Plant biodiversity differences between rainforest plots in different stages of recovery in the uplands of the Wet Tropics

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Abstract

Rainforests are one of the most diverse ecosystems in the world. In Australia, the Wet Tropics Rainforests of North Queensland are especially speciose, containing a wide range of flora and fauna, including a high number of endemic species. Unfortunately, the region has also been threatened by human impact such as land clearing. Relatively few studies have conducted full plot-level floristics in this region. In our study in the Gadgarra region of the Atherton Tablelands, Queensland, we looked at full floristics in 500m² plots that we established in four vegetation types: a relatively undisturbed Old growth rainforest, an Old secondary rainforest (recovering from clearance since 1947); a Young secondary rainforest (recovering from clearance since 1972), and an Abandoned Orchard area. Across all plots, we found a total of 214 species belonging to 162 genera and 74 families. We found that the Old growth forest had the highest number of species, genera and families. The diversity present in the Older secondary plot was comparable to that displayed by the Old growth forest plot. In general, our results indicate that previously cleared forests have a lower species richness, a decrease in endemism, and altered species composition due to the effects of clearing. However, over time secondary succession results in some recovery of both forest structural and species composition similar to that of an undisturbed forest. Our study is descriptive in nature due to the lack of replication in sampling plots within vegetation types. However, we present a plant biodiversity list for each plot that can serve as baseline data for further studies in the region.

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Handling editor: Gabriel Crowley

Citation: Mullin MV, Salecki EF, Li CR, Avinger AM, Landen EW, Thurnham JS, Pohlman CL, Tng DYP. 2020. Plant biodiversity differences between rainforest plots in different stages of recovery in the uplands of the Wet Tropics. *North Queensland Naturalist* 50: 25-37.

Introduction

Rainforests are one of the most valuable ecosystems on the planet as they provide habitat for about 80% of the world's documented species and play important roles in carbon cycle and in stabilizing ecosystems (Whitmore 1990; Leigh 1999; Alamgir *et al.* 2016). Forests in general contain about 80% of global terrestrial biodiversity, and tropical rainforests alone account for 59% of forest species richness (Whitworth *et al.* 2016). This diversity highlights the importance of protecting and observing these ecosystems.

Rainforests also store about 25% of the world's carbon, remaining a key component in mitigating CO² rises due to climate change (Global Forest Atlas 2019; Magnago *et al.* 2015). Degraded rainforests often store less carbon than intact forests, although with the proper rehabilitation they could store comparable amounts (Alamgir *et al.* 2016). This finding emphasizes the need to focus on rehabilitation and demonstrates the important role that these systems have in combatting climate change. However, despite their value, rainforests have been steadily impacted by human activities such as logging and land clearing (Goudie 2018; Whitworth *et al.* 2018).

The Wet Tropics region in North Queensland Australia, at 1,849,725 ha, represents a prime example of a highly threatened rainforest ecosystem upon which a variety of rainforest restoration projects have been focused (Neldner et al. 2017). Almost half of the Wet Tropics consists of the World Heritage Area (894,420 ha) which remains home to a wide range of endemic and rare species, including 16 of the ancient primitive flowering plant lineages and 700 endemic vascular plant species (Williams et al. 2011; Goosem & Tucker 2013). The geological history of the Australian continent, including large periods of isolation and contact with Asia, accounts for much of this diversity and the high endemism in the region (Common & Norton 1992). While the Wet Tropics accounts for only about 0.26% of the area of the Australian continent, the area hosts a disproportionate portion of certain groups of Australian plant species, including 30% of Australia's orchid species and 65% of Australia's fern species (Goosem & Tucker 2013). Furthermore, because a great level of diversity is present and because the region is threatened, the area is considered a biodiversity hotspot (Williams *et al.* 2011).

Unfortunately, over 70% of the natural areas in the Wet Tropics have already been cleared (Williams *et al.* 2011). Despite this clearing, the rest of the Wet Tropics still faces a range of threats from further land clearing and climate change which threatens some 739 native species in the region (Neldner *et al.* 2017). Further, such land clearing affects the local climate, such as temperature and precipitation and produces runoff that contaminates areas like the neighbouring Great Barrier Reef World Heritage Area (Neldner *et al.* 2017).

