

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

3
4 **Running head:** Recovering mammal diversity in restored forests

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27

28 **Abstract**

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

51

52 **Keywords:** Australia, ecological restoration, ecosystem functioning, functional guilds,
53 rainforest, Wet Tropics.

54

55 **Implications for Practice**

- 56 ● Restored tropical rainforests have the capacity to recover functionally diverse, rainforest-
57 like mammal communities in a relatively short period of time (10–17 years), which aids
58 the recovery of ecosystem functioning and thus ecosystem stability in recovering forests.
- 59 ● Restored tropical rainforests also appear to act as buffers for population declines of
60 terrestrial mammals within the ‘critical weight range’, considered most at risk from
61 extinction in Australia.
- 62 ● Traditional species-based metrics of diversity are insufficient to evaluate the efficacy of
63 restoration practices, and should be complemented with measures of community
64 structure, functional diversity and functional composition.

65

66 **Introduction**

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

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

87 Mammals play an integral role within rainforest ecosystems as consumers, dispersers of
88 seeds and spores, and as predators and prey. Changes in mammalian community structure
89 following ecological forest restoration are therefore likely to have consequences for the
90 integrity and stability of the ecosystem (Goheen et al. 2004). However, most ecological forest

91 restoration has focussed on the recovery of vegetation structure and floral species diversity
92 (Brudvig 2011). Invertebrate and vertebrate animals are important for ecosystem functioning,
93 so full evaluation of restoration success requires a more unified approach that integrates both
94 floral and faunal approaches (McAlpine et al. 2016).

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

107 Functional trait-based metrics capture differences in species' morphology, life-history
108 traits and ecological niches that affect community responses to disturbance and habitat
109 change (Mason et al. 2013) – complexities that traditional taxonomic indices do not capture.
110 Functional diversity is one such metric and is defined as the diversity and abundance
111 distribution of traits within a community (Mason et al. 2005). Functional diversity provides a
112 mechanistic link between diversity and ecological processes and has been shown to be a more
113 accurate predictor of ecosystem functioning than traditional species-based metrics (Cadotte et
114 al. 2011; Mouillot et al. 2011, 2013; Derhé et al. 2016). Furthermore, functional diversity,
115 rather than species richness, determines community assembly as it drives the processes that

116 structure biological communities (Mouchet et al. 2010). Although there have been studies of
117 faunal recovery in restored sites in the Wet Tropics of Australia (e.g. Nakamura et al. 2003;
118 Catterall et al. 2012; Leach et al. 2013; Lawes et al. 2017), including small–medium
119 mammals (Paetkau et al. 2009; Whitehead et al. 2014), these have focussed on species
120 diversity and composition recovery with only one study to date investigating the effect of
121 restoration on functional diversity and faunal-mediated ecosystem functions (Derhé et al.
122 2016).

123 The present study builds on previous research on the recovery of small–medium
124 mammal communities in the Wet Tropics by comparing measures of species and functional
125 diversity, and species and functional composition in response to tropical rainforest
126 restoration, and discusses the implications for ecological functioning and ecosystem health of
127 restored forests. This study specifically examines whether: (1) small–medium mammal (10g–
128 3kg) species diversity increases with restored forest age; (2) functional diversity increases
129 with restored forest age; and (3) restoration forests converge in species composition and
130 functional diversity on the ‘old-growth’ rainforest condition.

131 **Methods**

132 **STUDY AREA**

133 The study took place on the Atherton Tableland in the Wet Tropics bioregion, a hilly, mid-
134 elevation (500–1000 m) plateau in north-east Queensland, Australia (approximately 17°–
135 17°30' S, 145°30'–145°45' E). Mean annual rainfall is 1,300–3,000 mm and is distinctly
136 seasonal. The climate is predominantly humid tropical with temperatures of 10.2°C–29°C
137 (Bureau of Meteorology 2016). Original vegetation was predominantly tropical rainforests,
138 mostly complex notophyll to mesophyll vine-forest (Stanton & Stanton 2005; Queensland
139 Herbarium 2009). More than half the rainforests on the Tablelands were cleared for
140 agriculture, beginning in the early 1900s, and by 1983 over 76,000 ha of the original 177,000
141 ha forest had been cleared (Winter et al. 1987). Although many small patches (<1,000 ha) of
142 remnant rainforest remain, large (>3,000 ha) tracts of unfragmented rainforest survive only
143 on steeper hillsides (Laurance 1991). In recent decades there has been an increase in
144 rainforest restoration projects, with a high diversity (10–100+ species) of native rainforest
145 trees and shrubs planted at densities ranging from ~1,000 to 6,000 stems/ha, often in small
146 (<5 ha) patches and strips mainly in riparian areas (Goosem & Tucker 2013). The resulting
147 landscape is a mosaic of livestock pasture, croplands, urban settlements, remnant, natural
148 regrowth and planted forest patches.

