Title: Recovery of mammal diversity in tropical forests: a functional approach to measuring restoration

Running head: Recovering mammal diversity in restored forests

Mia A. Derhé 1,2, Helen T. Murphy2, Noel D. Preece3,4,5, Michael J. Lawes5, Rosa Menéndez

1 Lancaster Environment Centre, Lancaster University, Bailrigg, Lancaster, LA1 4YQ, UK.
2 CSIRO, Tropical Forest Research Centre, PO Box 780, Atherton, Qld 4883, Australia
3 Centre for Tropical Environmental & Sustainability Science, College of Marine & Environmental Sciences, James Cook University, Queensland 4811, Australia
4 Biome5 Pty Ltd., PO Box 1200, Atherton, Queensland 4883, Australia
5 Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northern Territory 0909, Australia

Corresponding author: Mia A. Derhé
Present address: Karisoke Research Centre, The Dian Fossey Gorilla Fund International, NR 4 RD 58, B.P. 105 Ruhengeri/Musanze, Rwanda.
Email: mia.derhe@gmail.com Phone: +250 788 319232

Author contributions: MAD, RM conceived and designed the research; MAD performed the fieldwork, analyzed the data; HM, NP, ML contributed tools, permit assistance, expertise in field identification techniques; MAD, RM, HM, NP, ML wrote the manuscript.
Abstract

Ecological restoration is increasingly applied in tropical forests to mitigate biodiversity loss and recover ecosystem functions. In restoration ecology, functional richness, rather than species richness, often determines community assembly, and measures of functional diversity provide a mechanistic link between diversity and ecological functioning of restored habitat. Vertebrate animals are important for ecosystem functioning. Here we examine the functional diversity of small-to-medium sized mammals to evaluate the diversity and functional recovery of tropical rainforest. We assess how mammal species diversity and composition, and functional diversity and composition vary along a restoration chronosequence from degraded pasture to ‘old-growth’ tropical rainforest in the Wet Tropics of Australia. Species richness, diversity, evenness and abundance did not vary, but total mammal biomass and mean species body mass increased with restoration age. Species composition in restoration forests converged on the composition of old-growth rainforest and diverged from pasture with increasing restoration age. Functional metrics provided a clearer pattern of recovery than traditional species metrics, with most functional metrics significantly increasing with restoration age when taxonomic-based metrics did not. Functional evenness and dispersion increased significantly with restoration age, suggesting that niche complementarity enhances species’ abundances in restored sites. The change in community composition represented a functional shift from invasive, herbivorous, terrestrial habitat generalists and open environment specialists in pasture and young restoration sites, to predominantly endemic, folivorous, arboreal and fossorial forest species in older restoration sites. This shift has positive implications for conservation and demonstrates the potential of tropical forest restoration to recover rainforest-like, diverse faunal communities.
Keywords: Australia, ecological restoration, ecosystem functioning, functional guilds, rainforest, Wet Tropics.

Implications for Practice

- Restored tropical rainforests have the capacity to recover functionally diverse, rainforest-like mammal communities in a relatively short period of time (10–17 years), which aids the recovery of ecosystem functioning and thus ecosystem stability in recovering forests.

- Restored tropical rainforests also appear to act as buffers for population declines of terrestrial mammals within the ‘critical weight range’, considered most at risk from extinction in Australia.

- Traditional species-based metrics of diversity are insufficient to evaluate the efficacy of restoration practices, and should be complemented with measures of community structure, functional diversity and functional composition.
**Introduction**

Half of the world’s mammal species are declining and one-quarter face extinction (Schipper et al. 2008). Australia’s highly distinctive and mostly endemic land mammal fauna has experienced greater declines, range contractions, and extinctions than any other taxonomic group, with more than 10% of the original 273 endemic mammals having gone extinct, the highest in the world in recent times (Woinarski et al. 2015). The drivers of these declines are varied and often cumulative or synergistic, for example habitat loss can cause extinctions directly but can also be indirectly lead to further extinctions by facilitating invasions, eliminating prey, altering biophysical conditions and increasing inbreeding depression (Brook et al. 2008). However, habitat alteration and loss are the most widespread drivers (Rands et al. 2010).

