Fig. 2.2A.

Fig. 2.2D.

Fig. 2.2B.

Fig. 2.2E.

Fig. 2.2C.

Fig. 2.2F.

Figure 2.2(A-F). Three weeks after Cyclone Yasi, the forests of Mission Beach, north Queensland, Australia showed almost complete defoliation of all canopy trees (Fig.2.2A), most trees snapped (Fig.2.2B) or uprooted (Fig.2.2C) or branches stripped from main stems and debris scattered across the forest floor (Figs.2.2D and 2.2E). All trees exhibited varying levels of damage with the most common being snapped main stem (bole snapped). This cyclone event also triggered mast flowering within weeks in some species, particularly palms (e.g. *Licuala ramsayi* var. *ramsayi*) (Fig.2.2F)

Sites were re-visited in October-November 2012 and all individuals (including all trees, palms and robust lianas) were assessed for delayed mortality. Stem diameters were not re-measured on the second visit. Live and dead stem counts were adjusted accordingly. For example, some long-lived, late-maturing canopy trees (including *Ailanthus integrifolia* subsp. *integrifolia, Dysoxylum pettigrewianum. D. alliaceum* and *Syzygium graveolens*) displayed a burst of epicormic growth immediately after suffering severe damage from uprooting or partial uprooting. This initial growth response however was followed by delayed mortality some months later and these individuals were recorded as dead in the subsequent re-census.

Table 2.1. Cyclone damage classes and definitions

minor	partial defoliation, twig-snapping and minor branches snapped or damaged
branch snaps	major branches in crown and/ or upper multiple stems snapped
bole snap	main stem (trunk) snapped and/or leaning with all major branches stripped or broken
uproot	tree uprooted and fallen to ground

Damage classes and definitions were adapted from previous studies (Curran et al., 2008a; Webb et al., 2014; Zimmerman et al., 1994). After Cyclone Yasi, all trees exhibited some level of damage (Figure 2.2). To detect an association of cyclone damage with habitat types, I assigned each individual tree encountered into the following damage classes: (1) partial defoliation, twig snapping and minor branches snapped or damaged; (2) major branches in crown and/ or upper multiple stems snapped; (3) main stem (trunk) snapped and/or leaning with all major branches stripped or broken; and (4) tree uprooted and fallen to ground (Table 2.1). The extent of multi-directional tree falls, depth of debris piles and prolific growth of rattan palms (*Calamus* spp.) within all sites, however, made it difficult to determine the cause of snapped main stems (i.e. direct wind damage or from other tree falls). Trees were separated from palms and other species which have stems with no secondary vascular tissue (e.g. *Pandanus* and *Musa* spp.) or limited or weak secondary thickening of stems (e.g. *Lepidozamia hopei*.).

2-2-5 Statistical analysis

I tested the appropriateness of the data to fit the assumptions of ANOVA with Shapiro-Wilk and Bartlett's tests. For three different habitat categories, I tested the null hypothesis that there was no difference in 1) total number of stems (all live and dead standing stems; N = 1,482); and 2) basal area (live tree stems, including multi-stemmed individuals; N = 1,163) using single factor (one-way) ANOVAs. Basal area calculations for all live tree stems were summed for each habitat category (i.e. basal area expressed as m^2 ha^{-1} for each habitat category). I divided live tree stems into four tree size classes (DBH): 5-24cm, 25-49cm, 50-74cm and 75-100cm+ and examined associations between stem DBH and habitat categories using Chi-square tests. For my second hypothesis, Chi-square tests were used to detect an association between the four damage classes and habitat categories. All statistical analyses were conducted in the R software environment for statistical computing and graphics (R Core Team, 2015).

Finally, I compared the types of damage divided into classes (1-4) sustained by the most abundant plant families and species of trees in the ≥ 5cm DBH size class. Thirteen families were considered abundant based on a threshold of ≥ 25 individual trees in total from all sites. For common tree species, I set the number of individuals ≥ 10, which included 31 species out of a total of 152 tree species (not including palms, cycads, non-woody species (e.g. *Musa* sp.) and robust lianas).

2-3 Results

2-3-1 Relative stem frequencies for different habitat categories

I recorded a total of 1,482 (live and dead) stems ≥ 5cm DBH, including 176 species identified from 1,424 live stems. Although all live stems sustained some level of damage (i.e. minor to severe) following the impact of Severe Tropical Cyclone Yasi, a total of 96% of stems ≥ 5cm DBH resprouted within weeks of this event and continued to maintain vigour throughout the following months. I found only 55 individual trees with multiple stems ≥ 5cm DBH (total additional stems = 68) representing only 5% of all live trees (excluding palms, cycads, non-woody species (e.g. *Musa* sp.) and robust lianas). Trees that coppiced or exhibited a shrubby multi-stemmed habit include *Alstonia muelleriana, Apodytes brachystylis, Davidsonia pruriens, Eupomatia laurina*, *Hibiscus tiliaceus* and *Rhodomyrtus macrocarpa*. As multi-stemmed individuals represented such a small portion of the total database, no further analyses of reponses were conducted for this group.

I found that stem frequencies did not differ significantly between habitat categories ($F_{2,15}$ = 2.68, P = 0.101; one-way ANOVA; Figure 2.3). Nevertheless, the frequency of stems in continuous forest was more variable and lower than fragmented forest. Edge sites from continuous forest recorded the highest mean stem count and lowest variability among the six replicate sites (Figure 2.3).

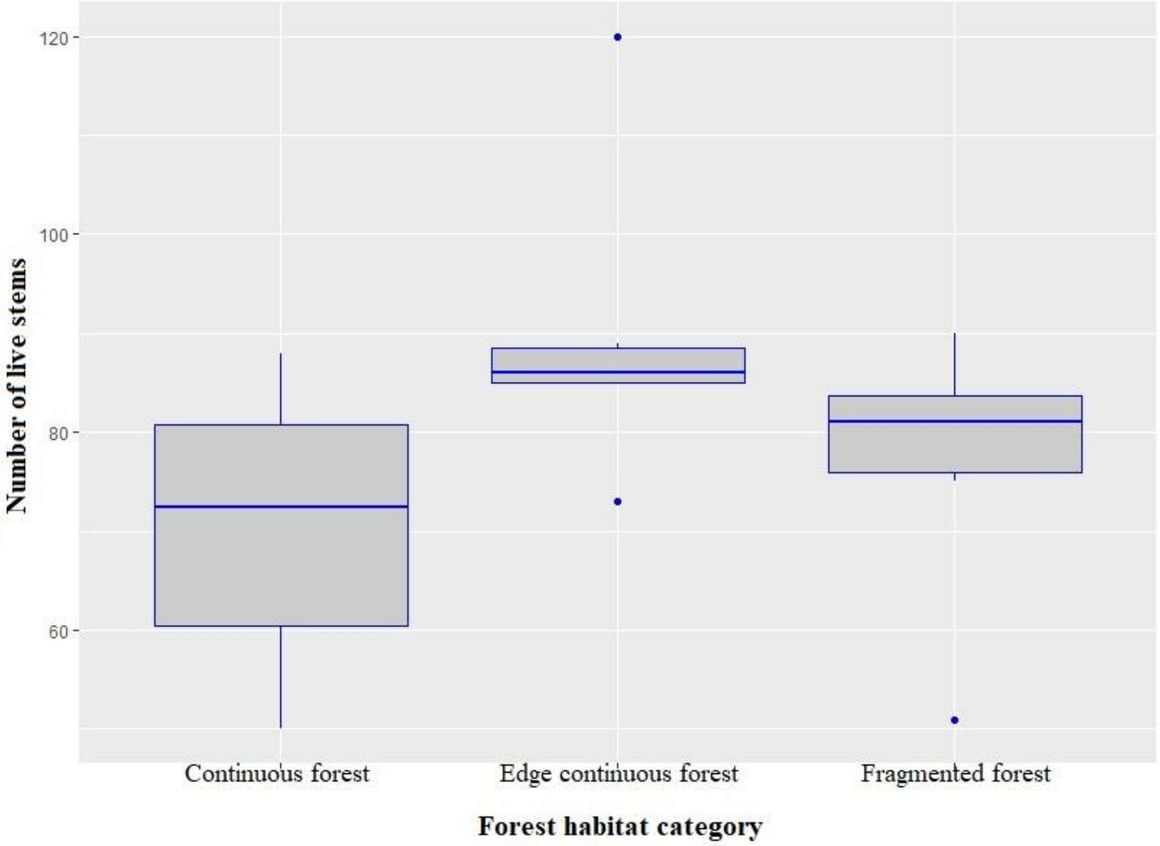

Figure 2.3. Boxplots showing relative stem frequencies for continuous forest, edge continuous forest and fragmented forest sites Mission Beach, north Queensland, Australia. Each box encompasses the 25th to 75th percentiles; the median is indicated by the boldest horizontal line and vertical lines outside the box indicate the 10th and 90th percentiles. Dots indicate outliers. A trend shows higher stem frequencies for forest edges and fragmented forest compared to continuous forest sites.

2-3-2 Relative basal areas of trees across different habitat categories

Basal area estimates showed a similar trend to stem number, with edge continuous forest sites recording the higher median values followed by fragmented forest sites, and then interior sites in continuous forest. No significant differences were detected in tree basal area values between habitat categories (One-way ANOVA, $F_{2,15} = 1.685$, $P = 0.219$; Figure 2.4).

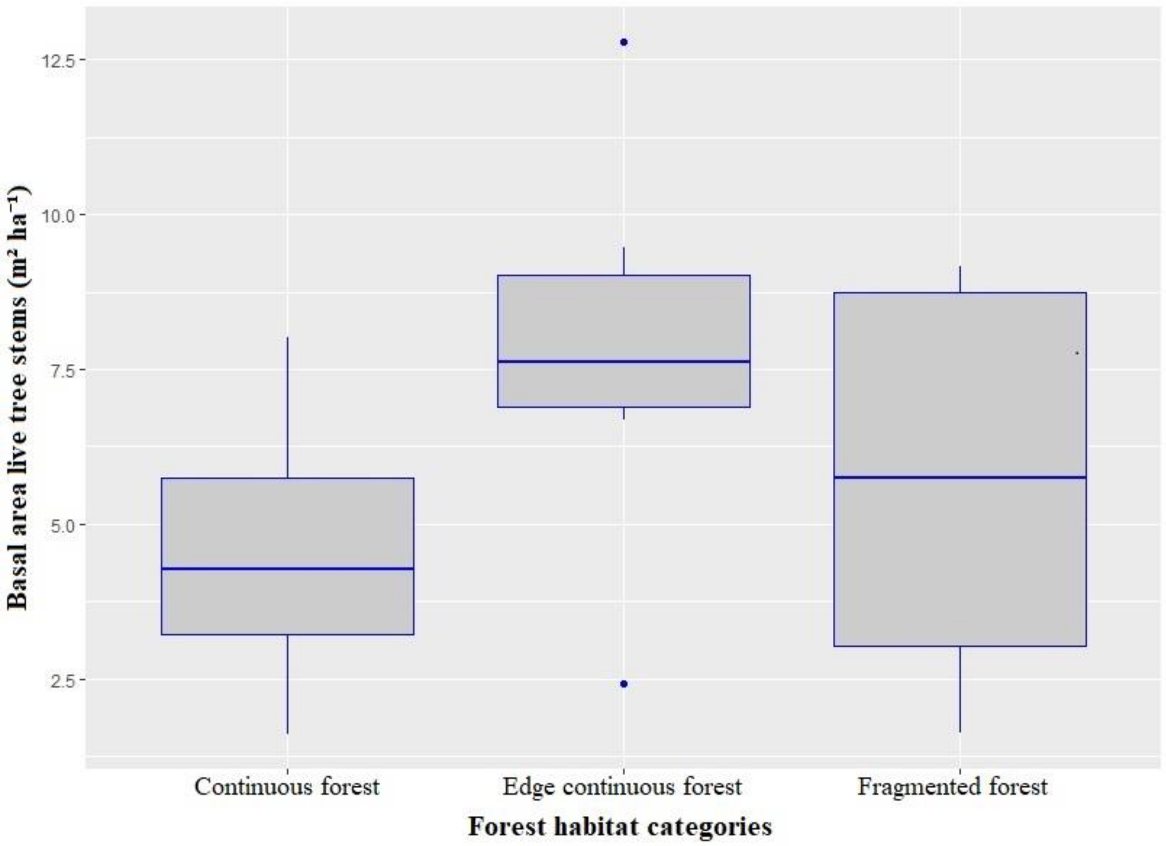

Figure 2.4. Boxplots showing the post-cyclone relative basal area of trees within continuous forest, edge continuous forest and fragmented forest sites. A trend shows relatively higher basal area of trees in forest edges and fragmented forest compared to continuous forest sites.

2-3-3 DBH classes and relative percentages of stems for different habitat categories

The demographic pattern in plant size classes were also similar across the three habitat types, with 83% of all live tree stems found in the smallest stem class (5-24cm DBH) and the number of stems decrease rapidly with increasing size class (Table 2.2; Figure 2.5). As a subset of this class, 48% of all tree stems are 5-9cm DBH, 19% are 10-14cm DBH, 9% are 15-19cm DBH and 7% are 20-24cm DBH (data not shown). A total of 5.5% of all live tree stems are ≥ 50cm DBH and half of these are found in edge continuous forest. By comparison, only 22% and 28% of this larger stem cohort (≥ 50cm DBH) occur in continuous forest and fragmented forest respectively. Tree stems ≥ 120cm DBH are rare (0.5% of all stems). None occur in fragmented forest sites; only 2 individuals were found in continuous forest and 4 in edge continuous forest (data not shown).

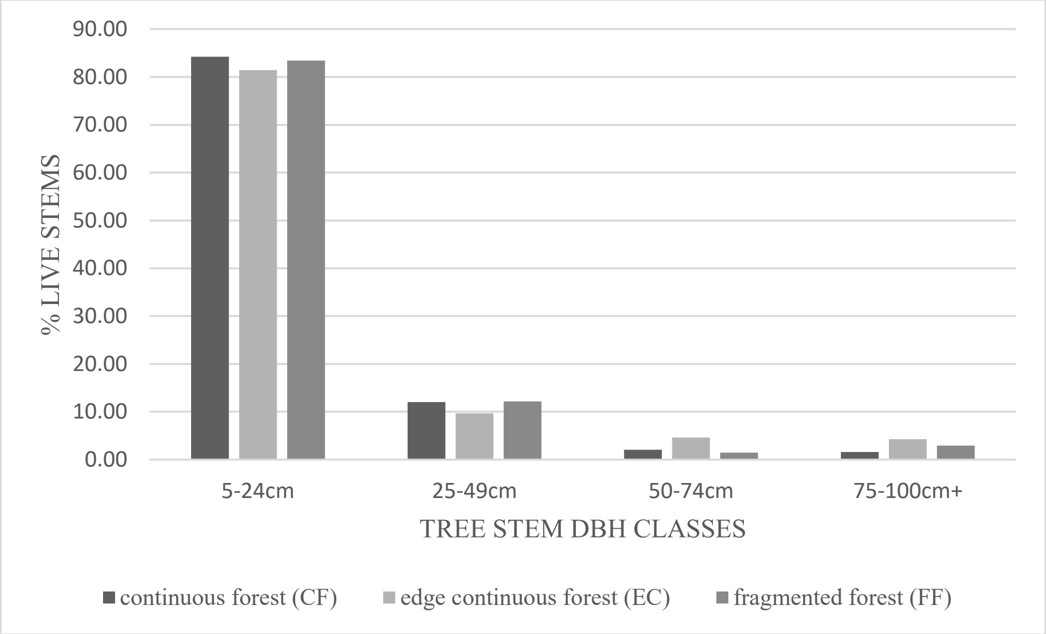

Figure 2.5. Percent of live tree stems for four DBH classes across three habitat categories.

Table 2.2. Three habitat categories showing the frequencies and percentages of tree stems for four DBH classes. A chi-square test indicated a significant relationship between habitat category and a single DBH class (50-74cm).

DBH class	**Continuous forest (CF)**		**Edge continuous forest (EC)**		**Fragmented forest (FF)**		**TOTAL**		**Chi-square test *(df = 2)***	
	n	**%**	**n**	**%**	**n**	**%**	**N**	%	X^2	***P***
5-24cm	321	84.25	302	81.40	343	83.45	966	83.06	2.61	0.27
25-49cm	46	12.07	36	9.70	50	12.17	132	11.35	2.36	0.31
50-74cm	8	2.10	17	4.59	6	1.46	31	2.67	6.65	**0.0361**
75-100cm+	6	1.58	16	4.31	12	2.92	34	2.92	4.47	0.11
Totals	**381**		**371**		**411**		**1163**			

I observed a significant relationship between habitat type and stem size class, with more larger stems observed in edge sites of continuous forest than expected, compared to the other habitats (size class 50-74cm DBH; $X^2 = 6.65$, $P = 0.0361$, $df = 2$; Table 2.2).

2-3-4 Habitat type influences the extent of damage to trees

All tree stems sustained some form of cyclone damage due to Severe Tropical Cyclone Yasi with 75% of stems showing stem or bole snapping (Table 2.3). Habitat type influences the level of cyclone damage to trees with greater numbers of less severe branch snaps ($X^2 = 14.27$, $P = 0.0008$, $df = 2$; Fig. 2.6B) recorded in continuous forest interior and edge sites compared to relatively higher numbers of snapped boles in fragmented forest sites ($X^2 = 11.10$, $P = 0.0039$, $df = 2$; Fig. 2.6C).

Table 2.3. Cyclone damage to tree stems across three habitat categories. A Chi-square test provided significant results for branch snaps and bole snap. Habitat categories influence damage classes.

Damage class	**Continuous forest (CF)**		**Edge continuous forest (EC)**		**Fragmented forest (FF)**		**TOTAL**		**Chi-square test *(df = 2)***	
	n	**%**	**n**	**%**	**n**	**%**	**N**	**%**	**X^2**	***p-value***
minor	30	7.88	48	12.94	42	10.22	120	10.32	4.20	0.12
branch snaps	57	14.96	52	14.02	24	5.84	133	11.44	14.27	**0.0008**
bole snap	273	71.65	260	70.08	335	81.51	868	74.63	11.10	**0.0039**
uproot	21	5.51	11	2.96	10	2.43	42	3.61	5.29	0.07
Totals	**381**		**371**		**411**		**1163**			

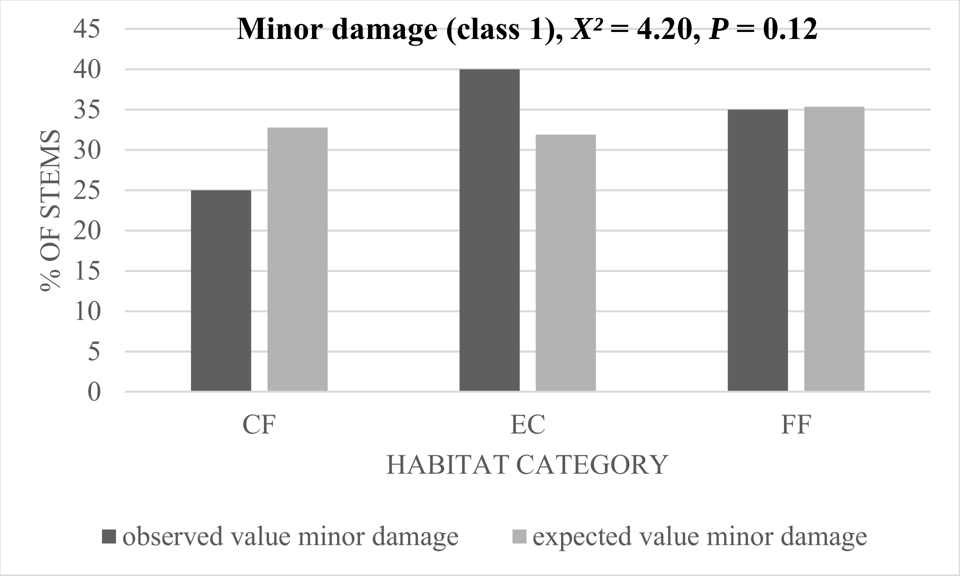

Figure 2.6A. Chi-square test showing differences in observed values (black bar) and expected values (grey bar) for minor damage across three habitat types: CF = Continuous forest, EC = Edge continuous forest; and FF = Fragmented forest. Only 10% of all stems showed minor damage (i.e. partial defoliation, twig-snapping and minor branches snapped or damaged). A Chi-square test however failed to find a significant result. Observed values were lower than expected values for continuous forest but higher for edge continuous forest and no difference for fragmented forest sites.