The continued conservation and management of these unique forests lies in having a good understanding, and a sound monitoring system, of plant biodiversity on the local scale (Boyle & Sayer 1995). Assessing and recording local plant diversity enables vegetation ecologists to produce better vegetation classification systems that will aid in informing vegetation management (Boyle & Sayer 1995). Biodiversity assessments also provide an important means by which rainforest systems can monitored for responses to changing be environments (Magurran et al. 2010). Investigating diversity in the Wet Tropics, a biodiversity hotspot, provides a great deal of valuable information. Additionally, studying the differences in diversity patterns between rainforest plots of different successional ages can help to better understand the effects of land clearing and forest regeneration (Yeo & Fensham 2014; Goosem et al. 2016). For instance, some studies indicate that it is fairly difficult for tropical rainforest soils to recover from this kind of disturbance (Rasiah et al. 2004; Shoo et al. 2016). However, other studies have shown that with sufficient time the forests can increase in both species and functional diversity (Bu et al. 2014). Disturbance in secondary successional forest e.g. land clearing, alters aspects such as soil and light availability (Crome et al. 1992; Paul et al. 2010). The alteration of these factors results in niches that favor different species than those of the original forest; consequently, intraspecific competition is likely to be a more significant driver of diversity in primary than in secondary forest (Fibich et al. 2016).

Comparing plant biodiversity at the plot level enables us to examine the sensitivity of different plant groups to disturbance. Certain groups of plants such as rainforest gymnosperms may not compete well with more competitive angiosperms (Alroy 2017; Becker 2000). The more primitive lineages of plants, such as ferns, rainforest gymnosperms, and basal angiosperms have less developed water conducting systems and may therefore be more susceptible to desiccation caused by disturbance (Boyce *et al.* 2009). Similarly, plot-based studies help to identify specific ecological niches in undisturbed rainforests that enable them to support a greater number of endemic species (Böehmer 2011).

Most plot-based vegetation monitoring studies have focused primarily on trees, or stems over 10 cm diameter at breast height (DBH), and investigations have included smaller stems (Whitmore 1990; Leigh 1999). Partly, this has been due to the difficulties of conducting such work in tropical regions and also the scarcity of information on the tropical flora. Even though the flora of the Wet Tropics of Australia is relatively well known, flora checklists of local areas are limited (Graham 2006; Tng et al. 2016), or are generally inaccessible to the public. This limited understanding of tropical flora also limits ecological research and consequently conservation planning on a larger scale (Phillips et al. 2003).

In this study, we investigate the local plant biodiversity of vegetation plots at different successional stages ranging from Old Growth forest to anthropogenically-managed landscapes. We expect that the species richness, diversity and aboveground biomass will be greater in an Old Growth forest compared to a forest recovering from disturbance. We also hypothesize that ferns, conifers, and basal angiosperms will be most diverse in undisturbed areas, which would also include the highest proportion of regional endemics, and the highest percentage of epiphytic and vine plant lifeforms.

Methods

Study site

This study was conducted within the property of the Centre for Rainforest Studies (CRS) of the School for Field Studies (17°12'S, 145°40'45"E). The Centre is located on the western edge of Gadgarra Forest Reserve (Fig. 1A), which is part of the Wet Tropics World Heritage Area of northeast Queensland, Australia. The CRS property encompasses an area of 62 hectares of upland rainforest at different stages of recovery from previous land clearing or logging activities, areas with replanted rainforest, and also a limited extent of abandoned orchard areas and built up areas (Fig. 1B). The dominant underlying geology within the CRS is granite, with small areas of basalt.

The older, least disturbed areas at the CRS consist of rainforests with a relatively simple structure and an even canopy layer, known as simple notophyll vine forest (Tracey & Webb 1959). The secondary forests within the property consist of recovering notophyll vine forest with *Acacia celsa* and *A. cincinnata* as dominants.

Mean annual temperature measured at the closest weather station (approximately 21.5 km due west) with long-term temperature and precipitation data (Atherton station: $17^{\circ}15'35''S$, $145^{\circ}28'50''E$, 753 m a.s.l elevation, data measured between 1992–2009) is 25.6 °C and the mean annual precipitation is 1369.3 mm, with a significant wet period (> 100 mm month⁻¹) from December through April (Australian Government Bureau of Meteorology 2019; Fig. 2). The CRS is probably slightly wetter than Atherton due to location.

Data collection

Our field sampling was conducted during the end of the dry season (November) in 2019. We surveyed four different vegetation plots within the CRS property, each located at least 162 m apart. The first plot consisted of old growth rainforest, which had never been cleared, although some selective extraction of timber may have occurred in these forests in the 1920-40s as was common in the region before World Heritage Area protection was implemented (e.g. Horne & Hickey 1991). The two secondary forest plots consisted of rainforest of the same type as the old growth plot which is recovering from clearance for pasture, but which were abandoned in 1947 and 1972 (Table 1). All plots were located on areas with underlying granitic geology, and ranged in altitude between 743-764m a.s.l (Table 1).