As a means of reversing or mitigating such biodiversity losses, as well as recovering ecosystem processes and services, ecological restoration is being increasingly applied in tropical rainforests worldwide (Holl & Aide 2011). A popular method of ecological restoration, particularly in the tropics, is the planting of native tree species on land previously cleared of rainforest (Chazdon 2008), with the aim of recovering the physical structure, biodiversity and ecosystem functions of the ecosystem (Goosem & Tucker 2013). Faunal recolonisation following ecological forest restoration is a major component of ecosystem recovery due to the ecological functions that they mediate. However, knowledge of faunal outcomes in ecological forest restoration plantings, and the factors that influence the direction of the restoration pathway, remains uncertain (Catterall et al. 2012).

Mammals play an integral role within rainforest ecosystems as consumers, dispersers of seeds and spores, and as predators and prey. Changes in mammalian community structure following ecological forest restoration are therefore likely to have consequences for the integrity and stability of the ecosystem (Goheen et al. 2004). However, most ecological forest
restoration has focussed on the recovery of vegetation structure and floral species diversity (Brudvig 2011). Invertebrate and vertebrate animals are important for ecosystem functioning, so full evaluation of restoration success requires a more unified approach that integrates both floral and faunal approaches (McAlpine et al. 2016).

Two of the main goals of ecological restoration projects are the recovery of biodiversity and the creation of functioning ecosystems (Montoya et al. 2012), so effective monitoring should incorporate measures of both. The range of functions provided by a community is thought to depend primarily on the diversity of functional characteristics or values of key traits (Hooper et al. 2005; Cadotte et al. 2011), rather than species richness or diversity per se. The number or diversity of species as a simple measure of biotic diversity has no real explanatory power, since ecosystem processes are affected by the functional traits of organisms involved rather than by taxonomic identity (Hooper et al. 2006). Functional traits operate in a variety of contexts, including competition, facilitation, mutualism, disease, and predation (Hooper et al. 2005). To assess how changes in diversity and composition (following restoration) influence ecosystem functions, an understanding of the functional traits of the species involved is required.

Functional trait-based metrics capture differences in species’ morphology, life-history traits and ecological niches that affect community responses to disturbance and habitat change (Mason et al. 2013) – complexities that traditional taxonomic indices do not capture. Functional diversity is one such metric and is defined as the diversity and abundance distribution of traits within a community (Mason et al. 2005). Functional diversity provides a mechanistic link between diversity and ecological processes and has been shown to be a more accurate predictor of ecosystem functioning than traditional species-based metrics (Cadotte et al. 2011; Mouillot et al. 2011, 2013; Derhé et al. 2016). Furthermore, functional diversity, rather than species richness, determines community assembly as it drives the processes that
structure biological communities (Mouchet et al. 2010). Although there have been studies of faunal recovery in restored sites in the Wet Tropics of Australia (e.g. Nakamura et al. 2003; Catterall et al. 2012; Leach et al. 2013; Lawes et al. 2017), including small–medium mammals (Paetkau et al. 2009; Whitehead et al. 2014), these have focussed on species diversity and composition recovery with only one study to date investigating the effect of restoration on functional diversity and faunal-mediated ecosystem functions (Derhé et al. 2016).

The present study builds on previous research on the recovery of small–medium mammal communities in the Wet Tropics by comparing measures of species and functional diversity, and species and functional composition in response to tropical rainforest restoration, and discusses the implications for ecological functioning and ecosystem health of restored forests. This study specifically examines whether: (1) small–medium mammal (10g–3kg) species diversity increases with restored forest age; (2) functional diversity increases with restored forest age; and (3) restoration forests converge in species composition and functional diversity on the ‘old-growth’ rainforest condition.
Methods

