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RESEARCH ARTICLE

Soil seed banks in three restored wildlife corridors; implications for linear habitats in tropical environments

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Restoring habitat corridors between fragments and continuous forests can potentially counter the effects of isolation, especially in tropical forests where species sensitivity to fragmentation is high. The ability of restored linear habitats to absorb natural disturbance in inimical surroundings potentially reflects resilience, an important aim of ecological restoration practice. Soil seed banks (SSBs) are reservoirs of plant life that can respond to disturbance and contribute to site recovery and resilience. Using seedling emergence, we compared SSB floristics in three restored wildlife corridors aged 10–26 years and their adjoining reference forest and adjacent pastures in tropical northern Australia. A total of 1427 seedlings from 69 species and 27 families were counted and identified from 131 samples. SSBs in restored corridors, while containing higher numbers of exotic species, were more similar in composition to reference forests than pastures, which are dominated by exotic species. Small, vertebrate-dispersed seeds of gap trees dominated reference forest SSBs and were also conspicuous in corridors. Exotic herbs and grasses occurred in all corridors, were most abundant in pastures, but rarely emerged in forest samples. Both distance from forest (z-value $= -2.641$, $p < 0.01$) and year of planting (z-value $= -4.213$, $p < 0.001$) had significant effects on the proportion of native species. Almost all of the exotic species recorded in corridors are benign. Few have a demonstrated ability to block or arrest native species regeneration, suggesting SSBs in linear restored habitats can make a significant contribution to resilience and recovery.

Key words: resilience, restored wildlife corridors, soil seed banks, weed invasion

Implications for Practice

- Soil seed banks (SSB) are a viable means to assess the development of resilience and recovery potential in linear restored areas.
- Gap species and *Ficus* spp. are common SSB components in restored and reference sites indicating their attractiveness to frugivorous dispersers.
- Dispersal is critical to natural regeneration and the development of connectivity in restored tropical environments.

Introduction

Forest fragmentation is a global issue with myriad negative effects (Haddad et al. 2015) including disruption to ecological connectivity, an essential element of landscape function (Taylor et al. 1993) and an important contributor to ecosystem resilience (Standish et al. 2014). Restoring habitat connectivity between fragments and larger intact areas can potentially alleviate negative fragmentation effects, enhancing the movement of pollen, seeds, and genetic material (Paetkau et al. 2009; Rivera-Ortíz et al. 2014; Tucker et al. 2024) and allowing range shifts in response to climate change (Heller & Zavaleta 2009; Senior et al. 2019). By implication, restoring connectivity may also contribute to ecosystem resilience.

Restoration practitioners should aim to restore resilience in the systems we reestablish and manage (Lake 2012). Soil seed banks (SSBs), the viable seeds present in forest soil and litter, represent reservoirs of potential life and ecological resilience within restored ecosystems (Mall & Singh 2014), being indicative of a component of the future plant community after disturbance occurs (Auffret & Cousins 2011). SSBs can be used to assess a restored area's inherent recovery capacity prior to initiating restoration actions (Gioria & Pyšek 2015; Florentine et al. 2023), to measure recovery in forests under active and passive pathways (Paul et al. 2012), and as an indicator of a restored area's accumulation of biological memory and recovery capacity over time (Ma et al. 2019, 2021); the ability of a restored area to absorb natural disturbance is an important indicator of restoration success.

In the tropical uplands of northeastern Queensland, historical fragmentation has resulted in the isolation of many patches of

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mature forest, embedded in a matrix of human settlement and extensive areas of cropping and grazing (Winter et al. 1987) dominated by exotic vegetation. With a demonstrated susceptibility to habitat isolation, faunal communities in local rainforest fragments are increasingly depauperate (Laurance 1997), lacking cassowaries (*Casuarius casuarius johnsoni*) and other endemic species responsible for specialist seed dispersal.

These fragments are often Protected Areas or Reserves, but intervening lands are all in private tenure. If connectivity is to be restored, landholder co-operation is required to provide the land for restoration and agree to its permanent protection. Locally, high land values and intensive land use preclude restoration of the consistent extent of land (i.e. width proportional to length) theoretically required to provide the core interior habitat required by rainforest species, Laurance and Laurance (1999) suggesting corridor widths up to 200 m may be required for some arboreal mammals. Are the narrow linear habitats that result from corridor restoration, especially those increasingly distant from native seed sources, more prone to weed invasion (White et al. 2004) because of their high edge-area ratio, and following disturbance, are the weed species present in SSBs likely to deflect or arrest natural recovery processes? In this paper, we examine SSB floristics in three restored wildlife corridors and ask three questions: (1) what is the SSB composition in corridors 10–26 years of age, (2) are there differences between SSBs in pastures, corridors, and reference forest(s), and (3) to what extent do age and proximity to forest affect SSB composition? From this analysis, we examine similarities and differences and extrapolate the role that SSBs in these restored linear habitats may have on their post-disturbance resilience and recovery capacity.