149

150 **STUDY DESIGN**

151 Twelve restoration sites of varying ages were selected: 2 years (n=2); 3 years (n=1); 5 years
152 (n=1); 9 years (n=1); 11 years (n=2); 12 years (n=1); 15 years (n=2); 16 years (n=1); 17 years
153 (n=1). These sites were classified as young (1–5 years), mid-age (6–12 years) and old (13–17
154 years). All sites were previously grazed pasture on cleared rainforest, which had been
155 abandoned for varying amounts of time. Remnant rainforest patches were reference target

156 sites, representing the desired end point of restoration (n = 4) and ungrazed, abandoned (for
157 3–10 years) pasture on previously cleared rainforest land were adopted as degraded reference
158 sites, representing the starting point of restoration (n = 4).

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

168 Sites were set up in four blocks within the landscape (Fig. 1), with each block
169 containing one site of each habitat category (i.e. the three restoration classes, and starting and
170 reference sites): pasture; young restoration; mid-age restoration; old restoration; and
171 rainforest. Blocks were selected to represent the maximum variation in topographic, climatic
172 and geological parameters in the landscape and all sites within a block were similar in these
173 parameters. Sites were separated by >300 m (mean = 2,513 m) and blocks by >1.5 km (mean
174 = 10.9 km). All restoration and degraded pasture sites were of similar size and shape (1–4 ha;
175 mean = 1.6 ha) and were 200–1,000 m (mean = 422 m) from intact rainforest, connected
176 through restored and remnant corridors. All rainforest sites were at least 300 ha (mean = 471
177 ha) in size.

178

179 MAMMAL TRAPPING

180 To determine the structure of small–medium mammal assemblages at the sites, small–
181 medium mammals were sampled over a consecutive three day/ three night period (Tasker &
182 Dickman 2002) on four separate occasions at each site, covering both the wet (Feb–Mar 2014
183 and Feb–Mar 2015) and dry season (Sept–Oct 2013 and Sept–Oct 2014). Trapping occurred
184 within a 50 × 10 m transect at the centre of each site, and comprised six cage traps (30 × 30 ×
185 60 cm; treadle wire-cage type; Mascot Wire Works, Enfield, New South Wales, Australia)
186 and 20 Elliott A traps (10 × 10 × 30 cm aluminium box traps; Elliott type A, Elliot Scientific,
187 Upwey, Victoria, Australia) baited with a mixture of oats, honey, vanilla essence, peanut
188 butter, sardines and apple. Elliott traps were set in two parallel lines, at 5 m intervals along
189 the outside edge of the transect. Wire cage traps were placed along the transect centre line at
190 0, 10, 20, 30, 40 and 50 m. The traps were placed 10 m apart as a compromise between
191 maximising captures and working within the constraints of transect length and site size. Traps
192 were checked in the morning between 0600 and 1000 h. Each animal trapped was identified
193 to species level, weighed, sexed, morphometrics measured and then released at the site of
194 capture. All animals were tagged with a passive integrated transponder (PIT) tag (7 × 1.35
195 mm; Loligo Systems) to identify recaptures and avoid recounting individuals (Gibbons &
196 Andrews 2004). The number of individuals caught at each site was used as an index of
197 relative abundance of each species. Recaptures were not included. Total biomass was
198 calculated as the total mass of all mammals captured at a site.

199 Bush rat (*Rattus fuscipes*) and Cape York rat (*R. leucopus*), two sympatric rat species
200 in the study area, are difficult to distinguish without examining their skulls. Because all
201 individuals could not be positively identified, records of these two species were combined in
202 the analyses, following the protocol of Williams et al. (2002), and are referred to as *R.*
203 *fuscipes/ leucopus*, although most individuals are likely *R. fuscipes* (Williams et al. 2002).
204 Grassland melomys (*Melomys burtoni*) and fawn-footed melomys (*M. cervinipes*) are broadly

205 sympatric in eastern Australia and are difficult to distinguish on external features. This study
206 used two hind foot plantar pad measurements suggested by Frost (2009) and Van Dyck et al.
207 (2013) to differentiate between the two *Melomys* species. All work on mammals was
208 performed under Charles Darwin University Animal Ethics Permit A13003 and Scientific
209 Permit WITK12678313.

210

211 DATA ANALYSIS

212 Species were classified into four functional roles that were relevant to regenerating forests:
213 feeding guild (herbivores; omnivores; folivores; insectivores; frugivores), foraging guild
214 (terrestrials; fossorials [digging species]; scansorials [capable of, or adapted for climbing];
215 arboreals), diel activity (nocturnal or diurnal) (Menkhorst & Knight 2011; Van Dyck et al.
216 2013) and species mean body mass (Table S1, Appendix S1). All calculations were carried
217 out using R version 3.1.1 (R Core Team 2014). Data from all four trapping rounds were
218 pooled for analysis.

219 The “FD” package for R was used to calculate four complementary measures of
220 functional diversity that describe a different functional aspect of biological communities: (1)
221 functional richness (FRic), is the range of functional roles in a community quantified by the
222 volume of functional trait space occupied; (2) functional evenness (FEve), which summarises
223 how species’ abundances are distributed throughout the occupied functional trait space; (3)
224 functional divergence (FDiv), which describes the variation in the distribution of species
225 abundances with respect to the centre of functional trait space (an abundance weighted
226 centroid) (Villéger et al. 2008); and (4) functional dispersion (FDis), which indicates the
227 distribution of abundances in functional trait space relative to an abundance weighted
228 centroid, and the volume of space occupied (Laliberté & Legendre 2010).