STUDY AREA

The study took place on the Atherton Tableland in the Wet Tropics bioregion, a hilly, mid-elevation (500–1000 m) plateau in north-east Queensland, Australia (approximately 17°–17°30’ S, 145°30’–145°45’ E). Mean annual rainfall is 1,300–3,000 mm and is distinctly seasonal. The climate is predominantly humid tropical with temperatures of 10.2°C–29°C (Bureau of Meteorology 2016). Original vegetation was predominantly tropical rainforests, mostly complex notophyll to mesophyll vine-forest (Stanton & Stanton 2005; Queensland Herbarium 2009). More than half the rainforests on the Tablelands were cleared for agriculture, beginning in the early 1900s, and by 1983 over 76,000 ha of the original 177,000 ha forest had been cleared (Winter et al. 1987). Although many small patches (<1,000 ha) of remnant rainforest remain, large (>3,000 ha) tracts of unfragmented rainforest survive only on steeper hillsides (Laurance 1991). In recent decades there has been an increase in rainforest restoration projects, with a high diversity (10–100+ species) of native rainforest trees and shrubs planted at densities ranging from ~1,000 to 6,000 stems/ha, often in small (<5 ha) patches and strips mainly in riparian areas (Goosem & Tucker 2013). The resulting landscape is a mosaic of livestock pasture, croplands, urban settlements, remnant, natural regrowth and planted forest patches.

STUDY DESIGN

Twelve restoration sites of varying ages were selected: 2 years (n=2); 3 years (n=1); 5 years (n=1); 9 years (n=1); 11 years (n=2); 12 years (n=1); 15 years (n=2); 16 years (n=1); 17 years (n=1). These sites were classified as young (1–5 years), mid-age (6–12 years) and old (13–17 years). All sites were previously grazed pasture on cleared rainforest, which had been abandoned for varying amounts of time. Remnant rainforest patches were reference target
sites, representing the desired end point of restoration (n = 4) and ungrazed, abandoned (for
3–10 years) pasture on previously cleared rainforest land were adopted as degraded reference
sites, representing the starting point of restoration (n = 4).

The natural regrowth rate in the Wet Tropics is known to be extremely slow, with
some abandoned pastures not exhibiting any natural regrowth of (mesophyll type) forest trees
even after 40 years (Florentine & Westbrooke 2004, Rasiah et al. 2004). Furthermore, when
grazing animals are removed from pastures, aggressive exotic grasses can invade and arrest
succession (reviewed in Holl & Cairns 2002), as is the case in the study area. As such, the
abandoned, ungrazed pasture sites in the study area represented both a pre-planting reference
state (pasture), as well as a control state (unassisted regeneration). All degraded pasture sites
lacked trees or shrubs and were comprised of dense grass dominated by non-native species
(principally Urochloa decumbens but also Megathyrsus maximus and Setaria sphacelata).

Sites were set up in four blocks within the landscape (Fig. 1), with each block
containing one site of each habitat category (i.e. the three restoration classes, and starting and
reference sites): pasture; young restoration; mid-age restoration; old restoration; and
rainforest. Blocks were selected to represent the maximum variation in topographic, climatic
and geological parameters in the landscape and all sites within a block were similar in these
parameters. Sites were separated by >300 m (mean = 2,513 m) and blocks by >1.5 km (mean
= 10.9 km). All restoration and degraded pasture sites were of similar size and shape (1–4 ha;
mean = 1.6 ha) and were 200–1,000 m (mean = 422 m) from intact rainforest, connected
through restored and remnant corridors. All rainforest sites were at least 300 ha (mean = 471
ha) in size.