Methods

Site Descriptions

The three corridors in this study are located on the southern Atherton Tablelands of tropical north Queensland, Australia. They were designed to restore habitat connectivity between three fragments—Lake Eacham, Lake Barrine (both around 500 ha and collectively forming Crater Lakes National Park) and Curtain Fig National Park (300 ha)—inter-linking these fragments to Gadgarra National Park, part of a continuous 80,000 ha forest block (Wooroonooran National Park) (Fig. 1). Forests within both Crater Lakes and Gadgarra are classified as Complex Mesophyll Vine Forest (Tracey 1982), occurring on basalt soils. Average annual rainfall is 1428 mm at Barrine (Tracey 1982). Curtain Fig N.P., while only 9 km distant, is marginally drier, resulting in elevated levels of deciduousness and reduced leaf size; forest classification is Complex Notophyll Vine Forest (Tracey 1982), also on basalt. Average temperatures vary from 15.5 to 25.0°C (Kairi Research Station, Tracey 1982). Each fragment is embedded in an anthropogenic landscape, largely surrounded by beef and dairy pastures, and all have been isolated since the 1940s.

Beginning in the mid-1990s restoration projects commenced to establish inter-connecting habitat between these fragments and the larger block, and there are features common to each corridor. Restored corridors were dominated by active cropping or grazing immediately prior to restoration, but permanent stock exclusion fencing was erected immediately after planting. All contained existing individual trees, patches of regrowth, and/or remnant forest to varying degrees (see Fig. 1). Plantings comprised mixtures of local pioneer and mature forest species; sites were prepared, planted, and maintained using techniques described in Goosem and Tucker (2013), and records were kept of planting locations and timing.

There are also differences. Apart from the obvious variation in corridor lengths, width is inconsistent, varying from a relatively constant 80 m at Donaghy's Corridor, from 60 to 350 m at Lakes Corridor, and between 25 and 350 m at Petersen Creek Corridor. As noted, floristics vary at the two ends of the Petersen Creek Corridor, and 400 m of the Lake Eacham end of the Petersen Creek Corridor was not completed until 2014 (due to landholder issues), despite the remainder of the corridor being in place for over 5 years. Donaghy's Corridor and the Petersen Creek Corridor are riparian in nature; Lakes Corridor bisects rather than follows a watercourse, and around one-third of that corridor (400 m) is comprised entirely of autogenic regrowth, albeit of the same age as plantings, with land abandonment occurring around the same time as the planting of the remaining 1 km. Table 1 summarizes key features of the three corridors.

Sampling

In the Wet Tropics of north Queensland, seasonal humid conditions are optimal in terms of both seed production and germination; for this reason, this seedling emergence study was completed during the three summer months of 2022–2023. In November 2022, 131 SSB samples were collected at 14 sites using hollow sections of polyvinyl chloride (PVC) pipe 100 mm wide and 50 mm deep (0.00039 m^3). Surface leaf litter was removed, and PVC cores were tapped into the ground to the depth of the pipe, gently levered out using a screwdriver, and wrapped firmly in sealed plastic bags. Cores were pre-labeled with permanent marker indicating the sampling point of each core and were collected every 100 m inside each corridor, 20 m from the corridor edge. Pasture samples were taken equidistant along the corridors, also at 20 m from the edge of the planting. Inside reference forests, samples were collected at 20 and 50 m from the edge to determine whether increased distance from the forest edge affected SSB composition, in both cases taking five samples 10 m apart along 50 m transects.

The day after collection, each soil core was removed from its plastic cover, retaining all the soil within the core, and then placed directly onto trays with 25 mm of sterile potting mix at the base of each tray to ensure soil and moisture retention in the cores. Trays were placed in a sealed germination room at the Qld Parks and Wildlife Service's Restoration Services Nursery and watered twice daily. Germinating seedlings were identified, counted, and removed at 30, 60, and 90 days; surface soil was lightly tilled after each census to encourage further germination. Any unidentified seedlings were potted on for later identification.

