

How does the forest structure, diversity and species composition of a restored rainforest 25 years after planting compare with that of mature rainforest?

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Abstract

Restoration of forest ecosystems is a global imperative, yet there are relatively few studies assessing the success of old forest restoration efforts in the tropics. We assessed the vegetation structure, species diversity and composition of a 25-year-old wildlife corridor restoration site linking two patches of mature rainforest in the uplands of the Wet Tropics of Australia. Our results show that the vegetation structure of the restored rainforest was similar to that of mature reference rainforest in profile, in the overall stem size class distribution, in plot level means of stem basal areas and in the number of individuals. Reference mature rainforest had significantly higher plot-level mean biomass than was found in restored rainforest. Species richness and diversity indices of the two forest types also showed differences, and these were significant in terms of species composition, with the mature rainforest having a higher percentage of wind or mechanically dispersed species, and restored rainforest having more animal dispersed species. Although the restored rainforest is not compositionally similar to mature rainforest, the habitat it provides for wildlife and the presence of many mature rainforest species recruiting in the restored rainforest are positive restoration outcomes. Future monitoring and comparisons with other revegetated sites or naturally regenerating forest will provide deeper insights into the processes of recovery in restored forests.

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Introduction

Tropical rainforest restoration is of paramount importance for potentially ameliorating the negative impacts of land clearing and buffering the effects of anthropogenically induced climate change and forest fragmentation (Haddad *et al.* 2015). Recognizing the urgency for restoring natural habitats, various conventions have set ambitious restoration agendas at the global scale such as the Aichi Biodiversity Targets, which

propose to restore 15% of the land area worldwide (Convention on Biological Diversity 2020), and the Bonn Challenge, which aims to restore tree cover on 350 million hectares of land by 2030 (Verdone & Seidl 2017). The goals of these efforts include biodiversity conservation, carbon sequestration to combat climate change, improvements to the quality of ecosystem services such as water quality and supply, and improved human livelihoods that

go hand in hand with healthy restored forest ecosystems (Chazdon *et al.* 2017).

Forest fragmentation is one of the leading causes of biodiversity decline and local extinctions in tropical rainforests; it disrupts the dispersal of plants and animals, subjects forest biota to edge effects, and facilitates invasion by pests and exotic species (Murcia 1995; Fahrig 2003; Goosem 2012). The effectiveness of restored habitat in buffering the negative impacts of landscape fragmentation and preventing further extinctions will likely depend on how similar the restored habitat is to the original rainforest (Rocha *et al.* 2018). Forest restoration is underpinned by ecological succession and community reassembly theory (e.g. Howe 2016). In an ecosystem restoration context, studying the recovery of restored forest provides a framework to monitor the development of ecosystem processes and function (Hobbs & Norton 1996).

Restoration success can be measured by examining vegetation structure, diversity and species composition, all widely-used indicators of recovery trajectory and self-maintenance of restored ecosystems (Ruiz-Jaen & Aide 2005; Wortley *et al.* 2013; Prach *et al.* 2019). For instance, the development of forest vegetation structure can reflect the recovery of various ecosystem attributes and ecological processes, such as microclimate (Milling *et al.* 2018), protection against soil erosion (Zhou *et al.* 2008) and sequestration of carbon (Wang *et al.* 2011; Chazdon *et al.* 2016). Restored vegetation structure can pave the way for the recovery of the composition and abundance of plant species (Suganuma & Durigan 2015), microorganisms (Banning *et al.* 2011), faunal groups (Whitehead *et al.* 2014; Lawes *et al.* 2017; Zachar *et al.* 2017; Derhé *et al.* 2018), and soil biology and chemistry (Rachmat *et al.* 2021), thus fulfilling several ecological restoration objectives (Palmer *et al.* 1997). Another assessment method commonly used is to estimate the number or abundance of new native species that have recruited in the restoration sites (Reid 2015; Catterall *et al.* 2004). This indicates natural regeneration or recruitment, and the extent to which ecological processes and self-organized sustainability or resilience of the ecosystem have been re-established (Prach *et al.* 2019). Finally, plant species composition is an indicator of fundamental ecosystem properties, and is regarded by some restoration ecologists to

be ‘the principal obligation of restorationists’ (Clewell & Aronson 2013; Rydgren *et al.* 2020). Although floristic composition of restored sites may not return to that of mature rainforest, it is useful to understand how closely the species composition of restoration sites approximates that of reference habitats (Crouzeilles *et al.* 2017; Meli *et al.* 2017; Prach *et al.* 2019).

Whilst restoration ecology has grown significantly over the last few decades, there are still comparatively few studies documenting success of restoration efforts on a decadal-scale. In part, this could be due to the paucity of old restoration sites (> 15 years old) established with a view for long-term monitoring (Kanowski *et al.* 2008; Wortley *et al.* 2013). For instance, most investigators evaluate restoration success 6–10 years after implementation (Freebody 2007; Gatica-Saavedra *et al.* 2017). A lack of funding (DeLuca *et al.* 2010) or good record keeping (McDonald 2006) can also hamper monitoring efforts.

The presence of a relatively well-documented and well-established rainforest restoration project in the Wet Tropics of Australia provides an opportunity to examine restoration success. Fortunately, the rainforest species in the region are relatively well-known and expertise in plant identification is available. In this study, we compare the structure, species diversity and species composition of forest plots in a restoration site (>20 years old) to forest plots in a nearby patch of intact reference forest (henceforth mature rainforest). Our research revolves around answering the following question: How similar is the (1) vegetation structure, (2) species diversity, and (3) species composition of this 25-year-old restoration planting in comparison to intact mature rainforest?

Methods

Study area and vegetation sampling

The study was conducted near the eastern edge of the Atherton Tablelands, northeast Queensland, Australia, within the Australian Wet Tropics Bioregion. Historically, the upland rainforests of the Atherton Tablelands and the lowland floodplains have been extensively cleared for agriculture and dairy farming (Winter *et al.* 1987; Collins 1994; Goosem *et al.* 1999). Our reference plots of mature rainforest were situated in the forest vegetation surrounding Lake Barrine (145° 38' E, 17° 15' S), a volcanic maar at an altitude of

c. 760 m a.s.l., and contained within a c. 500 ha section of the Crater Lakes National Park (NP), and our restoration plots in a revegetated forest (Donaghy's Corridor, see later) just southeast of the lake (Fig. 1). There is no long-term rainfall gauge data available in the vicinity; however mean annual rainfall is believed to be about 2.5 m; mean annual temperatures vary from 25°C in January to 15.5°C in July (Tracey 1982).

The Lake Barrine section of the Crater Lakes NP is comprised primarily of mature tropical rainforest known as complex mesophyll vine forest (Tracey 1982) and as Regional Ecosystem 7.8.2 (Goosem *et al.* 1999). This rainforest type grows over basaltic soils, and is characterized by well-developed canopy stratification, the conspicuous presence of trees with plank roots, numerous robust woody

lianas, and a high diversity of lifeforms (Tracey 1982). At a broader landscape scale, Lake Barrine is a forest fragment which in precolonial times was continuous with a larger block of rainforest in Gadgarra NP, due southeast (Fig. 1). However, in the 1930s, the forest growing over basaltic soils was mostly cleared to make way for agricultural expansion, leading to the Lake Barrine rainforest being reduced to its current extent and previously isolated from the larger block of forest at Gadgarra NP (totalling 80,000 ha when including Wooroonoran NP; Harrison *et al.* 2003). However, the hydrological system of the two forest blocks remained connected by Toohey Creek, which issues from Lake Barrine and flows across farmland into the Gadgarra NP (Fig. 1).