MAMMAL TRAPPING
To determine the structure of small–medium mammal assemblages at the sites, small–medium mammals were sampled over a consecutive three day/three night period (Tasker & Dickman 2002) on four separate occasions at each site, covering both the wet (Feb–Mar 2014 and Feb–Mar 2015) and dry season (Sept–Oct 2013 and Sept–Oct 2014). Trapping occurred within a 50 × 10 m transect at the centre of each site, and comprised six cage traps (30 × 30 × 60 cm; treadle wire-cage type; Mascot Wire Works, Enfield, New South Wales, Australia) and 20 Elliott A traps (10 × 10 × 30 cm aluminium box traps; Elliott type A, Elliot Scientific, Upwey, Victoria, Australia) baited with a mixture of oats, honey, vanilla essence, peanut butter, sardines and apple. Elliott traps were set in two parallel lines, at 5 m intervals along the outside edge of the transect. Wire cage traps were placed along the transect centre line at 0, 10, 20, 30, 40 and 50 m. The traps were placed 10 m apart as a compromise between maximising captures and working within the constraints of transect length and site size. Traps were checked in the morning between 0600 and 1000 h. Each animal trapped was identified to species level, weighed, sexed, morphometrics measured and then released at the site of capture. All animals were tagged with a passive integrated transponder (PIT) tag (7 × 1.35 mm; Loligo Systems) to identify recaptures and avoid recounting individuals (Gibbons & Andrews 2004). The number of individuals caught at each site was used as an index of relative abundance of each species. Recaptures were not included. Total biomass was calculated as the total mass of all mammals captured at a site.

Bush rat (*Rattus fuscipes*) and Cape York rat (*R. leucopus*), two sympatric rat species in the study area, are difficult to distinguish without examining their skulls. Because all individuals could not be positively identified, records of these two species were combined in the analyses, following the protocol of Williams et al. (2002), and are referred to as *R. fuscipes/leucopus*, although most individuals are likely *R. fuscipes* (Williams et al. 2002). Grassland melomys (*Melomys burtoni*) and fawn-footed melomys (*M. cervinipes*) are broadly
sympatric in eastern Australia and are difficult to distinguish on external features. This study used two hind foot plantar pad measurements suggested by Frost (2009) and Van Dyck et al. (2013) to differentiate between the two Melomys species. All work on mammals was performed under Charles Darwin University Animal Ethics Permit A13003 and Scientific Permit WITK12678313.

DATA ANALYSIS

Species were classified into four functional roles that were relevant to regenerating forests: feeding guild (herbivores; omnivores; folivores; insectivores; frugivores), foraging guild (terrestrials; fossorials [digging species]; scansorials [capable of, or adapted for climbing]; arboreals), diel activity (nocturnal or diurnal) (Menkhorst & Knight 2011; Van Dyck et al. 2013) and species mean body mass (Table S1, Appendix S1). All calculations were carried out using R version 3.1.1 (R Core Team 2014). Data from all four trapping rounds were pooled for analysis.

The “FD” package for R was used to calculate four complementary measures of functional diversity that describe a different functional aspect of biological communities: (1) functional richness (FRic), is the range of functional roles in a community quantified by the volume of functional trait space occupied; (2) functional evenness (FEve), which summarises how species’ abundances are distributed throughout the occupied functional trait space; (3) functional divergence (FDiv), which describes the variation in the distribution of species abundances with respect to the centre of functional trait space (an abundance weighted centroid) (Villéger et al. 2008); and (4) functional dispersion (FDis), which indicates the distribution of abundances in functional trait space relative to an abundance weighted centroid, and the volume of space occupied (Laliberté & Legendre 2010).
To estimate species richness in each habitat category and assess whether all mammal species had been sampled, we generated sample-based observed species richness rarefaction curves, with 95% confidence intervals. We also calculated the mean of four commonly used abundance based species richness estimators (ACE, CHAO1, JACK1 and Bootstrap), from 999 randomisations of observed species richness, using ESTIMATES v. 9.1.0 (Colwell 2013). We measured species diversity using the Shannon-Wiener index and calculated species evenness using Pielou’s evenness index. Species richness was rarefied to the minimum number of individuals sampled in a site (n = 9 individuals).

To test for effects of restoration age and habitat category on mammal species diversity and composition, functional diversity and functional composition, we used generalised linear mixed effects models (glmm) with sampling block as a random effect. Models were run separately, with each model containing one fixed effect and one dependent variable. We performed a contrast analysis on the glmms with habitat category as a predictor, by obtaining confidence intervals using parametric bootstrapping, to determine whether the response variables differed between the habitat categories. Appropriate error structures were applied for all models.

