

Structural and functional connectivity in a 25-year old restored wildlife corridor - an example from the upland Wet Tropics of north-eastern Australia

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Abstract

Re-establishing ecological connectivity between remnants and continuous forest can counter the effects of fragmentation and climate change by strategically increasing habitat area and improving movement potential. To evaluate the effect of restoring habitat between an isolated fragment and adjacent intact rainforest, we re-surveyed vegetation, birds and ground mammals in a restored wildlife corridor over a 12-month period in 2021, comparing results to data from 1996-1998 (birds) and 2000 (vegetation and mammals). Over 150 naturally regenerating plants were recorded; birds were primarily responsible for seed dispersal. Numbers of large-seeded (>30 mm dia.) and late successional species dispersed by birds and mammals have increased. Bird and mammal assemblages are increasingly similar to adjacent reference forest, although some endemic birds remain absent. Germination of some large-fruited species coincides with colonisation by the only mammals capable of their dispersal; generalist mammals have been replaced by rainforest specialists. After nearly 25 years, plantings have produced a structurally complex habitat inhabited by many species, and tropical restoration projects in similar settings may achieve comparable responses.

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Handling editor: Peter Valentine

Citation: Tucker NIJ, Freeman AND, Marshall TJ. 2024. Structural and functional connectivity in a 25-year old restored wildlife corridor – an example from the upland Wet Tropics of north-eastern Australia. *North Queensland Naturalist* 54: 69-78.

Introduction

Anthropogenic habitat is a significant barrier to the movement of rainforest species, posing risks to fragmentation sensitive species (Haddad *et al.* 2015) and those potentially requiring range shifts in response to climate change (Senior *et al.* 2019). Landscape connectivity (Taylor *et al.* 1993), a central tenet of ecosystem management, potentially counters some of the effects of fragmentation by

allowing the unimpeded flow of pollen, seeds and wildlife, with the review by Heller and Zavaleta (2009) finding that improving landscape connectivity was the ‘most frequent recommendation for climate change adaptation’. Despite this endorsement, long-term studies documenting outcomes from the actual restoration of connectivity in tropical environments are

uncommon. Instead, studies have tended to demonstrate colonisation of restored areas over time (Catterall *et al.* 2012; de la Peña-Domene *et al.* 2014; Holl *et al.* 2020), utilisation of existing elements of connectivity within the vegetation matrix (Crome *et al.* 1994; de la Peña-Cuéllar *et al.* 2015) or the function of existing corridors that have been experimentally manipulated (Tewksbury *et al.* 2002).

In the Wet Tropics of north-eastern Australia, restoration of wildlife corridors re-connecting habitat patches and continuous forests began in the mid-1990s, adopted as an adaptive management response specifically to improve habitat connectivity, rather than enlarging existing habitat or restoring riparian habitat. In a cooperative effort between landholders, community and government, a number of connectivity restoration projects have been, and continue to be, established. In some cases, base-line data was obtained relating to the plants and animals present prior to treatment, and records were kept relating to species planted and patterns of colonisation over time.

One example of this approach is the Donaghy's Corridor (DC) project. Base-line data was collected in 1994, prior to restoration of the corridor, and involved identifying all vascular plants along the proposed alignment and within a 100 m buffer. Live-trapping of ground mammals was also completed along the proposed alignment. At completion of planting in 1998, colonisation by plants and ground mammals were surveyed over a 3-year period. Birds were surveyed in 1996–1998 (Jansen 2005). Tucker and Simmons (2009) detailed colonisation of DC by small mammals and vegetation; at the same site, Paetkau *et al.* (2009) documented genetic exchange between previously separated populations of the Bush Rat (*Rattus fuscipes*). Both studies used base-line data and regular monitoring data to examine changes in community and/or genetic composition over the first 3 years of corridor establishment.

In this paper we re-examine DC vegetation and how its small mammal and bird communities have responded to the changes in habitat structure and connectivity since surveys were conducted over two decades ago.

Methods

Site description

Donaghy's Corridor is a 16.4 ha block of restored riparian-zone habitat linking the isolated 505 ha Lake Barrine section of Crater Lakes National Park to Wooroonooran National Park (80,000 ha). Located in the tropical highlands at 720 m a.s.l, the site receives annual rainfall of 1428 mm (mostly between November and March), with average temperatures varying from 17.1°C in winter to 27.3°C in summer (Tracey 1982). Planting of around 17,000 stems from 101 species was undertaken over four years from 1995 to 1998 to establish the corridor along Toohey Creek, converting cattle pasture and 1.75 ha of regrowth into a wildlife corridor between two World Heritage Area properties separated since the 1940s (Tucker & Simmons 2009). Planted species comprised those listed in Group 9 (Goosem & Tucker 2013), with Regional Ecosystem 7.8.2a (Complex mesophyll vine forest; uplands of the very wet and wet cloudy rainfall zones) being the reference forest ecosystem. At both ends of the planted corridor, vegetation had been previously cleared and variously developed regrowth was present, (totalling an additional 300 m) making the full corridor (from mature reference forest at both ends) c.1.2 km in length, with an average width of 80 m (Fig. 1).