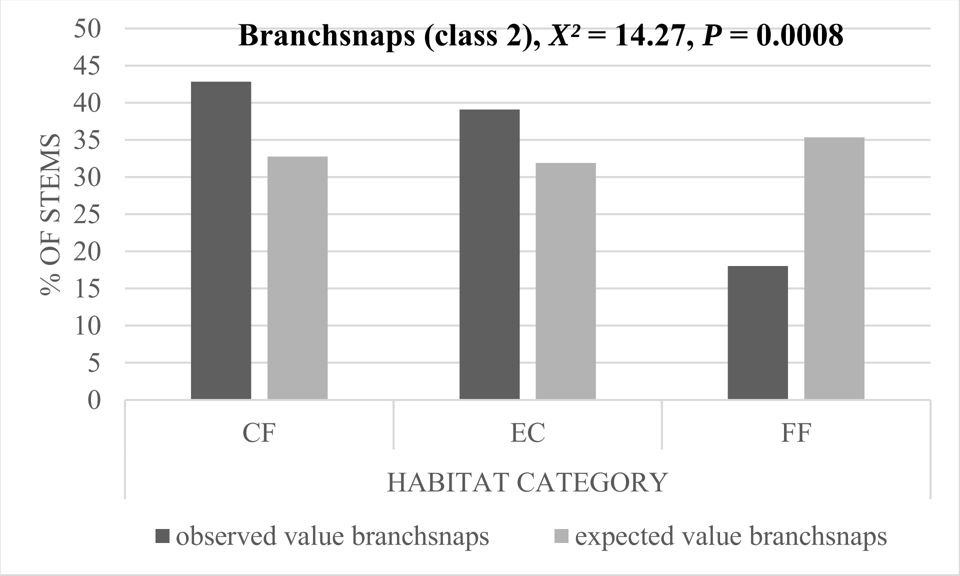

Figure 2.6B. A relatively small percentage of stems (11.4%) exhibit class 2 damage (i.e. major branches in crown and/ or upper multiple stems snapped). A Chi-square test detected an association between this class of damage and habitat type (P < 0.001). Continuous forest and edge continuous forest have significantly higher observed values for this damage class (43% and 39% of damaged stems) compared to fragmented forest (only 18% of stems) for continuous forest.

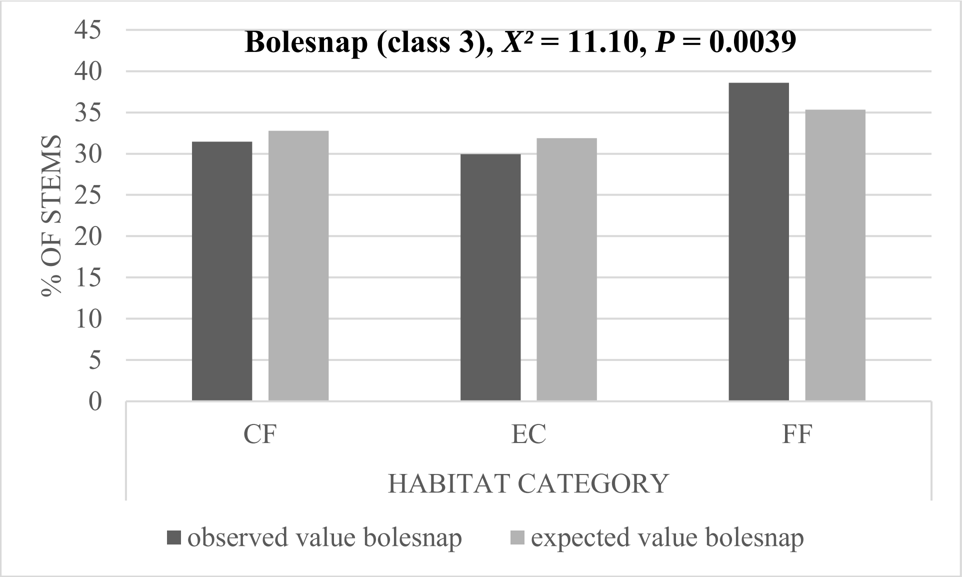

Figure 2.6C. Almost 75% of all stems exhibit class 3 damage (i.e. main stem (trunk) snapped and/or leaning with all major branches stripped or broken). This damage class is 6.5 times larger than the next damage class (i.e. class 2: major branches snapped). A Chi-square test detected an association between this class of damage and habitat type (P < 0.01). Fragmented forest has higher observed values (35%) compared to continuous forest and fragmented forest, 32% and 33% respectively. Observed values are slightly less than expected values for continuous forest and edge continuous forest but higher in fragmented forest.

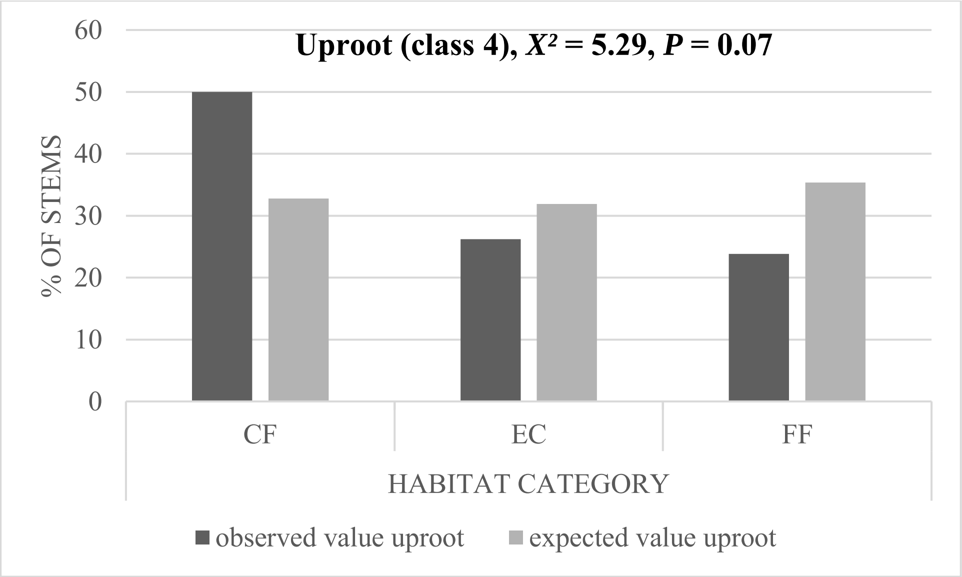

Figure 2.6D. Less than 4% of all stems were uprooted and fallen to ground (class 4 damage). This damage class has the smallest percentage of stems. A Chi-square test failed to find a significant result. Nevertheless, observed values were higher than expected values for continuous forest but lower for both edge continuous forest and fragmented forest sites. Continuous forest had about twice as many stems uprooted and fallen to ground compared to forest edges and fragmented forest.

2-3-5 Different types of cyclone damage across plant families and species

A comparison of different types of cyclone damage (classes 1-4) affecting the most common families of trees (not including palms) with ≥ 25 stems summed across all sites revealed some interesting trends (Table 2.4). All members of the Proteaceae family sustained some form of severe damage (i.e. snapping of main stem or bole, snapping of major branches or uprooting) whereas species within the Rutaceae and Anacardiaceae families demonstrated greater resistance to damage with approximately 1 in 5 stems recording only minor damage. The percentage of major branches and upper stems snapping varied markedly from 0-31% within these families. Snapping of the main stem (bole) is the dominant damage class for all families (av. 74.96 ± SD 9.68) ranging from 61% in Rutaceae to 87% in Sapindaceae. All trees in these families share vigorous resprouting strategies after cyclone damage. By comparison, relatively few stems were uprooted. Myrtaceae recorded the highest number of uprooted trees (7.25% of all trees) while not a single tree was uprooted in five families: Anacardiaceae, Elaeocarpaceae, Icacinaceae, Meliaceae and Sapindaceae.

Tree species showed different types of damage (Table 2.5). The most abundant tree species (i.e. species with ≥ 10 individuals summed across all sites) recorded snapped main stems as the major damage response (av.75.93 ±SD 14.55). *Citronella smythii* (Icacinaceae) and *Cryptocarya oblata* (Lauraceae) had snapped boles for all individuals. Other species with very high rates of snapped main stems (≥ 90% of all individuals) included *Apodytes brachystylis*, *Cryptocarya mackinnoniana*, *Dysoxylum alliaceum*, *Elaeocarpus angustifolius* and *Myristica insipida*. Species with the lowest proportion of snapped boles included *Dysoxylum pettigrewianum* (40.2%), *Castanospermum australe* (50%), *Polyscias australiana* (53%), *Intsia bijuga* (54.5%) and *Litsea leefeana* (56%). Notably, the tall canopy species *Dysoxylum pettigrewianum* had the lowest proportion of snapped boles but the highest proportion of snapped major branches (53%). *Litsea leefeana* had the highest proportion of uprooted individuals (25%). A total of 71% of the most abundant tree species did not record uprooting as a damage response.

Notably, the mid-to late successional canopy species, *Flindersia schottiana* showed exceptionally high resistance to wind damage with only minimal damage (class 1) to large compound leaves. This species is relatively uncommon in the Mission Beach study area. Only two *F. schottiana*, both mature specimens, were recorded in my study and these occurred within separate fragmented forest sites. No other canopy species were recorded in this damage class.

Table 2.4. Frequency and percentage distribution of damage classes (1-4) sustained by trees from the 13 most abundant plant families (≥ 25 stems present).

FAMILIES	**minor (1)**		**branch snaps (2)**		**bole snap (3)**		**uproot (4)**		**Totals**
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	
ANACARDIACEAE	5	20.00	0	0.00	20	80.00	0	0.00	25
APOCYNACEAE	3	4.48	7	10.45	53	79.10	4	5.97	67
ARALIACEAE	6	11.54	16	30.77	27	51.92	3	5.77	52
ELAEOCARPACEAE	2	7.14	4	14.29	22	78.57	0	0.00	28
EUPHORBIACEAE	6	10.71	4	7.14	43	76.79	3	5.36	56
ICACINACEAE	15	11.45	6	4.58	110	83.97	0	0.00	131
LAURACEAE	10	8.77	11	9.65	86	75.44	7	6.14	114
MELIACEAE	1	1.41	14	19.72	56	78.87	0	0.00	71
MYRISTICACEAE	10	8.06	10	8.06	102	82.26	2	1.61	124
MYRTACEAE	10	14.49	5	7.25	49	71.01	5	7.25	69
PROTEACEAE	0	0.00	10	25.64	27	69.23	2	5.13	39
RUTACEAE	24	22.86	14	13.33	64	60.95	3	2.86	105
SAPINDACEAE	2	5.26	3	7.89	33	86.84	0	0.00	38
TOTAL	**94**	**100.00**	**104**	**100.00**	**692**	**100.00**	**29**	**100.00**	**919**

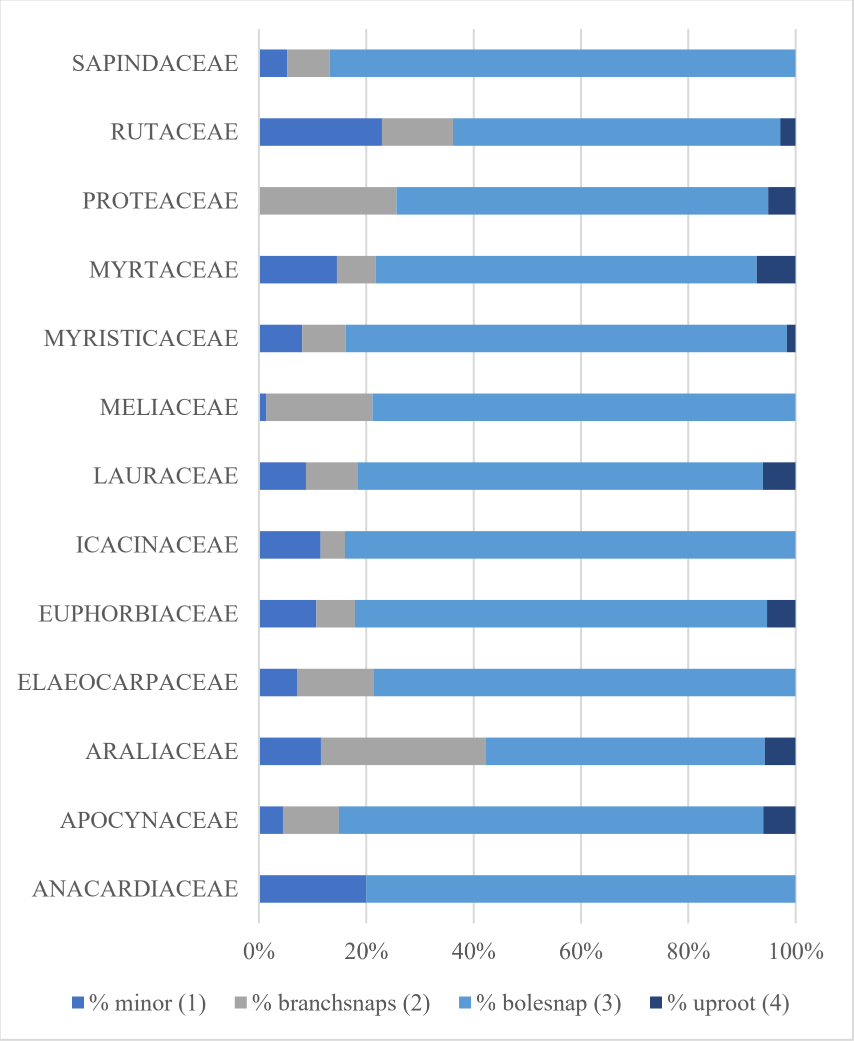

Figure 2.7. Percent of individuals within plant families in each of four damage classes. Families are arranged alphabetically (bottom to top). Damage classes from left to right are: (1) minor, (2) branch snaps, (3) bole snap, (4) uprooted.

Table 2.5. Frequency and percentage distribution of damage classes (1-4) sustained by the most abundant tree species ≥ 10 stems present.

TREE SPECIES ≥ 10 stems	**FAMILIES**	**minor (1)**		**branchsnaps (2)**		**bolesnap (3)**		**uproot (4)**		**Totals**
		n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	
Ailanthus integrifolia subsp. *integrifolia*	SIMOURABACEAE	2	16.67	1	8.33	9	75.00	0	0.00	**12**
Aleurites rockinghamensis	EUPHORBIACEAE	5	33.33	0	0.00	10	66.67	0	0.00	**15**
Alstonia muelleriana	APOCYNACEAE	0	0.00	1	4.76	16	76.19	4	19.05	**21**
Alstonia scholaris	APOCYNACEAE	2	11.76	3	17.65	12	70.59	0	0.00	**17**
Apodytes brachystylis	ICACINACEAE	0	0.00	1	6.25	15	93.75	0	0.00	**16**
Brombya platynema	RUTACEAE	17	23.29	11	15.07	45	61.64	0	0.00	**73**
Canarium vitiense	BURSERACEAE	1	5.56	4	22.22	13	72.22	0	0.00	**18**
Cardwellia sublimis	PROTEACEAE	0	0.00	3	27.27	8	72.73	0	0.00	**11**
Castanospermum australe	FABACEAE	2	12.50	5	31.25	8	50.00	1	6.25	**16**
Citronella smythii	ICACINACEAE	0	0.00	0	0.00	13	100.00	0	0.00	**13**
Cryptocarya mackinnoniana	LAURACEAE	1	10.00	0	0.00	9	90.00	0	0.00	**10**
Cryptocarya oblata	LAURACEAE	0	0.00	0	0.00	15	100.00	0	0.00	**15**
Davidsonia pruriens	CUNONIACEAE	0	0.00	3	25.00	9	75.00	0	0.00	**12**
Dysoxylum alliaceum	MELIACEAE	0	0.00	1	5.26	18	94.74	0	0.00	**19**
Dysoxylum pettigrewianum	MELIACEAE	1	5.89	9	52.94	7	41.17	0	0.00	**17**
Elaeocarpus angustifolius	ELAEOCARPACEAE	0	0.00	2	9.52	19	90.48	0	0.00	**21**
Endiandra hypotephra	LAURACEAE	0	0.00	4	23.53	13	76.47	0	0.00	**17**
Gomphandra australiana	ICACINACEAE	15	14.71	5	4.90	82	80.39	0	0.00	**102**
Intsia bijuga	CAESALPINIACEAE	2	18.18	3	27.27	6	54.55	0	0.00	**11**
Litsea leefeana	LAURACEAE	2	12.50	1	6.25	9	56.25	4	25.00	**16**
Macaranga inamoena	EUPHORBIACEAE	0	0.00	3	15.00	16	80.00	1	5.00	**20**
Musgravea heterophylla	PROTEACEAE	0	0.00	3	23.08	10	76.92	0	0.00	**13**
Myristica globosa subsp. *muelleri*	MYRISTICACEAE	10	9.17	10	9.17	88	80.73	1	0.93	**109**
Myristica insipida	MYRISTICACEAE	0	0.00	0	0.00	14	93.33	1	6.67	**15**
Polyscias australiana	ARALIACEAE	3	6.67	15	33.33	24	53.33	3	6.67	**45**
Rockinghamia angustifolia	EUPHORBIACEAE	0	0.00	1	7.69	11	84.62	1	7.69	**13**
Semecarpus australiensis	ANACARDIACEAE	4	23.53	0	0.00	13	76.47	0	0.00	**17**
Syzygium claviflorum	MYRTACEAE	4	26.67	0	0.00	11	73.33	0	0.00	**15**
Syzygium cormiflorum	MYRTACEAE	0	0.00	0	0.00	10	76.92	3	23.08	**13**
Toechima erythrocarpum	SAPINDACEAE	1	8.33	2	16.67	9	75.00	0	0.00	**12**
Wrightia laevis	APOCYNACEAE	1	3.70	3	11.11	23	85.19	0	0.00	**27**
TOTALS		73	100.00	94	100.00	565	100.00	19	100.00	**751**

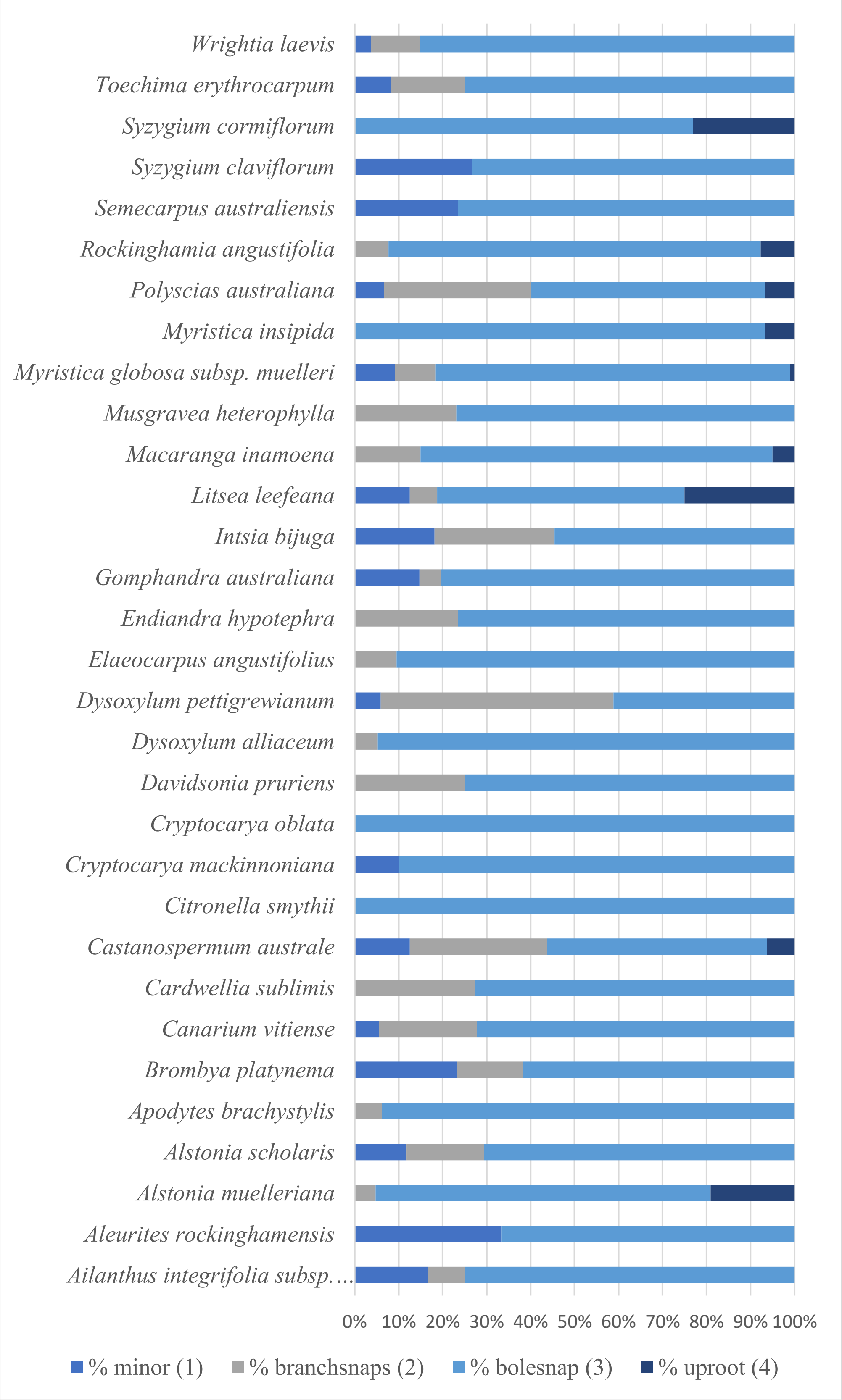

Figure 2.8. Percent of individuals within species in each of four damage classes. Species are arranged alphabetically (bottom to top). All trees sustained some level of damage. Damage classes from left to right are: (1) minor, (2) branch snaps, (3) bole snap, (4) uprooted.