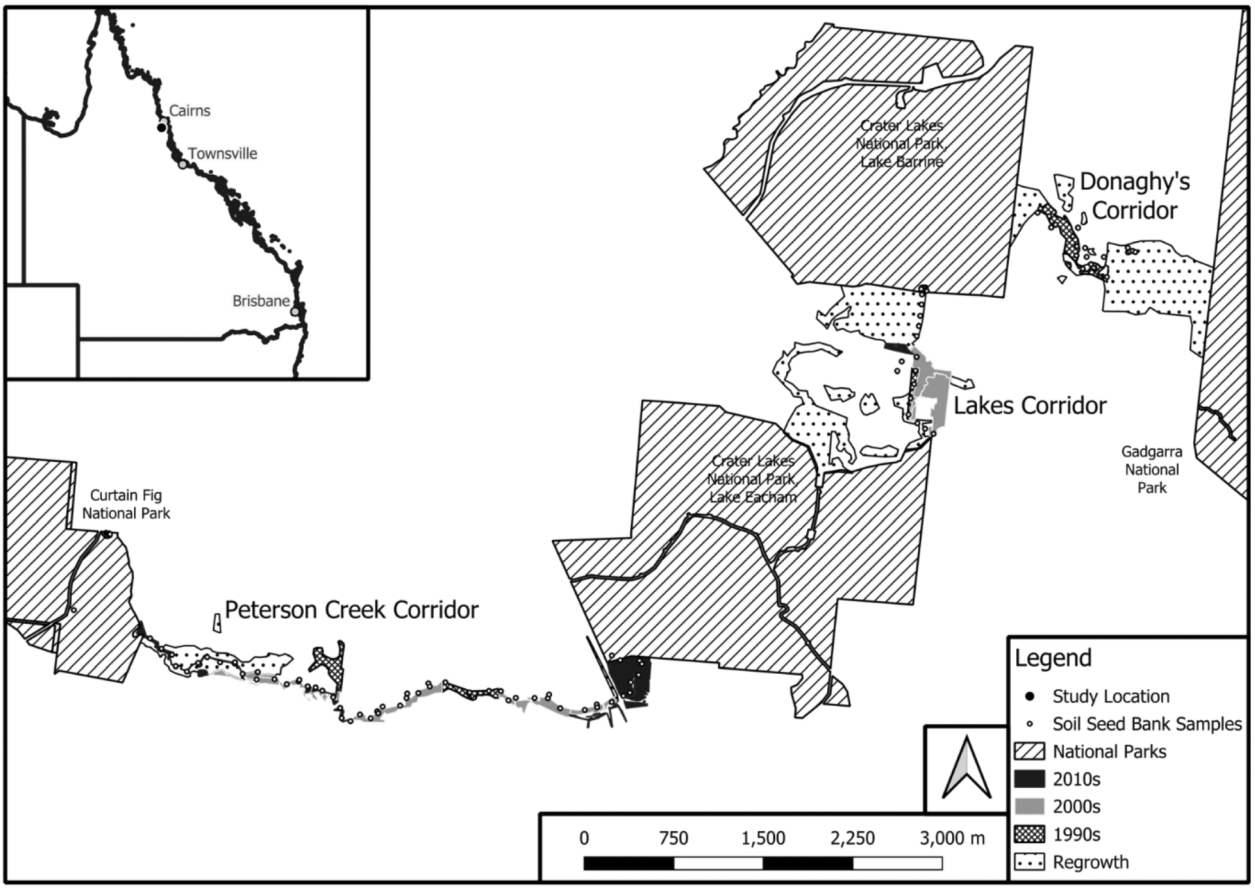

Figure 1. Study location showing existing vegetation, planting extents, and soil seed bank sampling points.

Table 1. Key features of each corridor showing the length, date of planting and the numbers of trees/species planted.

Corridor	*Joins*	*Length*	*Date of planting*	*Number of trees planted*	*Number of species planted*
Donaghy's	Gadgarra N.P to Lake Barrine	1.2 km	1995–1998	16,800	101
Lakes	Lake Barrine to Lake Eacham	1.4 km	1997–2005	17,000	n/a
Peterson Creek	Lake Eacham to Curtain Fig N.P	4.4 km	1998–2014	105,000	211

Data Analysis

Germinated seedlings were classified as woody or non-woody, native or exotic, and by life form, either a canopy tree, gap tree, shrub, vine, sedge, herb (dicots), or grass (a non-sedge monocot). Canopy trees are late successional species restricted to mature forest, while gap trees are pioneer species of abandoned pasture, regrowth, or large tree-fall gaps. We compared the percentage of native and exotic individuals from each life form among the three land uses (corridor, pasture, or reference forest) using a chi-squared test. The dispersal vector of each species was determined as either by vertebrate, wind, water, or combinations thereof; some species have multiple dispersers. Dispersal vector classifications were derived from Tucker and Murphy (1997), Tucker et al. (2024) and Cooper and Cooper (2004), and on-line resources at https://keys.lucidcentral.org. To calculate the differences between vectors across sites, vectors for each species were summed for each site (reference forest 20 m/50 m, corridor, and pasture) and directly compared.

To test for the effect of land use on (1) the number of species and (2) the Shannon biodiversity index separately, we conducted two generalized linear mixed models (GLMMs). Species origin (native or exotic) and land use were used as explanatory variables. To account for possible differences among the 14 study sites (Peterson Creek, Lakes, and Donaghy's Corridors, pasture and forest), we added site as a random effect. Additionally, the proportion of individual seedlings from native species found in soil cores from corridor, reference forest, and pasture was compared using a GLMM. The proportion of seeds from native species was used as the response variable and land

use as the explanatory variable, while site was added as the random effect.