Vegetation

To document vegetation change, 3 m wide permanent transects (three in each planting year – 1995/96/97/98, 12 in total) established across the corridor in 1998 were re-sampled in 2021. All vascular plants in 3 m x 5 m plots (n=180) were identified to species level along each transect (from outer fence to creek edge), and the species composition of the canopy, understorey (1–10 m high), and ground layer (<1 m high) were recorded.

Baseline data, relating to both planted and pre-existing species, was used to identify plants which had been dispersed into the corridor from outside the 100 m corridor survey buffer. To better understand the trajectory of the developing vegetation, each recruiting species was assigned to a typical stage of forest development depending on where it is most commonly encountered in local forests (Tucker & Murphy 1997). Gap-phase species are pioneer plants most commonly seen in young

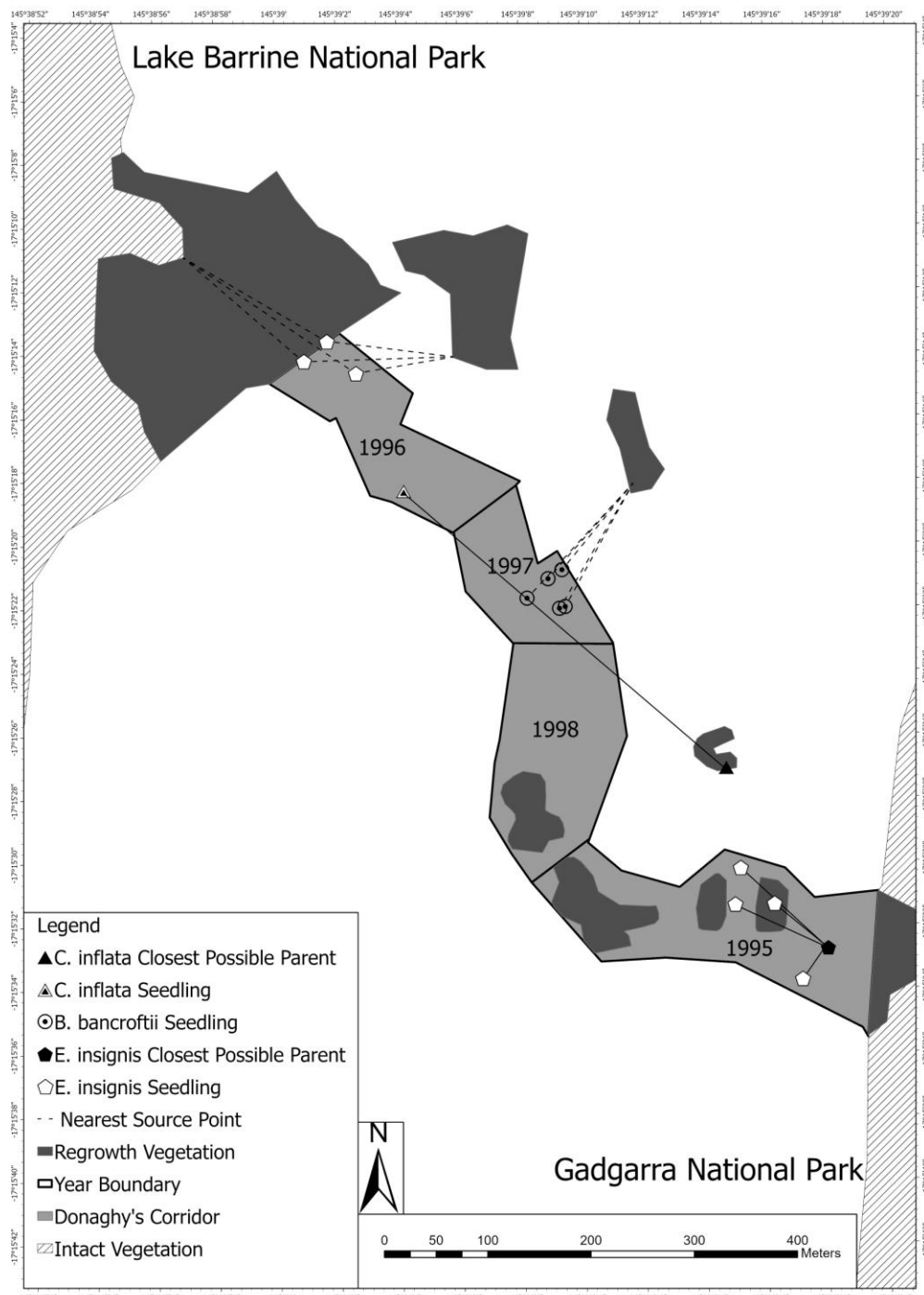


Figure 1. Site layout of Donaghy's Corridor with dispersal of three large-fruited plants from internal and external sources.

regrowth or abandoned pasture, species of intermediate and intermediate-late stages typically occur in well-developed regrowth and large tree-fall gaps, whereas late successional species are only encountered in mature forest. In each case, values for 2000 and 2021 were directly compared.

We also categorized regenerating plant species according to fruit size, previous studies showing that large fruited species are dispersal limited (Qie *et*

al. 2019; Albert *et al.* 2020). Fruit-size calculations are based on the span that limits swallowing (diameter of fruits swallowed whole or single seeds and associated pulp of soft-skinned fruit or arillate seed from self-opening fruit). Fruit size categories (small = 3–10 mm, medium = 10–30 mm and large = >30 mm) were derived from Tucker and Murphy (1997), Cooper and Cooper (2004) and on-line resources at <https://keys.lucidcentral.org>.

Birds

In the 1995, 1996 and 1998 planting sites, an area of 0.3 ha was established for bird surveys. Reference sites of the same dimensions were established in mature forest at Lake Barrine and in the pre-existing 1.75 ha of regrowth within the corridor (Fig 1).

Thirty-minute area searches of all terrestrial birds seen and heard in corridor habitat were completed, with six surveys conducted at approximately monthly intervals between May and December 2021, all in fine conditions. Surveys were conducted by one observer (AF), with additional incidental records obtained from motion-sensor cameras deployed for ground mammal survey.