2-4 Discussion

The effects of severe cyclone disturbance and fragmentation on community structure were explored in three different habitat types in the lowland rainforest of north-eastern Australia. Despite my expectations that tree stem frequencies would be lower in continuous forest sites compared to fragmented forest sites (especially as this study includes small stems ≥ 5cm DBH), I found no significant difference in tree stem frequencies between the three forest habitat categories.

As expected across all sites, tree stem frequency was far higher in the small size classes (DBH). As a subset of this smallest tree size class, 28% of all stems in my study were in the 10-19cm DBH class. If the 5-9cm DBH class is removed from the total stem count, the 10-19cm DBH class accounts for 58% of all stems. By comparison, a study of the impact of Cyclone Larry on the critically endangered Mabi Type 5b rainforest, in the Atherton Tablelands found about 40% of all tree stems were in the 10-20cm DBH size class and stem numbers generally decreased with increasing size class (Curran et al., 2008a). Similarly, Laurance et al. (2009), in a study of forest dynamics in the Amazon basin found that the smallest tree size class (10-20cm DBH) contained 64% of all stems. These studies show a similar trend in the frequency distribution curve for all tree size classes. Curran et al. (2008a) found that tree size classes had no influence on the type of damage sustained by trees whereas other studies have shown larger trees (as measured by DBH) sustain higher levels of wind damage and mortality (Basnet et al., 1992; Ostertag et al., 2005; Putz et al., 1983). Metcalfe et al. (2008) found only one out of ten plots in their study showed a correlation between damage-classes and stem size (DBH). Contrary to my hypothesis, no significant difference was detected in mean basal area $m^2\ ha^{-1}$ between habitat types, but overall a trend was observed with edge continuous forest recording the highest total ($46.61\ m^2\ ha^{-1}$) and interestingly, continuous forest recorded the lowest values (27.29 $m^2\ ha^{-1}$) rather than fragmented forest (34.17 $m^2\ ha^{-1}$).

2-4-1 Forest habitat categories influence type of damage sustained by trees

My results suggest that fragmented forest may be more susceptible to stem snapping but snapping of major branches and upper stems is more likely to occur in continuous forest and their edges. Some studies have shown that fragmented forests are more vulnerable to the effects of strong wind (Laurance & Curran, 2008; Laurance et al., 2006; Turton & Siegenthaler, 2004), while other studies have found no evidence to support the notion that edge effects increase the susceptibility of rainforest fragments to cyclone damage (Catterall et al., 2008; Grimbacher et al., 2008; Pohlman et al., 2008).

2-4-2 Uprooting vs. snapped boles (trunks)

Less than 4% of all trees in my study were uprooted compared to 75% of trees having their main stem or bole snapped. About 11% of trees had major branches in their crowns and/ or upper multiple stems snapped. Only 10% of all trees in my study sustained minor damage including partial defoliation, twig snapping and minor branches snapped or damaged. Putz et al. (1983) reported higher rates of uprooted trees (25% of all trees) but similar rates of snapped trees (75%) while Webb et al. (2014) found about 23% of all trees were uprooted and 35% snapped (32% sustained less severe damage) during Cyclone Olaf, a Category 5 cyclone. By comparison, Curran et al. (2008a) recorded severe limb (branch) failure as the most common form of damage (25% of all trees) followed by snapped main stems (20%). This is a surprisingly low figure for snapped main stems, particularly as Mabi forest, in the Australian Wet Tropics, has been subject to extensive fragmentation. My results showed snapping of main stems was higher in fragmented forest compared to continuous forest.

Furthermore, I found a 3.75-fold increase in snapped main stems following Cyclone Yasi, compared to results for Cyclone Larry (Curran et al., 2008a). Similar results for increased rates of snapped stems have been found in the Neotropics following repeated hurricane damage (Uriarte et al., 2019).

Catterall et al. (2008) reported that large trees >100cm DBH sustained the highest overall damage levels to standing stems of any tree size class and that standing tree density in this size class was reduced by an average of 53% across all sites. While some studies have reported similar high rates of wind damage for larger trees (Ostertag et al., 2005; Putz et al., 1983), others have found no evidence for tree size influencing mortality (Bellingham et al., 1995; Curran et al., 2008a). My observations support these findings that relatively few large trees were left standing after Cyclone Larry (2006) (N. Ruting, unpubl. data 2010), and this likely reduced the number of trees available for this damage class for Cyclone Yasi (2011).

Cyclone Larry followed months of relatively low rainfall with five out of six of the preceding months recording well below average rainfall (BOM Australian Government, 2018). It has been suggested that the high rate of snapped boles compared to uprooting may be attributed to stable ground conditions providing secure anchorage for tree roots (Metcalfe et al., 2008). Webb (1958) commented on the rarity of uprooted trees after Cyclone Agnes and linked the damage response to relatively dry soil conditions. Rainfall was below average over spring-early summer but slightly above average for the two months before Cyclone Agnes (BOM Australian Government, 2018). By contrast, Cyclone Yasi followed many months of above average rainfall. Yasi was preceded by more than double the average rainfall over six out of the seven previous months, recording 2,587mm compared to mean rainfall of 1,182mm for this period (BOM Australian Government, 2018). This cyclone also brought a further 471mm of rainfall over a 24-hour period (BOM Australian Government, 2017a). These relatively wet and potentially unstable conditions for root anchorage would suggest there should have been a far higher rate of uprooted trees in my study. I also expected far higher rates of mortality for all forest habitat types due to weakened trees succumbing to a second severe cyclone. However, my results showed most trees with snapped main stems resprouted vigorously within only a few weeks of cyclone damage. All cyclone-damaged forest habitats in my study show an exceptionally high level of resilience, with 96% of all standing stems displaying vigorous growth after eighteen months. By comparison, uprooted trees showed a mixed survival response, dependent upon the extent of damage to the root-plate (Zimmerman et al., 1994) and species traits (Webb et al., 2014). I found many smaller understorey species, including multi-stemmed individuals, had a capacity for resprouting after extensive root damage whereas, uprooted canopy tree species (75-100cm+ DBH) had high rates of mortality, with root-plates either largely, or completely, torn out of the ground.

2-4-3 Common species responses to cyclone damage

The main stems of most of the common tree species snapped during the cyclone event. All *Citronella smythii* (Icacinaceae) and *Cryptocarya oblata* (Lauraceae) recorded only this type of damage. Other species with very high proportions of snapped boles included *Apodytes brachystylis*, *Cryptocarya mackinnoniana*, *Dysoxylum alliaceum*, *Elaeocarpus angustifolius* and *Myristica insipida*. *Dysoxylum pettigrewianum*, a tall canopy species with some of the largest recorded tree sizes (as measured by DBH), was the only species to resist this trend, snapping more major branches and upper stems, (53% vs. 41% respectively). Zimmerman et al. (1994) noted that tree species resistant to stem damage were more likely to suffer branch failures (i.e. trees with higher wood density have less ability for their branches to bend and twist in high winds, thus leading to breakage). It was also suggested that this response is related to the relative size of lateral branches to the main stem (bole), or angle of branching. Another large canopy species in my study, *Castanospermum australe* exhibited extensive damage to upper crowns, including breakage of all major branches (31%) but a larger proportion had snapped boles (50%). All trees in these damage classes showed vigorous resprouting along the upper trunk and snapped branch stubs within weeks. Only 6% of *C. australe* were uprooted. Curran et al. (2008b) found very different cyclone damage responses in this canopy species in the Mabi forest community in the Atherton Tablelands: uprooting (~50%), snapped boles (~30%) and major branch damage (~20%).

In my study, only 9 out of 31 common species recorded uprooting as a damage response and the proportions of individuals tended to be very low. Two sub-dominant/ understorey species *Litsea leefeana* (Lauraceae) and *Alstonia muelleriana* (Apocynaceae) and the canopy species *Syzygium cormiflorum* (Myrtaceae) showed a tendency for uprooting. Other species with low proportions of uprooted individuals included *Castanospermum australe, Macaranga inamoena, Myristica globosa* subsp. *muelleri, Myristica insipida, Polyscias australiana* and *Rockinghamia angustifolia.* Amongst these species I found many partially uprooted trees which continued to grow vigorously. Some uprooted understorey species exhibit strategies for resprouting and coppicing from fallen stems providing they retain some undamaged roots (e.g. *Macaranga inamoena* and *Eupomatia laurina*). Putz et al. (1983) suggested that some uprooted trees have the capacity to resprout vigorously if some undamaged roots are retained in the soil and this gives them a positional advantage over seedlings. Webb et al. (2014) suggested survival rates after uprooting are exclusively underpinned by species traits. In my study, I found some tall canopy species (e.g. *Syzygium alliiligneum, Dysoxylum alliaceum* and *Flindersia pimenteliana*) showed an initial pulse of resprouting along fallen trunks but new growth withered and died within 3-4 months.

Some common species displayed a high level of resistance to cyclone damage (i.e. partial defoliation, twig-snapping and minor branches snapped or damaged) however this response within species occurred with no clear trend across different forest habitat types. These species included *Aleurites rockinghamensis, Semecarpus australiensis, Syzygium claviflorum* and *Brombya platynema.*

CHAPTER THREE

Community and species-level responses to fragmentation and severe cyclone disturbance in lowland tropical rainforest in north Queensland

3-1 Introduction

Habitat fragmentation is widely considered to be the greatest single threat to global tropical forests and biodiversity (Laurance et al., 2007; Laurance et al., 2006; Wright & Muller-Landau, 2006). Most of the world's tropical forest habitat (excluding the Congo and Amazon basins) has been transformed into archipelagos embedded within human-modified landscapes (Gascon et al., 2000; Oliveira et al., 2008; Tabarelli et al., 2008). Globally, old growth tropical forest is being replaced by secondary and logged forest (Wright & Muller-Landau, 2006), leading to a predominance of impoverished early-successional forest assemblages (Laurance et al., 2006; Pütz et al., 2011; Santos et al., 2008; Tabarelli et al., 2008).

Fragmented forest patches may fail to provide adequate habitat for rare or endangered species (e.g. local examples of endemism) (Wilcox & Murphy, 1985) or disrupt specialist mutualisms between plants and pollinators or seed-dispersers (Lopes et al., 2009; Williams & Adam, 2010), and particularly crucial is the loss of large-vertebrate frugivores that are vital for the dispersal of long-lived, shade-tolerant species (Costa et al., 2012; de Melo et al., 2006). Furthermore, edge-effects and surrounding matrix quality and extent will strongly influence fragment dynamics, species assemblages and connectivity (Gascon et al., 2000; Laurance et al., 1998; Laurance et al., 2007).

Few natural populations or communities persist in a static or near equilibrium condition (Sousa, 1984). These ecosystems are constantly being configured and reconfigured by extreme events rather than average conditions (Walker & Salt, 2006). Community responses to environmental or anthropogenic disturbance are often expressed as changes in species composition (Attiwill, 1994; Houseman et al., 2008), with disturbance events such as tropical cyclones often triggering varying responses in forest communities (Lugo et al., 1983; Lugo & Scatena, 1996). Succession may follow many paths to forest recovery (Lugo, 2009) and species composition will be influenced by environmental variables such as seed availability (Graham & Hopkins, 1990; Whitmore, 1998), pollination and dispersal mechanisms (Williams & Adam, 2010) and competition (Lugo, 2009). Furthermore, fragmentation may act synergistically with climate change, altering long-term species assemblages (Whitmore, 1998).

The rainforests of the Wet Tropics of north-eastern Queensland have a history of natural cyclonic disturbances which have shaped the evolution of life history strategies that influence the structure and composition of forest communities (Webb, 1958). In addition to natural hyper-disturbance, this region, particularly the narrow coastal strip, is increasingly impacted by fragmentation for urban development. The Mission Beach study area is undergoing a process of intensification of land uses with expansion of coastal urban development and infrastructure leading to further loss of habitat and fragmentation (Hill et al., 2010).

Fragmented rainforest occurs within an increasingly human-modified matrix, making these habitats particularly susceptible to further degradation, loss of biomass and species extinctions (Laurance, 1991; Laurance et al., 1998) and proliferation of successional species (Laurance et al., 2006). The process of fragmentation is marked by a progressive shift in floristic assemblages from long-lived, large-fruited forest-interior tree species with high wood density to disturbance-favoured pioneer and secondary tree species with relatively low wood density and low carbon storage (Laurance & Curran, 2008; Laurance et al., 2002; Laurance et al., 2006). Laurance et al, (2002) describes a shift in the communities of forest fragments towards “matrix-tolerant generalists, disturbance-adapted opportunists and species with small area requirements”. The structure and floristic composition is inevitably altered over time leading to mass recruitment of light-demanding species (Metcalfe et al., 2008) and hyper-abundance of edge-favoured generalists (i.e. pioneer and secondary species) and exclusion of forest-interior species (Laurance & Curran, 2008). Fragmented rainforest patches also display a dramatic loss of large canopy and emergent trees (Laurance et al., 2000).

I investigated differences in plant community structure and composition across three rainforest habitat types immediately following severe cyclone disturbance. I explored how life history traits, especially successional characteristics, predict changes in community and species level responses.

I hypothesised that fragmentation and severe cyclone disturbance would lead to a shift in the successional characteristics of fragmented forest and forest edges compared to continuous forest in the following ways: 1) lower species richness and abundances; 2) mass recruitment and hyper-abundance of disturbance-favoured, edge-generalists and opportunistic colonisers (i.e. pioneer and secondary species); 3) proliferation of smaller stems; 4) increased presence of invasive exotic species; and 5) dramatic loss of large-fruited, late-maturing and long-lived forest-interior canopy and emergent trees.

3-2 Methods

3-2-1 Study area and plant sampling

This study was undertaken in Mission Beach, north Queensland within the lowland rainforest complex below 100 metres a.s.l. This area experiences a tropical climate moderated by sea breezes. Annual rainfall of 3,090 mm/yr is strongly seasonal, with a wet season from December to May, and average monthly temperatures range from 19 - 26°C. I sampled a total of 18 sites comprising six sites each in the following habitat categories: 1) Continuous forest sites; 2) Continuous forest edge sites; and 3) Fragmented forest sites. Continuous forest is defined as non-fragmented lowland rainforest covering >100 hectares (ha) in area. Sampling sites within this habitat were located a minimum distance of 100 metres to forest edges (Laurance et al., 2006). Continuous forest edge sites are located within 100 metres of the forest edge and perpendicular to the edge. Fragmented forest sites are located within fragmented rainforest blocks, patches and narrow riparian corridors (area < 10ha). These sites are separated from continuous forest by a cleared or modified land matrix (e.g. pasture, plantations, residential development and other infrastructure).

For each site, along a 50-metre transect I established three 10 x 10m plots (300 m^2 total) spaced 10m apart. Within each plot I identified to species and measured the stem diameters and heights of all tree, palm and vine stems ≥ 5cm DBH at 1.3 m height above ground level. Uprooted or leaning stems were measured 1.3 m along the stem length from the base. Plant identifications were made on site, and where that was not possible, samples were taken for subsequent identification in the laboratory using the online interactive database and key of the Australian Tropical Rainforest Plants: Trees, Shrubs and Vines (Hyland et al., 2010) or the Australian Tropical Herbarium archival collection and Queensland Herbarium database.

3-2-2 Statistical analysis

I assessed the efficacy of my sampling methods for each habitat category using the ‘specaccum’ function (method: random, with 100 permutations) in the R software environment (R Core Team, 2015). I tested the appropriateness of the data to fit the assumptions of ANOVA with Shapiro-Wilk and Bartlett’s tests. Single factor (one-way) ANOVAs were used to test the null hypothesis that there was no difference in species richness for the three habitat categories for the following: 1) all species (176 spp./1,424 stems); 2) all trees (including palms, pandanus, cycads and non-woody stems (e.g. *Musa* sp.)) (161 spp./1,377 stems); 3) tree species (no palms) (157 spp./1,107 stems); 4) palms (Arecaceae) only (4 spp./270 stems); and 5) exotic tree species (5 spp./ 16 stems).

I calculated Shannon’s Diversity index *(H)* for each habitat category and the difference in diversity between categories were tested with one-way ANOVA. For community analysis, I calculated a Bray-Curtis dissimilarity matrix for all sites and tested for differences in dispersion (variance) among groups formed by habitat categories using function betadisper (in package Vegan v.2.3-3) (Anderson et al., 2006; Oksanen et al., 2016). I tested for variation in composition within groups using PERMANOVA (function permutest) based on the null hypothesis that the average within-group dispersion measured by the average distance to the group centroid was equivalent among groups. I used Principal Co-ordinates Analysis (PCoA function Adonis) to test for differences in composition between groups and SIMPER to look at the contribution of individual species to the Bray-Curtis dissimilarity.

Community composition was further assessed by ranking the ten highest species abundances for all forest habitat types (combined) and for each forest habitat category. I examined trends in the relative abundances (%) per habitat of these common species. Species ranked equally in 10th position were included for each habitat category.

Chi-square tests were used to detect an association between successional life-history traits and habitat categories using four successional groups: 1) early-mid; 2) mid-late; 3) late; and 4) early-mid-late. Group 1: colonising early successional, short-lived species/ light-demanding pioneers to early intermediate/ gap demanding species; Group 2: mixed intermediate species to late successional, shade-tolerant species; Group 3: long-lived/ late-maturing, slow-growing/ shade-tolerant species; and Group 4: species spanning all three successional stages (e.g. *Ailanthus integrifolia* subsp. *integrifolia, Aleurites rockinghamensis, Alstonia scholaris and Dysoxylum mollissimum* subsp. *molle*). The total database of species includes five exotic species, and these were removed for testing of successional attributes.

Successional groups were based on the Monitoring Toolkit spreadsheet (Kanowski et al., 2010). Attribute definitions (i.e. origin, life form and successional stages) are consistent with those shown in the Toolkit. Additional species data was provided by the online interactive database and key of the Australian Tropical Rainforest Plants: Trees, Shrubs and Vines (Hyland et al., 2010). All statistical analyses were conducted in the R software environment (R Core Team, 2015).