Time of abandonment of the secondary forest sites was estimated through observation of aerial photographs pertaining to the years 1942, 1952, 1965, 1978, 1986, 1992 and 1997, which are archived at CRS. We estimated pasture



Figure 1. An aerial map of the Centre for Rainforest Studies, School for Field Studies site in Gadgarra, Atherton Tablelands, Queensland where the study was conducted. (A) Points indicate the location of each study site. (B) Indicates the vegetation types in each area of the property.





Plot Type	Location	Canopy Openness (%)	Canopy Strata Height Range (m)	Elevation Range (m)	Slope (°)	Aspect (°)	Description
Old Growth	17.203151S 145.678807E	14.4 (± 3.8)	19.0 — 24.6	743 – 744	1.4	228	Selectively logged before 1942
Old Secondary	17.200556S 145.678553E	13.7 (± 6.4)	14.0 — 18.6	751 – 762	18.8	180.4	Cleared and abandoned ~ 1947
Young Secondary	17.203376S 145.675862E	29.3 (± 4.1)	17.2 – 23.4	751 – 764	13.2	261.6	Cleared and abandoned ~ 1972
Abandoned Orchard Area	17.204572S 145.679041E	42.5 (± 10.5)	7.5 – 14	740 – 747	11	30	Abandoned in early to mid 2000s but never allowed to fully regenerate due to anthropogenic disturbance

 Table 1. General descriptions of each of the four sampled plots at the School for Field Studies Centre for

 Rainforest Studies.

abandonment to have occurred if pasture was observed in one photo and signs of secondary succession were observed in the next; we then took the mid-point between the two years as the approximate pasture abandonment year. Our fourth site was an area that was originally planted as an orchard and then abandoned in 2008. This site consists of a number of planted exotic and native fruit trees and is regularly mown to control for non-native weeds.

At each site, a single 50 m x 10 m plot was established, consisting of five 10 m x 10 m subplots. Stakes were used to mark the corners of each subplot and the boundary of the entire plot was marked out with nylon string. GPS coordinates were taken at each corner. A single 25 m x 20 m plot was established in the orchard, which was of limited extent. For each of the forest plots, the slope in degrees was measured with a clinometer, and canopy cover percentage was estimated in the center of each subplot using a densitometer and averaged the canopy openness values. For the orchard plot, we measured these attributes at the center of 5m x 5m grids.

Within each plot, we recorded the stem diameters of trees, shrubs and vines with a stem diameter of ≥1cm DBH. In some cases, buttresses or deformities along the stem necessitated measurement be made slightly above or below the 1.3m mark. Tree height was measured using a Nikon Forestry Pro Laser Rangefinder (Nikon, Tokyo, Japan) to the nearest 0.1 m. Each tree was tagged, marked at the point of measurement with pink paint, and identified to species-level with the assistance of two authors (CP and DT).

In order to document the full floristics of each plot, we searched each subplot thoroughly for additional plant species that did not reach the DBH threshold for measurement. This included all nontree plant lifeforms such as shrubs, vines, ground herbs, graminoids (grasses and grass-like plants), and epiphytes (including parasitic plants). Voucher specimens were collected for each species found within each plot. We used an extension pole cutter to collect material from taller specimens (2-6m) and a slingshot to collect samples from trees that were too tall to identify from the ground or to retrieve with the extension cutter. These voucher specimens were then dried for three days at 75°C in a drying oven, mounted on 200 GSM A4-sized paper, and lodged in the field herbarium of the CRS. Specimens that could not be identified in the field were identified at the CRS laboratory using the online Australian Rainforest Plant Identification key (Zich et al. 2019), and where further verification was needed, we compared our specimens with collections at the Australian Tropical Herbarium, James Cook University, Cairns.

Data analysis

Using the full floristic data, we constructed Venn diagrams to visualize the number of species within each plot, and the number of species shared between plots. Biodiversity of the stems in each plot \geq 1cm (DBH), was calculated using Fisher's alpha diversity index (Schulte *et al.* 2005). Evenness, an indicator of species dominance (values close to 0 indicate a single dominant species and values close to 1 indicate all species are equally represented), was calculated using Pielou's (J') (Peet 1975). Plot dissimilarity was assessed using Whittaker β -diversity index (a value approaching 1 denotes very few shared species; Wilson & Shmida 1984). Fisher's alpha and Pielou's (J') evenness indexes were calculated in the Past 3.0 (Hammer *et al.* 2001) statistical program.