229 To estimate species richness in each habitat category and assess whether all mammal
230 species had been sampled, we generated sample-based observed species richness rarefaction
231 curves, with 95% confidence intervals. We also calculated the mean of four commonly used
232 abundance based species richness estimators (ACE, CHAO1, JACK1 and Bootstrap), from
233 999 randomisations of observed species richness, using ESTIMATES v. 9.1.0 (Colwell
234 2013). We measured species diversity using the Shannon-Wiener index and calculated
235 species evenness using Pielou's evenness index. Species richness was rarefied to the
236 minimum number of individuals sampled in a site ($n = 9$ individuals).

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

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

254

255 **Results**

256 SPECIES DIVERSITY AND COMPOSITION

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

268 Restoration age had no effect on the number of species (observed species richness: χ^2
269 = 0.00, $P = 0.997$; Fig. 2a), number of individuals ($\chi^2 = 0.038$, $P = 0.846$; Fig. 2b), Shannon-
270 Wiener species diversity ($\chi^2 = 0.20$, $P = 0.655$; Fig. S2c) or Pielou's species evenness ($\chi^2 =$
271 1.90, $P = 0.168$; Fig. S2d). However, increasing restoration age led to an overall increase in
272 total mammal biomass ($\chi^2 = 10.62$, $P = 0.001$; Fig. 2c), due to a greater mean body mass of
273 the dominant species occupying older restoration forests ($\chi^2 = 12.95$, $P < 0.001$; Fig. 2d), i.e.
274 there was a species shift with increasing age of the restored forest and a concomitant increase
275 in body size of these species.

276 Pasture sites supported the largest number of individuals ($\chi^2_4 = 10.83$, $P = 0.029$; Fig.
277 2f) but had the lowest total biomass ($\chi^2_4 = 16.16$, $P = 0.003$; Fig. 2g) and lowest mean body
278 mass of species ($\chi^2_4 = 21.74$, $P < 0.001$; Fig. 2h). However, species richness (observed species

279 richness: $\chi^2_4 = 1.89$, $P = 0.755$; Fig. 2e), Shannon-Wiener species diversity ($\chi^2_4 = 3.84$, $P =$
280 0.429 ; Fig. S2g) and Pielou's species evenness ($\chi^2_4 = 0.71$, $P = 0.950$; Fig. S2h) did not differ
281 among habitat classes.

282 Species composition differed significantly among habitat categories (ADONIS: $r^2 =$
283 0.351 , $df = 4$, $P = 0.002$; Fig. 3). The NMDS ordination represented 85.6% of the assemblage
284 dissimilarity on the first two principle axes, demonstrating that as restoration sites age they
285 become more similar to the rainforest sites ($\chi^2 = 7.33$, $P = 0.007$; Fig. S3b) and deviate from
286 the pasture sites ($\chi^2 = 10.21$, $P = 0.001$; Fig. S3a) in their community composition. Bray-
287 Curtis similarity to rainforest differed by habitat category ($\chi^2_4 = 10.42$, $P = 0.034$; Fig. S3d),
288 with the least similarity to forest composition in pasture.

289

290 FUNCTIONAL DIVERSITY AND COMPOSITION

291 Increasing restoration age led to an increase in functional evenness ($\chi^2 = 4.91$, $P = 0.027$; Fig.
292 4b) and dispersion ($\chi^2 = 10.62$, $P = 0.001$; Fig. 4d), but had no effect on functional richness
293 ($\chi^2 = 1.06$, $P = 0.303$; Fig. 4a) or divergence ($\chi^2 = 1.17$, $P = 0.279$; Fig. 4c). The lowest
294 functional divergence occurred in mid-restoration, and the highest in old-restoration and
295 rainforest sites ($\chi^2_4 = 12.71$, $P = 0.013$; Fig. 4g); whilst the highest functional dispersion
296 occurred in old-restoration and rainforest, and the lowest in pasture ($\chi^2_4 = 8.24$, $P = 0.083$;
297 Fig. 4h). Habitat category had no effect on functional richness ($\chi^2_4 = 1.35$, $P = 0.557$; Fig. 4e)
298 or evenness ($\chi^2_4 = 6.34$, $P = 0.175$; Fig. 4f).

299 The abundance of open environment specialists ($\chi^2 = 12.59$, $P < 0.001$; Fig. 5a),
300 invasive species ($\chi^2 = 18.49$, $P < 0.001$; Fig. 5d), herbivores ($\chi^2 = 8.85$, $P = 0.003$; Fig. 6e)
301 and terrestrial foragers ($\chi^2 = 9.37$, $P = 0.002$; Fig. 6a) declined with restoration age, but the
302 abundance of forest species ($\chi^2 = 7.97$, $P = 0.005$; Fig. 5c), Australian endemics ($\chi^2 = 11.45$, P
303 < 0.001 ; Fig. 5f), folivores ($\chi^2 = 6.01$, $P = 0.014$; Fig. 6g) and arboreal foragers ($\chi^2 = 6.01$, P

304 = 0.014; Fig. 6d) increased. The abundance of habitat generalists ($\chi^2 = 0.00$, $P = 0.992$; Fig.
305 5b), Australian natives ($\chi^2 = 0.00$, $P = 0.996$; Fig. 5e), omnivores ($\chi^2 = 0.14$, $P = 0.706$; Fig.
306 6f), scansorial foragers ($\chi^2 = 0.03$, $P = 0.852$; Fig. 6b) and fossorial foragers ($\chi^2 = 0.34$, $P =$
307 0.562; Fig. 6c) did not vary with restoration age.