3-3 Results

From three rainforest habitat types in north-eastern Queensland, I sampled eighteen sites (0.54 ha total area) recording a total of 1,424 live stems ≥ 5cm DBH and 176 species from 58 families. Fragmented forest sites recorded the highest total plant diversity with 47 plant families (81% of all families) and 107 species (61% of all species), with only marginally fewer species detected at edge continuous forest sites with 44 plant families (76% of all families) and 102 species (58% of all species). Continuous forest sites had the lowest counts with 36 families (62% of all families) and 92 species (52% of all species). Palms (Arecaceae family), represented by only 4 different species have the highest proportion of stems in the dataset (19%). Only 1% of all stems were exotic species.

Species-accumulation curves for each habitat type (Fig. 3.1) showed new species accrued more rapidly for fragmented forest and edge continuous forest sites compared to continuous forest sites. Stem frequencies are similar for all three habitat types (see Chapter 2) suggesting that the species accumulation curves are not being driven by number of stems present. Fisher's Alpha values supported these findings.

I found no significant difference in species richness between habitat categories for 1) all plant species (including trees, palms, cycads, non-woody species (e.g. *Musa* sp.) and lianas) (Table 3.1, Fig. 3.2A, $P = 0.5235$; N.S.); 2) all trees (including palms) (Fig. 3.2B, $P = 0.4349$; N.S.); 3) trees (no palms) (Fig. 3.2C, $P = 0.4357$; N.S.); 4) palms (Arecaceae) only (Fig. 3.2D, $P = 0.2063$; N.S.); and 5) exotic tree species (Fig. 3.2E, $P = 0.222$; N.S.; all one-way ANOVAs).

Shannon’s Diversity Index (H) showed no significant difference in species composition between forest habitat categories ($F_{2,15} = 1.428$, $P = 0.271$; N.S.). A permutational ANOVA (PERMANOVA) on the Bray-Curtis dissimilarity matrix showed no significant difference in variance between sites within groups formed by the habitat categories ($F_{2,15} = 0.082$, $P = 0.934$; N.S.) but I found significant differences in composition between groups using Principal Co-ordinates Analysis (PCoA) (function Adonis) (Fig. 3.3, $F_{2,15} = 0.199$, $P = 0.022$). The ordination plot (Fig. 3.4) and SIMPER identified the contribution of individual species to the Bray-Curtis dissimilarity. Three palm species including *Archontophoenix alexandrae, Licuala ramsayi* var. *ramsayi* and *Ptychosperma elegans* were identified as outlying species driving significant differences in composition between habitat categories. *Archontophoenix alexandrae* was the most abundant species in edge continuous forest sites, which included riparian corridors. *Licuala ramsayi* var. *ramsayi* was locally abundant in two sites within continuous forest and edge continuous forest. *Ptychosperma elegans* was the most abundant species occurring in all habitat types (7.65% of all live stems). Other tree and shrub species driving these compositional differences included *Myristica globosa* subsp. *muelleri, Gomphandra australiana* and *Brombya platynema.*

The ten most abundant species accounted for 46% of all live stems. Three palm species and seven tree species dominated all forest habitat types (combined) and shared a broad range of successional life-history traits (Table 3.2A; Fig. 3.5A). Continuous forest sites were dominated by a single, disturbance-favoured species, *Brombya platynema* and two palm species *Ptychosperma elegans* and *Licuala ramsayi* var. *ramsayi* and included mainly mid-to late successional tree species (Table 3.2B; Fig. 3.5B). Edge continuous forest sites were characterised by dominant palm assemblages, especially *Archontophoenix alexandrae* together with the mid-to late and late successional tree species, *Gomphandra australiana* and *Myristica globosa* subsp. *muelleri* (Table 3.2C; Fig. 3.5C). Fragmented forest sites were also dominated by *Gomphandra australiana* and *Myristica globosa* subsp. *muelleri* (i.e. mid-to late and late successional tree species), and in addition, one palm species, *Ptychosperma elegans* (Table 3.2D; Fig. 3.5D).

Chi-square tests detected a significant relationship between habitat category and successional life-history traits (Table 3.3). The early-mid successional group showed a significant difference between observed and expected values, especially for edge continuous forest, but also for fragmented forest and continuous forest (Fig. 3.6A; $X^2 = 26.23$, $P < 0.001$, $df = 2$); Similarly, the early-mid-late successional group, including long-lived canopy and emergent species, spanning all successional groups showed a significant relationship, particularly with continuous forest and fragmented forest sites (Fig. 3.6D; $X^2 = 20.11$, $P < 0.001$, $df = 2$). The mid-late successional group, accounting for almost 47% of all stems, also showed a significant relationship between all habitat types (Fig. 3.6B; $X^2 = 11.98$, $P = 0.003$, $df = 2$). No effect was found for late successional species (Fig. 3.6C; $X^2 = 1.01$, $P = 0.6045$, $df = 2$; all chi-square tests).

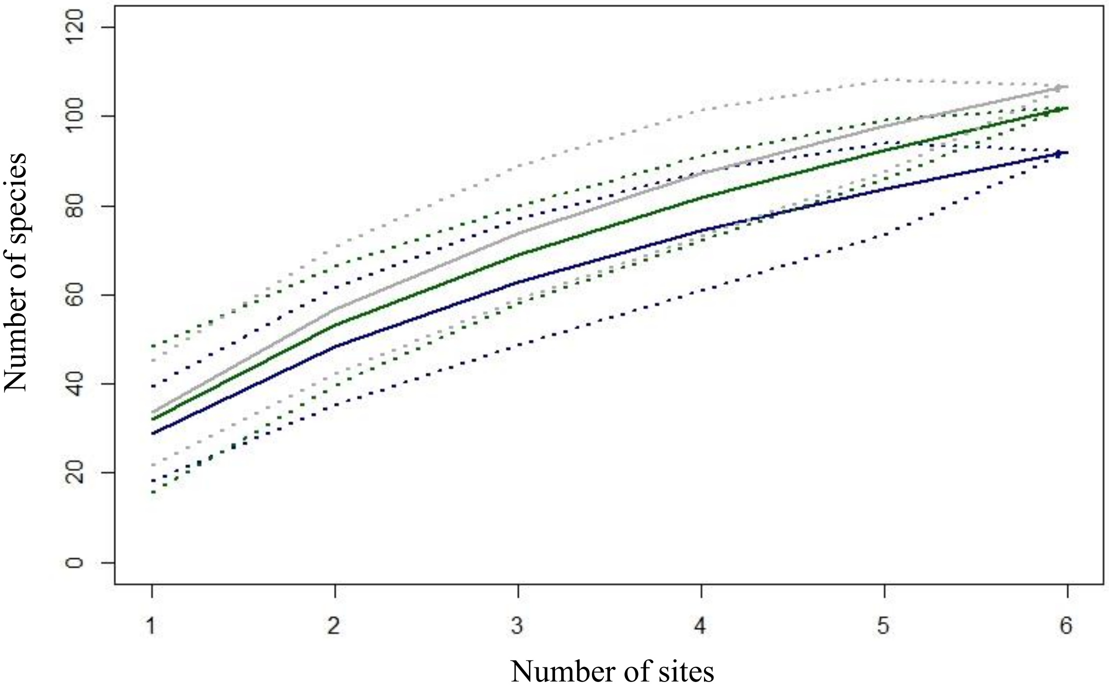

Figure 3.1. Species-accumulation curves are shown for three habitat types (i.e. 6 sites each for continuous forest, edge continuous forest and fragmented forest) in lowland tropical rainforest, Mission Beach, north-eastern Australia. Lines indicate the median and dotted lines are confidence intervals for continuous forest (dark blue), edge continuous forest (dark green) and fragmented forest (dark grey). The trend shows a higher rate of diversity accumulation in fragmented forest and edge continuous forest sites compared to continuous forest sites. The species-accumulation curves suggest that further sampling would have only marginally increased the number of species in each habitat type. A total of 176 species were sampled from eighteen sites.

Table 3.1. One-way ANOVA results in plant species richness for the five groups of species testing for differences between the three forest habitat categories in cyclone-damaged lowland tropical rainforest of north-eastern Australia.

Response variable	**Term**	**df**	**SS**	**MS**	**F**	**P**
All species	habitat	2	69.33	34.667	0.6761	0.5235
	Residual	15	769.17	51.278		
All trees (incl. palms, etc.)	habitat	2	85.78	42.889	0.8807	0.4349
	Residual	15	730.50	48.700		
Trees (no palms)	habitat	2	83.44	41.722	0.8786	0.4357
	Residual	15	712.33	47.489		
Palms only	habitat	2	1.4444	0.7222	1.7568	0.2063
	Residual	15	6.1667	0.4111		
Exotic trees	habitat	2	0.7778	0.3889	1.6667	0.222
	Residual	15	3.500	0.2333		

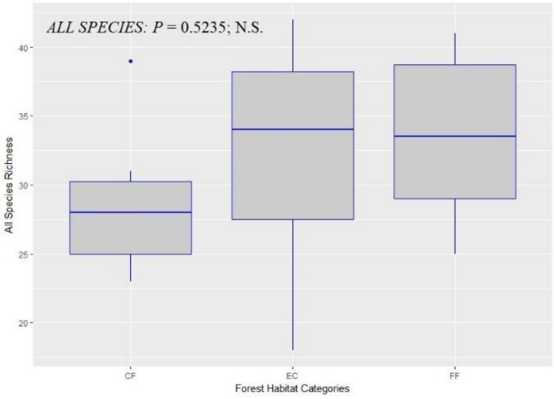

Fig. 3.2A. All species

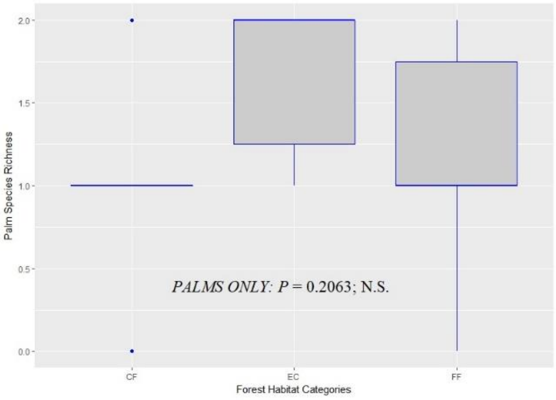

Fig. 3.2D. Palm spp. (Arecaceae)

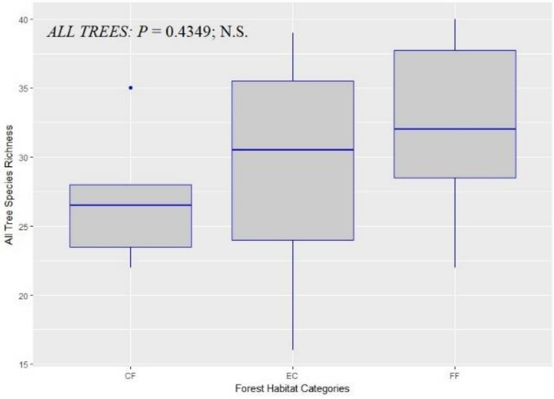

Fig. 3.2B. All tree species (incl. palms)

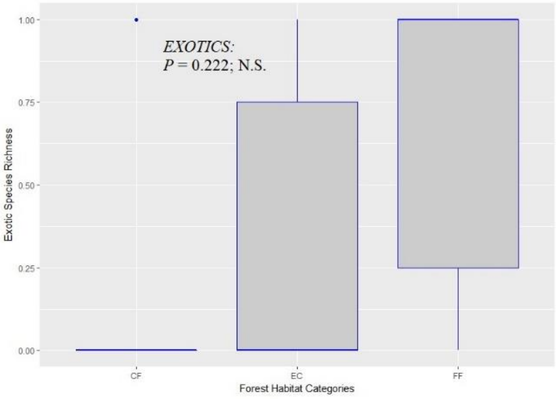

Fig. 3.2E. Exotic spp. (weed species)

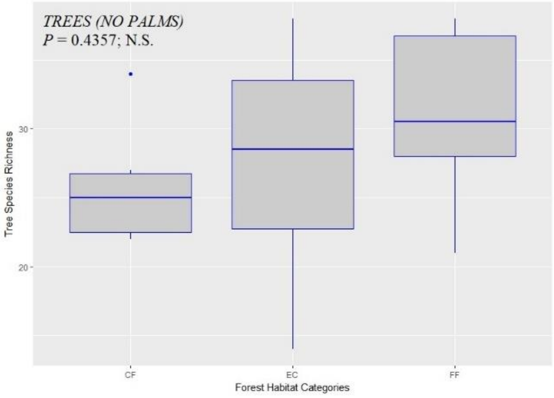

Fig. 3.2C. Tree spp. (no palms)

Figure 3.2(A-E). Boxplots showing relative species richness within continuous forest, edge continuous forest and fragmented forest sites. Each box encompasses the 25th to 75th percentiles; the median is indicated by the boldest horizontal line and vertical lines outside the box indicate the 10th and 90th percentiles. Dots indicate outliers. The trend showed broadly higher species richness in edge continuous forest and fragmented forest compared to continuous forest sites (Figs. 3.2A-C). Palm (Arecaceae family) (4 spp.) (Fig. 3.2D) and exotic species (5 spp.) (Fig. 3.2E) form small subsets of broader species richness.

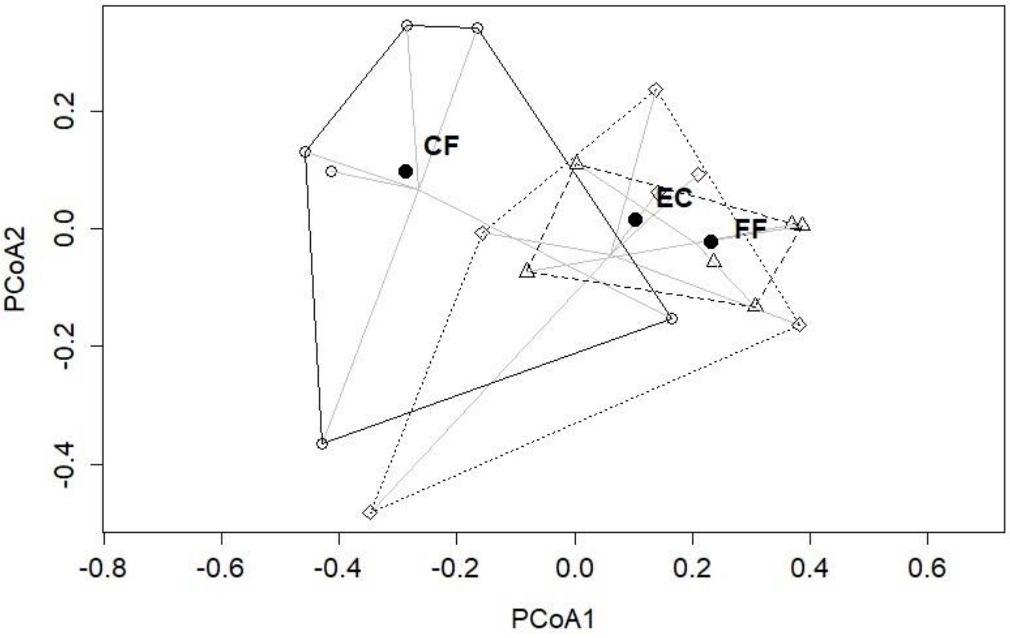

Figure 3.3. Principal Co-ordinates Analysis (PCoA) plot of community diversity for three forest habitat categories, each identified with a different polygon and centroids shown: CF = continuous forest (solid line and open circles), EC = edge continuous forest (dotted line and open diamonds), FF = fragmented forest (dashed line and triangles). This plot shows the relative distances apart for each of the centroids. Community dispersion is highest for continuous forest sites and lowest for fragmented forest sites. There is considerable overlap in community composition for all habitat categories, particularly edge continuous forest. Fragmented forest and edge continuous forest sites share a high level of similarity in species composition.

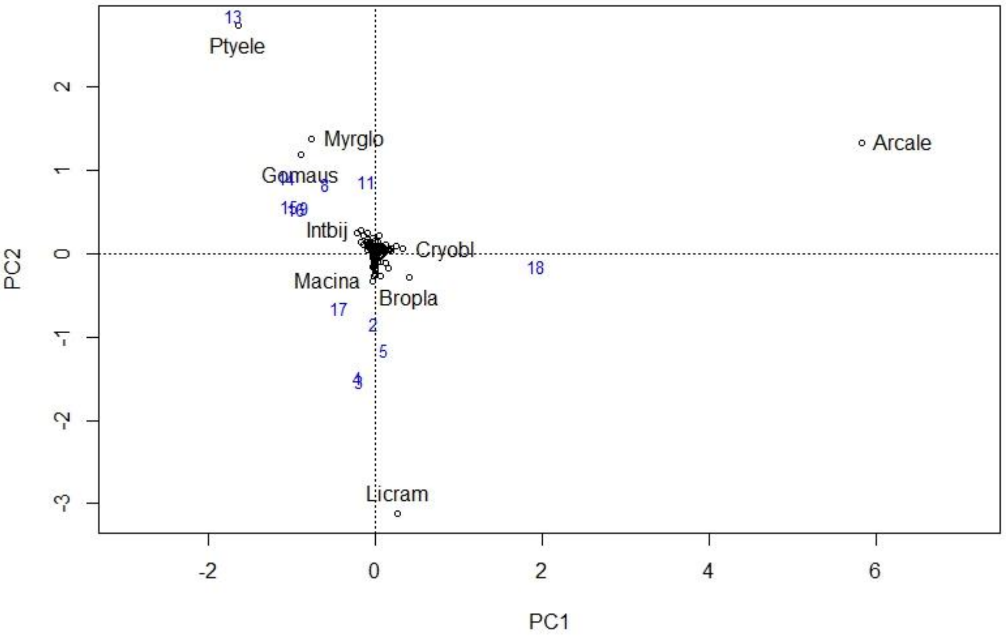

Figure 3.4. Ordination plot of community diversity identifies the contribution of individual species to the Bray-Curtis dissimilarity. Outlying sites (blue font) and species (black font) include Arcale= *Archontophoenix alexandrae*, Licram= *Licuala ramsayi var. ramsayi*, Ptyele= *Ptychosperma elegans*, Myrglo= *Myristica globosa* subsp. *muelleri*, Gomaus= *Gomphandra australiana*, Bropla= *Brombya platynema.* These species are driving significant differences in composition between groups.

Table 3.2A. All forest habitat categories: Ten highest species abundances for three habitat categories (combined) are shown including family, life form, successional life-history traits, number of stems for each species and % proportion of total species (≥ 5cm DBH) recorded in all plots (*N* =176). This group of 10 species accounts for 45.7% of all live stems.

SPECIES	FAMILY	Life form	Successional stage	All habitat categories	
				n	%
Ptychosperma elegans	ARECACEAE	palm	mid	109	7.65
Myristica globosa subsp. *muelleri*	MYRISTICACEAE	tree	late	108	7.58
Gomphandra australiana	ICACINACEAE	tree	mid-late	102	7.16
Archontophoenix alexandrae	ARECACEAE	palm	early-mid	89	6.25
Brombya platynema	RUTACEAE	shrub/tree	mid-late	73	5.13
Licuala ramsayi var. *ramsayi*	ARECACEAE	palm	mid-late	63	4.42
Polyscias australiana	ARALIACEAE	shrub/tree	early-mid	40	2.81
Wrightia laevis	APOCYNACEAE	tree	late	27	1.90
Elaeocarpus angustifolius	ELAEOCARPACEAE	tree	mid	21	1.47
Dysoxylum alliaceum	MELIACEAE	tree	late	19	1.33

% abundance ranked out of 176 species (**Appendix 3.1**).

Table 3.2B. Continuous forest: Ten highest ranked species abundances for continuous forest sites.

SPECIES	FAMILY	Life form	Successional stage	All habitat categories n	All habitat categories %
Brombya platynema	RUTACEAE	shrub/tree	mid-late	44	10.40
Ptychosperma elegans	ARECACEAE	palm	mid	33	7.80
Myristica globosa subsp. *muelleri*	MYRISTICACEAE	tree	late	21	4.96
Polyscias australiana	ARALIACEAE	shrub/tree	early-mid	21	4.96
Licuala ramsayi var. *ramsayi*	ARECACEAE	palm	mid-late	19	4.49
Macaranga inamoena	EUPHORBIACEAE	tree	mid-late	17	4.02
Musgravea heterophylla	PROTEACEAE	tree	late	13	3.07
Rockinghamia angustifolia	EUPHORBIACEAE	tree	late	13	3.07
Apodytes brachystylis	ICACINACEAE	shrub/tree	late	12	2.84
Alstonia muelleriana	APOCYNACEAE	tree	early-mid	10	2.36
Litsea leefeana	LAURACEAE	tree	mid	10	2.36
Citronella smythii	ICACINACEAE	tree	mid	10	2.36

Three species are equal ranked No.10.