Each species was categorized into broad biogeographical groups (Northeast Queensland (NQ) endemic, Australian endemic, widespread for species with distributions beyond Australia, or nonnative), phylogenetic groups (ferns, gymnosperms, basal angiosperms (following Metcalfe & Ford 2009); (iv) monocots, and (v) eudicots) and lifeform groups (trees, shrubs, vines, and epiphytes).

We calculated the Aboveground Biomass (AGB) for each stem in megagrams (Mg) dry mass, following the allometric equation by Chave *et al.* (2014), as follows: AGB = $0.0673 \times (\rho D^2 H)^{0.976}$, where ρ = wood density (in g cm⁻³), D = DBH (in cm) and H = height (in metres). The total AGB was then obtained by summing up the individual AGB for all trees in each plot (Mg ha⁻¹). Wood density values for each species were obtained from a wood density database developed for the nearby Robson Creek 25-ha long-term monitoring plot (Matt Bradford, CSIRO, personal communication, April 2013; Ilic *et al.* 2000; Bradford *et al.* 2014).

Results

We documented a total of 213 species belonging to 161 genera and 73 families. The Old growth forest plot had the highest number of species, genera and families, followed by the Old and Young secondary forest plots, and the plot in the Abandoned Orchard area had the lowest species count (Table 2). This pattern was similar for stems \geq 1cm diameter DBH. Non-native species (12 spp.) were only present in the plot within the Abandoned Orchard area (Table S1).

	Old growth forest	Old secondary forest	Young secondary forest	Abandoned Orchard area
Full floristics				
Families	62	45	31	11
Genera	108	75	45	30
Species	137	96	53	42
Only stems ≥ 1cm DBH				
Families	34	21	14	10
Genera	67	40	20	14
Species	89	56	26	15
Number of stems	328	231	243	29
Species diversity (Fishers alpha index)	40.17	23.39	7.38	15.83
Evenness	0.97	0.95	0.88	0.9
Basal area (m ² ha ⁻¹)	465.61	450.46	518.19	193.73
Aboveground biomass (Mg ha ⁻¹)	335.92	253.45	342.22	63.87

Table 2. Breakdown of the number of plant families, genera, species, diversity indices and structural variable measured from vegetation plots within the Centre for Rainforest Research, School for Field Studies, Gadgarra, north Queensland.

The Old growth forest had the greatest number of unique species and also that the highest number of shared species was between the Old growth and Old secondary forest plots (Fig. 3A). In contrast, no species were shared only between the Old growth forest and Abandoned Orchard area plot (Fig. 3B). Further, our beta-diversity analyses indicate that the Old growth forest plot was most similar to the Old secondary forest plot (β -diversity = 0.456) and most dissimilar to the Abandoned Orchard area plot (β -diversity = 0.908). Seven common native species, namely Calamus australis (Arecaceae), Drynaria rigidula (Polypodiaceae) Guioa acutifolia, G. lasioneura (Sapindaceae), Litsea leefeana (Lauraceae), Polyscias australiana (Araliaceae) and Rhodomyrtus pervagata (Myrtaceae), were shared among all plots.

The most species-rich familes were Sapindaceae (in all plots), Lauraceae (in all three forest plots), and Myrtaceae in the Old growth forest and the Old secondary forest (Table 3). Species-rich families in the Young secondary forest plot also included Proteaceae and Polypodiaceae, and in the Abandoned Orchard area included Rutaceae.

The eudicot lineages were the dominant phylogenetic grouping (>58.5% - 69.8% of the species across all plots; Table 4). Representation of eudicots, primitive angiosperm and monocot lineages were quite similar across all plots, but the Young Secondary forest plot and the Abandoned Orchard area had no gymnosperms. Additionally, ferns made up a higher proportion of species in the Young Secondary forest plot than in the other plots because of an abundance of high-light-adapted epiphytic fern species in the Polypodiaceae.

Trees were the most abundant lifeform in all plots. The Old growth and Old secondary forest plots exhibited the greatest similarity in lifeform spectra, in relation to their relative proportions of trees, shrubs, vines and epiphytes. However, graminoids (grass-like plants) were represented by a single species in the Old growth forest. Northeast Queensland and Australian endemic species made up the greatest percentage of species in the Old growth forest and Old secondary forest plots. The largest number of both Northeast Queensland and Australian endemics were found in the Old growth forest plot.

Discussion

Although there have been several plot-level studies of tree diversity in the tropics, full floristics studies are relatively rare. In our study we examined the full floristics in plots of different successional stages within a tropical upland rainforest region. We acknowledge that because we only sampled within a small area, broad extrapolation of our results should be cautioned against. Nevertheless, this study will allow for continued monitoring of the region over time and provides a baseline for future research of diversity at CRS.