We tested the similarity of species composition calculating the Sørensen index *R* (Sorensen, 1948) comparing corridor × forest, corridor × pasture, and forest × pasture. We then conducted a Bray–Curtis ordination analysis, testing for dissimilarity in species composition among pasture, corridor, and forest and using the packages "vegan" (Oksanen et al. 2024) and "ape" (Paradis & Schliep 2019) in R (R Core Team 2022).

We additionally tested the effect of "year of planting" and "distance from forest" on (1) the proportion of individuals of native species, and (2) proportion of individuals from late successional species. We tested using a GLMM (beta distribution family) with site added as the random effect in all models. All GLMMs were conducted using the package "glmmTMB" (Brooks et al. 2017) and residuals analyzed using "DHARMa" (Hartig 2022) in R (R Core Team 2022).

Lastly, the two sections of Lakes Corridor were analyzed to compare autogenic regrowth against manual planting. To do this, we tested for differences between Transect "A" (0–400 m from the Lake Barrine end), representing natural regrowth, and Transect "B" (500–1400 m to the Eacham end), representing sites that were manually planted. We used a Kruskal–Wallis test, as the data did not present a normal distribution after analysis with the Shapiro–Wilk test, with the number of individual seedlings by plant origin as the response variable, and corridor origin (LC0-400 or LC500-1400), plant origin (native or exotic), and the interaction of corridor and plant origin as the explanatory variables.

Results

Floristics

A total of 1427 seedlings were identified and counted, representing 32 native and 37 exotic species from 27 families, 34 species being woody and 35 non-woody (Table 2). Comparing reference forest sites, continuous forest at Gadgarra N.P. had the lowest species diversity (native and exotic), but the highest number of individuals. Exotic species diversity in fragments was higher than in the continuous forest, but greater in corridors, particularly Petersen Creek Corridor where exotic seedling numbers were highest, reaching greater than 50% of total diversity. Pasture sites had the lowest complement of native species (Table 2).

Three native species were prominent. Red-leaf fig (*Ficus congesta*: Moraceae) (nine sites, 54 individuals) occurred in all corridor and 20 m/50 m reference forest samples, though none germinated in any pasture samples. Native sarsaparilla (*Alphitonia petriei*: Rhamnaceae) (seven sites, 63 individuals) occurred in all corridors, in two pasture samples, and in all 20 and 50 m reference forest samples except Curtain Fig N.P, where it was replaced by the closely related Pink ash (*A. whitei*). Brown salwood (*Acacia celsa*: Fabaceae) (seven sites, 19 individuals) occurred in the same range of corridor and reference forest sites, but was also absent at Curtain Fig N.P. With 78 individuals from seven species, Moraceae was the most common native family, recorded in all corridor and reference forests but never in pastures.

The dicot herb Blue-top (*Ageratum conyzoides*: Asteraceae) (five sites, 277 individuals), and South African pigeon grass (*Setaria sphacelata*: Poaceae) (five sites, 273 individuals) accounted for 38.5% of total germination, occurring in all corridors and pasture sites, but absent from reference forest sites except Curtain Fig N.P (20 m, three individuals of Blue-top). Sedges (*Cyperus* spp.: Cyperaceae) were the most common exotic genus with 112 individuals across four species, in addition to the native sedge *Rhynchospora corymbosa*. Asteraceae and Poaceae were the most common exotic families (eight species from each).

There were no consistent differences in the composition, abundance, or diversity of native and exotic species at sites 20 or 50 m from the edge of reference forests. Native species were more common than exotics at both distances (Table 2).

Life Forms

Dicotyledonous herbs (19 species) were most prominent, followed by gap trees and shrubs (both 13 species), canopy trees and grasses (both eight species), sedges (five species), and vines (three species).

Most SSB canopy trees were strangler figs (*Ficus* spp.); only one of the eight canopy species recorded, the Mulberry-leaf stinger (*Dendrocnide photinophylla*: Urticaceae, Barrine 50 m), was not a fig. Strangler figs are a conspicuous canopy emergent in reference forests and were recorded in some SSB reference sites, and in the Donaghy's and Petersen Creek Corridors.

Similar to other tropical seed bank studies, herbs were a common life form (Weerasinghe et al. 2018; Benitez-Malvido 2023). In this study, only two are native (*Alpinia caerulea*: Zingiberaceae Donaghy's Corridor; *Commelina ensifolia*: Commelinaceae, Petersen Creek Corridor). Most SSB herbs are ephemeral annuals of small stature, mainly Blue-top and other Asteraceae. Of the 13 shrubs, 6 are native and 7 are exotic. Giant bramble (*Rubus alceifolius*: Rosaceae, Gadgarra 50 m) is the only shrub recorded that is locally invasive and capable of arresting natural regeneration.