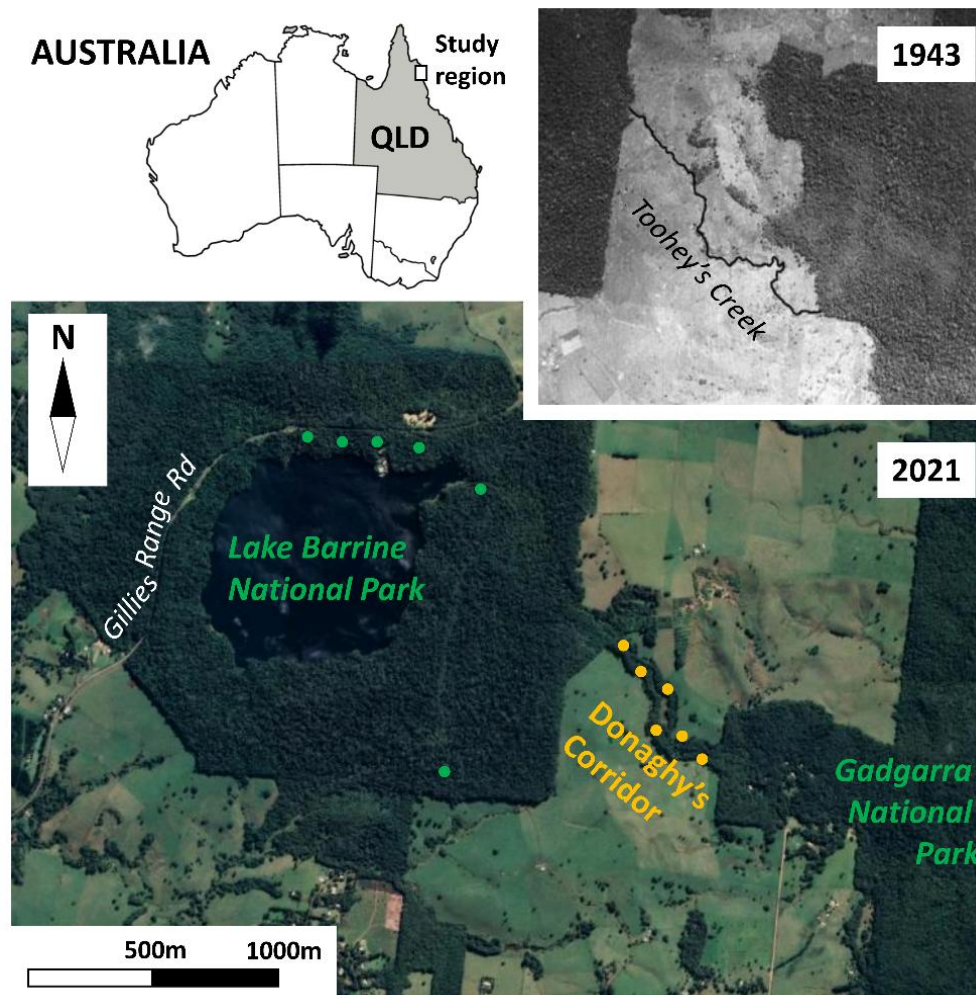


Figure 1. The study site at Donaghy's Corridor and Lake Barrine National Park, Atherton Tablelands, Australia. The inset on the top right shows state of deforestation at the Donaghy's Corridor area in the 1940s, and the outline of Toohey Creek is highlighted in black for emphasis. Location of the study plots are indicated in yellow dots denoting restored rainforest plots (n = 6) and green dots denoting mature rainforest reference plots (n = 6).

Between 1995 and 1998, a reforestation planting project was undertaken to establish Donaghy's Habitat Linkage (hereafter Donaghy's Corridor). Donaghy's Corridor is a 1.2 km x 100 m planting of rainforest species along both flanks of Toohey Creek on basalt soils (Fig. 1; Tucker & Simmons 2009), and represents one of the earliest large-scale efforts to reinstate rainforest on cleared land in the Australian Wet Tropics (Catterall & Harrison 2006). The objective of the planting was to create a habitat linkage between the forests of Lake Barrine and Gadgarra NP and to provide habitat for forest fauna species potentially affected by fragmentation (Tucker & Simmons 2009). A baseline survey recorded all vascular plants on the site before treatment, including vegetation along the creek, isolated paddock trees and other vegetation within 100 m of re-planted areas (but excluding forests at either end of Donaghy's Corridor). The forest restoration at Donaghy's Corridor employed a diverse planting model approach (Tucker & Simmons 2009), which in this case involved planting around 16,800 selected seedlings from 100 native tree species within the c. 16 ha area (c. 3000 stems ha⁻¹). Motorised augurs were used to drill holes into sites where weeds had been sprayed out prior to planting. Plants were spaced 1.7 m apart. Following the planting, weeds were treated with herbicide until canopy closure at c. 18 months. The species planted consisted of trees that would have been present on basaltic soil that occurs in the area (Goosem & Tucker 2013; see also Supplementary Table S1). By 2006, a vegetation strip with a closed forest canopy had formed, linking Lake Barrine and Gadgarra NP (Tucker & Simmons 2009). A number of studies has also since been carried out to monitor wildlife use of the habitat corridor (Tucker 2000; Paetkau *et al.* 2009).

Our overarching objective was to assess restoration success by comparing the current vegetation in restored rainforest in Donaghy's Corridor (restoration treatment) with that of mature rainforest in Lake Barrine NP (control treatment). To accomplish this, we sampled six 50 m x 3 m plots in each area between August and December 2021 (Fig. 1). Spacing between plots was at least 150 m. We did not sample plots in the Gadgarra NP area to the southeast of Donaghy's Corridor, as this reserve is situated on granitic substrates, and its rainforest has a simpler structure (simple notophyll vine forest; Tracey 1982) than the complex

rainforest that would have historically vegetated Donaghy's Corridor. Consequently, the two areas could not be expected to have similar vegetation structure, species diversity or species composition.

In each plot, we established a 50 m long transect and identified all tree, shrub and vine stems ≥ 1 cm diameter at breast height (1.3 m; DBH) within 1.5 m either side of the centre line. Stem diameters were measured with a DBH tape, and stem heights were estimated using a Nikon Laser Rangefinder. We deviated from other studies that measured only stems > 10 cm DBH because we wanted to account for the diversity and basal area of plants in smaller stem size classes (1–10 cm DBH), which can be important for more comprehensive biomass accounting (Preece *et al.* 2012). Within the sampled transects, we also distinguished between species that were part of the original planting, and those that had naturally recruited, possible because records of the species planted in each year had been maintained.

To obtain a measure of the density of small plants (< 1 cm DBH), we marked out a 5 m x 3 m subplot (15 m²) at the midpoint of each plot, and used callipers to measure the basal diameter of all herbs, grasses, shrubs and tree seedling and sapling stems within this subplot. We made an inventory of all additional species occurring within each plot. We also opportunistically noted any additional species in both the corridor and in the reference forests in the rainforests surrounding Lake Barrine and include them in the species list in the Supporting Information (Table S1). Within each plot, we estimated leaf litter cover and canopy cover. Leaf litter was visually estimated in five 1 m x 1 m subplots at points 5 m, 15 m, 25 m, 35 m, 45 m along the transect centre line using a modified Braun-Blanquet scale (van der Maarel 1979), as follows: 1 – $< 5\%$; 2 – 5 to 25%; 3 – 25 to 50%; 4 – 50 to 75%; 5 – $> 75\%$ cover. Percent canopy cover was also estimated at the same points along the transect from photographs taken 1.3 m above the ground using the CanopyCapture app (Patel 2018) installed in a Samsung S9 mobile phone. The CanopyCapture app estimates the vertical tree crown projection per unit area of the ground surface (Winsen & Hamilton 2023).

A representative plot was selected from each of the restored and mature rainforest plots for the purpose of creating a profile diagram. To do this, we collected extra information from each tree

stem ≥ 1 cm DBH. The location of each stem was recorded using the measuring tape as a Y-axis (between 0 – 50 m), and another measuring tape to record the X-axis (between -1.5 – 1.5 m). For each stem, we also recorded height to first branch, an estimate of crown width, and basal stem diameter parallel to or intercepting the Y-axis.