Table 3.2C. Edge continuous forest: Ten highest ranked species abundances for edge continuous forest.

SPECIES	FAMILY	Life form	Successional stage	All habitat categories n	All habitat categories %
Archontophoenix alexandrae	ARECACEAE	palm	early-mid	70	12.99
Myristica globosa subsp. *muelleri*	MYRISTICACEAE	tree	late	43	7.98
Gomphandra australiana	ICACINACEAE	tree	mid-late	43	7.98
Licuala ramsayi var. *ramsayi*	ARECACEAE	palm	mid-late	43	7.98
Ptychosperma elegans	ARECACEAE	palm	mid	42	7.79
Brombya platynema	RUTACEAE	shrub/tree	mid-late	25	4.64
Polyscias australiana	ARALIACEAE	shrub/tree	early-mid	15	2.78
Wrightia laevis	APOCYNACEAE	tree	late	13	2.41
Dysoxylum pettigrewianum	MELIACEAE	tree	late	8	1.48
Intsia bijuga	CAESALPINIACEAE	tree	mid-late	8	1.48
Cryptocarya laevigata	LAURACEAE	shrub/tree	mid-late	8	1.48

Two species are equal ranked No.10.

Table 3.2D. Fragmented forest: Ten highest ranked species abundances for fragmented forest sites.

SPECIES	FAMILY	Life form	Successional stage	All habitat categories n	All habitat categories %
Gomphandra australiana	ICACINACEAE	tree	mid-late	56	12.12
Myristica globosa subsp. *muelleri*	MYRISTICACEAE	tree	late	44	9.52
Ptychosperma elegans	ARECACEAE	palm	mid	34	7.36
Archontophoenix alexandrae	ARECACEAE	palm	early-mid	15	3.25
Myristica insipida	MYRISTICACEAE	tree	late	15	3.25
Dysoxylum alliaceum	MELIACEAE	tree	late	13	2.81
Canarium vitiense	BURSERACEAE	tree	mid-late	13	2.81
Elaeocarpus angustifolius	ELAEOCARPACEAE	tree	mid	12	2.60
Wrightia laevis	APOCYNACEAE	tree	late	11	2.38
Semecarpus australiensis	ANACARDIACEAE	tree	mid-late	9	1.95
Castanospermum australe	FABACEAE	tree	late	9	1.95
Syzygium cormiflorum	MYRTACEAE	tree	late	9	1.95

Three species are equal ranked No.10.

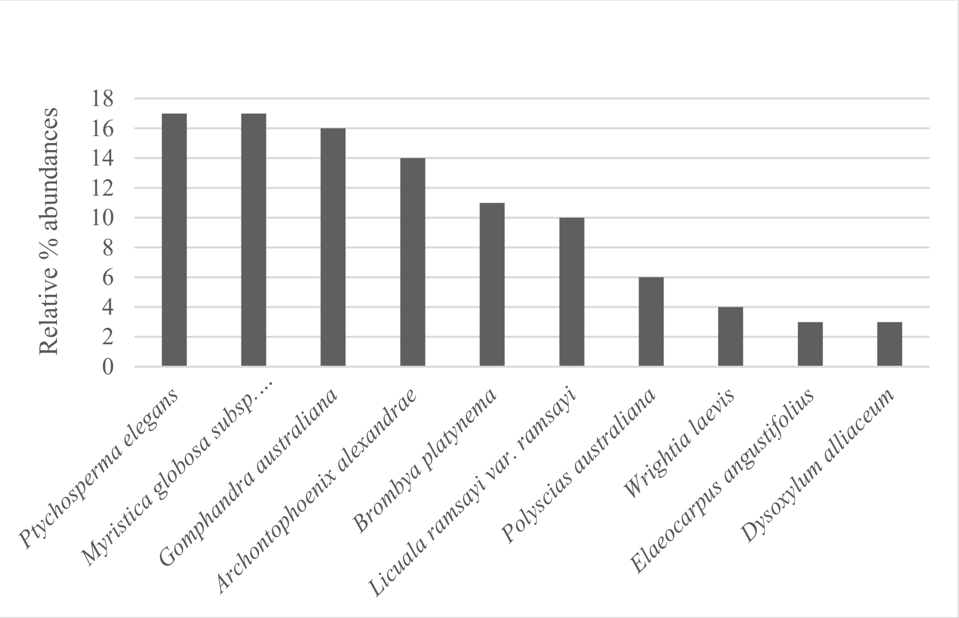

Figure 3.5A. All forest habitat categories: Relative % abundances are shown for the ten most abundant tree species for all forest habitat types combined. The curve shows hyper-abundance of only a few dominant species. Three palm species (Arecaceae family) dominated these rankings - *Ptychosperma elegans, Archontophoenix alexandrae* and *Licuala ramsayi* var. *ramsayi*. Eight out of ten species shown belong to mid- to late successional groups.

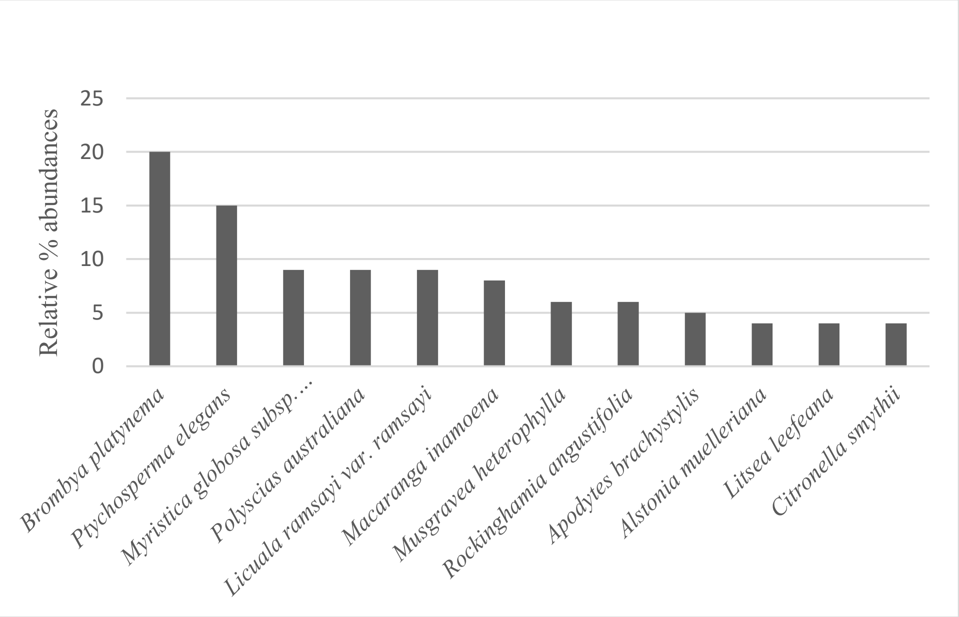

Figure 3.5B. Continuous forest: Relative % abundances are shown for the ten highest ranked tree species (three species ranked equal No.10) for continuous forest sites. The disturbance-favoured, understorey shrub/ tree species, *Brombya platynema* (mid-late successional) makes up 20% of all stems in this group. Two palm species, *Ptychosperma elegans* and *Licuala ramsayi* var. *ramsayi* were also important components (24% of stems in this group). Most of the species are mid-to late successional canopy and sub-canopy trees.

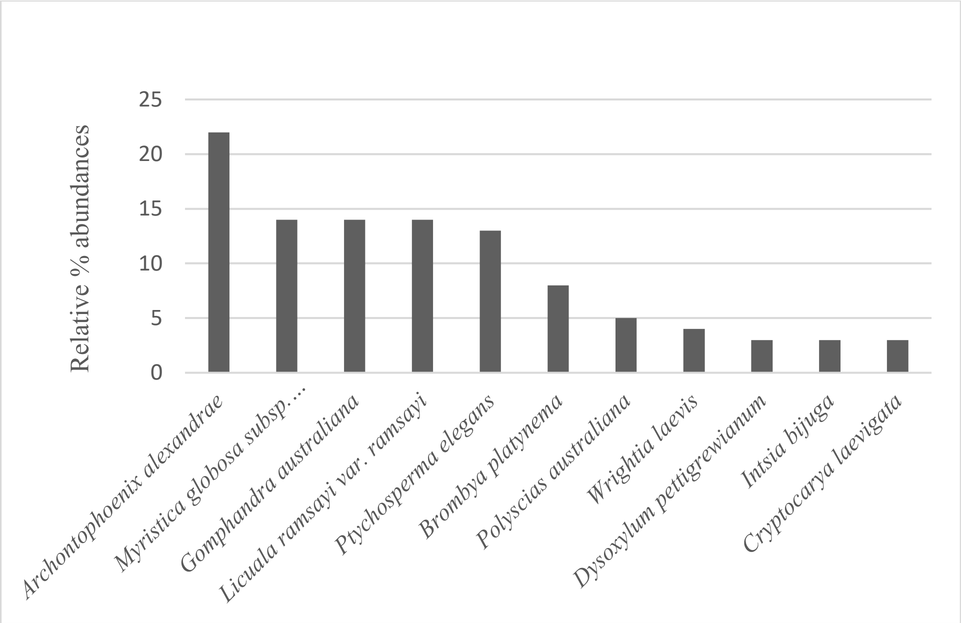

Figure 3.5C. Edge continuous forest: Relative % abundances are shown for ten highest ranked tree species (two species ranked equal No.10) for edge continuous forest sites. This group is characterized by dominant palms, especially the early-mid successional species, *Archontophoenix alexandrae* (22%) and two mid- to late successional species, *Licuala ramsayi* var. *ramsayi* (14%) and *Ptychosperma elegans* (13%). Two mid- to late successional canopy and sub-canopy species, *Myristica globosa* subsp. *muelleri* and *Gomphandra australiana* make up 28% of this group.

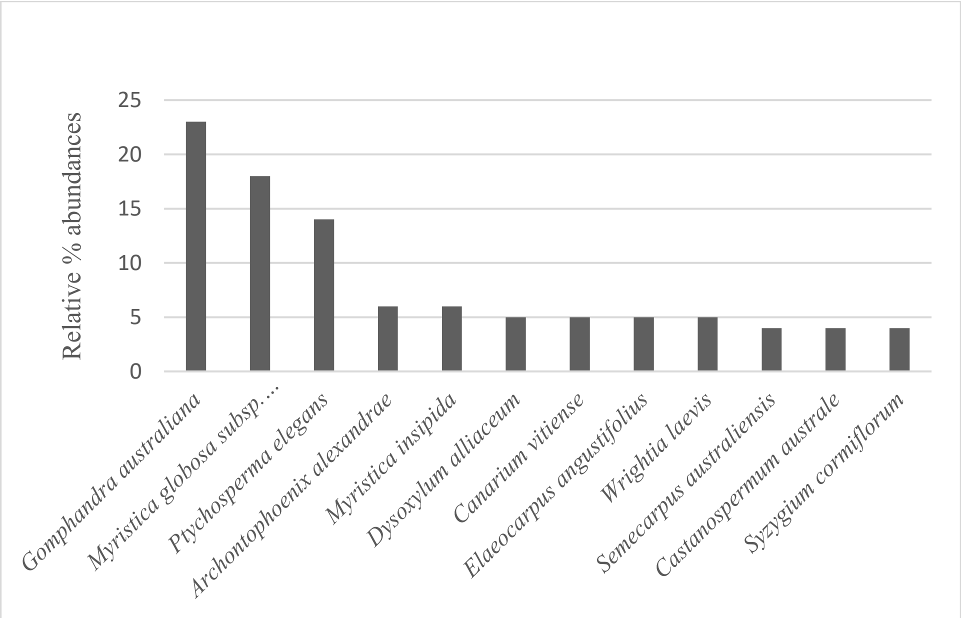

Figure 3.5D. Fragmented forest: Relative % abundances are shown for ten highest ranked species (three species ranked equal No.10) for fragmented forest sites. This group is dominated by two mid- to late successional canopy and sub-canopy species, *Myristica globosa* subsp. *muelleri* and *Gomphandra australiana* (combined 41% for this group) and the mid-successional palm, *Ptychosperma elegans* (14%). Notably, most species are mid-late and late successional species.

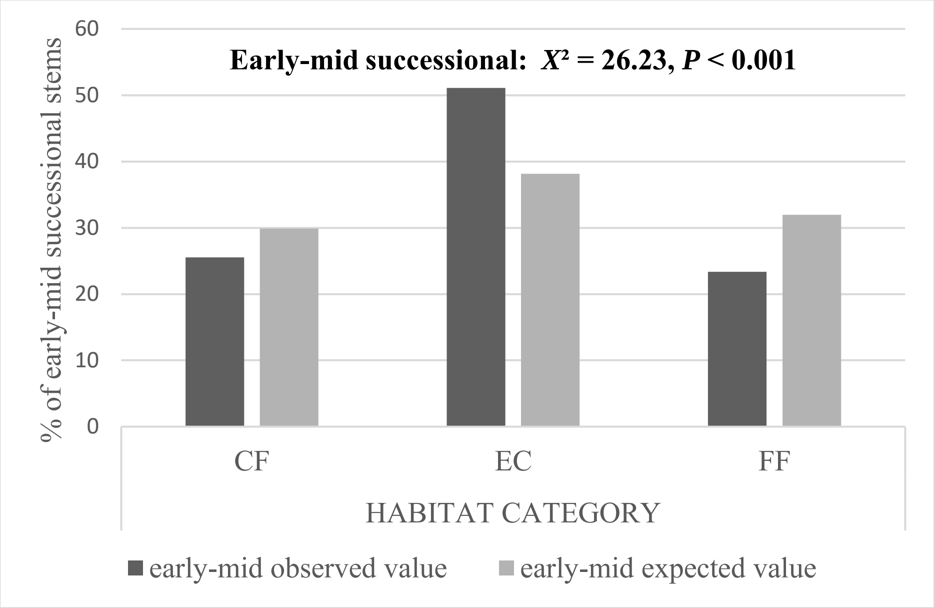

Figure 3.6A. Chi-square test showing % differences in observed values (black bar) and expected values (grey bar) for early-mid successional stems from three habitat types: CF = Continuous forest, EC = Edge continuous forest; and FF = Fragmented forest. Early to mid-successional stems account for only 13% of all stems. The chi-square test showed a significant difference between observed and expected values, especially for edge continuous forest (13%). Edge continuous forest also has a significantly higher proportion of stems (51%) compared to the other habitat types. Notably, there is little difference between continuous forest and fragmented forest, 26% and 23% respectively. A far greater proportion of early-mid successional stems was expected for fragmented forest.

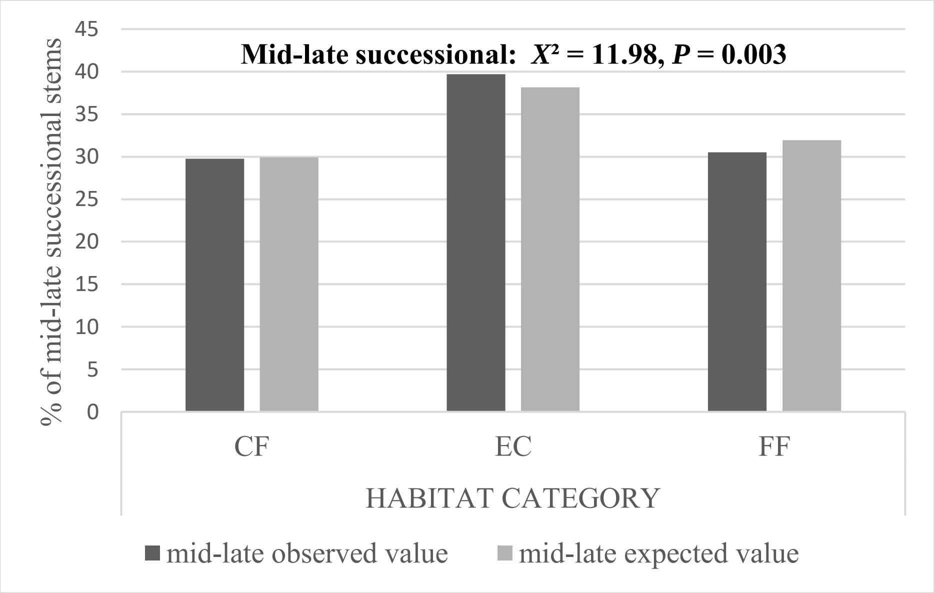

Figure 3.6B. Almost 47% of all stems were assigned to the mid-late successional group. This was the largest group. Edge continuous forest showed higher observed values (40%) compared to continuous forest and fragmented forest, 30% and 31% respectively. Observed and expected values showed only a relatively small difference for edge continuous forest and fragmented forest and no difference for continuous forest but the chi-square test identified a relationship between mid-late successional species and habitat type.

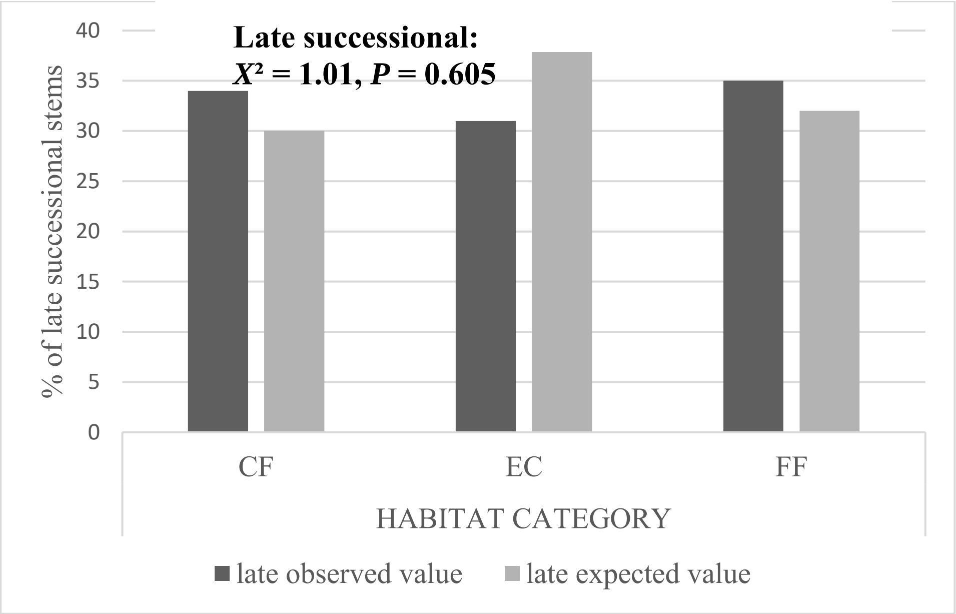

Figure 3.6C. Late successional species make up almost 37% of all stems and are the second most abundant successional group. A Chi-square test however failed to find a significant result. Observed values were lower than expected values for edge continuous forest but higher for continuous forest and fragmented forest.