SSB grasses were dominated by exotics; only one native grass was recorded (*Oplismenus aemulus*: Poaceae) in all corridors and Curtain Fig. Of the exotic grasses recorded, Guinea grass (*Megathyrsus maximus* var. *maximum*: Poaceae, one sample in Petersen Creek Corridor) is locally invasive and capable of arresting natural regeneration (Rhodes et al. 2021). Adjacent to these corridors, South African pigeon grass and Signal grass (*Urochloa decumbens*: Poaceae) are the dominant pasture grasses, but both species are lower growing, shade intolerant, and, compared to Guinea grass, are less invasive and probably less favored by seed dispersing birds.

Vines were the least common SSB life form and the three species recorded are all exotic. Two are common pasture legumes, often seen on forest margins but are intolerant of shade and not considered invasive. Brazilian nightshade (*Solanum seaforthianum*: Solanaceae) was only recorded in the Petersen Creek Corridor, and is locally conspicuous in restored areas and the

Table 2. The number of samples, species, and individuals recorded at each of the 14 SSB sampling sites along with their status as native or exoti.

Site	*# Samples*	*# Species*	*# Individuals*	*# Native*	*# Exotic*
Gadgarra 20 m	5	6	22	5	1
Gadgarra 50 m	5	4	35	3	1
Barrine 20 m	5	6	17	3	3
Barrine 50 m	5	9	11	6	3
Eacham 20 m	5	7	10	5	2
Eacham 50 m	5	10	14	5	5
Curtain Fig 20 m	5	10	27	5	5
Curtain Fig 50 m	5	10	22	7	3
Donaghy's Corridor	9	16	75	9	7
Lakes Corridor	14	26	115	13	13
Petersen Creek Corridor	44	49	611	17	32
Donaghy's Pasture	6	3	77	0	3
Lakes Pasture	6	13	167	3	10
Petersen Creek Pasture	12	20	224	4	16

disturbed margins of fragments. Figure 2 summarizes life form diversity. The composition of life form diversity in each site was significantly different from one another, as per chi-squared test.

Dispersal

Vertebrate dispersal was the main vector across all site types, and more dominant in 50 m forest sites where other vectors were uncommon. Wind, water, and "all vectors" were more likely in corridors and pastures (Table 3).

Land Use Effects on Species Diversity

Analysis confirms exotic species were more common in corridor and pasture SSBs than forest SSBs (Fig. 3A). Plant origin, land use, and the interaction between plant origin and land use were significant in both models (Table 5). Post hoc tests showed that, within pastures and corridors, the number of exotic species was higher than that of native species, but lower in forest (Fig. 3A). Shannon's diversity index was greater for exotic species in both pastures and corridors, but less in forest (Fig. 3B). Pasture had the lowest Shannon's index values, significantly different from forest (Fig. 3B).

The proportion of native species was highest in forest, followed by corridor and pasture. Corridor and forest were not significantly different from each other, but both were significantly different from pasture (Fig. 4). However, the proportion of native species was lower in corridors than in continuous forest.

Both distance from forest (z-value $= -2.641$, $p < 0.01$) and year of planting (z-value $= -4.213$, $p < 0.0001$) had significant effects on the proportion of individuals of native species (GLMM with beta distribution, Efron $r^2 = 0.77$). The relationships were negative for both dependent variables (marginal effects are presented in Fig. 5), with proportion of native species decreasing from 0.7 in 1995 to 0.1 in 2014 (Fig. 5A), and decreasing from circa 0.6 to circa 0.2 from 0 to 20 m from forest (Fig. 5B).