We defined successional species as those that are associated with disturbance or regrowth and are typically shade intolerant, and mature forest species as those that are not found in early successional environments, and have seedlings or mature adults that are shade tolerant (e.g. Whitmore 1990; Van Breugel *et al.* 2007). We based this classification on local knowledge of species ecologies (Goosem & Tucker 2013; Zich *et al.* 2020). We also considered a number of epiphytes (e.g. ferns and herbs) to be mature forest species as they are not typically associated with successional environments (Table S1). We classified species as wind-, animal- or mechanically dispersed based on Tucker & Murphy (1997), Cooper & Cooper (2004), and Seale & Nakayama (2020).

Data management and analysis

We compared vegetation structure between the two forest types qualitatively and quantitatively. We produced profile diagrams (visual tools for examining and comparing forest stand stratification and development; Richards 1996; Larsen & Nielsen 2007) to compare forest structure. Plot-level stem density was compared using a t-test. We calculated stem basal areas (m^2) for each plot using the measured DBH values for each stem and the π rule, and compared treatment means using a t-test. In cases where individuals had multiple stems, we calculated the basal area of each stem and then summed the basal areas of all the stems to obtain the basal area of the individual plant. Tree above-ground biomass of each stem was calculated for each plot using an allometric equation developed by Chave *et al.* (2014), and treatment means were compared using a t-test. Data on wood density were obtained from a national wood density database (Ilic *et al.* 2000). Species-level wood density values were lacking for some species, and in these cases, we used genus-level average values. The mean stem size class distributions of restored and mature rainforest plots were visualized with a histogram, and the treatment means within each respective size class were compared using t-tests.

Species richness and Shannon and Pielou's evenness indices for the measured stems ≥ 1 cm DBH in each plot were computed for each study area, and compared using student t-tests. Treatment medians of leaf litter cover were compared using a Mann Whitney test. To visualize and compare species richness between the two treatments, we also plotted rarefied species abundance curves.

Overall species composition in the two treatments was compared by creating a species list for each forest type based on presence-absence, including all additional species in the sampling plots that were undetected during stem measurements. We then plotted Venn diagrams to visualize differences between treatments in the number of shared and unique species, and the overall species composition of small plants. We also report the number of new species found in Donaghy's Corridor that were not previously planted.

To examine plant community structure and plot-level species composition, we performed a non-metric multidimensional scaling ordination using a Bray-Curtis similarity distance matrix and transformed (Wisconsin standardization and square root transformation) abundance data for all tree, shrub and liana species. After discarding third and fourth dimensions with little biological information, and a maximum of 200 random starts, the ordinations resulted in highly orthogonal principal axes in two dimensions using a Bray-Curtis similarity distance matrix. The axes were correlated with the percentages of species types (successional or mature forest species) and dispersal syndrome (animal, wind or mechanically dispersed seeds) using Bonferroni adjusted P values. We used a PERMANOVA to test for significant differences in species composition between treatments. All analyses were performed in R (R Core Team 2022). Ordinations were performed using the *metaMDS* function, and PERMANOVAs were run using the *adonis* function in the package 'vegan'.

Results

Vegetation structure

We recorded a total of 912 large stems within the plots across the two sites, with slightly more stems in the mature rainforest than in the restored rainforest (Table 1). We recorded a total of 1,128 small stems within the subplots, with slightly more plants in the restored rainforest. The number of

Table 1. Structural and diversity measures of plants in a restored rainforest corridor at Donaghy's Corridor and nearby mature rainforest in Lake Barrine National Park. Study plots were 150 m²; subplots were 15 m². Error terms are standard errors of means. Comparison of leaf litter cover were made using a Mann Whitney test; all other comparisons were made using t-tests. *ns* indicates $P > 0.05$. See Methods and Table S1 for definitions of successional and mature forest species, and dispersal syndromes.

	Donaghy's Corridor (restored rainforest)	Lake Barrine (mature rainforest)	Significance of difference
Whole of site measures			
Species richness (species site ⁻¹)	157	199	-
Leaf litter cover (median Braun-Blanquet class)	4-5	4-5	<i>ns</i>
Canopy cover (%)	85.7 (±2.17)	83.6 (±0.77)	$P < 0.05$
Large plants (≥ 1 cm DBH)			
No. stems (stems measured site ⁻¹)	446	466	-
No. of plants (plants plot ⁻¹)	78.3 (±34.9)	86.7 (±21.7)	<i>ns</i>
Basal area (m ² ha ⁻¹)	825.3 (±333.6)	1212.1 (±405.8)	<i>ns</i>
Biomass (t plot ⁻¹)	7.81 (±3.91)	16.94 (±6.71)	$P < 0.05$
Species richness (species site ⁻¹)	92	111	-
Species richness (species plot ⁻¹)	31.8 (±5.6)	34.2 (±7.5)	<i>ns</i>
Shannon's Diversity (H')	2.989 (±0.358)	2.986 (±0.237)	<i>ns</i>
Pielou's Evenness (J')	0.869 (±0.111)	0.85 (±0.029)	<i>ns</i>
Successional species (% plants)	51.8 (±7.9)	48.2 (±7.9)	$P < 0.05$
Mature forest species (% plants)	20.7 (±7.2)	79.3 (±7.2)	$P < 0.05$
Animal-dispersed species (% plants)	75.7 (±4.5)	75.8 (± 5.1)	<i>ns</i>
Wind-dispersed species (% plants)	19.3 (±5.0)	15.0 (± 6.7)	<i>ns</i>
Mechanically-dispersed species (% plants)	5.0 (±3.4)	9.2 (± 3.1)	<i>ns</i>
Small plants (<1cm DBH or <1.3m high)			
No. stems (stems measured site ⁻¹)	621	507	-
No. of stems (stems subplot ⁻¹)	103.5 (±32.9)	84.5 (±25.2)	<i>ns</i>
Basal area (cm ² subplot ⁻¹)	29.5 (±15.1)	39.5 (±56.0)	<i>ns</i>
Species richness (species site ⁻¹)	21.7 (±1.5)	18.5 (±3.2)	<i>ns</i>
Successional species (% plants)	50.9 (±9.7)	27.7 (±8.8)	$P < 0.05$
Mature forest species (% plants)	49.1 (±9.7)	72.3 (±8.8)	$P < 0.05$
Animal-dispersed species (% plants)	87.3 (±2.8)	69.9 (±7.3)	$P < 0.05$
Wind-dispersed species (% plants)	6.2 (±6.2)	8.6 (±2.7)	<i>ns</i>
Mechanically-dispersed species (% plants)	6.5 (±3.9)	21.5 (±7.3)	$P < 0.05$

large and small stems, large stem basal area, small plant basal area, and leaf litter cover did not differ significantly between the treatments. The mature rainforest plots had twice the biomass as the restored rainforest plots, and this difference was significant. Conversely, the restored rainforest plots had marginally, but significantly, higher canopy cover than the mature rainforest had.