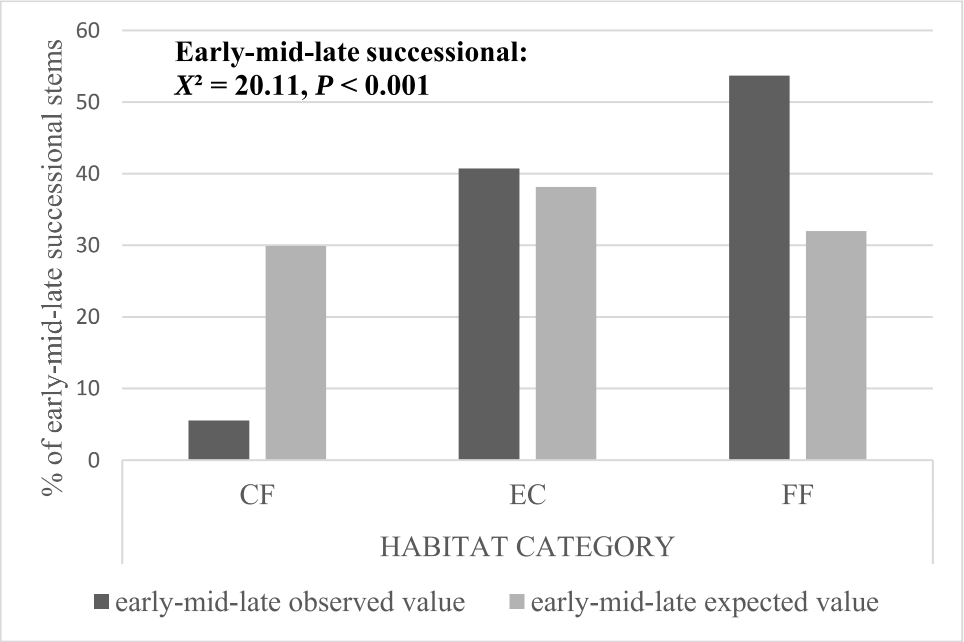

Figure 3.6D. Species spanning early-mid-late successional stages were the smallest group with only 3.83% of stems. Nevertheless, as a group they formed a very important cohort of long-lived canopy and emergent species. The Chi-square test showed a very significant result. Observed values ranged from only 6% for continuous forest to 54% for fragmented forest. The difference between observed and expected values for continuous forest and fragmented forest was 24% and 22% respectively with a much smaller difference (3%) shown in edge continuous forest. This early-mid-late successional group showed a highly significant relationship with habitat type.

Table 3.3. Plant abundances and successional strategies for three forest habitat categories in cyclone-damaged lowland tropical rainforest of north-eastern Australia.

Successional	**Continuous forest**		**Edge continuous forest**		**Fragmented forest**		**TOTAL**		**Chi-square test *(df = 2)***	
stages	**n**	**%**	**n**	**%**	**n**	**%**	**N**	**%**	X^2	***p-value***
early-mid	47	11.16	94	17.50	43	9.56	184	13.07	26.23	< 0.001
mid-late	195	46.32	260	48.42	200	44.44	655	46.52	11.98	0.003
late	176	41.81	161	29.98	178	39.56	515	36.58	1.01	0.605
early-mid-late	3	0.71	22	4.10	29	6.44	54	3.84	20.11	< 0.001
Totals	421		537		450		1408			

3-4 Discussion

The effects of fragmentation and severe cyclone disturbance on community structure and composition were explored across different habitat types in the lowland rainforest of north-eastern Australia.

3-4-1 Distribution of early successional species for different habitat types

Only 13% of tree stems for all habitat types were identified as early-mid successional species, whereas a total of 83% of stems belonged to mid-late and late successional species groups. A further 4% of all stems were canopy and emergent tree species, spanning early-mid-late successional stages. Notably, early-mid successional species showed little difference in the proportion of stems found in continuous forest and fragmented forest, 26% and 23% respectively. Fragmented forest however, should have a far higher proportion of stems assigned to this group of pioneer and early intermediate species, compared to continuous forest (Laurance & Curran, 2008; Metcalfe et al., 2008). My study found no evidence of this expected shift in floristic composition, or distinctive bias towards disturbance-adapted pioneer or secondary species over slow-growing, late-maturing species (Laurance et al., 2006). Two consecutive severe cyclones, less than five years apart, removed many early successional species and provided opportunities for small stemmed, mid-late and late successional species (already present in the understorey), to dominate all habitat types.

Early successional species including *Acacia crassicarpa, A. mangium, Alphitonia petriei* and *A. excelsa* were absent from all forest habitat types while other early successional species were rare. I recorded *Alphitonia whitei,* continuous forest sites only (1.2% of recorded species in this habitat type), *Commersonia bartramia,* continuous forest sites (0.5%) and fragmented forest sites (0.2%), *Macaranga involucrata* var. *mallotoides* in edge continuous forest only (0.2%) and *M. tanarius,* fragmented forest sites (1.1%) (APPENDIX 3.1). Nevertheless, it is possible that canopy gaps created by cyclone disturbance may have presented opportunities for germination and establishment of some light-demanding, fast-growing pioneer species since the study was completed.

3-4-2 Fragmented forest sites show no shift towards early-successional strategies

I found no evidence to support my hypotheses that fragmented forests would show a shift towards: 1) mass recruitment and hyper-abundance of edge-favoured generalists; 2) proliferation of disturbance-favoured species and exclusion of forest-interior plant species; and 3) dramatic loss of large-fruited, late-maturing and long-lived canopy and emergent trees. My data suggest that forest habitat categories influence the life-history characteristics of plant communities but show no shift towards a proliferation of light-demanding, edge-favoured generalists (i.e. early pioneer species), within the time-frame of this study. A total of 84% of all tree stems in fragmented forest sites belonged to mid-late and late successional groups while only 9.5% of stems were early-mid successional species and 6.5% of stems were in the early-mid-late successional group (Table 3.3). Fragmented forest sites were dominated by two mid-to late successional canopy and sub-canopy species, *Myristica globosa* subsp.

muelleri (12.1% of all stems in this habitat type) and *Gomphandra australiana* (9.5%) and the mid-successional palm, *Ptychosperma elegans* (7.4%) (Table 3.2D).

3-4-3 Different habitat categories share high abundances of a few species

Although these forests demonstrate exceptional diversity (176 species ≥ 5cm DBH recorded within 18 sites covering an area of only 0.54 ha) my results for all forest habitat categories demonstrated that as few as ten species dominated (46%) of all live stems (N = 1,424). *Myristica globosa* subsp. *muelleri* (late-successional) and *Gomphandra australiana*, (mid-late successional), a sub-canopy and canopy species respectively, shared markedly high abundances (7.6% and 7.2% respectively, for all habitat categories combined). Other species that were highly ranked in abundances included *Wrightia laevis* (1.9%), *Elaeocarpus angustifolius* (1.5%) and *Dysoxylum alliaceum* (1.3%), all of which have mid- and late successional strategies. Similar findings of unusual and localised dominance of some mid-late successional species (e.g. *Backhousia bancroftii* – not present in this study) were described in a study located in the foothills west of Mission Beach, following Cyclone Winifred (1986) (Hopkins & Graham, 1987). It was suggested that cyclone events may promote random opportunities, which favour some species over others and re-shaping future successional trajectories.

Three out of the ten most abundant species were palms (Arecaceae family). These include: *Ptychosperma elegans* (ranked No.1), *Archontophoenix alexandrae* (ranked No.4) and *Licuala ramsayi* var. *ramsayi* (ranked No.6). These early-mid and mid-successional palm species are highly adapted to infrequent severe wind damage and cyclonic disturbance. Palm fronds may be damaged or shed during high winds, but providing the apical meristem is undamaged, these species respond rapidly with new fronds only a few weeks after disturbance. Synchronised mass flowering (i.e. mast flowering) in these species also occurred within a few weeks after both cyclone events, however, fruit set appeared sporadic possibly due to loss of pollinators.

Similar resistance by palms to cyclone (or hurricane) mortality have been described in studies of Neo-tropical forests (Frangi & Lugo, 1991; Zimmerman et al., 1994). A recent study of the impact of three severe tropical storms (Hugo in 1989, Georges in 1998, and Maria in 2017) on secondary forest in Puerto Rico, found a common palm species, *Prestoea acuminata* var. *montana*, had the lowest rates of stem break of all species, and abundances of these palms doubled over the past two decades (Uriarte et al., 2019). These studies suggest that more severe tropical storms may favour wind-resistant species, such as palms.

The disturbance-favoured, understorey shrub/ tree species, *Brombya platynema* (mid-late successional) and *Polyscias australiana* (early-mid-successional) shared high total abundances (5.1% and 2.8% respectively). Whilst *P. australiana* is a pioneer/ intermediate successional species, *B. platynema* typically persists as a shade-tolerant, understorey specialist. For *B. platynema*, the effects of severe cyclone disturbance, including canopy shredding and removal of most of the canopy, dramatically increased light levels to the understorey and forest floor, triggering similar massed flowering as observed in the palms but *P. australiana* showed little flowering response. Unlike the mast flowering of many different species observed after Cyclone Winifred (1986) (Hopkins & Graham, 1987) only a very restricted suite of species, as described here, responded in this way after successive cyclone events. Notably, in the months immediately following cyclones Larry and Yasi, monthly rainfall was above average (BOM Australian Government, 2018), promoting foliage regrowth over flowering and fruiting. These events contrasted sharply with the unseasonal cloudless skies and sustained hot, dry weather conditions following Cyclone Winifred as described by Hopkins and Graham (1987). The flora of Queensland's Wet Tropics shows a diversity of flowering patterns with a general peak in activity coinciding with the end of the dry season (i.e. start of the wet season) (Hopkins & Graham, 1987). Different families and species respond in very different ways to a combination of abiotic, biotic and evolutionary factors however the causes of individual species responses remain an area for future research (Boulter et al., 2006).

3-4-4 Continuous forest habitat – ranked highest abundances

A disturbance-favoured understorey shrub/ tree species, *Brombya platynema* (mid-late successional) was ranked No.1 (10.4% of all stems). Almost 1 in 4 stems in this group were palms (Arecaceae family) and included two species, *Ptychosperma elegans* (7.8%, ranked No.2) and *Licuala ramsayi* var. *ramsayi* (4.5%, ranked No.5). These were mid and mid-late successional species respectively. The broader group was comprised of a mix of mid to late successional canopy and sub-canopy tree species including *Myristica globosa* subsp. *muelleri, Macaranga inamoena, Musgravea heterophylla, Rockinghamia angustifolia, Apodytes brachystylis, Litsea leefeana and Citronella smythii.* Notably, two early-mid successional species, *Polyscias australiana* (5%, ranked No.4) and *Alstonia muelleriana* (2.4%, ranked equal No.10) were important components of species assemblages in this habitat type.

3-4-5 Edge continuous forest habitat – ranked highest abundances

This group was characterised by dominant palm (Arecaceae) assemblages including the early-mid successional species, *Archontophoenix alexandrae* (13%, ranked No.1), and mid-to late successional species, *Licuala ramsayi var. ramsayi* (8%, ranked No.4) and

Ptychosperma elegans (7.8%, ranked No.5). Four key species including *Myristica globosa* subsp. *muelleri* (late successional), *Gomphandra australiana* (mid-late successional), *Brombya platynema* (mid-late successional) and *Polyscias australiana* (early-mid successional) accounted for almost 1 in 4 stems in this group. Two late successional canopy species, *Wrightia laevis* and *Dysoxylum pettigrewianum* and the mid-late successional species, *Intsia bijuga* (canopy) and *Cryptocarya laevigata* (understorey) were also important components.

3-4-6 Fragmented forest habitat – ranked highest abundances

Notably, fragmented forest is dominated by mid-late and late successional species. This was an unexpected result and contrary to my original hypothesis. The mid-late successional species, *Gomphandra australiana* (ranked No.1) and late successional species, *Myristica globosa* subsp. *muelleri* (ranked No.2) contributed almost 22% of all stems in this forest habitat type. Furthermore, the congener and late successional species, *Myristica insipida* (ranked No.5) recorded 3.25% of all stems in this habitat type. Two palms (Arecaceae), the mid successional species, *Ptychosperma elegans* (7.4%, ranked No.3) and early-mid successional species, *Archontophoenix alexandrae* (3.25%, ranked No.4) were also important components of this habitat type. The palm, *A. alexandrae* was the only early-mid successional species present in the group. Moreover, mid-late and late successional canopy and sub-canopy species make up all the remaining members within this group. These include *Dysoxylum alliaceum, Canarium vitiense, Elaeocarpus angustifolius, Wrightia laevis, Semecarpus australiensis, Castanospermum australe* and *Syzygium cormiflorum.*

CHAPTER FOUR

Discussion: community and species-level responses to severe cyclone disturbance and fragmentation in lowland tropical rainforest in north Queensland

4-1 Severe tropical cyclones Larry (2006) and Yasi (2011)

My study followed two severe tropical cyclone events, Cyclones Larry (2006) and Yasi (2011) in the Australian Wet Tropics. To date, no comparable investigation has measured the effects of successive severe tropical cyclone events on different forest habitat types in lowland mesophyll rainforest. Cyclone Larry (Category 4 cyclone) crossed the coast only 28 km north of the study area's northern boundary with the most severe damage occurring immediately south of the eye-wall near Clump Point, Mission Beach (Callaghan & Otto, 2006). Maximum wind gusts were in the order of 55 ms^{-1} (~200 km/h) (BOM Australian Government, 2013) and possibly as high as 65-67 ms^{-1} (~235-240 km/h) (Geoscience Australia, 2006; Turton, 2008) . Less than five years later Cyclone Yasi (a marginal Category 5 cyclone) crossed the coast directly over the Mission Beach study area, recording a sustained wind speed of 57 ms^{-1} (~205 km/h) with maximum wind gusts of 79 ms^{-1} (~285 km/h) (BOM Australian Government, 2013). Cyclone Yasi was a massive system in comparison to Cyclone Larry (Turton, 2012) and believed to be one of the most powerful cyclones to affect north Queensland since records commenced, comparable to Cyclone Mahina (1899) and the two cyclones which devastated Mackay and Innisfail in 1918 (BOM Australian Government, 2013, 2017a).

4-2 Cyclone disturbance: tree mortality and life-history traits

In Chapter 2, I predicted that continuous forest would have larger trees with fewer small stems and less severe canopy damage compared to fragmented forest and forest edges. I expected all forest habitat types would have high rates of mortality (i.e. dead snapped and standing trees or dead uprooted trees) due to weakened trees succumbing to a second severe cyclone. In addition, higher levels of severe damage in fragmented forests compared to continuous forest were expected due to inherent vulnerability to wind-storms and proliferation of early successional species. Finally, I predicted that different tree families and species would show varying levels of cyclone damage across habitat types.

Although I expected tree stem frequencies would be lower in continuous forest sites (i.e. fewer trees with larger diameter stems) compared to fragmented forest sites (i.e. many trees with smaller diameter stems), I found no significant difference between the three forest habitat categories. Nevertheless, my data confirmed far higher tree stem frequencies in the smallest size classes (DBH) for all three habitats, and that stem numbers generally decreased with increasing size class, similar to findings in other studies (Curran et al., 2008a; Laurance et al., 2009).

Large trees (>60cm DBH) in fragmented forests are considered particularly vulnerable to cyclone damage compared to continuous forest (Laurance & Curran, 2008; Laurance et al., 2000). Large diameter trees were largely absent from all habitat types, not just fragmented forest. No significant difference was detected in mean basal area between habitat types, but overall a trend was observed with edge continuous forest recording the highest total (46.61 $m^2\ ha^{-1}$). Interestingly, fragmented forest recorded a relatively high basal area (34.17 $m^2\ ha^{-1}$) compared to continuous forest (27.29 $m^2\ ha^{-1}$). I would suggest that the relatively low basal area for continuous forest is related to the dramatic loss of larger canopy trees in continuous forest sites, following the impact of two severe cyclones. Structurally, all three habitat types showed no significant differences following two successive severe cyclones (i.e. continuous forest sites had become more like the forest edges and fragmented forest sites).

Catterall et al. (2008) reported that large trees >100cm DBH sustained the highest overall damage levels to standing stems of any tree size class and that standing tree density in this size class had been reduced by about half for all sites, after the impact of Cyclone Larry. Notably, other studies have reported higher vulnerability to wind damage for large diameter trees (Ostertag et al., 2005; Putz et al., 1983; Uriarte et al., 2019), but others have found no evidence for tree size influencing mortality (Bellingham et al., 1995; Curran et al., 2008a). My observations, however, support findings that there was a dramatic loss of large canopy trees during and after Cyclone Larry (2006) (N. Ruting, unpubl. data 2010), and this event likely reduced the number of trees available for this damage class for Cyclone Yasi (2011).

All forest habitat types in my study displayed multi-directional tree falls, shredding and defoliation of almost all canopy trees, snapped boles, or branches stripped or broken from main stems, or uprooted and debris scattered across the forest floor. My results showed all stems (≥ 5cm DBH) sustained some level of damage (i.e. minor to severe). My data suggest habitat type influences the level of cyclone damage to trees, with greater numbers of major snapped branches recorded in continuous forest (interior) and edge sites compared to higher numbers of snapped main stems in fragmented forest sites. In total, for all forest habitat types, 75% of standing trees had snapped main stems and a further 11% of trees had snapped major branches and/ or multiple branch breakages. Only 10% of trees sustained minor damage including partial defoliation, twig-snapping and minor branches snapped or damaged. Less than 4% of all trees in my study were uprooted. Putz et al. (1983) recorded higher rates of uprooted trees (25% of all trees) but similar rates of snapped trees (75%). Webb et al. (2014) found about 23% of all trees were uprooted and 35% had snapped main stems while a study in the Australian Wet Tropics, following Cyclone Larry, recorded only 20% of trees with snapped main stems (Curran et al., 2008a). A recent study in Puerto Rico, following three hurricanes over 30 years, found up to 2- to 12-fold more stems were snapped in the most recent hurricane (Uriarte et al., 2019). Similarly, my study showed a 3.75-fold increase in snapped main stems following Cyclone Yasi, compared to the results for Cyclone Larry (Curran et al., 2008a). Rates of severe damage depend on the degree of forest recovery following previous tropical storms as well as successional specialization (Canham et al., 2010; Uriarte et al., 2019; Zimmerman et al., 1994).

I recorded a tree (≥ 5cm DBH) mortality rate of 4% over 18 months. Notably, some long-lived, late-maturing, large-diameter canopy and emergent trees (including *Ailanthus integrifolia* subsp. *integrifolia, Dysoxylum pettigrewianum. D. alliaceum* and *Syzygium graveolens*) displayed a burst of epicormic growth immediately after suffering severe damage from uprooting or partial uprooting. This initial growth response, however was followed by delayed mortality months later and these individuals were recorded as dead in the subsequent re-census in my study. Background mortality rates for trees (≥ 10cm DBH), in wet tropical forests, range between 1 and 2% per year (rarely exceeding 3% per year) but may rise to between 7 and 14% per year following severe windstorms (Brokaw & Walker, 1991; Lugo & Scatena, 1996; Uriarte et al., 2019). Delayed rates of mortality however, may continue for some years after these storm events, suggesting that 18 months to assess delayed mortality may have been too short (Frangi & Lugo, 1991; Lugo & Scatena, 1996; Zimmerman et al., 1994). Nevertheless, it is plausible that low mortality rates recorded in my study reflect the dynamic successional characteristics of these forest habitats. Following Cyclone Yasi, early successional or pioneer species suffered very high rates of mortality, while wind-resistant, disturbance-favoured tree species resprouted vigorously after the cyclone, and continued to flourish alongside emerging slow-growing, late-maturing saplings previously suppressed in the understorey.

After the impact of hurricanes or severe wind-storms on tropical forests, resprouting is the most common response followed by sapling regrowth (Bellingham et al., 1994; Yih et al., 1991; Zimmerman et al., 1994). In my study, a total of 96% of all tree stems resprouted within a few weeks after Cyclone Yasi and maintained vigour over the following 18 months. Many trees with stems ≥ 10cm DBH displayed a recent history of stem breakage during Cyclone Larry (2006) followed by resprouting and snapping again during Cyclone Yasi (2011), higher up the main stem.

Tree species affected by cyclones display life-history strategies which are geared to either high resistance (i.e. slow-growing, late-maturing, shade-tolerant species with relatively high wood density) or low resistance with trade-offs linked to rapid growth and tree turn-over (i.e. early-successional, light-demanding species with low wood density) (Curran et al., 2008a; Curran et al., 2008b; Ostertag et al., 2005; Zimmerman et al., 1994). Tree species which display rapid growth rates sustain greater cyclone damage, reflecting these life-history strategies or trade-offs (Ostertag et al., 2005). These ‘trade-offs’ however allow these species to retain a positional advantage over smaller trees and seedlings after cyclone damage (Putz et al., 1983). Rapid recovery involving resprouting from snapped and leaning stems or damaged crowns typically occurs in species with low resistance, but high resilience to severe cyclone disturbance (Bellingham et al., 1994; Zimmerman et al., 1994).