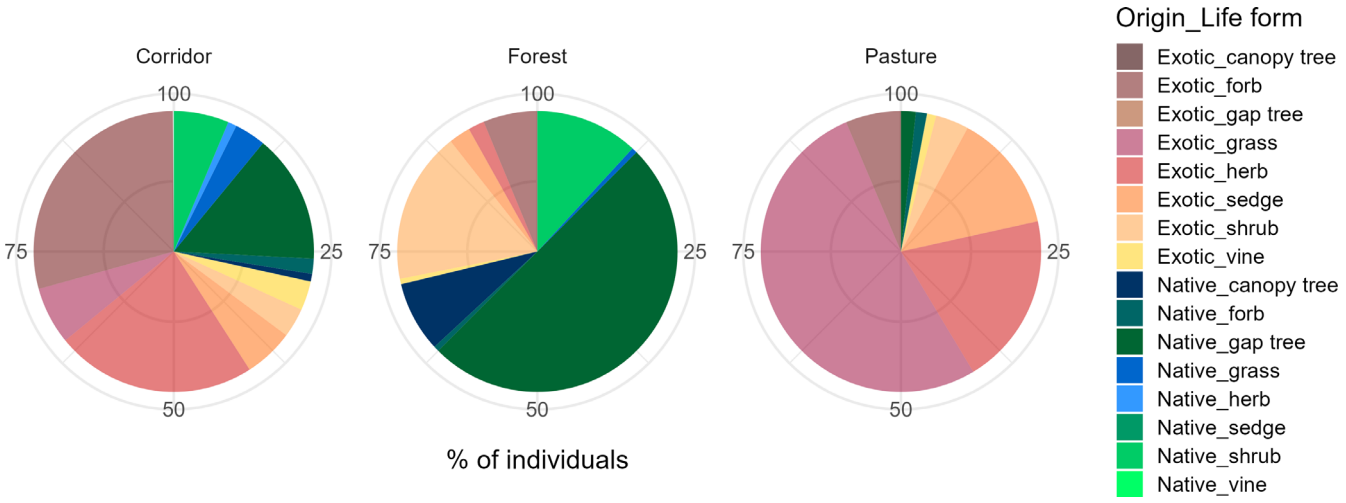

Figure 2. The abundance of native and exotic life forms germinated from SSBs in corridors, reference forest, and pasture. Corridor, pasture, and forest all differ from each other as per chi-squared test.

Table 3. Dispersal vectors of germinated SSB species recorded in the four site types.

Site type	*Vertebrate*	*Wind*	*Water*	*Wind/water*	*Vertebrate/water*	*All vectors*
Reference forests (50 m)	31	2	0	0	1	0
Reference forests (20 m)	19	4	0	2	4	0
Corridors	44	12	2	23	5	7
Pastures	21	4	1	9	1	7

Land use, plant origin, and the interaction between land use and plant origin had a significant effect on the number of individuals and the number of species (Table 4). Biodiversity was also significantly influenced by plant origin, land use, and the interaction between land use and plant origin (Table 4).

The Sørensen index between each pair of land uses characterizes variation in β-diversity between corridor and forest, corridor and pasture, and pasture and forest. The most similar pair was corridor and forest, with a Sørensen index of 0.53, followed by corridor and pasture, with a Sørensen index of 0.50. The most dissimilar pair was forest and pasture, with a Sørensen index of 0.30. The high similarity between corridor and forest is supported by the Bray–Curtis ordination seen in Figure 6, which shows high similarity between corridor and forest, both differing from pasture.

Regrowth SSBs

Finally, we found evidence for differences between autogenic regrowth and manual planting in the Lakes Corridor data. Autogenic regrowth was significantly different from planted areas, as shown in the Kruskal–Wallis test (Table 5) with significant differences in seedling abundance of plant origin within the two sections of the corridor (Table 5). Transect "A" (regrowth) had higher numbers of woody and non-woody exotic individuals (across eight species with only two natives), while Transect "B" (planted) recorded nine woody and non-woody native individuals and six exotic individuals (Tables 5 & S1).

Discussion

This study shows SSBs in restored corridors, while containing higher numbers of exotic species, are more similar in composition to reference forests than pastures, which are dominated by exotic species. This finding broadly suggests there may be some similarity in SSB disturbance responses in corridors and reference forests. In this respect, the SSB contribution to forest recovery and resilience may also be similar in the two site types.

Collections captured the wide variations in corridor width. Although the effect of corridor width was not tested, SSB abundance and diversity were lowest around the mid-section of the Petersen Creek Corridor, where it is bisected by a single-lane road, corridor width is at its narrowest point (25 m), and the distance to fragments is greatest. Proximity to fragments and the age of plantings both affect SSB development. Increasing distance lowers both abundance and diversity, and the youngest sites (Petersen Creek Corridor 2014) had reduced diversity and abundance, despite adjoining the Lake Eacham fragment. Donaghy's Corridor is the shortest and longest established and the only corridor where native species diversity was higher than exotics.

Floristics

Persistent seeds (Thompson & Grime 1979) of native gap trees are a conspicuous component of SSBs in planted corridors and reference forests. With likely life spans of 20+ years, the small (3 mm diameter) vertebrate-dispersed native sarsaparilla and brown salwood, both producing abundant, annual seed crops, were present in most corridor and reference forest SSBs. Hopkins et al. (1990) recorded similar abundances of small seeded gap trees in the SSBs of local fragments, including the Curtain Fig N.P remnant used in this study. These gap trees respond rapidly to moderate–major disturbances and are conspicuous elements of local regrowth, but are rare in local reference forest (Tng et al. 2023). While neither species was recorded in Curtain Fig N.P, Pink ash and other pioneers in SSBs at that site indicate disturbance would likely elicit comparable germination responses. An individual of Candle-nut (*Aleurites rockinghamensis*: Euphorbiaceae, 20 mm seed diameter—Eacham 50 m) was the only large seed that emerged.