To assess whether restoration sites were progressing towards the reference sites in terms of their species composition, we used a non-metric multidimensional scaling (NMDS) ordination analysis using Bray-Curtis pairwise distances based on standardised, square root transformed abundance data (to reduce the influence of the most dominant species). To test for differences in Bray-Curtis similarity to rainforest among habitat categories, we used a permutational multivariate analysis of variance (ADONIS). We used glmms to explore the relationship between restoration age and Bray-Curtis similarity to rainforest and the total number of individuals of four different functional guilds: habitat specialists; geographic range status; feeding guild; and foraging guild (see Table S1 for species classification).
**Results**

**SPECIES DIVERSITY AND COMPOSITION**

A total of 657 small–medium mammals from 12 species and 9 genera were recorded (excluding recaptures). The most commonly captured species was the house mouse (*Mus musculus*) which was also the smallest species (mean mass = 12 g) and recorded only in pasture and young restoration sites. The largest species was the common brushtail possum (*Trichosurus vulpecula*), recorded only in restoration (young, medium and old) and rainforest sites (mean mass = 2.1 kg). Species accumulation curves revealed that sampling effort was adequate to characterise the local mammal community (Fig. S1). The four common estimators of species richness suggest that between 74% of species in mid-restoration plantings to 99% in young restoration plantings were sampled (Table S2). The community attributes (abundance, total biomass, species richness, FRic, FEve, FDiv, FDis) across the experimental plots were not strongly correlated.

Restoration age had no effect on the number of species (observed species richness: $\chi^2 = 0.00, P = 0.997$; Fig. 2a), number of individuals ($\chi^2 = 0.038, P = 0.846$; Fig. 2b), Shannon-Wiener species diversity ($\chi^2 = 0.20, P = 0.655$; Fig. S2c) or Pielou’s species evenness ($\chi^2 = 1.90, P = 0.168$; Fig. S2d). However, increasing restoration age led to an overall increase in total mammal biomass ($\chi^2 = 10.62, P = 0.001$; Fig. 2c), due to a greater mean body mass of the dominant species occupying older restoration forests ($\chi^2 = 12.95, P < 0.001$; Fig. 2d), i.e. there was a species shift with increasing age of the restored forest and a concomitant increase in body size of these species.

Pasture sites supported the largest number of individuals ($\chi^2 = 10.83, P = 0.029$; Fig. 2f) but had the lowest total biomass ($\chi^2 = 16.16, P = 0.003$; Fig. 2g) and lowest mean body mass of species ($\chi^2 = 21.74, P < 0.001$; Fig. 2h). However, species richness (observed species
richness: $\chi^2_4 = 1.89, P = 0.755$; Fig. 2e), Shannon-Wiener species diversity ($\chi^2_4 = 3.84, P = 0.429$; Fig. S2g) and Pielou’s species evenness ($\chi^2_4 = 0.71, P = 0.950$; Fig. S2h) did not differ among habitat classes.

Species composition differed significantly among habitat categories (ADONIS: $r^2 = 0.351$, df = 4, $P = 0.002$; Fig. 3). The NMDS ordination represented 85.6% of the assemblage dissimilarity on the first two principle axes, demonstrating that as restoration sites age they become more similar to the rainforest sites ($\chi^2 = 7.33, P = 0.007$; Fig. S3b) and deviate from the pasture sites ($\chi^2 = 10.21, P = 0.001$; Fig. S3a) in their community composition. Bray-Curtis similarity to rainforest differed by habitat category ($\chi^2_4 = 10.42, P = 0.034$; Fig. S3d), with the least similarity to forest composition in pasture.