Early successional tree species however, are most likely to have the highest mortality rates following severe tropical storms (Carrington et al., 2015; Uriarte et al., 2012; Yih et al., 1991; Zimmerman et al., 1994). My results are consistent with post-hurricane studies which show a negative impact on early successional species (i.e. pioneer species) compared to vigorous resprouting strategies by mid-late successional species (Yih et al., 1991; Zimmerman et al., 1994). Pioneer species tend to snap stems but not resprout which leads to tree death (Zimmerman et al., 1994). Within a few months after Hurricane Joan impacted the tropical rainforests of Nicaragua, Central America, the proportions of different tree species and size distributions were altered but species composition and richness remained the same (Yih et al., 1991). Notably, Yih et al. (1991) found that secondary regrowth species were rare and early-successional species were almost totally absent. A decade later, the competition for canopy space by a surviving and diverse range of upper canopy trees, resprouting mid-level trees, sapling and seedling regeneration, was intense (Vandermeer et al., 2000). The results suggest that large-scale disturbances, such as severe tropical storms, play a pivotal role in maintaining and promoting species composition and diversity (Lugo, 2008; Vandermeer et al., 2000).

In my study, I expected to find early successional species, particularly in fragmented forest sites, including *Acacia crassicarpa, A. mangium, Alphitonia petriei* and *A. excelsa* but these species were absent from all forest habitat types while other early successional species such as *Alphitonia whitei, Commersonia bartramia, Macaranga involucrata* var. *mallotoides* and *M. tanarius* were recorded for some sites but rare following successive cyclone events. By comparison, I observed non-pioneer tree species vigorously resprouting and sustaining growth of new main stems and branches during the post-cyclone recovery phase. Gaps in the canopy created by cyclone disturbance may have initiated germination and establishment of some light-demanding, fast-growing pioneer tree species since the study was completed. This response however, is limited by the speed of canopy closure of dominant mid-late and late successional tree species, including surviving upper canopy trees, resprouting stems and sapling recruitment.

I observed high rates of herbivory within the first weeks after Cyclone Yasi. Coley (1983) found that leaves of pioneer species are less tough and have shorter life-spans than the leaves of shade-tolerant species, and this in turn leads to high rates of herbivory. In my study, family taxa such as Lauraceae, Rhamnaceae, Malvaceae, Rosaceae and Euphorbiaceae were particularly impacted by post-cyclone herbivory. Vigorous resprouting, post-cyclone, is typical of these families and reflects a 'trade-off' between resistance and resilience (Coley, 1983). Notably, many mid-to late successional species in the Lauraceae family displayed a marked pattern of vulnerability to this early post-cyclone phase of herbivory. These species included *Litsea leefeana* (mid), *Cryptocarya vulgaris* (mid-late), *Beilschmiedia bancroftii* (late), *B. obtusifolia* (late), *B. recurva* (late), *Endiandra sankeyana* (late), *E. wolfei* (late), *E. compressa* (late) *and E. cowleyana* (late).

In a study of species and community-level impacts after Cyclone Larry, Metcalfe et al. (2008) reported significantly different responses to increasing wind speed for two species, *Myristica globosa* ssp. *muelleri* and *Rockinghamia angustifolia.* The results showed a tendency for *M. globosa* ssp. *muelleri* to snap boles or branches (severe damage) in the most severe damage category whereas *R. angustifolia* lost whole leaves and twigs (minor damage) and fewer snapped branches and boles (severe damage) with increasing wind speed (Metcalfe et al., 2008). It would appear that a 'trade-off' exists between snapping of stems at relatively low cyclone intensity, therefore reducing the chances of uprooting and allowing rapid resprouting vs. retaining full canopy and risking catastrophic uprooting (Metcalfe et al., 2008). Contrary to these findings however, I found *M. globosa* subsp. *muelleri* and *R. angustifolia* shared very similar damage responses after Cyclone Yasi. Both species sustained very high rates of snapped boles (81% and 85% respectively) and low rates of snapped branches (9% and 7.5%) but uprooting was more common in *R. angustifolia.* Whilst *M. globosa* subsp. *muelleri* recorded 9% of trees with minor damage (i.e. partial defoliation, twig snapping and minor branches snapped), *R. angustifolia* had no trees in this class. All trees showed vigorous resprouting and sustained growth after cyclone damage.

Metcalfe et al. (2008) suggested that under a future climate change scenario of more frequent intense cyclones, a shift may occur in species assemblages with an increase in abundance of disturbance-favoured vines, climbing palms (*Calamus* spp.) and expansion of ‘cyclone scrubs’ (Webb, 1958) on the exposed coastal lowlands. Metcalfe et al. (2008) made the prediction that ‘susceptible species’ such as *M. globosa* ssp. *muelleri* may retreat from lowland rainforests altogether or face a restricted distribution on leeward facing slopes of lowland ranges. In my study area at Mission Beach, *M. globosa* subsp. *muelleri* is the most common tree species across all habitat types making up 7.6% of all stems while *R. angustifolia* is one of the most common species in continuous forest plots. Both trees are late successional species dominating the canopy/ sub-canopy and sub-canopy levels respectively. Following successive severe cyclones, *M. globosa* subsp. *muelleri* together with its congener, *Myristica insipida,* a locally abundant littoral rainforest species, continue to demonstrate high rates of survivorship and resilience in these coastal communities. Furthermore, my results show no shift towards a decline in abundances or ‘retreat’ of these dominant late-maturing species.

4-3 No evidence for fragmented forest shift to early-successional species

In Chapter 3, my results failed to find support for my earlier hypotheses that fragmented forests would show a shift towards: 1) mass recruitment and hyper-abundance of edge-favoured generalists; 2) a proliferation of disturbance-favoured species and exclusion of forest-interior plant species; and 3) dramatic loss of large-fruited, late-maturing and long-lived canopy and emergent trees. Forest habitat categories influenced successional characteristics but showed no shift towards the proliferation of light-demanding, edge-favoured generalists (i.e. pioneer species), within the time-frame of this study.

4-4 Dominance of species with mid- to late successional life-history traits

My results showed tree assemblages across all three habitat types were dominated by mid-to late successional species (i.e. shade-tolerant, late-maturing species). Although there was a dramatic loss of large canopy and emergent trees during Cyclone Larry five years earlier (Catterall et al., 2008), 83% of all stems in my plots were identified as belonging to mid-late and late successional species. Only 13% of stems were early-mid successional species and showed little difference in the proportion of stems between continuous forest and fragmented forest, 26% and 23% respectively. Mid-late successional tree species showed a significantly higher proportion of stems for edge continuous forest compared to continuous forest and fragmented forest, however, the differences between habitat types were not as pronounced in the late successional group. Trees which span all successional stages (i.e. early-mid-late successional) were comprised largely of long-lived canopy and emergent species. These species showed a significantly higher proportion of trees in fragmented forest sites compared to continuous forest sites.

In my study, mid-late and late successional tree species were largely represented by small stem saplings (≤ 10-20cm DBH), which were present in the understorey before the impact of Cyclone Yasi. Most of these saplings have survived recent successive severe cyclone events protected within the understorey ‘vine tangles’ (Webb, 1958). Laurance et al. (2009), in a study of forest dynamics in the Amazon basin found that the smallest tree size class (10-20cm DBH) dominated the structure of these forests. In the Australian Wet Tropics, Curran et al. (2008a) also reported higher proportions of tree stems in smaller tree size classes compared to large stem classes and that individual species demonstrated ‘trade-offs’ between cyclone resistance and resilience. Following severe tropical storms, tree size distributions are altered but species composition and richness remain the same (Yih et al., 1991), or increase as a result of the large-scale disturbance (Vandermeer et al., 2000). Long-lived, late-maturing (primary) species increase in abundances while pioneer and secondary regrowth species decrease (Lugo, 2008; Vandermeer et al., 2000).

Carrington et al. (2015) also noted the dominance of late successional species post-hurricane disturbance and suggested preferential seed dispersal likely plays a role in accelerated succession, especially if mature trees are present in the ecosystem. Mid-late and late successional species, including many large-fruited species, are dispersed predominantly by bats, birds and particularly the southern cassowary *(Casuarius casuarius johnsonii)* (Catterall et al., 2008; Westcott et al., 2005) across all forest habitat types in the study area. These mid-late and late successional species are preferentially dispersed into these communities and grow slowly, establishing a positional advantage over smaller trees and seedlings as well as restricting opportunities for germination and establishment of light-demanding pioneer species after cyclone damage (Putz et al., 1983). Furthermore, tropical wind-storms may impact different stages of an individual’s life-history (i.e. short-lived vs. long-lived species) and in particular, may influence outcomes for long-lived, late-maturing species many times during their life-cycle (Bellingham et al., 1995).

4-5 No evidence of significant exotic shrub/ tree invasion

Contrary to predictions of weed invasion after Cyclone Larry (Catterall et al., 2008; Murphy & Metcalfe, 2016; Murphy et al., 2008), I found no evidence to support my hypothesis that these cyclone-disturbed forests are particularly vulnerable to exotic plant invasion within the time-frame of this study. Only 1.16% of all live stems ≥ 5cm DBH are exotic or alien species. The results broadly show a high level of resilience to alien plant invasion, but fragmented forest appears to be more vulnerable compared to continuous forest. Sixteen exotic tree stems ≥ 5cm DBH were recorded including five families and five species. Exotic tree stems include *Mangifera indica*, *Spathodea campanulata, Bauhinia monandra*, *Carica papaya* and *Ravenala madagascariensis*. These species have a horticultural origin as either fruit trees or ornamentals. Most of the smaller stemmed exotic species present are shade averse and transient (e.g. perennial grasses, herbs, slender soft-stem climbers and scramblers). As canopy cover re-establishes following cyclone disturbance, the amount of shade increases reducing opportunities for heliophytic species within the ground layer and lower stratum. The seed bank however is retained in the topsoil (Murphy et al., 2008).

The capacity for invasive species to establish and potentially transform an ecosystem appears to be dependent on complex interactions between species assemblages, gap dynamics, disturbance history and successional life-history traits of individual species (Baret et al., 2008; Martin et al., 2009). Many invasive species are disturbance-favoured, existing mostly as a transient component of the flora following disturbance (i.e. possessing early successional life-history traits) (Murphy et al., 2008). As canopy cover and shade increases these species disappear from the assemblages, however, some species may have much longer-term effects (Murphy et al., 2008; Tng et al., 2016). In the Wet Tropics, invasion by potential 'transformer' weed species (e.g. *Miconia calvescens*, *Rubus alceifolius, Annona glabra* and *Mikania micrantha)* may retard the successional trajectories of native species, altering forest structure and species assemblages. In a recent study comparing mature rainforests and successional sites on the Atherton Tablelands, the potentially invasive exotic shrub, *Psidium cattleianum* (strawberry guava) was found to be largely restricted to early successional or secondary forests (Tng et al., 2016). Similarly, diversity and abundance of invasive species was found to be highest in the most severely cyclone-damaged forests (Murphy et al., 2008), raising questions over the future of storm-damaged forests in fragmented landscapes (Murphy & Metcalfe, 2016).

4-6 Maintaining mega-frugivore dispersal of late successional, large-fruited trees

Seed dispersal, seedling establishment and spatial distribution of seedlings, away from parent trees, are strongly affected by frugivore diversity and behaviour (Bleher & Boehning-Gaese, 2001). Large-fruited, late-successional tropical forest tree species, which rely on seed dispersal by a few, or possibly a single large-bodied frugivore, may become vulnerable to local and regional extinction with the decline or disappearance of these animal or bird species (Bueno et al., 2013; Costa et al., 2012; de Melo et al., 2006). Strategies for protecting critical forest habitat for large-bodied frugivores, and improving connectivity with smaller forest fragments, are vitally important for managing these threatened tropical landscapes (Costa et al., 2012; Williams & Adam, 2010).

The southern cassowary *(Casuarius casuarius johnsonii),* is considered an iconic keystone species of the Australian Wet Tropics Bioregion (Buosi & Burnett, 2006; Latch, 2007; Moore, 2007; Westcott et al., 2005). This large-bodied frugivore is crucial to dispersal and post-cyclone seedling recruitment, maintaining forest assemblages and floristic diversity (Catterall et al., 2008; Westcott et al., 2005). Importantly, the southern cassowary, listed as endangered under the Environmental Protection and Biodiversity Act (EPBC Act 1999) (Australian Government, 2017), is capable of dispersing large-fruited, late-successional, shade-tolerant tree species. Key plant families in these frugivore-dispersed relationships include Lauraceae, Meliaceae, Sapindaceae and Sapotaceae. A total of 55 of 176 recorded plant species in this study are known to be dispersed by the southern cassowary (Cooper & Cooper, 2004).

The southern cassowary is not restricted to continuous (interior) rainforest, moving freely between a mosaic of varying habitats. This ability to move between continuous forest and fragmented forest patches, including traversing a harsh matrix of roads, cleared paddocks and urban subdivisions, has important implications for dispersal and germination of large-fruited, late-successional (interior) tree species and long-term resilience of fragmented forests in the Mission Beach study area (Catterall et al., 2008; DEWHA, 2009; Hill et al., 2010; Westcott et al., 2005).

4-7 Conclusion

My research demonstrates that severely storm-damaged and fragmented tropical forests are remarkably resilient, showing a capacity for rebuilding and maintaining plant species composition and diversity. After two successive severe cyclones, within less than 5-years, the structural characteristics for all three habitat types were altered dramatically, with the loss of many large canopy trees, and a severely lowered and damaged understorey, dominated by smaller-stemmed trees and sapling recruitment. All trees sustained some level of cyclone damage (i.e. minor to severe). The three habitat types shared similar basal areas and high ratio of small stems. Structurally, continuous forest sites had become more like the forest edges and fragmented forest sites after two successive cyclones. I found no evidence however, to suggest that cyclone disturbance and fragmentation are driving species assemblages towards early successional states.

Tropical-storm damaged forests respond rapidly to these new opportunities, usually with a very high level of resilience (Lugo, 2008; Ostertag et al., 2005). These natural disturbances influence species composition and diversity (Attiwill, 1994; Keppel et al., 2010; Vandermeer et al., 2000) and redirect successional trajectories (Lugo, 2008). I recorded an exceptionally high level of tree species diversity (176 tree species) across three habitat types (total 0.54 Ha) within lowland tropical rainforest. My data suggest that forest habitat types influence the life-history characteristics of these plant communities, but there was no evidence for a shift in composition or bias towards pioneer or secondary species (Laurance et al., 2006). My data show no proliferation of these light-demanding, short-lived generalist and early-successional species (Laurance & Curran, 2008; Laurance et al., 2006; Metcalfe et al., 2008). By comparison, I recorded a marked absence, or near absence (<1%) of early-pioneer tree species in the study sites, including forest fragments. A total of 84% of all tree stems in fragmented forest sites belonged to mid-late and late successional groups. These two severe cyclones provided opportunities for small stemmed, mid-late and late successional species (already present in the understorey), to dominate all habitat types. Furthermore, no evidence was found for exotic woody or non-woody weed invasion, with these species comprising less than 1% of total assemblages.

Following Cyclone Larry in 2006, many studies predicted that cyclone-damaged tropical forest fragments would be locked into declining successional trajectories, with greater vulnerability to windstorm damage, proliferation of edge-favoured, early-successional pioneer species, exclusion of late-successional, shade-tolerant interior species, and exotic weed invasion (Laurance & Curran, 2008; Metcalfe et al., 2008; Murphy & Metcalfe, 2016; Murphy et al., 2008). Other studies found no evidence of increased susceptibility of rainforest fragments to cyclone damage (Catterall et al., 2008; Grimbacher et al., 2008; Pohlman et al., 2008). One study however, examined how these tropical storms influence renewal of species assemblages, maintain diversity and alter successional trajectories (Lugo, 2008).

Studies which have focused on impoverishment of tree species assemblages, ecosystem collapse, exotic invasion and local extinctions, have largely ignored the vital role of fragmented and secondary tropical forests providing opportunities for succession towards mature forests. Lugo (2009) argues that devaluing fragmented and secondary forests gives the impression that the biota is incapable of adjusting, adapting or coping with the modified environmental conditions. After Cyclone Larry, predictions of seriously compromised ecological outcomes provided a strong argument for land-clearing on public and privately-owned land, especially within small and highly disturbed parcels of forest habitat. This narrative, based solely on declining ecological trajectories, continues to diminish the conservation values of fragmented forest habitat, despite their essential role in rebuilding resilience, regenerating and connecting habitat in these modified landscapes.

In the Mission Beach study area, fragmented rainforests occur primarily on privately-owned land. These small forest patches represent the most threatened parcels of habitat in this coastal landscape. In recent decades, fragmented forests have come under increasing pressure for urban development, particularly along the narrow coastal strip. However, the landscape matrix still retains exceptional opportunities for improved habitat and enhanced connectivity, ensuring better conservation outcomes for threatened and iconic keystone species, such as the southern cassowary *(Casuarius casuarius johnsonii).*

I believe that a focus on only the negative aspects of fragmented forests feeds directly into a loop of expendability and poor policy-making decisions. Fragmented forests are increasingly an important part of human-modified tropical landscapes, particularly highly contested landscapes such as Mission Beach, north Queensland. Their loss would have a significant impact upon a range of social-ecological values across a range of scales. The Mission Beach area is internationally recognised for its exceptional biodiversity, scenic and natural heritage values, but it would be a very different place without these forest habitat mosaics in the landscape. It is important that policy-makers recognise the ecological significance of fragmented forest habitat, (including its plant diversity, successional specialization and potential for rebuilding resilience in the landscape), and to ensure delivery of strategies which will protect and manage these habitats, as integral components of broader local and regional conservation measures.

APPENDIX 3.1. Abundance and successional characteristics of 176 plant species (stems ≥ 5cm DBH) from three rainforest habitat types in north Queensland.