Species richness and vegetation structure comparisons with other studies

Various studies have used plot-based methods to assess biodiversity in the Northeast Queensland region of Australia (e.g. Connell & Green 2000; Laidlaw et al. 2007; Goosem et al. 2016; Green & Connell 2018), but full floristic data within a plot area including all lifeforms has thus far only been reported for twenty 0.5 ha plots in various localities by Graham (2006), one 1 ha plot by Bradford et al. (2014) and a 2 ha plot by Tng et al. (2016), although other unpublished material may exist. Among the studies most comparable to our own are those located in the vicinity of Robson Creek (Graham 2006; Bradford et al. 2014) approximately 8 km in linear distance from the CRS. In the Robson Creek area, one 0.5 ha plot established in 1972 has a species count of 189 species (Graham 2006), while 266 species were recorded in the larger 1 ha plot by Bradford et al. (2014). Assessment of a species-area curve for our plots indicates that the maximum diversity had not yet been achieved at a plot size of 500 m^2 , suggesting that diversity in the Old Growth rainforest at CRS is comparable to that found in these former studies (Fig. S1). Our structural parameters such as basal area and aboveground biomass for the Old growth forest are well within the ranges reported by Bradford et al. (2014), Laidlaw et al. (2007) and Tng et al. (2016) for undisturbed rainforests within the Atherton Tablelands and the lowlands region in the Daintree.

Recovery from disturbance

In our study, species-, family-, and genus-richness were greatest in the Old Growth plot, followed by the Old Secondary plot and the Young Secondary plot, consistent with our predictions based on



Figure 3. (A) Venn diagram showing the extent of shared and unique species between vegetation plots within the Centre for Rainforest Studies, School for Field Studies property. (B) Whittaker's beta-diversity indices denote the extent of dissimilarity in the floristic composition between plots.

0.747

forest

Table 3. The three most prevalent families in the four different plots.

The number of species recorded from each family is given in parentheses. Four families are listed for the Young secondary forest because of the even distribution of three families; the Abandoned Orchard area includes only two as other families, which dominated the plot.

	Old growth	Old secondary	Young secondary	Abandoned
	forest	forest	forest	Orchard area
Families	Myrtaceae (13) Sapindaceae (11) Lauraceae (8)	Lauraceae (10) Myrtaceae (8) Sapindaceae (8)	Sapindaceae (5) Proteaceae (4) Polypodiaceae (4) Lauraceae (4)	Sapindaceae (17) Rutaceae (11)

Table 4. Representation of species groupings (no. of species) within each plot.

	Old growth forest	Old secondary forest	Young secondary forest	Abandoned Orchard area
Biogeography				
NEQ endemic	39	31	9	6
Australian endemic	48	39	20	9
Widespread	40	21	21	16
Non-native	0	0	0	12
Phylogeny				
Fern	6	2	5	2
Gymnosperm	1	2	0	0
Basal angiosperm	22	17	7	1
Monocot	11	10	9	8
Eudicot	97	66	32	32
Lifeform				
Tree	85	61	27	13
Shrub	20	14	4	13
Vine	24	15	11	3
Epiphyte	4	3	8	3
Herb	3	1	0	7
Graminoid	1	3	3	4

levels of disturbance and period of recovery. This pattern is consistent with other studies, and reflects the way abiotic factors affected by clearing, such as light and soil, alters species composition (Congdon & Herbohn 1993; Bu *et al.* 2014; Yeo & Fensham 2014; Chua & Potts 2018). This finding also supports earlier work indicating that it takes a long time for rainforest to recover in species richness from disturbances like clearing (Rasiah *et al.* 2004). The longer recovery time experienced by the Old Secondary plot likely resulted in richer soil and a denser canopy, which allowed for an environment more similar to the Old Growth plot, and thus the high number of shared species. The structural characteristics such as basal area and aboveground biomass in the Old

secondary forests had recovered to a greater extent and approached that of the Old growth forest. This is in line with the estimate by Horne & Hickey (1991) that logged forests take at least 60 years for canopy and below canopy conditions to be restored. The Young secondary forest plot had a higher basal area than either the Old growth and Old secondary forest plot as a result of the contribution of a number of large but senescing *Acacia* trees (Fig. S2)