Birds were classified into *a priori* functional habitat groups based on their use of intact vegetation within the study region (Kanowski *et al.* 2010). Mixed Forest (MF) species occur in a range of forested habitats from rainforest to more open-canopied sclerophyll communities. Rainforest-dependent (RF) species are largely confined to, or dependent on, rainforest. A subgroup of rainforest species is endemic to the Wet Tropics bioregion (RWT). The presence of rainforest-dependent species in corridor sites was compared to those recorded in 1996-1998 by Jansen (2005).

Effective seed dispersers and their gape width were identified by reference to Moran *et al.* (2004) and Dennis and Westcott (2006). Effective seed dispersers include species for which fruit forms the major part of the diet (frugivores), and species consuming fruit as part of a mixed diet (mixed). We classified effective seed dispersers into three gape width categories; small (<10 mm), medium (10–15 mm), and large (>15 mm).

Analysis of bird community composition used species' presence (recorded on one or more surveys), while abundance (number of individuals averaged across all six surveys at a site) was used to compare seed disperser numbers between sites.

Mammals

Terrestrial mammals were surveyed at four-monthly intervals (Apr/Aug/Dec) using Reconyx motion-sensor cameras baited with fresh chicken-necks. Ten cameras were randomly positioned either side of the corridor, two in each yearly planting (n=4) and the regrowth patch. Recording

was conducted over four nights/five days for a total of 120 nights. To remove bias caused by the different sampling methods used in the two time periods, we consider presence/absence only and exclude species that could not be live-trapped but were recorded by motion sensor cameras. These were Feral Pig (*Sus scrofa*), Feral Cat (*Felis catus*) and Echidna (*Tachyglossus aculeata*). No attempt was made to distinguish between the Bush Rat (*Rattus fuscipes*) and the closely related, nearly identical, Cape York Rat (*R. leucopus*), both of which had been previously recorded in the corridor (Paetkau *et al.* 2009).

Forest dependence of terrestrial mammal species followed the classification scheme developed by Williams (2006), as follows:

- 0 = does not occur in rainforest;
- 1 = occasionally recorded in rainforest;
- 2 = use rainforest as sub-optimal/marginal habitat;
- 3 = commonly recorded in rainforest but not the species' core habitat;
- 4 = rainforest is a main habitat, however also common in other forest environments;
- 5 = rainforest is core habitat, however, also occur in wet sclerophyll forests; and
- 6 = occurs in rainforest habitat only.