308

309 **Discussion**

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

318

319 SPECIES DIVERSITY AND COMPOSITION

320 We found that species richness, number of individuals and species diversity in the restored
321 and reference rainforest sites were similar to or lower than in pasture sites. These results are
322 commensurate with recent studies reporting similar species richness and abundance of small–
323 medium mammals in restored habitats compared to reference remnant and degraded sites
324 (Golet et al. 2011; Whitehead et al. 2014; Méréo et al. 2015). We found a marked increase in
325 total biomass and mean body mass of mammal species in the restored sites, due to increased
326 abundances of common brushtail possums and giant white-tailed rats (*Uromys*
327 *caudimaculatus*) in older restoration and rainforest sites. This indicates that as restoration
328 sites age, they recover sufficient resources to support these larger-bodied mammal species

329 typical of tropical rainforests. Increased total biomass and mean body mass of species in the
330 older restoration sites may be related to higher levels of productivity. Large body size is one
331 of the most important global predictors of extinction risk in mammals (Cardillo et al. 2005;
332 Hoffmann et al. 2011). The increase in total biomass and mean body mass of species with
333 restoration age suggests that restoration sites may act as buffers for population declines of
334 terrestrial mammals within the ‘critical weight range’ of between 100 g and 5 kg - those
335 considered most at risk from extinction in Australia (Murphy & Davies 2014).

336 While secondary and recovering forests may harbour a similar number of species as
337 mature forests (e.g. Dent & Wright 2009), communities in secondary forests are usually
338 dominated by generalist species (Barlow et al. 2007). Indeed, we found that restoration sites
339 were progressing towards rainforest and deviating from pasture sites in their small–medium
340 mammal composition, confirming patterns found by similar studies in the area on mammals
341 (Whitehead et al. 2014), birds (Catterall et al. 2012), ants (Leach et al. 2013; Lawes et al.
342 2017) and dung beetles (Derhé et al. 2016). The shift from pasture-like to more rainforest-like
343 mammal communities began at approximately five years after planting, corresponding with
344 the age at which canopy closure begins to occur (Goosem & Tucker 2013). Indeed, this
345 composition shift may be driven by canopy development, as small–medium mammal
346 assemblage structure is known to be closely related to vegetation structure, particularly
347 canopy cover (Williams et al. 2002).

348

349 FUNCTIONAL DIVERSITY AND COMPOSITION

350 We found an increase in functional evenness (FEve) with restoration age, consistent with
351 previous studies that report declines in FEve with increasing disturbance levels (Mouillot et
352 al. 2013; Magnago et al. 2014). This increase in FEve with restoration age indicates that in
353 older restoration sites, species are evenly distributed along a gradient of ecosystem functions

354 performed by those species and that dominant species differ in their contribution to the
355 ecosystem functions. We also found an increase in functional dispersion with restoration age,
356 indicating a higher degree of niche differentiation, and thus lower resource competition in the
357 older restoration sites, suggesting that niche complementarity enhances species' occurrence
358 probabilities and/or abundances in the restoration sites (Mason et al. 2013).

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

373 Although there were similar levels of functional richness in the restored and reference
374 sites, the identity of the functional groups changed with restoration age. There was a clear
375 shift from communities dominated by small-bodied, invasive, herbivorous, terrestrial open-
376 environment specialist species in young restoration and pasture sites, to communities
377 dominated by larger bodied, endemic, folivorous, arboreal, rainforest species in the mid-age
378 and old-restoration sites. The invasive house mouse was the dominant species in pasture,

379 whereas the endemic bush rat/ Cape York rat and giant white-tailed rat were dominant in
380 rainforest. The house mouse is one of the world's worst invasive alien mammal species
381 (Lowe et al. 2000) and so this community structural shift will have further positive effects on
382 biodiversity as invasive alien species are one of the key pressures driving biodiversity loss
383 today (Butchart et al. 2010).

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

392 Mammals are mediators of key ecosystem functions important to forest dynamics,
393 including nutrient cycling through dung deposition (Bardgett et al. 1998), and soil
394 bioturbation (Fleming et al. 2014). These functions are particularly important for previously
395 cleared forests that are known to have altered soil properties (Sahani & Behera 2001), which
396 can strongly affect growth of tree seedlings, especially in their early stages (Tilman 1986).
397 Mammals also contribute to nutrient recycling by returning organic matter and nutrients to
398 the soil in relatively labile forms as dung and urine, which improves plant access to essential
399 soil elements (Loreau 1995) and may stimulate soil activity (Bardgett et al. 1998). The
400 increased total biomass of mammals in older restored sites suggests that larger amounts of
401 dung will be deposited in those sites, which may increase productivity (Williams & Haynes
402 1995) and have positive effects on seedling recruitment and forest regeneration.