Functional Diversity and Composition

Increasing restoration age led to an increase in functional evenness ($\chi^2 = 4.91, P = 0.027$; Fig. 2b) and dispersion ($\chi^2 = 10.62, P = 0.001$; Fig. 4d), but had no effect on functional richness ($\chi^2 = 1.06, P = 0.303$; Fig. 4a) or divergence ($\chi^2 = 1.17, P = 0.279$; Fig. 4c). The lowest functional divergence occurred in mid-restoration, and the highest in old-restoration and rainforest sites ($\chi^2_4 = 12.71, P = 0.013$; Fig. 4g); whilst the highest functional dispersion occurred in old-restoration and rainforest, and the lowest in pasture ($\chi^2_4 = 8.24, P = 0.083$; Fig. 4h). Habitat category had no effect on functional richness ($\chi^2_4 = 1.35, P = 0.557$; Fig. 4e) or evenness ($\chi^2_4 = 6.34, P = 0.175$; Fig. 4f).

The abundance of open environment specialists ($\chi^2 = 12.59, P < 0.001$; Fig. 5a), invasive species ($\chi^2 = 18.49, P < 0.001$; Fig. 5d), herbivores ($\chi^2 = 8.85, P = 0.003$; Fig. 6e) and terrestrial foragers ($\chi^2 = 9.37, P = 0.002$; Fig. 6a) declined with restoration age, but the abundance of forest species ($\chi^2 = 7.97, P = 0.005$; Fig. 5c), Australian endemics ($\chi^2 = 11.45, P < 0.001$; Fig. 5f), folivores ($\chi^2 = 6.01, P = 0.014$; Fig. 6g) and arboreal foragers ($\chi^2 = 6.01, P < 0.001$; Fig. 5f),
The abundance of habitat generalists ($\chi^2 = 0.00, P = 0.992$; Fig. 6d) increased. The abundance of Australian natives ($\chi^2 = 0.00, P = 0.996$; Fig. 5b), omnivores ($\chi^2 = 0.14, P = 0.706$; Fig. 6f), scansorial foragers ($\chi^2 = 0.03, P = 0.852$; Fig. 6b) and fossorial foragers ($\chi^2 = 0.34, P = 0.562$; Fig. 6c) did not vary with restoration age.

**Discussion**

The patterns in species and functional diversity recovery reported here demonstrate that restoration plantings can restore functionally diverse, rainforest-like small–medium mammal communities in a relatively short period of time, which may potentially enhance the recovery of ecosystem functioning and thus ecosystem viability in recovering tropical rainforests. We also show that traditional species-based metrics of diversity do not reveal the whole picture, and that by complementing these with measures of species composition, and functional diversity and composition, we gain a better understanding of the efficacy of restoration practices.

**SPECIES DIVERSITY AND COMPOSITION**

We found that species richness, number of individuals and species diversity in the restored and reference rainforest sites were similar to or lower than in pasture sites. These results are commensurate with recent studies reporting similar species richness and abundance of small–medium mammals in restored habitats compared to reference remnant and degraded sites (Golet et al. 2011; Whitehead et al. 2014; Mérő et al. 2015). We found a marked increase in total biomass and mean body mass of mammal species in the restored sites, due to increased abundances of common brushtail possums and giant white-tailed rats (*Uromys caudimaculatus*) in older restoration and rainforest sites. This indicates that as restoration sites age, they recover sufficient resources to support these larger-bodied mammal species.
typical of tropical rainforests. Increased total biomass and mean body mass of species in the older restoration sites may be related to higher levels of productivity. Large body size is one of the most important global predictors of extinction risk in mammals (Cardillo et al. 2005; Hoffmann et al. 2011). The increase in total biomass and mean body mass of species with restoration age suggests that restoration sites may act as buffers for population declines of terrestrial mammals within the ‘critical weight range’ of between 100 g and 5 kg - those considered most at risk from extinction in Australia (Murphy & Davies 2014).