Our forest profile diagrams show the similarity between the vegetation structure of the two treatments (Fig. 2). Both profiles show a well-developed canopy around 30 m high with well-developed subcanopy and understorey strata. Other structural elements such as plank buttresses, lianas and epiphytes were also conspicuous. Both sites exhibited similar median abundances in each stem size class and had an overall reverse-J shaped

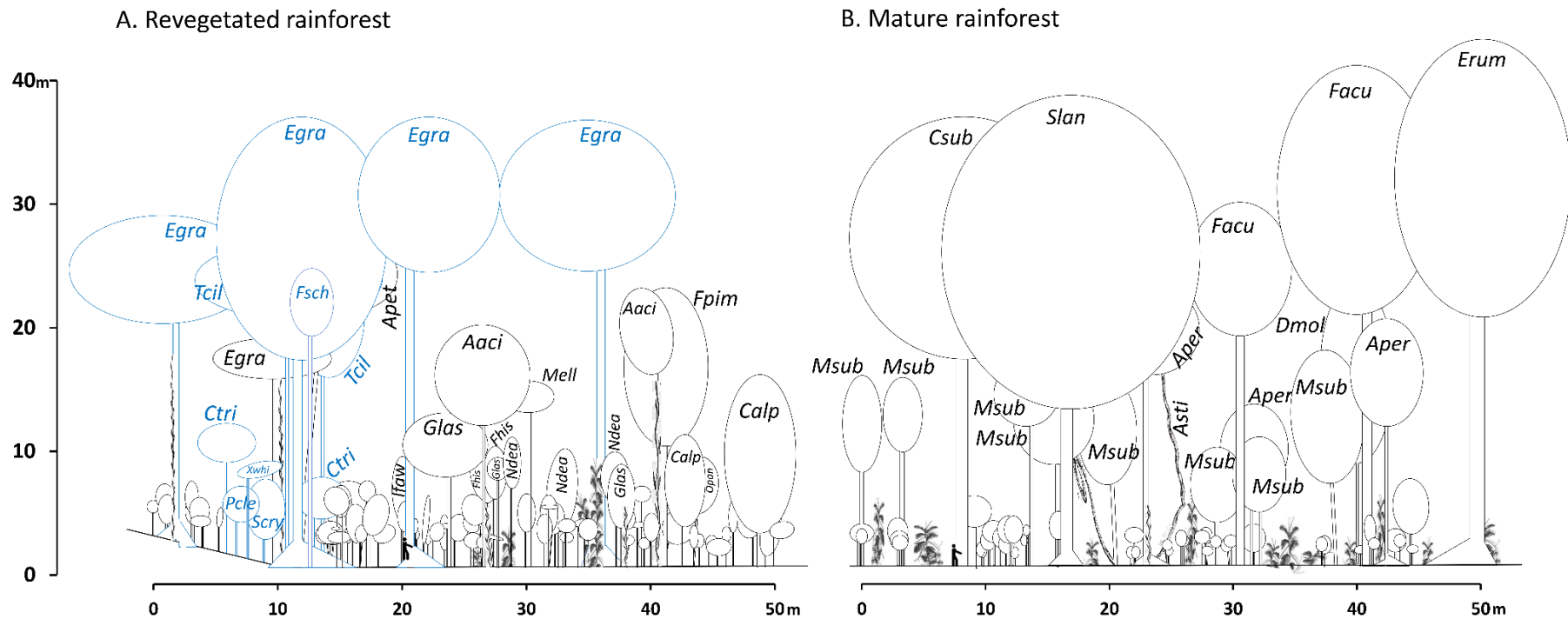


Figure 2. Profile diagrams of a representative vegetation transect in A. a 25-year-old restored rainforest in Donaghy’s Corridor, and B. mature rainforest in Lake Barrine National Park, Atherton Tablelands, Australia. Canopy trees in the revegetated corridor that were originally planted are in shown in blue. Species abbreviations: Aaci = *Acronychia acidula*; Aper = *Argyrodendron peralatum*; Apet = *Alphitonia petriei*; Asti = *Austrostenisia stipularis*; Calp = *Castanospora alphanthii*; Csub = *Cardwellia sublimis*; Ctri = *Cryptocarya triplinervis*; Dmol = *Dysoxylum mollissimum*; Egra = *Elaeocarpus grandis*; Erum = *E. ruminatus*; Facu = *Flindersia acuminata*; Fhis = *Ficus hispida*; Fpim = *Flindersia pimenteliana*; Fsch = *Flindersia schottiana*; Glas = *Guioa lasioneura*; Lfaw = *Litsea fawcettiana*; Mell = *Melicope elleryana*; Msub = *Macaranga subdentata*; Ndea = *Neolitsea dealbata*; Opan = *Olea paniculata*; Pcle = *Phaleria clerodendron*; Scry = *Syzygium cryptophlebium*; Slan = *Sloanea langii*; Tcil = *Toona ciliata*; Xwhi = *Xanthostemon whitei*.

size class distribution (Fig. 3). The only exception was the number of stems in the 20–29.9 cm DBH class, in which the restored rainforest had a marginally, but significantly, higher number of stems than the mature rainforest ($t = 2.424$, $P < 0.05$; Fig. 3). Life form distribution was similar between the two sites, although the mature rainforest had a slightly higher percentage of epiphytes, and a lower percentage of trees than the restored rainforest (Fig. 4A).

Species richness and composition

A total of 257 plant species was recorded across all plots (Table S1). Species in the mature rainforest site were nearly evenly divided between those unique to this site and those shared with the restored rainforest (Fig. 4B). The restored rainforest also had several unique species, although fewer than the mature rainforest. Of the 137 species found in the Donaghy's Corridor plots, 69 species (50.4%) were part of the original planting list, while 68 (49.6%) were species that had not been planted (Table S1). Many of these new species were herbs, epiphytes and vines that were also shared with the reference mature rainforest (Table S1). At both sites, estimated species richness

of both large and small plants increased with the number of individuals recorded (Fig. 5). However, the failure of rarefaction curves to reach an asymptote suggests that all our measures of species richness were underestimates. Rate of species accumulation of both plant size classes (as interpreted from the slope) was higher in mature rainforest than in restored rainforest, suggesting greater actual richness the mature rainforest site.

No significant differences were found between the two treatments in any diversity measures of large plants (Table 1). However, the restored rainforest had significantly fewer mature forest species and significantly more successional species than those found in the mature rainforest site. This pattern held for both large and small plants. However, the restored rainforest included five mature rainforest species that were not present in the mature rainforest, and had not been part of the original plantings (Table S1).

Animal-dispersal was the most abundant dispersal mechanism in both treatments. Among large plants, wind-dispersed species were the next most abundant and mechanically-dispersed species the least, with no differences in their relative abundance