Species scoring four or higher are considered most likely to benefit from enhanced connectivity of rainforest habitat.

Results

Vegetation

Surveys of naturally regenerating species in 2000 identified 115 species from 4472 individuals within the 180x15 m² plots, with 25 'new' species sourced from forests outside the corridor (i.e., not pre-existing or planted species) (Tucker & Simmons 2009). In 2021, re-census of the same plots revealed 153 species from 4501 individuals again with 25 'new' species (in addition to the 25 'new' species recorded in 2000). Seventeen seedlings (all <25 mm) were unidentified. Laurels (Lauraceae) (17 species), and tamarinds (Sapindaceae) (13 species), were the most common regenerating species. Both plant families are characteristic of well-developed rainforest, producing fleshy fruits dispersed by many birds and mammals.

Vegetation growth and colonisation has resulted in increased structural complexity. Canopy height is c. 30 m across the corridor, with a distinctive under-

storey and ground layer now present (Tng *et al.* 2023). In 2000, canopy height varied from 3–5 m, no understorey was present and regenerating vegetation was all <0.5 m.

A shift has also occurred in the typical successional stage of recruiting vegetation. Numbers of gap-phase trees and species of intermediate succession have remained relatively stable, but numbers of late successional species have increased (Fig. 2). Most recruits have seeds in the 3–10 mm size class (Fig. 3). Surveys in 2000 showed similar bias, although by 2021, medium (10–30 mm) and large (>30 mm) seeds had increased by 27% and 50% respectively. Wind-dispersed species increased by 58% (Fig. 3.) but this appears mostly attributable to reproduction from planted species.

Birds

A total of 511 records of 47 species of birds were collected (Supplementary Table S1). Forty species were recorded across the three planting sites, 27 species were recorded in the regrowth patch and 29 species in the mature forest reference site. The regrowth, 1995 and 1996 planting sites shared 66-76% of the species recorded in the mature forest site while the 1998 planting shared only 45% of those species.

Bird species richness, and the numbers of rainforest-dependent and mixed forest species were broadly similar between the forest reference and regrowth site and the 1995 and 1996 plantings. The 1998 planting had lower bird species

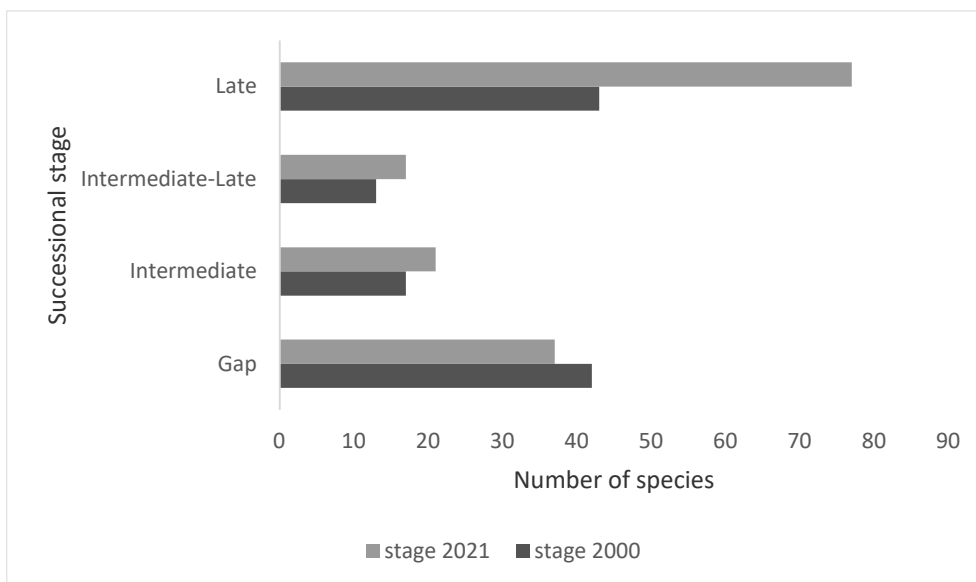


Figure 2. Changes in the successional stage of regenerating vegetation at Donaghy’s Corridor, all planting years combined, 2000-2021.