403 Mammals also influence biological processes by the ingestion and movement of seeds
404 and fungal spores (Williams et al. 2000). Seed-caching behaviour occurs in Australian native
405 rodents and marsupials (Elmoultie & Mather 2012), playing a critical role in dispersing plant
406 seeds and influencing germination rates (Midgley et al. 2002). Most mammals recorded in
407 older restoration sites are species which are known to cache seeds and have been shown to
408 increase germination rates, including the giant white tailed rat (Theimer 2001), bush rat and
409 fawn footed melomys (*Melomys cervinipes*) (Elmoultie & Mather 2012).

410

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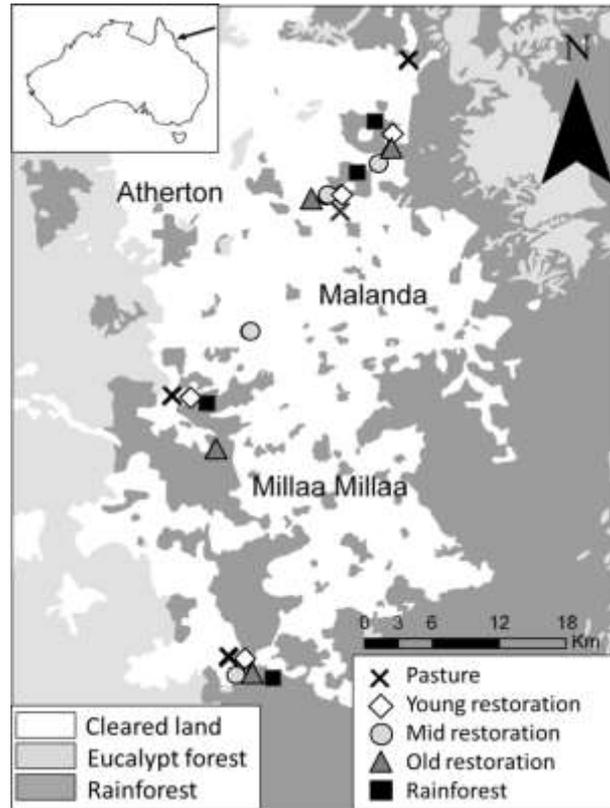
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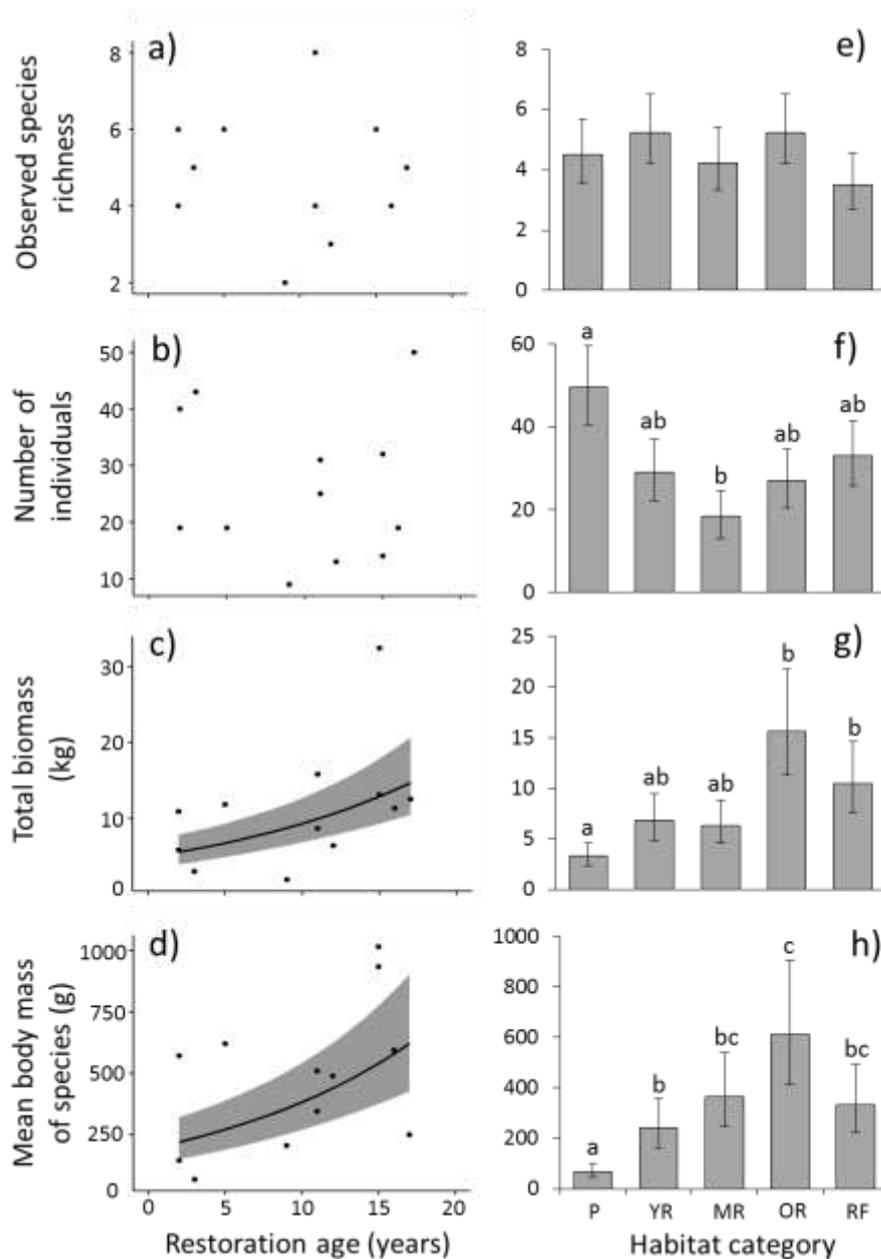
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589