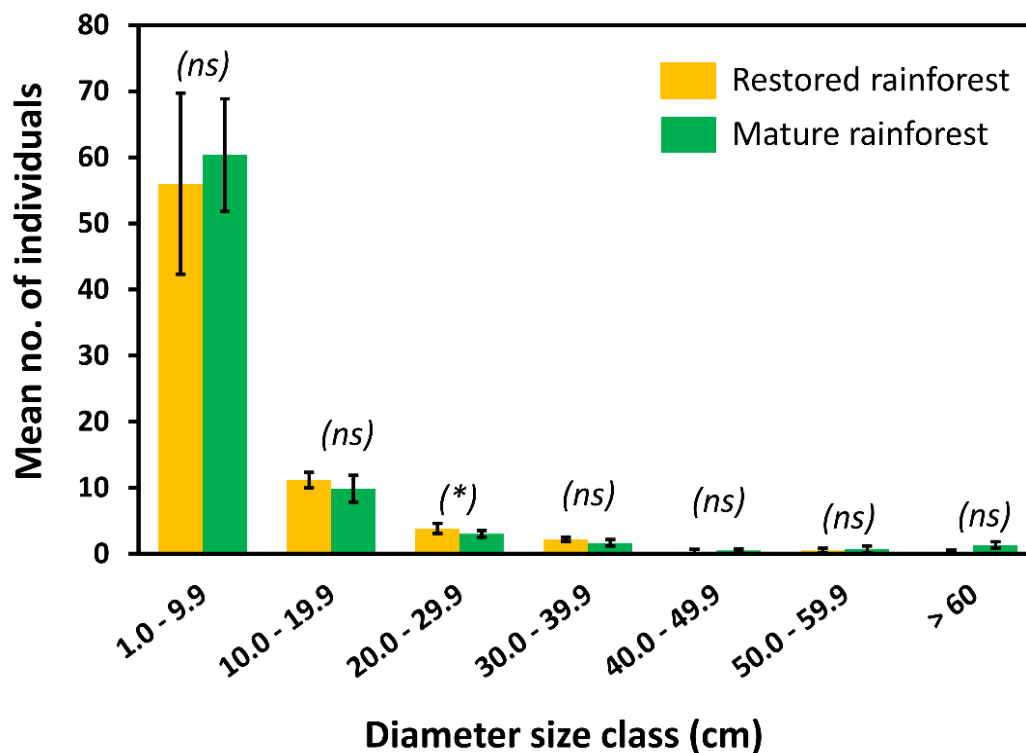
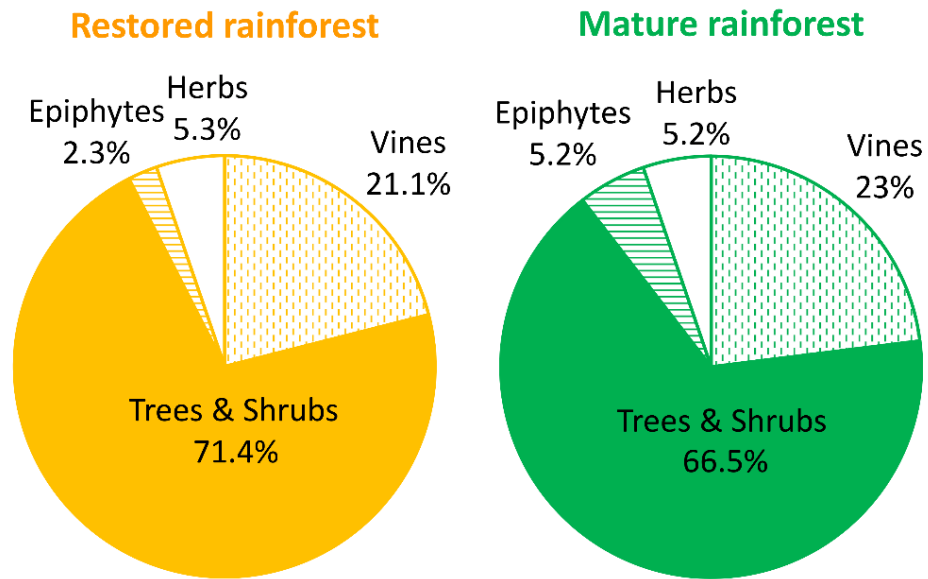


Figure 3. Mean abundances of trees (≥ 1 cm DBH) by diameter class in restored rainforest plots at Donaghy's Corridor ($n = 6$) and mature rainforest plots at Lake Barrine National Park ($n = 6$), on the Atherton Tablelands, Australia. Each size class is annotated with the significance class for t-tests (ns = not significant, * $P < 0.05$).

A. Lifeform breakdown



B. Species composition

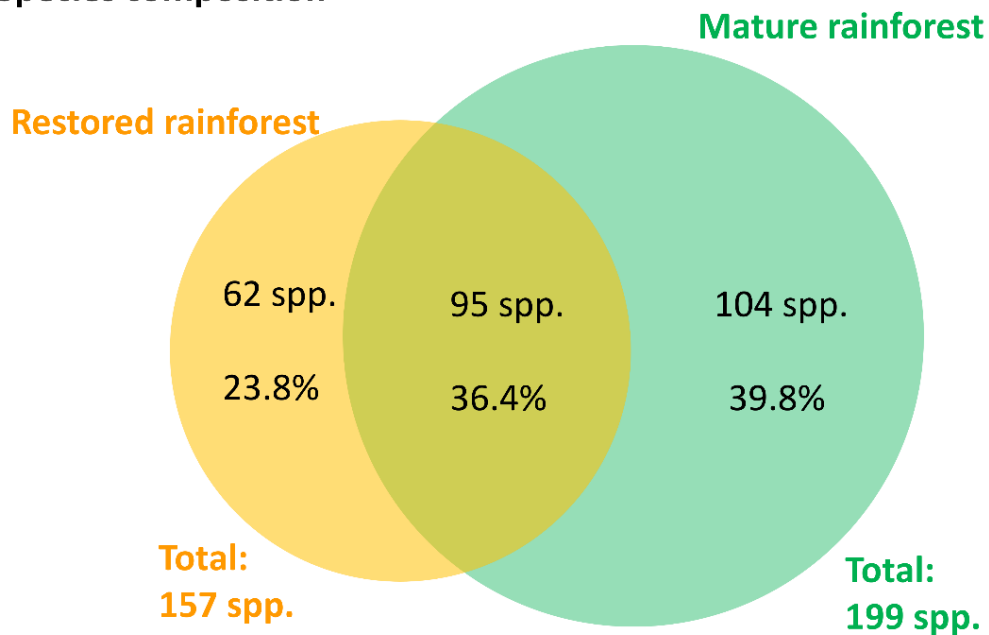


Figure 4. A. Piechart of the relative abundance of lifeforms; and B. Venn diagrams showing the total shared and unique species of all plants in plots in the restored rainforest at Donaghy’s Corridor (yellow circles) and mature rainforest at Lake Barrine National Park (green circles), Atherton Tablelands, Australia.

between treatments. However, among the small plants, the restored rainforest had a significantly higher percentage of animal-dispersed species, (mainly of small seeded species; e.g. *Guioa* spp.), with no significant differences in the relative abundance of wind-dispersed species (notably *Argyrodendron*). While large seeded, animal-

dispersed species were more abundant in the mature rainforest, some were also found in the restored rainforest (e.g. *Beilschmiedia bancroftii*), but only as seedlings or scattered individuals of the original plantings, and these were too few to allow statistical comparison with mature forests.