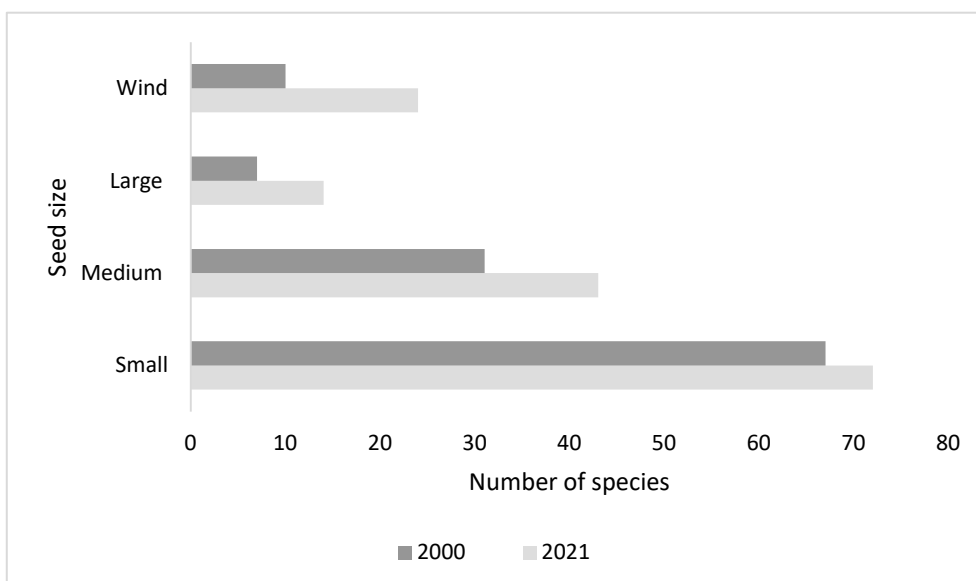


Figure 3. Size of seeds in natural recruitment, across all planting years (inc. wind dispersed species), in 2000 and 2021, at Donaghy’s Corridor. Small = 3–10 mm, Medium = 10–30 mm, Large = >30 mm.

richness overall and fewer rainforest-dependent species (Fig. 4; Supplementary Table S1).

Fewer Wet Tropics endemics were recorded outside the mature forest site. The regrowth site, 1995 and 1996 plantings had 3–5 of the eight endemic species recorded in mature forest, but no endemics were recorded in the 1998 planting (Fig. 4). The endemic Bower's Shrike-thrush (*Colluricincla boweri*), Chowchilla (*Orthonyx spaldingii*) and the Fern Wren (*Oreoscopus gutturalis*), were only recorded in reference forest (Supplementary Table S1).

Fourteen species were classified as effective seed-dispersers (Supplementary Table S1). Numbers were highly variable; there was no significant difference between sites in the average number of seed-dispersers recorded per survey (ANOVA; $p=0.15$; $F=1.87$; $df=4$). The 1996 and 1998 plantings had lower abundances of large-gaped seed-dispersers and higher abundances of small-gaped seed-dispersers than the other sites though these differences were not statistically significant. The 1995 planting had a higher abundance of medium-gaped frugivores than the other sites (Fig. 5; Supplementary Table S1).