While secondary and recovering forests may harbour a similar number of species as mature forests (e.g. Dent & Wright 2009), communities in secondary forests are usually dominated by generalist species (Barlow et al. 2007). Indeed, we found that restoration sites were progressing towards rainforest and deviating from pasture sites in their small–medium mammal composition, confirming patterns found by similar studies in the area on mammals (Whitehead et al. 2014), birds (Catterall et al. 2012), ants (Leach et al. 2013; Lawes et al. 2017) and dung beetles (Derhé et al. 2016). The shift from pasture-like to more rainforest-like mammal communities began at approximately five years after planting, corresponding with the age at which canopy closure begins to occur (Goosem & Tucker 2013). Indeed, this composition shift may be driven by canopy development, as small–medium mammal assemblage structure is known to be closely related to vegetation structure, particularly canopy cover (Williams et al. 2002).

FUNCTIONAL DIVERSITY AND COMPOSITION

We found an increase in functional evenness (FEve) with restoration age, consistent with previous studies that report declines in FEve with increasing disturbance levels (Mouillot et al. 2013; Magnago et al. 2014). This increase in FEve with restoration age indicates that in older restoration sites, species are evenly distributed along a gradient of ecosystem functions
performed by those species and that dominant species differ in their contribution to the ecosystem functions. We also found an increase in functional dispersion with restoration age, indicating a higher degree of niche differentiation, and thus lower resource competition in the older restoration sites, suggesting that niche complementarity enhances species’ occurrence probabilities and/or abundances in the restoration sites (Mason et al. 2013).

The functional metrics reveal that overall there is an increase in mammalian functional diversity as the restoration sites age; whereas the traditional species metrics failed to show a clear response with restoration age. Species richness measures do not reflect functional or ecological differences that determine species-specific response patterns, or the functional implications of species loss and recovery, and can therefore lead to misleading conclusions about trends in biodiversity (Mouillot et al. 2013; Derhé et al. 2016). These findings support previous meta-analyses showing that land use intensification and disturbance can reduce the functional diversity of mammal communities beyond changes in species richness alone (Flynn et al. 2009) - potentially further imperilling the provision of ecosystem processes and services. Moreover, it has been demonstrated that functional diversity responds differently to environmental, spatial and temporal processes compared to species abundance and biomass (da Silva & Hernández 2015). We recommend that functional diversity measures be used as a complementary tool to investigate faunal species distribution and recovery.

Although there were similar levels of functional richness in the restored and reference sites, the identity of the functional groups changed with restoration age. There was a clear shift from communities dominated by small-bodied, invasive, herbivorous, terrestrial open-environment specialist species in young restoration and pasture sites, to communities dominated by larger bodied, endemic, folivorous, arboreal, rainforest species in the mid-age and old-restoration sites. The invasive house mouse was the dominant species in pasture,
whereas the endemic bush rat/ Cape York rat and giant white-tailed rat were dominant in rainforest. The house mouse is one of the world’s worst invasive alien mammal species (Lowe et al. 2000) and so this community structural shift will have further positive effects on biodiversity as invasive alien species are one of the key pressures driving biodiversity loss today (Butchart et al. 2010).

The locally endemic musky rat kangaroo (*Hypsiprymnodon moschatus*), a forest specialist restricted to the tropical forests of north-eastern Queensland, was recorded only in rainforest. Forest mammal species are relatively specialised and intolerant of the surrounding landscape matrix, which makes them more prone to extinction (Laurance 1991). The recovery of forest species in the restoration sites therefore has positive conservation implications and also suggests that the habitat of restored sites is becoming structurally more similar to rainforest, as vegetation structure and habitat complexity have a strong influence on small-mammal community structure (Williams et al. 2002).