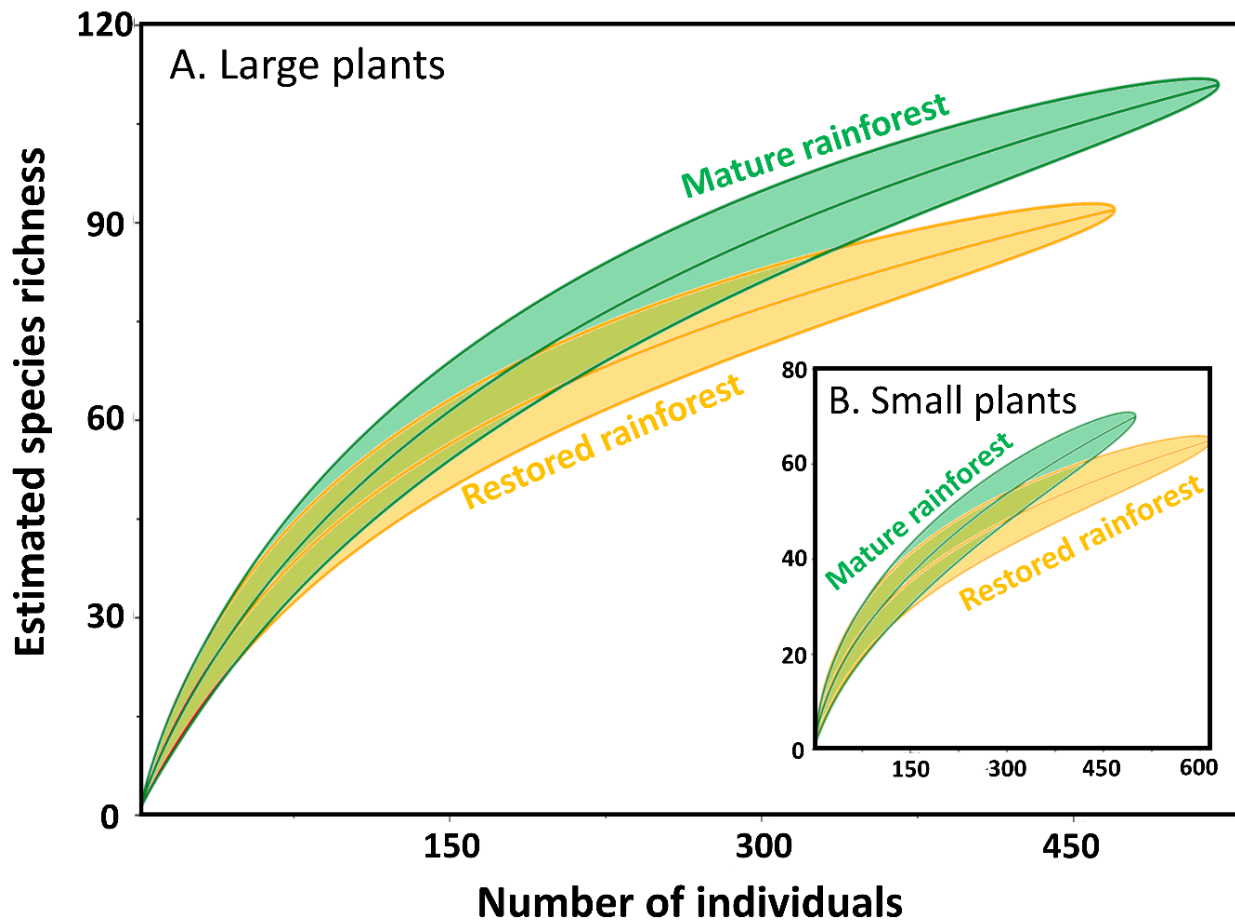


Figure 5. Rarefaction curves with 95% confidence intervals of estimated species richness of (A) large plants ($\geq 1\text{cm}$ DBH) and (B) small plants in restored rainforest plots at Donaghy's Corridor ($n = 6$) and mature rainforest plots at Lake Barrine National Park ($n = 6$), Atherton Tablelands, Australia.

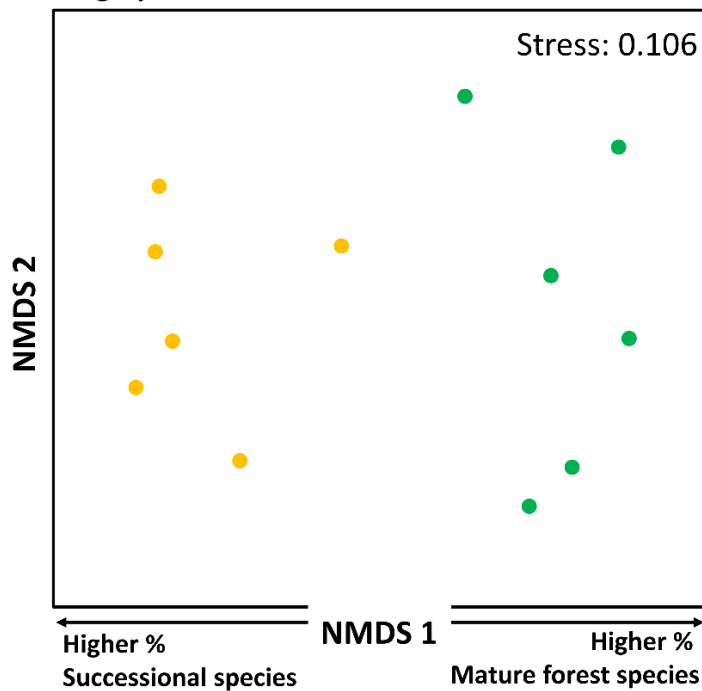
Even though the two treatments shared $>36\%$ of total species, their plot-level species composition differed markedly, as can be seen in the segregation of the mature rainforest and restored rainforest plots in both NMDS ordinations (Fig. 6). The PERMANOVA analysis indicated that these species compositional differences were significant (Large plants: $F_{1,11} = 4.181$, $P = 0.005$; Small plants: $F_{1,11} = 3.072$, $P = 0.005$). In the large-plant ordination, NMDS axis 1 was negatively correlated with the percentages of successional forest species, and positively correlated with the percentage of mature forest species (Fig. 6A). In the small-plant ordination, NMDS axis 1 was found to be negatively correlated with the percentage of animal-dispersed species, and positively correlated with the percentage of wind-dispersed species (Fig. 6B).

Discussion

Our findings demonstrate the results that can be achieved in the restoration of Australian tropical rainforests, but that even after a concerted revegetation program and 25 years restored rainforests will be different to intact remnant rainforest. While many aspects of vegetation structure and species diversity in the restored rainforest approximated those of the mature rainforest, the plot-based species composition of the two forest types remains dissimilar.

It is not surprising that the structure of the restored rainforest approximated that of the mature rainforest, while the floristics did not. This phenomenon also occurs in naturally regenerating secondary forests, which exhibit structural similarities to mature rainforest but lag in floristic recovery (Yeo & Fensham 2014; Goosem *et al.* 2016; Mullin *et al.* 2020). Kanowski *et al.* (2003)

A. Large plants



B. Small plants

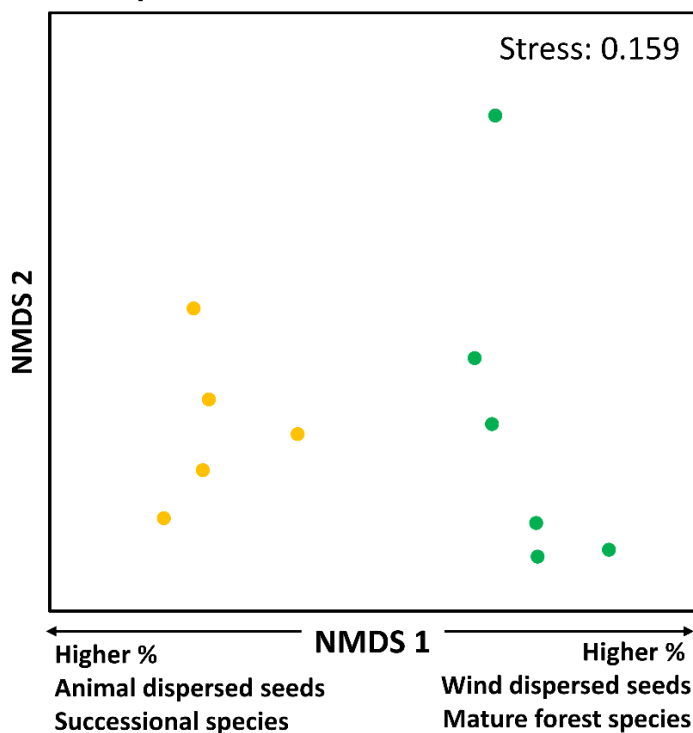


Figure 6. Two-dimensional non-metric multidimensional scaling (NMDS) ordination of A. large plants and B. small plants in plots in restored rainforest at Donaghy’s Corridor (yellow circles) and mature rainforest in Lake Barrine National Park (green circles), Atherton Tablelands, Australia.

found that rainforest structure recovered within 5–22 years of planting. However, there is scant information on the recovery of aboveground biomass. We demonstrated that 25-year-old restored rainforest still had substantially and significantly lower above-ground biomass than was found in the nearby mature rainforest. This

difference is likely due to the presence of a few very large and old trees in the largest size class in mature rainforest plots, including *Agathis microstachya*, *Aleurites rockinghamensis*, *Argyrodendron* spp., *Cardwellia sublimis* and *Elaeocarpus ruminatus* (e.g. Fig. 2 and Table S1). These species are particularly important for carbon sequestration because

of their dense wood, large size, and great longevity (Bello *et al.* 2015; Peres *et al.* 2016). The low density of such trees meant that this biomass difference was obscured in the size class comparison between sites.