Seed Dispersal

Results show that seed movement into pasture from corridors and adjacent forests is occurring at low rates, consistent with other tropical studies (Holl 1999; Cubiña & Aide 2001; Charles et al. 2016). In this study, of the limited numbers present in pasture SSBs, all native trees are vertebrate (bird) dispersed, suggesting that bird movements outside restored habitats occur, but at low frequency; incorporation of native shrubs and wind dispersed seeds into the soil of active pasture is also infrequent. However, within corridors, it is likely that restored vegetation has stimulated vertebrate colonization and dispersal, and the availability of resources in the developing plantings, reference forest, and elsewhere has contributed to SSB development. In a study at Donaghy's Corridor, Tucker et al. (2024) recorded 40 bird species within the corridor, including large- and small-gaped frugivores, in addition to ground mammals undertaking dispersal of larger fruits and seeds.

Disturbance Impacts

Within corridors and reference forest, SSBs occur in conjunction with established trees, saplings, and seedlings. Only

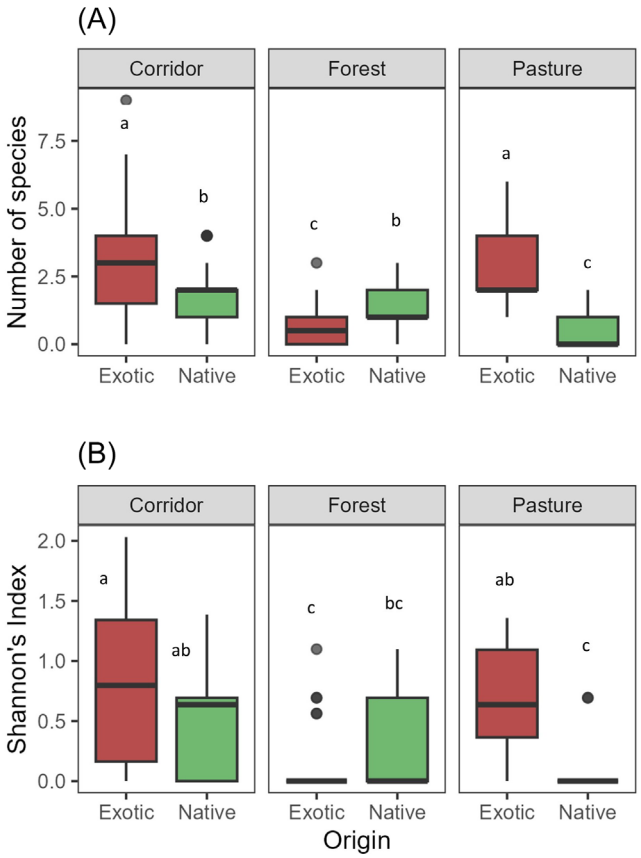

Figure 3. Boxplots of (A) number of species that grouped as exotic and native, and (B) Shannon's biodiversity index within exotic and species origin, found in each sampled core. Letters indicate significant differences as per GLMM results.

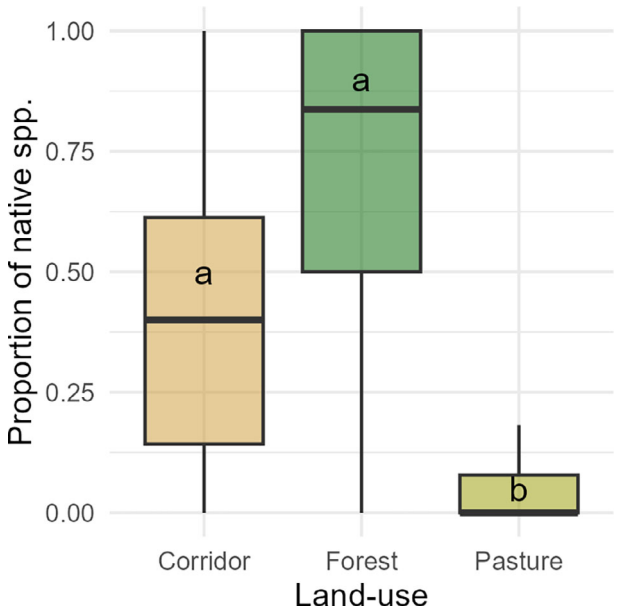

Figure 4. Proportion of individuals from native species found in cores from corridor, forest, and pasture. Letters indicate significant difference as per GLMM at α less than 0.05.

massive disturbances (e.g. landslides) are likely to remove both above- and belowground components. Natural disturbances, ranging from cyclones to tree-fall gaps, are more likely to leave seedlings and re-sprouting stumps that contribute to natural recovery in restored and natural forests (Kanowski et al. 2008). In corridors and reference forests, existing aboveground vegetation, coupled with SSBs comprising woody pioneers and relatively benign exotics, hint that recovery pathways may be similar in both systems.

This response is unlikely to be uniform. Where corridor width is narrow and/or bisected by a road or powerline, disturbance resulting in the loss of canopy cover will tend to favor in situ exotic species, especially vines. Germination of competitive exotic vines from the SSB is likely to inhibit native species germination and reduce habitat value (Bernich et al. 2024). In such cases, natural recovery may only be facilitated by direct intervention (e.g. César et al. 2016) to release residual vegetation and the SSB from weed competition. In addition to exotic vines, Guinea grass and Giant bramble are locally capable of arresting or delaying natural recovery and establishing elsewhere post-disturbance. Linear environments may be more susceptible to invasion by such species; however, their low abundance in this study suggests the effect of in situ SSBs may be minor. The degree to which disturbed linear habitats can withstand invasion from ex situ exotics is unknown.