590 **Fig. 1** Map of the study area, showing the 20 study sites and areas of cleared forest, Eucalypt forest and
 591 rainforest. One 50m transect line was set up in each site comprising 20 Elliott traps and 6 wire cage traps.

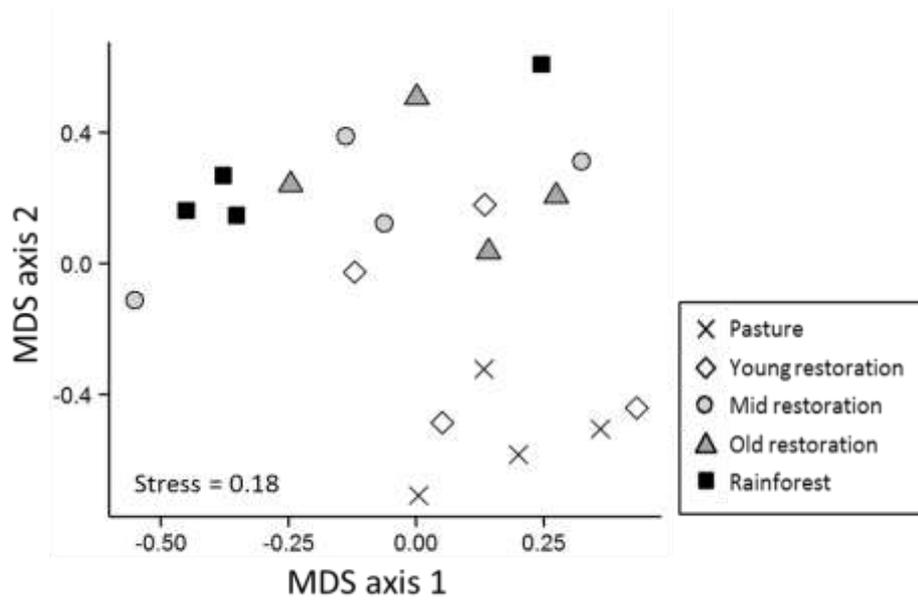
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594 **Fig. 2** Relationship between restoration age and observed species richness, number of individuals, total biomass
 595 and mean body mass of species (a–d), showing model-predicted mean (black line) \pm SE (grey shade) where
 596 relationships were significant ($p < 0.05$). Mean \pm SE observed species richness, number of individuals, total
 597 biomass and mean body mass of species in the different habitat categories (e–h). P = pasture; YR = young
 598 restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant
 599 differences ($P < 0.05$).

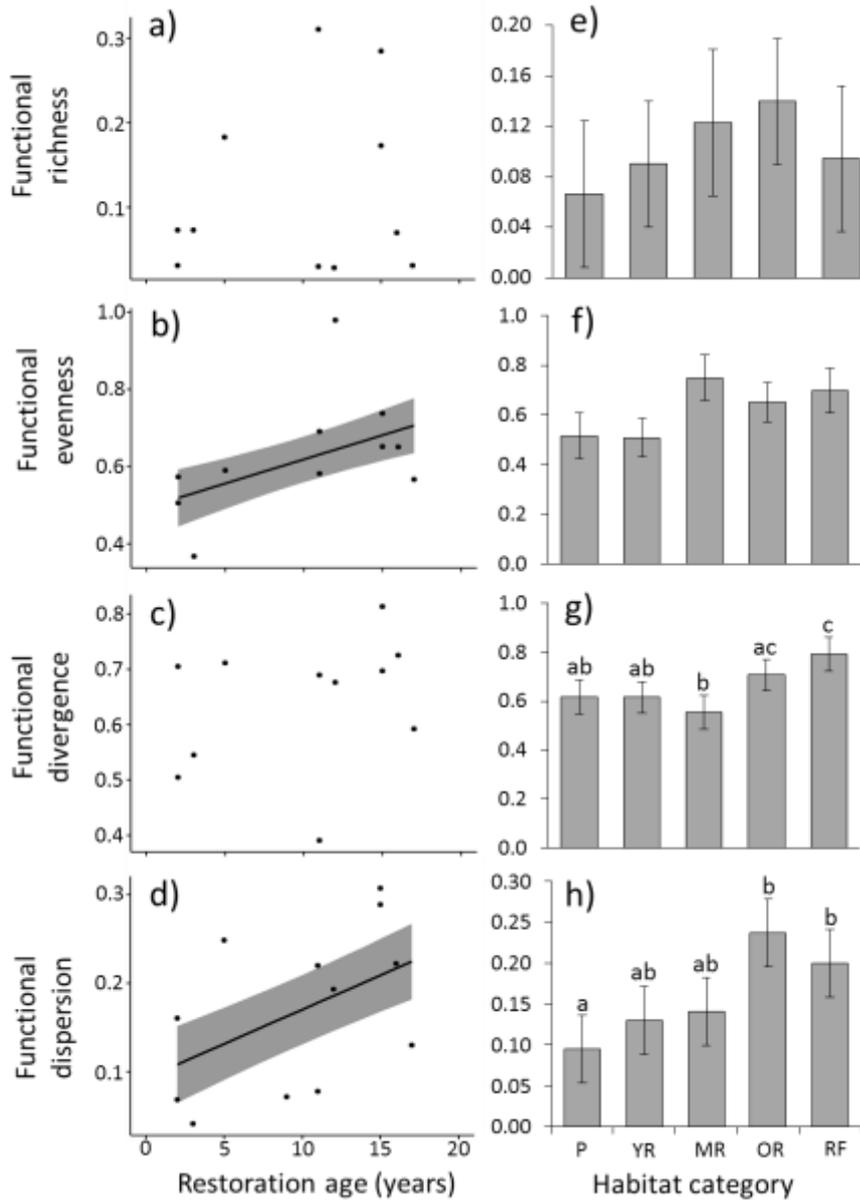
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601