Restored forest may also take decades or centuries before its species composition approaches that of intact forest, and may never do so. Lack of convergence in floristic composition has even been found in naturally regenerated secondary rainforest after 60 years (Goosem *et al.* 2016). In our study, lack of convergence in species composition was particularly marked in the canopy and subcanopy trees, with successional species being more important in restored rainforest and mature rainforest species in the mature rainforest. However, relative abundance of species within each of the dispersal classes only differed significantly among plants in the smallest size class. Presence of only low numbers of large-seeded, animal-dispersed in the restored rainforest has also been found in other studies, reflecting their limited dispersal capacity (Silva & Tabarelli 2000; Reid *et al.* 2015). However, Tucker *et al.* (unpublished data) did find evidence of large-fruited Lauraceae being dispersed internally and from forests outside the corridor.

The lack of plot-level similarity in species composition between the 25-year old restored rainforest and mature-phase reference forest should not be interpreted as a failure to achieve positive restoration outcomes. In the first instance, there is not information about the pre-clearing vegetation composition, and some spatial variation between sites is likely. Secondly, establishment of vegetation structure can pave the way for later natural regeneration through dispersal from surrounding intact rainforests. Strategic placement of restoration sites, along with the use of carefully selected species mixtures can facilitate dispersal across landscapes, and the presence of small plants of mature rainforest species that had not initially been planted in the restored corridor is evidence of this. Re-establishing habitat connectivity between fragments can enhance the likelihood of maintaining dispersal at the landscape scale by providing 'stepping stones' for large frugivores to travel between remnants. Wildlife use of Donaghy's Corridor since the initial planting includes species likely to disperse the seeds of rainforest plants (Paetkau *et al.* 2009; Tucker & Simmons 2009;

Tucker & Ford 2023); and instances of seed caching have been observed (authors' unpublished data). Maintaining frugivore populations – and the dispersal services they provide – appears to be essential for the restoration of species diversity and ecological functioning that typify mature tropical forests (Moran *et al.* 2009). Rainforest species recorded in the restoration site that had not been planted must have arrived through seed dispersal from the surrounding intact rainforest. This was particularly the case for animal-dispersed species. A heterogeneous and ecologically-connected landscape is likely to favour the persistence of large frugivores and increase the probability that dispersal, and hence continue to aid natural development of functionality and resilience in restored areas.

Our finding that almost half the species found in the restored rainforest were not part of the list of initial plantings was a positive result for restoration, and confirms the developing conservation value of Donaghy's Corridor and its ecological function. Although the majority of these new species were vines, epiphytes and herbs, there were also promising numbers of large-fruited mature rainforest species (e.g. *Beilschmiedia bancroftii*). Tucker and Murphy (1997) similarly found high levels of recruitment of rainforest species in restoration sites close to mature rainforest. In contrast, plantings at a greater distance from mature rainforests may have slower recruitment of mature rainforest species (Pohlman *et al.* 2021).

Despite this evidence of dispersal, representation of mature forest species in our restoration site was still lower than that in the mature rainforest. Engert *et al.* (2020) made similar findings, and discussed them in terms of functional trait representation differences between restoration plantings and mature rainforest. Assessing the functional trajectories of restored rainforests (e.g. Brancalion & Holl 2016; Manhães *et al.* 2022) could therefore be a productive avenue for future research.

Despite numerous rainforest restoration projects in the Wet Tropics bioregion, there has been no routine, systematic, long-term monitoring of their success (Goosem & Tucker 2013). This study provides a model for assessing rainforest recovery through the use of standard sized plots for assessing vegetation structure and floristics. We hope that it stimulates others to undertake similar assessments of restoration efforts throughout the region and beyond.

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Supplementary file

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

- Table S1. List of species found in restored forest in Donaghy's Corridor (DC) and mature forest (RF) in Lake Barrine.

References

- Banning NC, Gleeson DB, *et al.* 2011. Soil microbial community successional patterns during forest ecosystem restoration. *Applied and Environmental Microbiology* 77: 6158-6164.
- Bello C, Galetti M, *et al.* 2015. Defaunation affects carbon storage in tropical forests. *Science Advances* 1: e150110.
- Brancalion PH, Holl KD. 2016. Functional composition trajectory: a resolution to the debate between Suganuma, Durigan, and Reid. *Restoration Ecology* 24: 1-3.
- Catterall C, Harrison DA. 2006. *Rainforest Restoration Activities in Australia's Tropics and Subtropics*. Rainforest CRC: Queensland, Australia.
- Catterall C, Kanowski J, *et al.* 2004. Quantifying the biodiversity values of reforestation: perspectives, design issues and outcomes in Australian rainforest landscapes. In *Conservation of Australia's Forest Fauna*, ed. D Lunney pp. 359-393. Royal Zoological Society of New South Wales.
- 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.
- Chazdon RL, Broadbent EN, *et al.* 2016. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances* 2: e1501639.
- Chazdon RL, Brancalion PHS, *et al.* 2017. A policy-driven knowledge agenda for global forest and landscape restoration. *Conservation Letters* 10: 125-132.
- Clewell AF, Aronson J. 2013. *Ecological Restoration: Principles, Values, and Structure of an Emerging Profession*, 2nd edition. Island Press: Washington.
- Collins MJ. 1994. Patterns and rates of rainforest conversion on the Atherton and Evelyn Tablelands, north-eastern Queensland, 1978-1988. *Proceedings of the Royal Society of Queensland* 104: 1-10.
- Convention on Biological Diversity. 2020. *Aichi Biodiversity Targets*. <https://www.cbd.int/sp/targets>, viewed 19 March 2022.
- Cooper W, Cooper WT. 2004. *Fruits of the Australian Tropical Rainforest*. Nokomis Editions: Melbourne.
- Crouzeilles R, Ferreira MS, *et al.* 2017. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances* 3: e1701345.
- DeLuca TH, Aplet GH, Wilmer B, Burchfield J. 2010. The unknown trajectory of forest restoration: a call for ecosystem monitoring. *Journal of Forestry* 108: 288-295.
- Derhé MA, Murphy HT, Preece ND, Lawes MJ, Menéndez R. 2018. Recovery of mammal diversity in tropical forests: a functional approach to measuring restoration. *Restoration Ecology* 26: 778-786.
- Engert JE, Vogado NO, *et al.* 2020. Functional trait representation differs between restoration plantings and mature tropical rainforest. *Forest Ecology and Management* 473: 118304.
- Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* 34: 487-515.
- Freebody K. 2007. Rainforest revegetation in the uplands of the Australian Wet Tropics: The Eacham Shire experience with planting models, outcomes and monitoring issues. *Ecological Management and Restoration* 8: 140-143.
- Gatica-Saavedra P, Echeverría C, Nelson CR. 2017. Ecological indicators for assessing ecological success of forest restoration: a world review. *Restoration Ecology* 25: 850-857.
- Goosem M. 2012. Mitigating the impacts of rainforest roads in Queensland's Wet Tropics: Effective or are further evaluations and new mitigation strategies required? *Ecological Management and Restoration* 13: 254-258.
- Goosem S, Morgan G, Kemp JE. 1999. Wet Tropics. In *The Conservation Status of Queensland's Bioregional Ecosystems*, eds P Sattler, R Williams, pp. 7/0-7/73. Environmental Protection Agency: Brisbane.
- 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 edition. Wet Tropics Management Authority and Biotropica Australia: Cairns.
- Haddad NM, Brudvig LA, *et al.* 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances* 1: e1500052.
- Harrison R, Wardell-Johnson G, McAlpine C. 2003. Rainforest reforestation and biodiversity benefits: A case study from the Australian Wet Tropics. *Annals of Tropical Research* 25: 65-76.
- Hobbs RJ, Norton DA. 1996. Towards a conceptual framework for restoration ecology. *Restoration Ecology* 4: 93-110.
- Howe HF. 2016. Making dispersal syndromes and networks useful in tropical conservation and restoration. *Global Ecology and Conservation* 6: 152-178.
- Ilic J, Boland D, McDonald M, Downes G, Blakemore P. 2000. Wood Density Phase 1. National Carbon Accounting System, Technical Report No. 18. Australian Greenhouse Office: Canberra.
- Kanowski J, Catterall CP, Wardell-Johnson GW, Proctor H, Reis T. 2003. Development of forest structure on cleared rainforest land in eastern Australia under different styles of reforestation. *Forest Ecology and Management* 183: 265-280.
- Kanowski J, Catterall CP, Harrison DA. 2008. Monitoring the outcomes of reforestation for biodiversity conservation. In *Living in a Dynamic Tropical Forest Landscape*, eds NE Stork, SM Turton, pp. 526-536. Blackwell Publishing: Malden, MA, USA.
- Larsen JB, Nielsen AB. 2007. Nature-based forest management—Where are we going?: Elaborating forest development types in and with practice. *Forest Ecology and Management* 238: 107-117.
- Lawes MJ, Moore A, Andersen AN, Preece ND, Franklin D. 2017. Ants as ecological indicators of rainforest restoration: community convergence and the development of an Ant Forest Indicator Index in the Australian wet tropics. *Ecology and Evolution* 7: 8442-8455.
- Manhães AP, Pantaleão LC, *et al.* 2022. Functional trajectory for the assessment of ecological restoration success. *Restoration Ecology* 30: e13665.
- McDonald T. 2006. Preparing for restoration success: Are we ready? *Ecological Management and Restoration* 7: 76.
- Meli P, Holl KD, *et al.* 2017. A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. *PLoS One* 12: e0171368.
- Milling CR, Rachlow JL, *et al.* 2018. Habitat structure modifies microclimate: an approach for mapping fine-scale thermal refuge. *Methods in Ecology and Evolution* 9: 1648-1657.
- Moran C, Catterall CP, Kanowski J. 2009. Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biological Conservation* 142: 541-552.
- Mullin MV, Salecki EF, *et al.* 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.
- Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. *Trends in Ecology and Evolution* 10: 58-63.
- Paetkau D, Vázquez-Domínguez E, Tucker NI, Moritz C. 2009. Monitoring movement into and through a newly planted rainforest corridor using genetic analysis of natal origin. *Ecological Management and Restoration* 10: 210-216.
- Palmer MA, Ambrose R, Poff NL. 1997. Ecological theory and community restoration ecology. *Restoration Ecology* 5: 291-300.
- Patel N. 2018. *CanopyCapture*. [Mobile Application Software] <https://nikp29.github.io/CanopyCapture>, viewed 15 Aug 2021.
- Peres CA, Emilio T, Schiatti J, Desmouliere SJM, Levi T. 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences of the United States of America* 113: 892-897.
- Pohlman CP, Tng DYP, Florentine SK. 2021. Do primary rainforest tree species recruit into passively and actively restored tropical rainforest? *Forest Ecology and Management* 496: 119453.
- Prach K, Durigan G, *et al.* 2019. A primer on choosing goals and indicators to evaluate ecological restoration success. *Restoration Ecology* 27: 917-923.
- Preece ND, Crowley GM, Lawes MJ, Van Oosterzee P. 2012. Comparing above-ground biomass among forest types in the Wet Tropics: Small stems and plantation types matter in carbon accounting. *Forest Ecology and Management* 264: 228-237.
- R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing: Vienna, Austria. <https://www.R-project.org>, downloaded 15 Aug 2022.
- Rachmat HH, Ginoga KL, *et al.* 2021. What can native trees provide in revegetating tropical degraded land? An experience of man-made Dipterocarp forest in Indonesia. *Environmental Sciences Proceedings* 3: 79.
- Reid JL. 2015. Indicators of success should be sensitive to compositional failures: reply to Suganuma and Durigan (2015). *Restoration Ecology* 23: 519-520.