Regrowth SSBs

The autogenic regrowth comprising around 30% of Lakes Corridor indicates natural regeneration has been a viable restoration approach, almost certainly because at this site, (1) active grazing had ceased, (2) there was protection from any ongoing disturbance, and (3) forest seeds and their vertebrate dispersers were directly adjacent. However, SSBs in regrowth had higher exotic species diversity and lower native species diversity compared to planted sections, and *Ficus* was notably absent. Slower recovery of the autogenic SSB is consistent with other local comparisons of regrowth and restoration. Shoo et al. (2015) reported lower values for wood volume and species richness in regrowth compared to restoration plantings of similar age. Longer-term studies will be required to determine the time required for regrowth SSBs to attain similar values to restored and reference forests.

While the future survival of germinated seedlings may nevertheless be affected by edge (Benítez-Malvido et al. 2023), predation by mammals (Molofsky & Fisher 1993), insects (Kulikowski et al. 2022) or abiotic effects, this study reveals established SSBs in these linear restoration sites. Based on composition and diversity, their capacity to stimulate recovery is potentially similar to adjacent reference forests, and they differ significantly from pasture SSBs which contain few native species. Moreover, the exotic component of corridor SSBs consists mostly of benign species with little capacity to out-compete

Figure 5. Marginal effects of year of planting, and distance to forest (m), on the proportion of individuals of native species in corridor SSBs.

Table 4. Effects of origin (native/exotic) and land use (corridor/pasture/forest) on the number of species and biodiversity index. Results are from GLMMs with Site added as a random effect. *df*, degrees of freedom.

	Variable	χ^2	df	*Pr*(>χ^2)
Number of species	Origin	18.009	1	<0.0001
	Land use	13.402	2	<0.0001
	Origin:Land use	47.919	2	<0.0001
Shannon's index	Origin	14.635	1	<0.0001
	Land use	22.015	2	<0.0001
	Origin:Land use	33.409	2	<0.0001

Table 5. Results of Kruskal–Wallis test comparing corridor A (LC100-400) with corridor B (LC500-1400) on the number of individuals in each plant origin (native woody, native non-woody, exotic woody, and exotic non-woody), and the interaction between corridor and plant origin. Values are means ± SEM (). [a,b]Means in a row without a common superscript letter differ ($p < 0.05$) as analyzed by Dunn's test.

	LC 0-400			
Variable	*Exotic Non-woody* (n = *5*)	*Exotic Woody* (n = *5*)	*Native Non-woody* (n = *5*)	*Native Woody* (n = *5*)
Nind	8 ± 2.51^{a}	0.4 ± 0.245^{ab}	0 ± 0^{b}	2.8 ± 0.735^{a}
	LC 500-1400			
Variable	*Exotic Non-woody* (n = *9*)	*Exotic Woody* (n = *9*)	*Native Non-woody* (n = *9*)	*Native Woody* (n = *9*)
Nind	0.222 ± 0.222^{b}	0.111 ± 0.111^{b}	0.889 ± 0.889^{b}	1.56 ± 0.818^{ab}

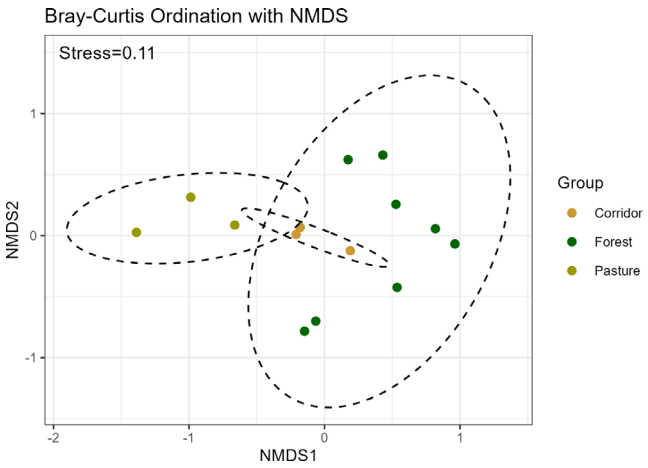

Figure 6. Non-metric Multidimensional Scaling ordination plot of the Bray–Curtis dissimilarity matrix in relation to species abundance in corridors, reference forest, and pasture (stress = 0.11, 95% confidence limit).

woody native species after natural disturbance events. Post-disturbance studies of restored corridor habitats would be valuable in determining SSB responses, and linear habitat resilience and recovery.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. The number of species and individuals germinated from soil cores at each of the 14 sites, and the life form type of each species.

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