SPECIES	FAMILY	Life form	Successional stage	Continuous forest		Edge continuous forest		Fragmented forest		TOTAL	
				n	%	n	%	n	%	N	%
Aceratium megalospermum	ELAEOCARPACEAE	tree	late	1	0.24	0	0.00	0	0.00	1	0.07
Acronychia acronychioides	RUTACEAE	tree	mid-late	0	0.00	1	0.19	0	0.00	1	0.07
Aglaia elaeagnoidea	MELIACEAE	tree	mid-late	0	0.00	0	0.00	1	0.22	1	0.07
Aidia racemosa	RUBIACEAE	tree	late	1	0.24	0	0.00	0	0.00	1	0.07
Ailanthus integrifolia subsp. *integrifolia*	SIMAROUBACEAE	tree	early-mid-late	0	0.00	4	0.74	7	1.52	11	0.77
Aleurites rockinghamensis	EUPHORBIACEAE	tree	early-mid-late	0	0.00	5	0.93	8	1.73	13	0.91
Alphitonia whitei	RHAMNACEAE	tree	early-mid	5	1.18	0	0.00	0	0.00	5	0.35
Alstonia muelleriana	APOCYNACEAE	tree	early-mid	10	2.36	2	0.37	5	1.08	17	1.19
Alstonia scholaris	APOCYNACEAE	tree	early-mid-late	3	0.71	7	1.30	7	1.52	17	1.19
Anthocarapa nitidula	MELIACEAE	tree	late	0	0.00	0	0.00	2	0.43	2	0.14
Antirhea tenuiflora	RUBIACEAE	shrub/tree	late	1	0.24	0	0.00	1	0.22	2	0.14
Apodytes brachystylis	ICACINACEAE	shrub/tree	late	12	2.84	0	0.00	0	0.00	12	0.84
Archidendron lucyi	MIMOSACEAE	shrub/tree	late	0	0.00	1	0.19	2	0.43	3	0.21
Archidendron vaillantii	MIMOSACEAE	tree	late	0	0.00	1	0.19	0	0.00	1	0.07
Archontophoenix alexandrae	ARECACEAE	palm	early-mid	4	0.95	70	12.99	15	3.25	89	6.25
Ardisia brevipedata	MYRSINACEAE	shrub	late	3	0.71	0	0.00	0	0.00	3	0.21
Arenga australasica	ARECACEAE	palm	late	2	0.47	4	0.74	3	0.65	9	0.63
Atractocarpus fitzallanii subsp. *fitzallanii*	RUBIACEAE	tree	late	2	0.47	0	0.00	2	0.43	4	0.28
Austrosteenisia blackii	FABACEAE	liana	mid	0	0.00	1	0.19	0	0.00	1	0.07
*Bauhinia monandra**	CAESALPINIACEAE	tree	n/a	0	0.00	0	0.00	1	0.22	1	0.07
Beilschmiedia bancroftii	LAURACEAE	tree	late	2	0.47	5	0.93	2	0.43	9	0.63
Beilschmiedia obtusifolia	LAURACEAE	tree	late	0	0.00	1	0.19	3	0.65	4	0.28
Beilschmiedia recurva	LAURACEAE	tree	late	5	1.18	0	0.00	0	0.00	5	0.35
Beilschmiedia tooram	LAURACEAE	tree	late	4	0.95	3	0.56	0	0.00	7	0.49
Bridelia insulana	PHYLLANTHACEAE	shrub/tree	late	2	0.47	0	0.00	0	0.00	2	0.14
Brombya platynema	RUTACEAE	shrub/tree	mid-late	44	10.40	25	4.64	4	0.87	73	5.13
Calophyllum sil	CLUSIACEAE	tree	late	0	0.00	2	0.37	1	0.22	3	0.21
Cananga odorata	ANNONACEAE	tree	mid-late	0	0.00	0	0.00	3	0.65	3	0.21
Canarium vitiense	BURSERACEAE	tree	mid-late	0	0.00	5	0.93	13	2.81	18	1.26
Carallia brachiata	RHIZOPHORACEAE	tree	mid-late	1	0.24	0	0.00	4	0.87	5	0.35
Cardwellia sublimis	PROTEACEAE	tree	late	6	1.42	4	0.74	1	0.22	11	0.77
*Carica papaya**	CARICACEAE	tree	n/a	0	0.00	0	0.00	2	0.43	2	0.14
Carnarvonia araliifolia var. *araliifolia*	PROTEACEAE	tree	late	6	1.42	1	0.19	0	0.00	7	0.49

Castanospermum australe	FABACEAE	tree	late	1	0.24	5	0.93	9	1.95	15	1.05
Castanospora alphandii	SAPINDACEAE	tree	late	0	0.00	0	0.00	1	0.22	1	0.07
Chionanthus ramiflorus	OLEACEAE	tree	mid-late	0	0.00	4	0.74	4	0.87	8	0.56
Chisocheton longistipitatus	MELIACEAE	tree	late	1	0.24	0	0.00	6	1.30	7	0.49
Cissus penninervis	VITACEAE	liana	mid	0	0.00	1	0.19	0	0.00	1	0.07
Citronella smythii	ICACINACEAE	tree	mid	10	2.36	1	0.19	0	0.00	11	0.77
Claoxylon hillii	EUPHORBIACEAE	shrub	mid	0	0.00	1	0.19	1	0.22	2	0.14
Cnesmocarpon dasyantha	SAPINDACEAE	tree	late	1	0.24	0	0.00	0	0.00	1	0.07
Commersonia bartramia	MALVACEAE	tree	early-mid	2	0.47	0	0.00	1	0.22	3	0.21
Connarus conchocarpus ssp. *conchocarpus*	CONNARACEAE	liana	mid-late	1	0.24	0	0.00	0	0.00	1	0.07
Cryptocarya grandis	LAURACEAE	tree	late	2	0.47	0	0.00	2	0.43	4	0.28
Cryptocarya hypospodia	LAURACEAE	tree	mid-late	0	0.00	1	0.19	4	0.87	5	0.35
Cryptocarya laevigata	LAURACEAE	shrub/tree	mid-late	0	0.00	8	1.48	1	0.22	9	0.63
Cryptocarya mackinnoniana	LAURACEAE	tree	late	3	0.71	5	0.93	2	0.43	10	0.70
Cryptocarya oblata	LAURACEAE	tree	late	4	0.95	7	1.30	3	0.65	14	0.98
Cryptocarya vulgaris	LAURACEAE	shrub/tree	mid-late	0	0.00	1	0.19	0	0.00	1	0.07
Cupaniopsis foveolata	SAPINDACEAE	tree	late	0	0.00	0	0.00	3	0.65	3	0.21
Daphnandra repandula	ATHEROSPERMATACEAE	tree	late	0	0.00	3	0.56	0	0.00	3	0.21
Davidsonia pruriens	CUNONIACEAE	tree	mid-late	6	1.42	0	0.00	1	0.22	7	0.49
Decaspermum humile	MYRTACEAE	shrub/tree	late	1	0.24	0	0.00	0	0.00	1	0.07
Delarbrea michieana	ARALIACEAE	shrub/tree	mid-late	1	0.24	0	0.00	0	0.00	1	0.07
Dendrocnide moroides	URTICACEAE	shrub	early-mid	0	0.00	0	0.00	1	0.22	1	0.07
Deplanchea tetraphylla	BIGNONIACEAE	tree	mid	0	0.00	2	0.37	0	0.00	2	0.14
Diospyros cupulosa	EBENACEAE	tree	late	2	0.47	1	0.19	2	0.43	5	0.35
Diploglottis diphyllostegia	SAPINDACEAE	tree	mid-late	0	0.00	1	0.19	0	0.00	1	0.07
Doryphora aromatica	ATHEROSPERMATACEAE	tree	late	0	0.00	1	0.19	0	0.00	1	0.07
Dysoxylum alliaceum	MELIACEAE	tree	late	0	0.00	6	1.11	13	2.81	19	1.33
Dysoxylum arborescens	MELIACEAE	tree	late	1	0.24	0	0.00	1	0.22	2	0.14
Dysoxylum klanderi	MELIACEAE	tree	late	3	0.71	1	0.19	1	0.22	5	0.35
Dysoxylum mollissimum subsp. *molle*	MELIACEAE	tree	early-mid-late	0	0.00	6	1.11	0	0.00	6	0.42
Dysoxylum oppositifolium	MELIACEAE	tree	late	1	0.24	3	0.56	2	0.43	6	0.42
Dysoxylum parasiticum	MELIACEAE	tree	late	3	0.71	1	0.19	0	0.00	4	0.28
Dysoxylum pettigrewianum	MELIACEAE	tree	late	4	0.95	8	1.48	5	1.08	17	1.19
Elaeocarpus angustifolius	ELAEOCARPACEAE	tree	mid	2	0.47	7	1.30	12	2.60	21	1.47
Embelia caulialata	PRIMULACEAE	liana	mid	1	0.24	1	0.19	0	0.00	2	0.14
Emmenosperma cunninghamii	RHAMNACEAE	tree	late	1	0.24	1	0.19	0	0.00	2	0.14
Endiandra compressa	LAURACEAE	tree	late	0	0.00	1	0.19	0	0.00	1	0.07
Endiandra cowleyana	LAURACEAE	tree	late	0	0.00	1	0.19	0	0.00	1	0.07

Endiandra hypotephra	LAURACEAE	tree	mid	8	1.89	5	0.93	3	0.65	16	1.12
Endiandra montana	LAURACEAE	tree	late	2	0.47	0	0.00	0	0.00	2	0.14
Endiandra sankeyana	LAURACEAE	tree	late	3	0.71	0	0.00	0	0.00	3	0.21
Endiandra wolfei	LAURACEAE	tree	late	1	0.24	0	0.00	0	0.00	1	0.07
Entada phaseoloides	MIMOSACEAE	liana	mid	2	0.47	6	1.11	5	1.08	13	0.91
Epipremnum pinnatum	ARACEAE	aroid	mid-late	0	0.00	1	0.19	0	0.00	1	0.07
Erycibe coccinea	CONVOLVULACEAE	liana	mid-late	0	0.00	2	0.37	1	0.22	3	0.21
Eupomatia laurina	EUPOMATIACEAE	shrub	mid	2	0.47	1	0.19	1	0.22	4	0.28
Faradaya splendida	LAMIACEAE	liana	mid-late	3	0.71	7	1.30	4	0.87	14	0.98
Ficus congesta var. *congesta*	MORACEAE	shrub/tree	early-mid	0	0.00	1	0.19	0	0.00	1	0.07
Ficus destruens	MORACEAE	tree	mid	0	0.00	1	0.19	0	0.00	1	0.07
Ficus racemosa	MORACEAE	tree	mid	0	0.00	0	0.00	1	0.22	1	0.07
Ficus septica	MORACEAE	shrub/tree	early-mid	0	0.00	0	0.00	1	0.22	1	0.07
Ficus variegata	MORACEAE	tree	late	0	0.00	3	0.56	0	0.00	3	0.21
Flindersia bourjotiana	RUTACEAE	tree	late	6	1.42	1	0.19	0	0.00	7	0.49
Flindersia pimenteliana	RUTACEAE	tree	late	7	1.65	1	0.19	0	0.00	8	0.56
Flindersia schottiana	RUTACEAE	tree	mid	0	0.00	0	0.00	2	0.43	2	0.14
Franciscodendron laurifolium	MALVACEAE	tree	late	0	0.00	0	0.00	1	0.22	1	0.07
Ganophyllum falcatum	SAPINDACEAE	tree	mid-late	2	0.47	3	0.56	1	0.22	6	0.42
Gillbeea adenopetala	CUNONIACEAE	tree	mid-late	5	1.18	0	0.00	0	0.00	5	0.35
Glochidion sumatranum	PHYLLANTHACEAE	tree	early-mid	2	0.47	3	0.56	3	0.65	8	0.56
Glycosmis trifoliata	RUTACEAE	shrub/tree	late	1	0.24	3	0.56	0	0.00	4	0.28
Gmelina dalrympleana	LAMIACEAE	tree	mid	0	0.00	0	0.00	1	0.22	1	0.07
Gomphandra australiana	ICACINACEAE	tree	mid-late	3	0.71	43	7.98	56	12.12	102	7.16
Gossia myrsinocarpa	MYRTACEAE	shrub/tree	late	0	0.00	1	0.19	0	0.00	1	0.07
Guioa acutiflolia	SAPINDACEAE	tree	early-mid	0	0.00	0	0.00	1	0.22	1	0.07
Guioa lasioneura	SAPINDACEAE	tree	mid-late	1	0.24	0	0.00	0	0.00	1	0.07
Helicia nortoniana	PROTEACEAE	tree	late	2	0.47	0	0.00	1	0.22	3	0.21
Hernandia nymphaeifolia	HERNANDIACEAE	shrub/tree	early-mid-late	0	0.00	0	0.00	3	0.65	3	0.21
Hibiscus tiliaceus	MALVACEAE	tree	mid	2	0.47	1	0.19	1	0.22	4	0.28
Hypserpa decumbens	MENISPERMACEAE	liana	mid	1	0.24	1	0.19	0	0.00	2	0.14
Intsia bijuga	CAESALPINIACEAE	tree	mid-late	0	0.00	8	1.48	3	0.65	11	0.77
Jagera pseudorhus var. *pseudorhus*	SAPINDACEAE	tree	mid	1	0.24	0	0.00	0	0.00	1	0.07
Kopsia arborea	APOCYNACEAE	shrub/tree	late	0	0.00	0	0.00	2	0.43	2	0.14
Lepidozamia hopei	ZAMIACEAE	tree	late	0	0.00	2	0.37	0	0.00	2	0.14
Licuala ramsayi var. *ramsayi*	ARECACEAE	palm	mid-late	19	4.49	43	7.98	1	0.22	63	4.42
Lindera queenslandica	LAURACEAE	tree	late	0	0.00	0	0.00	2	0.43	2	0.14
Litsea bindoniana	LAURACEAE	tree	late	0	0.00	0	0.00	1	0.22	1	0.07

Litsea leefeana	LAURACEAE	tree	mid	10	2.36	1	0.19	5	1.08	16	1.12
Macaranga inamoena	EUPHORBIACEAE	tree	mid-late	17	4.02	1	0.19	0	0.00	18	1.26
Macaranga involucrata var. *mallotoides*	EUPHORBIACEAE	shrub/tree	early-mid	0	0.00	1	0.19	0	0.00	1	0.07
Macaranga tanarius	EUPHORBIACEAE	shrub/tree	early-mid	0	0.00	0	0.00	5	1.08	5	0.35
*Mangifera indica**	ANACARDIACEAE	tree	n/a	2	0.47	2	0.37	3	0.65	7	0.49
Melia azedarach	MELIACEAE	tree	early-mid-late	0	0.00	0	0.00	1	0.22	1	0.07
Melicope vitiflora	RUTACEAE	tree	mid	3	0.71	0	0.00	0	0.00	3	0.21
Melicope xanthoxyloides	RUTACEAE	tree	mid	1	0.24	3	0.56	1	0.22	5	0.35
Melodinus australis	APOCYNACEAE	liana	early-mid	0	0.00	1	0.19	0	0.00	1	0.07
Merremia peltata	CONVOLVULACEAE	liana	early-mid-late	0	0.00	0	0.00	1	0.22	1	0.07
Mischocarpus exangulatus	SAPINDACEAE	tree	mid-late	0	0.00	0	0.00	1	0.22	1	0.07
Musa banksii	MUSACEAE	tree	early	0	0.00	0	0.00	1	0.22	1	0.07
Musgravea heterophylla	PROTEACEAE	tree	late	13	3.07	0	0.00	0	0.00	13	0.91
Myristica globosa subsp. *muelleri*	MYRISTICACEAE	tree	late	21	4.96	43	7.98	44	9.52	108	7.58
Myristica insipida	MYRISTICACEAE	tree	late	0	0.00	0	0.00	15	3.25	15	1.05
Nauclea orientalis	RUBIACEAE	tree	mid-late	0	0.00	1	0.19	0	0.00	1	0.07
Neosepicaea jucunda	BIGNONIACEAE	liana	mid	1	0.24	0	0.00	0	0.00	1	0.07
Opisthiolepis heterophylla	PROTEACEAE	tree	late	5	1.18	0	0.00	0	0.00	5	0.35
Palaquium galactoxylum	SAPOTACEAE	tree	late	1	0.24	0	0.00	4	0.87	5	0.35
Pandanus monticola	PANDANACEAE	shrub	mid	0	0.00	2	0.37	4	0.87	6	0.42
Pilidiostigma tropicum	MYRTACEAE	shrub	late	0	0.00	1	0.19	0	0.00	1	0.07
Pisonia umbellifera	NYCTAGINACEAE	tree	mid-late	0	0.00	2	0.37	6	1.30	8	0.56
Planchonella chartacea	SAPOTACEAE	tree	mid-late	0	0.00	2	0.37	0	0.00	2	0.14
Planchonella obovata	SAPOTACEAE	shrub/tree	early-mid-late	0	0.00	0	0.00	1	0.22	1	0.07
Podocarpus grayae	PODOCARPACEAE	tree	late	2	0.47	0	0.00	0	0.00	2	0.14
Polyalthia australis	ANNONACEAE	tree	mid-late	1	0.24	1	0.19	3	0.65	5	0.35
Polyathia nitidissima	ANNONACEAE	shrub/tree	mid-late	0	0.00	0	0.00	1	0.22	1	0.07
Polyscias australiana	ARALIACEAE	shrub/tree	early-mid	21	4.96	15	2.78	4	0.87	40	2.81
Polyscias elegans	ARALIACEAE	tree	early-mid	0	0.00	1	0.19	2	0.43	3	0.21
Polyscias murrayi	ARALIACEAE	tree	early-mid	3	0.71	0	0.00	0	0.00	3	0.21
Prunus turneriana	ROSACEAE	tree	late	3	0.71	0	0.00	0	0.00	3	0.21
Ptychosperma elegans	ARECACEAE	palm	mid	33	7.80	42	7.79	34	7.36	109	7.65
*Ravenala madagascariensis**	STRELITZIACEAE	tree	n/a	0	0.00	0	0.00	1	0.22	1	0.07
Rhodamnia sessiliflora	MYRTACEAE	shrub/tree	mid-late	3	0.71	2	0.37	4	0.87	9	0.63
Rhodomyrtus macrocarpa	MYRTACEAE	tree	mid-late	0	0.00	1	0.19	1	0.22	2	0.14
Rhus taitensis	ANACARDIACEAE	shrub/tree	early-mid	0	0.00	0	0.00	1	0.22	1	0.07
Rhysotoechia robertsonii	SAPINDACEAE	tree	mid-late	0	0.00	1	0.19	0	0.00	1	0.07
Rockinghamia angustifolia	EUPHORBIACEAE	tree	late	13	3.07	0	0.00	0	0.00	13	0.91

Rourea brachyandra	CONNARACEAE	liana	mid-late	1	0.24	0	0.00	0	0.00	1	0.07
Sarcotoechia protracta	SAPINDACEAE	tree	late	1	0.24	0	0.00	0	0.00	1	0.07
Semecarpus australiensis	ANACARDIACEAE	tree	mid-late	1	0.24	7	1.30	9	1.95	17	1.19
Sloanea langii	ELAEOCARPACEAE	tree	late	0	0.00	1	0.19	1	0.22	2	0.14
Sloanea macbrydei	ELAEOCARPACEAE	tree	late	4	0.95	0	0.00	0	0.00	4	0.28
Solanum viridifolium	SOLANACEAE	shrub	early-mid	0	0.00	0	0.00	1	0.22	1	0.07
*Spathodea campanulata**	BIGNONIACEAE	tree	n/a	0	0.00	0	0.00	5	1.08	5	0.35
Strychnos minor	LOGANIACEAE	liana	mid-late	2	0.47	0	0.00	0	0.00	2	0.14
Symplocos cochinchinensis var. *pilosiuscula*	SYMPLOCACEAE	tree	mid-late	0	0.00	3	0.56	1	0.22	4	0.28
Symplocos paucistaminea	SYMPLOCACEAE	tree	mid-late	6	1.42	1	0.19	0	0.00	7	0.49
Synima cordierorum	SAPINDACEAE	tree	late	0	0.00	2	0.37	3	0.65	5	0.35
Synima macrophylla	SAPINDACEAE	tree	late	0	0.00	1	0.19	1	0.22	2	0.14
Syzygium alliiligneum	MYRTACEAE	tree	late	1	0.24	2	0.37	3	0.65	6	0.42
Syzygium claviflorum	MYRTACEAE	tree	late	1	0.24	4	0.74	6	1.30	11	0.77
Syzygium cormiflorum	MYRTACEAE	tree	late	0	0.00	4	0.74	9	1.95	13	0.91
Syzygium graveolens	MYRTACEAE	tree	late	0	0.00	1	0.19	1	0.22	2	0.14
Syzygium hemilamprum ssp. *hemilamprum*	MYRTACEAE	tree	mid-late	0	0.00	3	0.56	0	0.00	3	0.21
Syzygium kuranda	MYRTACEAE	tree	late	6	1.42	0	0.00	0	0.00	6	0.42
Syzygium luehmannii	MYRTACEAE	tree	late	1	0.24	2	0.37	0	0.00	3	0.21
Terminalia catappa	COMBRETACEAE	tree	early-mid	0	0.00	0	0.00	1	0.22	1	0.07
Terminalia microcarpa	COMBRETACEAE	tree	early-mid-late	0	0.00	0	0.00	1	0.22	1	0.07
Tetrastigma nitens	VITACEAE	liana	mid	0	0.00	3	0.56	0	0.00	3	0.21
Toechima erythrocarpum	SAPINDACEAE	tree	late	3	0.71	7	1.30	1	0.22	11	0.77
Trema orientalis	CANNABACEAE	tree	early-mid	0	0.00	0	0.00	1	0.22	1	0.07
Vitex queenslandica	LAMIACEAE	tree	late	1	0.24	0	0.00	1	0.22	2	0.14
Wilkiea longipes	MONIMIACEAE	shrub/tree	late	0	0.00	1	0.19	2	0.43	3	0.21
Wilkiea pubescens	MONIMIACEAE	shrub/tree	mid-late	1	0.24	2	0.37	2	0.43	5	0.35
Wrightia laevis	APOCYNACEAE	tree	late	3	0.71	13	2.41	11	2.38	27	1.90
Xanthophyllum octandrum	POLYGALACEAE	tree	late	0	0.00	2	0.37	2	0.43	4	0.28
Totals				**423**	100.00	**539**	100.00	**462**	100.00	**1424**	100.00

Successional stages: early = early successional/ light-demanding pioneer spp.; mid = intermediate/ gap demanding spp.; late = late successional/ late maturing, shade-tolerant spp.; n/a = exotic spp. Many species have successional characteristics spanning two or three stages.

* Exotic weed species.

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