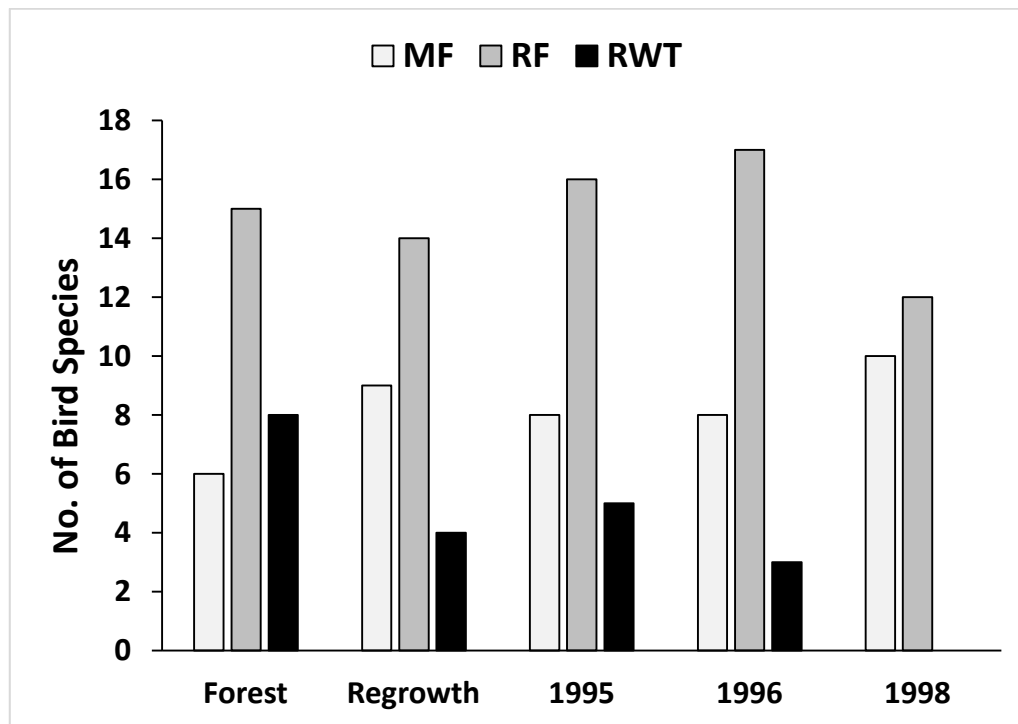


Figure 4. Species richness in functional habitat class recorded in Donaghy's Corridor planting (1995; 1996; 1998) and reference sites (Forest; Regrowth). MF = mixed forest; RF = rainforest species; RWT = endemic Wet Tropics.

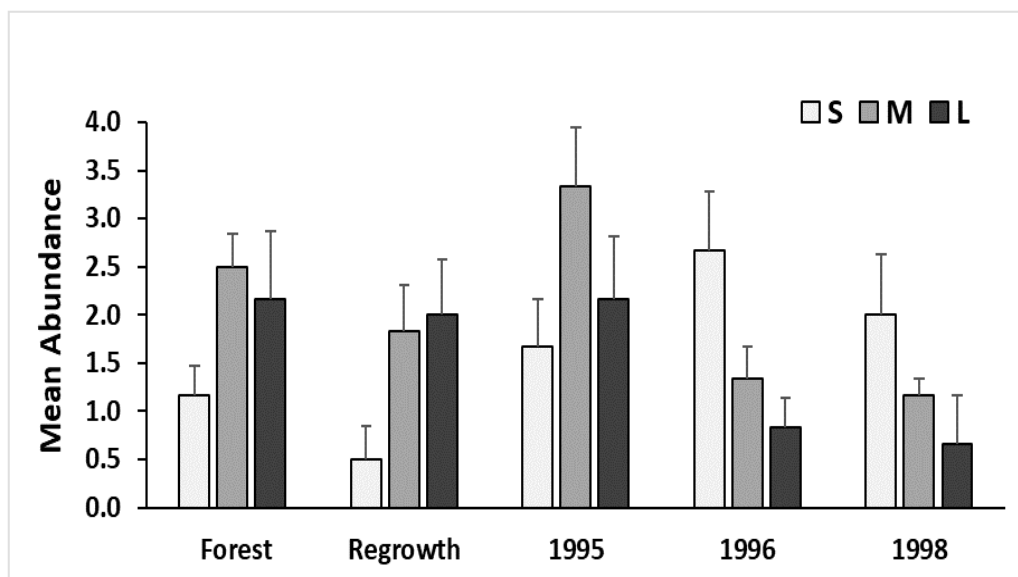


Figure 5. Mean abundance per count (n=6) + SE of seed-dispersers in gape width categories (S = small <10 mm; M = medium 10–15 mm; L = large >15 mm) recorded in Donaghy's Corridor planting (1995; 1996; 1998) and reference sites (Forest; Regrowth).

Twenty-five rainforest-dependent species, including five Wet Tropics endemics, were recorded in corridor sites. This represents a threefold increase in rainforest species richness compared to Jansen (2005), who recorded eight rainforest-dependent species, none of which are Wet Tropics endemics (Supplementary Table S1).

Mammals

Table 1 details ground mammals recorded by live-trapping in 2000 and remote camera in 2021. Present in base-line surveys and early establishment stages, the House Mouse (*Mus musculus*), Cane-field Rat (*Rattus sordidus*) and Grassland Melomys (*Melomys burtoni*) were not recorded. Tucker and Simmons (2009) demonstrated the replacement of Grassland Melomys by the Fawn-footed Melomys (*M. cervinipes*) within three years, almost certainly attributable to the shading out of grasses and weeds (*M. burtoni* habitat) and establishment of woody vegetation (*M. cervinipes* habitat). The loss of grasses and weeds in the corridor is also likely to be the main factor influencing the disappearance of Cane-field Rats and House Mice. Water Rats (*Hydromys chrysogaster*) were seen throughout the corridor in 2021 but were never captured between 1998 and 2000.

Musky Rat-kangaroo (*Hypsiprymnodon moschatus*) was recorded in the corridor but in 2000 the species was only trapped once in mature forest. A key disperser of large fruits (Dennis 2003), this is a regional endemic of mature forest and was detected in the 1995 and 1998 plantings (Fig. 1).