We found that the Old growth forest plot contained the highest number of species not shared with any of the other plots, followed by Old secondary forest, and then the Young secondary forest. In line with our expectations that more basal plant lineages and regional endemics would be found in less disturbed forest, because of the impact of disturbance and recovery time (Paul et al. 2010), many of these species were north Queensland endemics. This pattern is particularly apparent in representation of gymnosperms and also basal angiosperms. For example, basal Angiosperms Atherospermataceae, Lauraceae and Monimiaceae were present in the Old growth and Old secondary plots but not in the Young secondary plot, possibly because these plant lineages are more sensitive to drying conditions (Boyce et al. 2009). The Whittaker diversity indices further support these findings as the Old growth forest and Old secondary forest had the greatest number of species in common followed by the Old secondary forest and Young secondary forest. Lowest number of shared species between Old Growth forest and the Abandoned Orchard area, followed by the Old secondary forest and the Abandoned Orchard area, reflect the increase diversity in secondary growth forests over time, as previous studies have found (Smith et al. 2005; Bu et al. 2014; Goosem et al. 2016).

The high number of unique species present in the Abandoned Orchard area resulted from the presence of a large number of non-native herbaceous species in the plot, and also the planting of some Australian native, but not regionally-occurring species such as *Citrus garrawaye* (Rutaceae) and *Diploglottis campbellii* (Sapindaceae). Nevertheless, the Abandoned Orchard area also contained various early pioneer and native tree and shrub species such as *Breynia stipitata* (Phyllanthaceae) and *Mallotus paniculatus* (Euphorbiaceae) which we did not find in any of the secondary forest or old growth plots.

The lifeform spectra were similar in the Old growth and the Old secondary forests, with trees being the most prevalent, followed by shrubs and vines. A similar life form distribution was found in the Robson Creek plot surveyed by Graham (2006). Unexpectedly, epiphytes had higher representation in the Young secondary plot than in either the Old growth and Old secondary forest plots. However, the epiphytes in the Young secondary plot (notably Drynaria rigidula and Pyrrosia rupestris (Polypodiaceae)) are species widespread even in drier forest communities and which prefer high light conditions. In contrast, some of the epiphytic species found in the Old growth and Old secondary forests such as Crepidomanes vitiense (Hymenophyllaceae) (Fig. 4A) and Peristeranthus hillii (Orchidaceae) (Fig. 4B) probably require more filtered light or moister microclimates (Nasrulhaq-Boyce & Duckett 1991). Additionally, there is also a high likelihood that the density of the canopy in the Old growth and Old secondary plots made it difficult for us to record all possible epiphytic species, and thus we may have overlooked some species that were present.

In summary, the greatest similarity at all taxonomic levels occurred between the Old growth and Old secondary plots. These two plots had a very similar composition and shared the same three most prevalent families: Myrtaceae, Sapindaceae, and Lauraceae. These findings are in line with Bradford who reported et al. (2014), Lauraceae, Sapindaceae, and Myrtaceae as 3 of the 10 most important families in the Robson Creek plot. The Young Secondary forest plot also contained many of the families present in the Old Growth and Old Secondary forest plots, although one conspicuous family, the Goodeniaceae represented by the vine Scaevola enantophylla, was restricted to the Young secondary forest plot. The Abandoned Orchard area plot did not share many species in common with the other plots because of the combination of more recent clearing and deliberate planting of non-native and native fruit trees. Additionally, the open conditions of the Abandoned Orchard area favored the presence of various non-native weeds from the Asteraceae and Poaceae.

We conclude that full floristic surveys of tropical forests within can provide high quality distribution data for rainforest plants, and in particular



Figure 4. The filmy fern *Crepidomanes vitiense* (Hymenophyllaceae) (A) and the Beetle orchid, *Peristeranthus hillii* (Orchidaceae) (B) were encountered only in the Old growth forest and Old secondary forest respectively. Inset in (B) shows a close up of the flower details.

lifeforms that are typically overlooked in monitoring plots that apply a cut-off criteria for stems that are measured. Although the current study used plots of a comparatively small size, the biodiversity data generated can serve as a baseline for future biodiversity studies and comparisons.

Acknowledgements

We thank Erin Dodd, Allison Hren, Jack Dimmock, Delaney Brubaker and Bill Johnson for their assistance while in the field, Ashley Field for confirming the identifications of some fern specimens, and Fanie Venter and Gabriel Crowley for their constructive comments on the manuscript. The first six authors contributed equally to the fieldwork, data analysis and writing of the manuscript as part of their Directed Research projects while on a field semester course at the Centre for Rainforest Studies.

Supplementary file

A supplementary pdf file accompanies this paper on its web-page. It contains:

- Fig. S1: species-area rarefaction curves;
- Fig. S2: number and biomass of trees; and
- Table S1: list of plant species and attributes.