- Reid JL, Holl KD, Zahawi RA. 2015. Seed dispersal limitations shift over time in tropical forest restoration. *Ecological Applications* 25: 1072-1082.
- Richards PW. 1996. *The Tropical Rain Forest: An Ecological Study*. Cambridge University Press: Cambridge.
- Rocha R, Ovaskainen O, *et al.* 2018. Secondary forest regeneration benefits old-growth specialist bats in a fragmented tropical landscape. *Scientific Reports* 8: article 3819.
- Ruiz-Jaen MC, Aide TM. 2005. Restoration success: how is it being measured? *Restoration Ecology* 13: 569-577.
- Rydgren K, Auestad I, *et al.* 2020. Assessing restoration success by predicting time to recovery—But by which metric? *Journal of Applied Ecology* 57: 390-401.
- Seale M, Nakayama N. 2020. From passive to informed: mechanical mechanisms of seed dispersal. *New Phytologist* 225: 653-658.
- Silva JMC, Tabarelli M. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404: 72-74.
- Suganuma MS, Durigan G. 2015. Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. *Restoration Ecology* 23: 238-251.
- Tracey JG. 1982. *The Vegetation of the Humid Tropical Region of North Queensland*. CSIRO: Melbourne.
- Tucker NIJ. 2000. Monitoring and evaluation at Donaghy's wildlife corridor: measures used and questions asked. *Ecological Management and Restoration* 1: 61-62.
- Tucker N, Ford G. 2023. Observations on the utilisation of a restored wildlife corridor by echo-locating microbats in North Queensland's Wet Tropics. *Ecological Management and Restoration* 24: 7-11.
- Tucker NIJ, Murphy TM. 1997. The effects of ecological rehabilitation on vegetation recruitment: some observations from the Wet Tropics of North Queensland. *Forest Ecology and Management* 99: 133-152.
- Tucker NIJ, Simmons T. 2009. Restoring a rainforest habitat linkage in north Queensland: Donaghy's Corridor. *Ecological Management and Restoration* 10: 98-112.
- Van Breugel M, Bongers F, Martínez-Ramos M. 2007. Species dynamics during early secondary forest succession: Recruitment, mortality and species turnover. *Biotropica* 39: 610-619.
- Van der Maarel E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97-114.
- Verdone M, Seidl A. 2017. Time, space, place, and the Bonn Challenge global forest restoration target. *Restoration Ecology* 2: 903-911.
- Wang Y, Fu B, Lü Y, Chen L. 2011. Effects of vegetation restoration on soil organic carbon sequestration at multiple scales in semi-arid Loess Plateau, China. *Catena* 85: 58-66.
- Whitehead T, Goosem M, Preece ND. 2014. Use by small mammals of a chronosequence of tropical rainforest revegetation. *Wildlife Research* 41: 233-242.
- Whitmore TC. 1990. *An Introduction to Tropical Rain Forests*. Clarendon Press: Oxford, UK.
- Winsen M, Hamilton G. 2023. A comparison of UAV-derived dense point clouds using LiDAR and NIR photogrammetry in an Australian eucalypt forest. *Remote Sensing* 15: 1694.
- Winter JW, Bell FC, Pahl LI, Atherton RG. 1987. Rainforest clearfelling in northeastern Australia. *Proceedings of the Royal Society of Queensland* 98: 41-57.
- Wortley L, Hero JM, Howes M. 2013. Evaluating ecological restoration success: a review of the literature. *Restoration Ecology* 21: 537-543.
- Yeo WLJ, Fensham RJ. 2014. Will *Acacia* secondary forest become rainforest in the Australian Wet Tropics? *Forest Ecology and Management* 331: 208-217.
- Zachar S, Grant J, Winter J, McCaffrey M. 2017. Use of reforested rainforest by arboreal marsupials on the Atherton Tablelands, North-Eastern Australia – a preliminary assessment. *North Queensland Naturalist* 47: 21-27.
- Zhou P, Luukkanen O, Tokola T, Nieminen J. 2008. Effect of vegetation cover on soil erosion in a mountainous watershed. *Catena* 75: 319-325.
- Zich FA, Hyland BPM, Whiffin T, Kerrigan RA. 2020. *Australian Tropical Rainforest Plants*, 8th Edition. <https://apps.lucidcentral.org/rainforest/text/intro/index.html>, viewed 30 Nov. 2022.