Two exotic species (Feral Cat, Feral Pig) were recorded, along with an Echidna photographed at the two ends of the corridor on consecutive nights in the 2021 autumn sampling. Pre-treatment use of the site by these species is unknown and they are excluded from Table 1.

Discussion

This study shows that after two decades, vegetation, bird and mammal communities colonising the restored corridor are becoming increasingly similar to the target reference ecosystem.

Vegetation studies indicate that corridor vegetation is structurally similar to reference forest but differs in terms of biomass and composition (Tng *et al.* 2023). Structural similarity is known to develop quickly in restored sites (Kanowski *et al.* 2003). Indeed, corridor vegetation is now multi-layered with plank buttresses, vines, lianas and epiphytes, and juvenile strangler figs on planted trees. Higher biomass in reference forest reflects

Table 1. The presence of terrestrial mammals in Donaghy's Corridor in 2000 (by live trapping) and 2021 (by camera trapping). VAC provides a ranking of rainforest dependency from 0 = non-dependent to 6 = highly forest-dependent. VAC: Wet Tropics Vertebrate Atlas Classification (Williams 2006).

Species	VAC	2000	2021
<i>Antechinus flavipes</i> Yellow-footed Antechinus	4	*	
<i>Hydromys chrysogaster</i> Water Rat	2		*
<i>Hypsiprymnodon moschatus</i> Musky Rat-kangaroo	6		*
<i>Isoodon macrourus</i> Brown Bandicoot	1	*	*
<i>Melomys burtoni</i> Grassland Melomys	0	*	
<i>Melomys cervinipes</i> Fawn-footed Melomys	4	*	*
<i>Mus musculus</i> House Mouse	0	*	
<i>Perameles pallescens</i> Long-nosed Bandicoot	5	* ¹	*
<i>Rattus fuscipes/R. leucopus</i> Bush Rat/Cape York Rat	4/5	*	*
<i>Rattus sordidus</i> Cane-field Rat	0	*	
<i>Uromys caudimaculatus</i> Giant White-tail Rat	5	*	*

¹ reported as *P. nasuta*

the larger number of mature canopy trees, and given that restored forest is likely to take centuries to attain the same diversity, it is unsurprising that composition is dissimilar.

Bird communities have become more rainforest-like since Jansen's 1996-1998 surveys (Jansen 2005). Now in their third decade, the 1995 and 1996 planting sites respectively share three-quarters and two thirds of the bird species recorded in the forest reference site, with comparable numbers of rainforest-dependent species. This contrasts with younger restoration sites in the region which, at around 10 years of age, have only about 50% of old growth rainforest-dependent bird species (Catterall *et al.* 2012).

Wet Tropics endemics tend to be poorly represented in replanted sites, probably due to species' restricted movement and edge-avoidance, and the quality of replanted habitat being insufficient to meet the needs of some specialists (Catterall *et al.* 2012). Five of the eight endemic species recorded in reference forest were also recorded in restored forest, which is somewhat encouraging considering the 'stalling' of avifaunal recovery observed in restoration sites during their second decade (Freeman *et al.* 2009, 2015).

The loss of rodents of grassland and/or disturbed habitats is the main change to the corridor's ground mammal fauna. Whilst most other ground mammals were already present by 2000, colonisation by Musky Rat-kangaroos parallels increases in structural complexity and resource provisioning, reflected in fruit availability and dispersal. Similarly, the previously unrecorded Water Rat suggests riparian restoration has created suitable terrestrial habitat and improved the quality of aquatic habitat. Whilst no reference forest surveys were undertaken, the corridor's ground mammal fauna is increasingly similar to the adjacent rainforest fauna recorded by Tucker and Simmons (2009).

Dispersal

Whilst some plant groups (e.g. figs) have multiple dispersers, we suggest frugivorous birds were the mobile links primarily responsible for internally and externally-sourced seeds. Numbers of species with medium sized fruits (10–30 mm) have increased, facilitated by birds with medium (10–15 mm) and large gape widths (>15 mm). They include Wompoo (*Ptilinopus magnificus*) and Superb (*Ptilinopus*

superbus) Fruit-doves, known to disperse a diverse range of species (Crome 1975), typically for short distances within forest, as well as wide-ranging species, e.g. Australasian Figbirds (*Sphecothebes viridis*) that are capable of landscape-scale dispersal (Dennis & Westcott 2006). We consider this wide-ranging, specialised disperser fauna is supporting the development of both structural and functional connectivity (Tischendorf & Fahrig 2000).