References

- Alamgir M, Campbell MJ *et al.* 2016. Degraded tropical rain forests possess valuable carbon storage opportunities in a complex, forested landscape. *Scientific Reports* 6: 30012.
- Alroy J. 2017. Effects of habitat disturbance on tropical forest biodiversity. *PNAS* 114: 6056-6061.
- Australian Government Bureau of Meteorology. 2019. *Climate Statistics for Australian Locations: Atherton. http://www.bom.gov.au/climate/averages/tables/cw* _031193.shtml, downloaded 30 Nov. 2019.

- Becker P. 2000. Competition in the regeneration niche between conifers and angiosperms: Bond's slow seedling hypothesis. *Functional Ecology* 14: 401-412.
- Böehmer HJ. 2011. Vulnerability of tropical montane rain forest ecosystems due to climate change. In *Coping with Global Environmental Change, Disasters and Security,* eds. HG Brauch *et al.,* pp. 789-802. Springer: Berlin, Heidelberg.
- Boyce CK, Brodribb TJ, Feild TS, Zwieniecki MA. 2009. Angiosperm leaf vein evolution was physiologically and environmentally transformative. *Proceedings of the Royal Society of London Series B* 276: 1771-1776.
- Boyle TJB, Sayer JA. 1995. Measuring, monitoring and conserving biodiversity in managed tropical forests. *The Commonwealth Forestry Review* 74: 20-25.
- Bradford MG, Metcalfe DJ, Ford A, Liddell MJ, McKeown A. 2014. Floristics, stand structure and aboveground biomass of a 25-ha rainforest plot in the wet tropics of Australia. *Journal of Tropical Forest Science* 26: 543-553.
- Bu W, Zang R, Ding Y. 2014. Functional diversity increases with species diversity along successional gradient in a secondary tropical lowland rainforest. *Tropical Ecology* 55: 393-401.
- Chave J, Réjou-Méchain M *et al.* 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20: 3177-3190.
- Chua SC, Potts MD. 2018. The role of plant functional traits in understanding forest recovery in wet tropical secondary forests. *Science of the Total Environment* 642: 1252-1262.
- Common MS, Norton TW. 1992. Biodiversity: its conservation in Australia. *Ambio* 21: 258-265.
- Congdon RA, Herbohn JL. 1993. Ecosystem dynamics of disturbed and undisturbed sites in north Queensland wet tropical rain forest. I. Floristic composition, climate and soil chemistry. *Journal of Tropical Ecology* 9: 349-363.
- Connell JH, Green PT. 2000. Seedling dynamics over thirty-two years in a tropical rain forest tree. *Ecology* 81: 568-584
- Crome FHJ, Moore LA, Richards GC. 1992. A study of logging damage in upland rainforest in north Queensland. *Forest Ecology and Management* 49: 1-29.
- Fibich P, Leps J *et al.* 2016. Spatial patterns of tree species distribution in New Guinea primary and secondary lowland rain forest. *Journal of Vegetation Science* 27: 328-339.

- Global Forest Atlas. 2019. *Climate Change and Tropical Forests*. Yale School of Forestry and Environmental Studies. *https://globalforestatlas.yale.edu/climatechange/climate-change-and-tropical-forests*, viewed 30 Nov. 2019.
- Goosem M, Paz C *et al.* 2016. Forest age and isolation affect the rate of recovery of plant species diversity and community composition in secondary rain forests in tropical Australia. *Journal of Vegetation Science* 27: 504-514.
- Goosem S, Tucker NIJ. 2013. *Repairing the Rainforest* (2nd Ed.). Wet Tropics Management Authority and Biotropica Australia Pty. Ltd.: Cairns.
- Goudie, AS. 2018. *Human Impact on the Natural Environment* (8th Ed.). John Wiley & Sons. UK
- Graham AW (ed.) 2006. The CSIRO Rainforest Permanent Plots of North Queensland – Site, Structural, Floristic and Edaphic Descriptions. CSIRO and the Cooperative Research Centre for Tropical Rainforest Ecology and Management. Rainforest CRC: Cairns.
- Green PT, Connell JH 2018. Connell Rainforest Plot Network: Davies Creek Data Packages, 1963-2018. https://openresearch-repository.anu.edu.au/handle/ 1885/151946, viewed 20 May 2020.
- Hammer Ø, Harper DA, Ryan PD. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4: art. 4.
- Horne R, Hickey J. 1991. Ecological sensitivity of Australian rainforests to selective logging. *Australian Journal of Ecology* 16: 119-129.
- Ilic J, Boland D, McDonald M, Downes G, Blakemore P. 2000. Wood Density Phase 1 - State of Knowledge. Australian Greenhouse Office Technical Report 18: Canberra.
- Laidlaw M, Kitching R, Goodall K, Small A, Stork N. 2007. Temporal and spatial variation in an Australian tropical rainforest. *Austral Ecology* 32: 10-20.
- Leigh JEG. 1999. *Tropical Forest Ecology: A View from Barro Colorado Island*. Oxford University Press: Oxford.
- Magnago LFS, Magrach A *et al.* 2015. Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? *Global Change Biology* 21: 3455-3468.
- Magurran AE, Baillie SR *et al.* 2010. Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. *Trends in Ecology & Evolution* 25: 574-582.
- Metcalfe DJ, Ford AJ. 2009. A re-evaluation of Queensland's Wet Tropics based on primitive plants. *Pacific Conservation Biology* 15: 80-86.