602 **Fig. 3** Non-metric multidimensional scaling (MDS) ordination of community assemblages between the different
 603 habitat categories (pasture; young restoration; mid-age restoration; old restoration; and rainforest) at the site
 604 scale, based on square-root transformed, standardised abundance data ($r^2 = 0.86$).

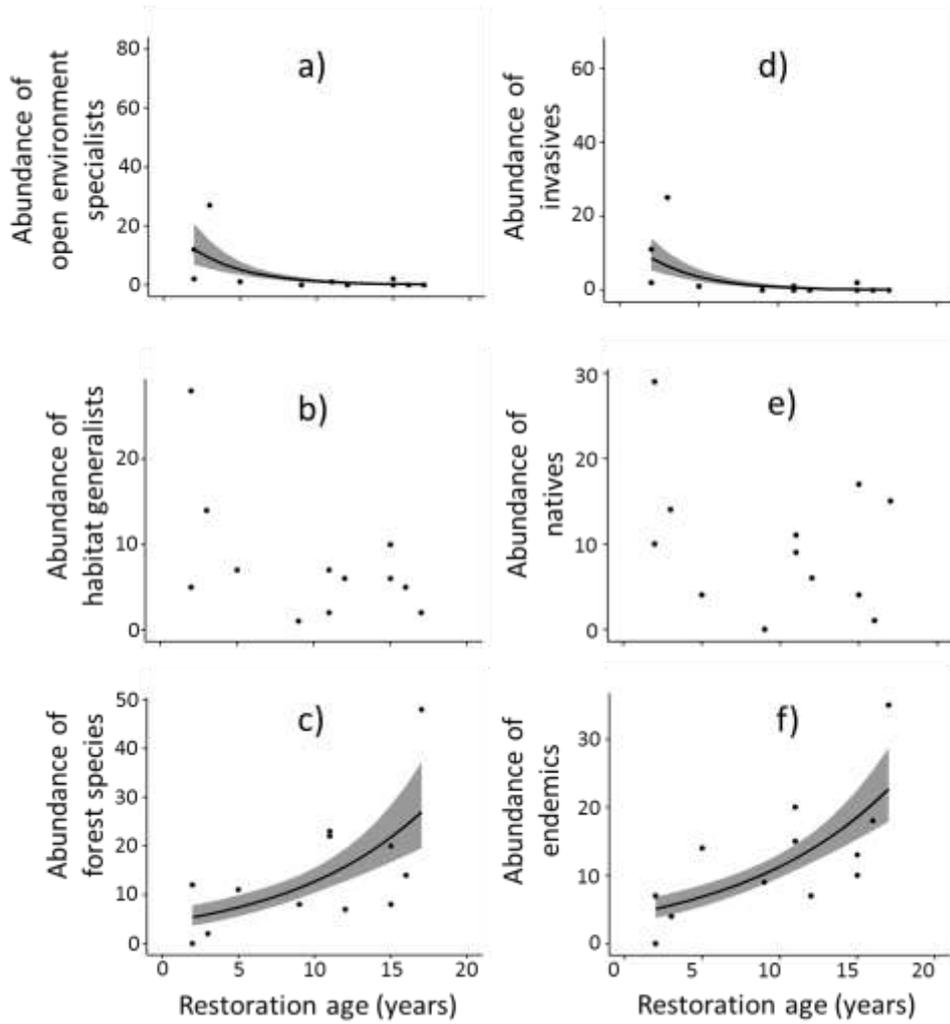
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607 **Fig. 4** Relationship between restoration age and functional richness, functional evenness, functional divergence
 608 and functional dispersion (a–d), showing model-predicted mean (black line) ± SE (grey shade) where
 609 relationships were significant ($p < 0.05$). Mean ± SE functional richness, functional evenness, functional
 610 divergence and functional dispersion in the different habitat categories (e–h). P = pasture; YR = young
 611 restoration; MR = mid-age restoration; OR = old restoration; RF = rainforest. Unlike letters indicate significant
 612 differences ($P < 0.05$).