However, the frugivorous bird community at DC cannot be responsible for the dispersal of the largest-fruited rainforest trees.

Figure 1 indicates the location and extent of pre-existing vegetation and, as noted, the identity of all this vegetation was determined prior to planting to better understand the source(s) of colonising vegetation. During plot surveys, seedlings of three large-fruited species were recorded. Additional 1 ha surveys (i.e. 100 m around each seedling) were subsequently undertaken to locate potential parent trees, none of which were in the original planting, although two were pre-existing.

Black Walnut (*Endiandra insignis*) (50–90 x 50–100 mm, weight 125–240 grams) seedlings were recorded in four 1995 plots, representing dispersal distances of 39, 64, 97 and 112 m from the only mature plant located in the 100 m surrounds survey (Fig. 1). Seedlings of black walnut were also recorded in two plots in the 1996 planting where an unknown parent tree is >100 m from the germination point(s) (Fig. 1).

A single seedling of Cassowary Plum (*Cerbera inflata*; Apocynaceae) (60–70 x 20–35 mm) was recorded in the 1996 planting. No potential parent was located in the surrounding 100 m survey; the closest individual known is a paddock tree (located within the 100 m buffer) situated 411 m from the juvenile plant (Fig. 1). The potential disperser of this fruit is unknown.

Five seedlings of Yellow Walnut (*Beilschmiedia bancroftii*) (65–75 x 50–60 mm, weight 30–90 gms), a species neither planted nor pre-existing, were recorded in the 1997 planting. No potential parent could be found in the 100 m surrounds survey. Dispersal distances of 100, 127, 131 and 143 m from the nearest potential seed source are therefore likely (Fig. 1), exceeding the 50 m distances reported by Theimer (2003). It is possible that these juveniles and the closest identified potential parents are not related – the actual

parent trees may be more distant (Hardesty 2006), but cannot be closer.

Dispersal of these large-seeded species into DC is evidence of ground mammals acting as dispersal vectors both within and beyond the corridor. Two endemic species, the Giant White-tail Rat (*Uromys caudimaculatus*) and Musky Rat-kangaroo are the only rainforest mammals capable of moving these fruits an effective dispersal distance (Theimer 2001; Dennis 2003). Yellow Walnut was neither pre-existing nor within the corridor buffer, but is a known diet item of Giant White-tail Rats, the most likely disperser (Theimer 2003). Their habit of scatter-hoarding Yellow and Black Walnut, and other large-fruited Lauraceae seedlings recorded during survey, e.g. Coach Walnut (*Beilschmiedia tooram*) (pre-existing) and Sankey's Walnut (*Endiandra sankeyana*) (planted), is probably undervalued. In fragments where long-lived, large-fruited tree species remain, but neither Musky Rat-kangaroos nor Cassowaries (*Casuaris casuaris johnsoni*) (the only bird capable of dispersing many large fruits) persist, Giant White-tail Rats are almost certainly legitimate dispersers. Germination of Yellow Walnut and Cassowary Plum seedlings also emphasises the influence and value of the surrounding matrix vegetation on the recruitment of new species (Zahawi *et al.* 2021).

Summary

In concluding, we acknowledge that the use of a single restored corridor with unique biophysical features limits firm conclusions about the ability of such projects to ameliorate fragmentation and/or climate change effects. However, two decades of corridor development does provide some insights.

Firstly, the restored corridor contains structurally complex vegetation but lacks the biomass and plant species diversity of reference forest (Tng *et al.* 2023); these deficiencies appear to selectively affect intact forest specialists, in particular some endemic rainforest birds. Terrestrial mammals appear less constrained. This suggests structural and functional connectivity has been achieved for a subset of the groups studied, and the composition of these groups includes species essential for ongoing ecological interactions.

Secondly, patterns reflect features that are keys to successful rainforest restoration: (i) the proximity of mature reference forest as a source of colonising plants, birds and animals, and (ii) the

presence of specialised vertebrate dispersers to disperse rainforest seeds.

Thirdly, within two decades, restored habitat is supporting wildlife that includes threatened and edge-avoiding plants, birds and animals which must have entered the corridor from the forests with which it is now continuous. In this sense, the corridor is fulfilling the dual roles of providing both connectivity and habitat *per se*.

Acknowledgements

The authors thank an anonymous reviewer for valuable comments on this paper. We thank the Donaghy family for continued access to the site and acknowledge the Dulgubbara Yidinji as Traditional Owners of the Lake Barrine area. Damon Colman assisted with data collection and prepared the accompanying map.

Supplementary file

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

- Table S1: Bird species richness, habitat, and disperser characteristics.

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