Mammals are mediators of key ecosystem functions important to forest dynamics, including nutrient cycling through dung deposition (Bardgett et al. 1998), and soil bioturbation (Fleming et al. 2014). These functions are particularly important for previously cleared forests that are known to have altered soil properties (Sahani & Behera 2001), which can strongly affect growth of tree seedlings, especially in their early stages (Tilman 1986). Mammals also contribute to nutrient recycling by returning organic matter and nutrients to the soil in relatively labile forms as dung and urine, which improves plant access to essential soil elements (Loreau 1995) and may stimulate soil activity (Bardgett et al. 1998). The increased total biomass of mammals in older restored sites suggests that larger amounts of dung will be deposited in those sites, which may increase productivity (Williams & Haynes 1995) and have positive effects on seedling recruitment and forest regeneration.
Mammals also influence biological processes by the ingestion and movement of seeds and fungal spores (Williams et al. 2000). Seed-caching behaviour occurs in Australian native rodents and marsupials (Elmouttie & Mather 2012), playing a critical role in dispersing plant seeds and influencing germination rates (Midgley et al. 2002). Most mammals recorded in older restoration sites are species which are known to cache seeds and have been shown to increase germination rates, including the giant white tailed rat (Theimer 2001), bush rat and fawn footed melomys (*Melomys cervinipes*) (Elmouttie & Mather 2012).

**Acknowledgements**

We gratefully thank all the landowners who allowed us unlimited access to their properties, without which this study would not have been possible. We would like to dedicate this work to the memory of I. Freeman. We also thank Trees for Evelyn and Atherton Tablelands (TREAT), Tablelands Regional Council (TRC) nursery and QPWS Lake Eacham nursery. We are very grateful to D. Jones for invaluable training and support in the field, as well as to M. Miller, R. Hart, S. Hart, F. Loughran and J. Tait for fieldwork assistance. We also thank Dr P. van Oosterzee for her support, assistance and her instrumental role in establishing the ARC project. A large section of this study has been published as a requirement of a PhD award completed in 2016 at Lancaster University (U.K.) in collaboration with CSIRO (Australia). This work was funded by a studentship awarded to M. D. by the National Environment Research Council (U.K.), and supported partly by and contributes to Australian Research Council Linkage project (LP0989161).
Literature cited


Bureau of Meteorology (2016) Kairi Weather Station #031034, Commonwealth of Australia, Bureau of Meteorology


Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples


Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world’s worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group Auckland


Murphy BP, Davies HF (2014) There is a critical weight range for Australia’s declining tropical mammals. Global Ecological Biogeography 23:1058–1061


Queensland Herbarium (2009) Survey and Mapping of Vegetation Communities and Regional Ecosystems of Queensland. Brisbane


Fig. 1 Map of the study area, showing the 20 study sites and areas of cleared forest, Eucalypt forest and rainforest. One 50m transect line was set up in each site comprising 20 Elliott traps and 6 wire cage traps.
Fig. 2 Relationship between restoration age and observed species richness, number of individuals, total biomass and mean body mass of species (a–d), showing model-predicted mean (black line) ± SE (grey shade) where relationships were significant (p < 0.05). Mean ± SE observed species richness, number of individuals, total biomass and mean body mass of species in the different habitat categories (e–h). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P < 0.05).
Fig. 3 Non-metric multidimensional scaling (MDS) ordination of community assemblages between the different habitat categories (pasture; young restoration; mid-age restoration; old restoration; and rainforest) at the site scale, based on square-root transformed, standardised abundance data ($r^2 = 0.86$).
**Fig. 4** Relationship between restoration age and functional richness, functional evenness, functional divergence and functional dispersion (a–d), showing model-predicted mean (black line) ± SE (grey shade) where relationships were significant (p < 0.05). Mean ± SE functional richness, functional evenness, functional divergence and functional dispersion in the different habitat categories (e–h). P = pasture; YR = young restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant differences (P <0.05).
Fig. 5 Relationship between restoration age and the total abundance of different functional guilds. Habitat specialisms: open environment specialists (a), habitat generalists (b) and forest species (c). Geographic range status: invasives (d), natives (e) and endemics (f), showing model-predicted mean (black line) ± SE (grey shade) where relationships were significant (p < 0.05).
Fig. 6 Relationship between restoration age and the total abundance of different foraging guilds: Foraging guild: terrestrial foragers (a), scansorial foragers (b), fossorial foragers (c) and arboreal foragers (d). Feeding guild: herbivores (e), omnivores (f), and folivores (g), showing model-predicted mean (black line) ± SE (grey shade) where relationships were significant (p < 0.05).