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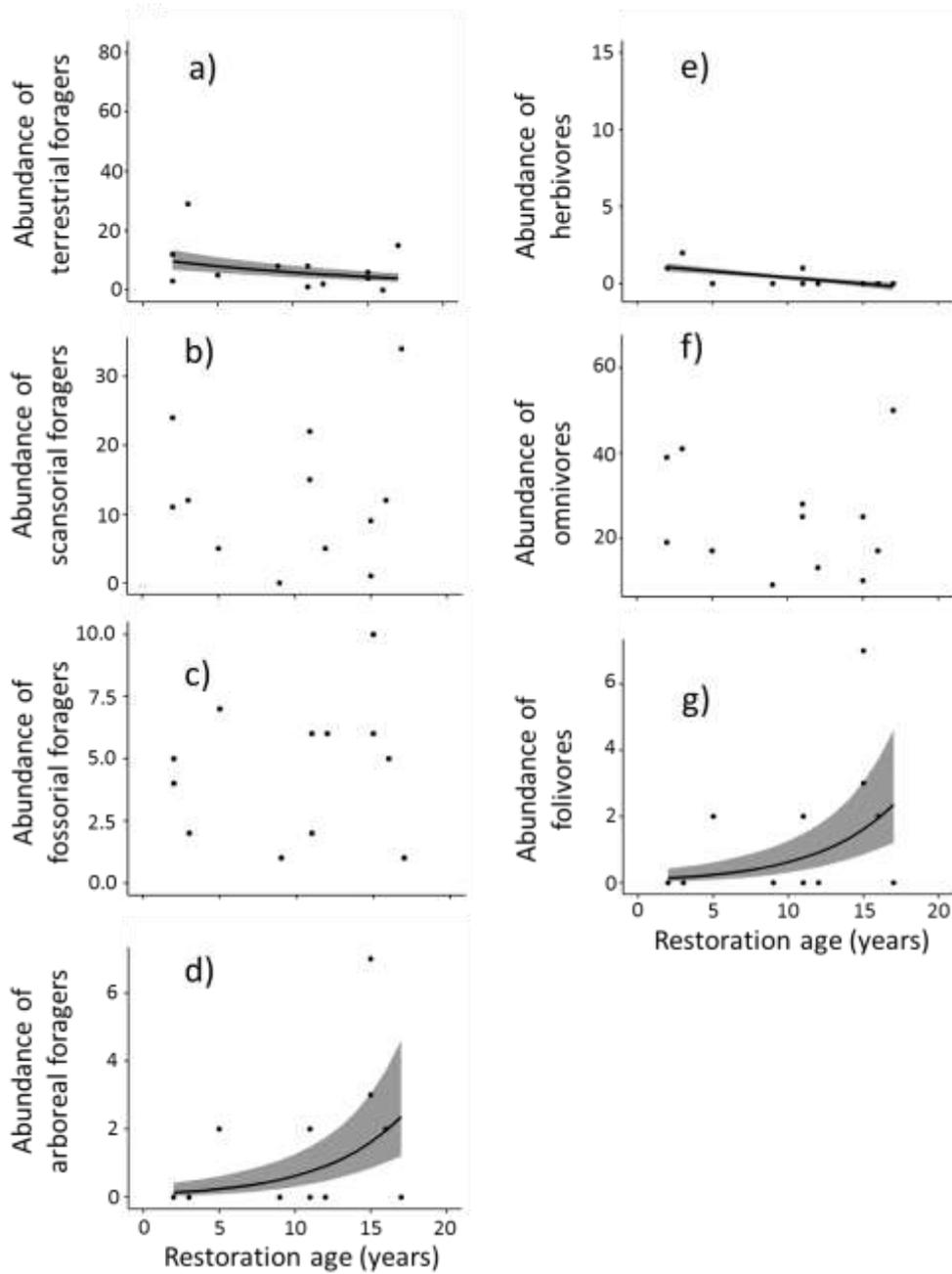


614

615 **Fig. 5** Relationship between restoration age and the total abundance of different functional guilds. Habitat
 616 specialisms: open environment specialists (a), habitat generalists (b) and forest species (c). Geographic range
 617 status: invasives (d), natives (e) and endemics (f), showing model-predicted mean (black line) \pm SE (grey
 618 shade) where relationships were significant ($p < 0.05$).

619

620



621

622 **Fig. 6** Relationship between restoration age and the total abundance of different foraging guilds: Foraging guild:
 623 terrestrial foragers (a), scansorial foragers (b), fossorial foragers (c) and arboreal foragers (d). Feeding guild:
 624 herbivores (e), omnivores (f), and folivores (g), showing model-predicted mean (black line) \pm SE (grey shade)
 625 where relationships were significant ($p < 0.05$).