- Nasrulhaq-Boyce A, Duckett JG. 1991. Dimorphic epidermal cell chloroplasts in the mesophyll-less leaves of an extreme-shade tropical fern, *Teratophyllum rotundifoliatum* (R. Bonap.) Holtt.: a light and electron microscope study. *New Phytologist* 119: 433-444.
- Neldner VJ, Laidlaw M *et al.* 2017. *Scientific Review of the Impacts of Land Clearing on Threatened Species in Queensland*. Department of Science, Information Technology and Innovation: Brisbane.
- Paul M, Catterall CP, Pollard PC, Kanowski, J. 2010. Recovery of soil properties and functions in different rainforest restoration pathways. *Forest Ecology and Management* 259: 2083-2092.
- Peet RK. 1975. Relative diversity indices. *Ecology* 56: 496-498.
- Phillips OL, Martinez RV *et al.* 2003. Efficient plot-based floristic assessment of tropical forests. *Journal of Tropical Ecology* 19: 629-645.
- Rasiah V, Florentine SK, Williams BL, Westbrooke ME. 2004. The impact of deforestation and pasture abandonment on soil properties in the wet tropics of Australia. *Geoderma* 120: 35-45.
- Schulte RP, Lantinga EA, Hawkins MJ. 2005. A new family of Fisher-curves estimates Fisher's alpha more accurately. *Journal of Theoretical Biology* 232: 305-313.
- Shoo LP, Freebody K, Kanowski J, Catterall CP. 2016. Slow recovery of tropical old-field rainforest regrowth and the value and limitations of active restoration. *Conservation Biology* 30: 121-132.
- Smith RGB, Nichols JD, Vanclay JK. 2005. Dynamics of tree diversity in undisturbed and logged subtropical rainforest in Australia. *Biodiversity and Conservation* 14: 2447-2463.
- Tng D, Apgaua D *et al.* 2016. Vegetation and floristics of a lowland tropical rainforest in northeast Australia. *Biodiversity Data Journal* 4: e7599.
- Tracy JG, Webb LJ. 1975. Vegetation of the Humid Tropical Region of North Queensland (15 maps at 1:100,000 scale + key). CSIRO Long Pocket Laboratory: Indooroopilly, Brisbane.
- Whitmore TC. 1990. *An Introduction to Tropical Rain Forests*. Clarendon Press: UK.
- Whitworth A, Downie R, von May R, Villacampa J, MacLeod R. 2016. How much potential biodiversity and conservation value can a regenerating rainforest provide? A 'Best-case scenario' approach from the Peruvian Amazon. *Tropical Conservation Science* 9: 224-245.

- Whitworth A, Pillco-Huarcaya R *et al.* 2018. Long lasting impressions: After decades of regeneration rainforest biodiversity remains differentially affected following selective logging and clearance for agriculture. *Global Ecology and Conservation* 13: e00375.
- Williams KJ, Ford A *et al.* 2011. Forests of east Australia: the 35th biodiversity hotspot. In *Biodiversity Hotspots*, eds. F Zachos, J Habel, pp. 295-310.
- Wilson MV, Shmida A. 1984. Measuring beta diversity with presence-absence data. *Journal of Ecology* 72: 1055-1064.
- Yeo WLJ, Fensham RJ. 2014. Will Acacia secondary forest become rainforest in the Australian Wet Tropics? *Forest Ecology and Management* 331: 208-217.
- Zich FA, Hyland BPM, Whiffin T, Kerrigan RA. 2019. *Australian Tropical Rainforest Plants, Edition 7. http://www.canbr.gov.au/cpbr/cd-keys/RFK7/key/ RFK7/Media/Html/index_rfk.htm*, viewed 30 Nov. 2019.