RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

RESEARCH ARTICLE

Identifying the best method for restoring dung beetle biodiversity and function in the early stages of rainforest restoration

Rosa Menéndez[1,2], Geoff B. Monteith[3], Penny van Oosterzee[4,5], Noel D. Preece[4,5]

With less than half of the world's tropical forests remaining, ecological restoration is urgently needed to halt biodiversity loss. However, the efficacy of different active reforestation methods remains largely untested particularly with respect to the recovery of fauna during the early years of restoration. Here, we present the results of a long-term restoration project in the Australian Wet Tropics after 6 years of planting. Using dung beetles as bioindicators of restoration success, we investigated how the diversity and density of trees in experimental plots influence the recovery of dung beetle diversity and their ecological functions (dung removal and secondary seed dispersal). We found that after only 6 years since planting, a native dung beetle community, representing around 41% of the species found in the adjacent rainforest, has colonized the experimental plots. Plots with the highest diversity of trees (24 species planted) showed higher dung beetle diversity, dung removal, and seed dispersal but only when the density of trees on the plots was low. These plots also have higher species richness, diversity, and abundance of rainforest species, while the opposite trend was found for open-habitat species. Therefore, planting a higher diversity of trees appears to be the best method for the early recovery of rainforest dung beetle communities and their functions. This is particularly crucial at low tree density, which is a common issue in active restoration projects as tree mortality is relatively high in the early years.

Key words: biodiversity, dung removal, ecological restoration, ecosystem functioning, fauna recovery, secondary seed dispersal

Implications for Practice

- Assessing early stages of faunal recovery in a long-term active rainforest reforestation project provides insights on the most efficient restoration methods.
- The interaction between tree diversity and tree density appears crucial, with dung beetle diversity and functionality heading toward recovery early in diverse plantings but only when tree density is low. Different species of trees may provide complementary canopy structure which could create the right conditions for rainforest dung beetles even when tree density is low.
- We recommend assessing both biodiversity metrics and functions to fully monitor the recovery of highly functional and resilient rainforest in future ecological restoration projects.
- It remains to be seen how these early recovery trajectories translate to long-term restoration success.

Introduction

Tropical rainforests support two-third of terrestrial biodiversity (Dirzo & Raven 2003) and sequester large amounts of carbon (Watson et al. 2018), making them crucial for halting biodiversity loss and mitigating climate change globally. However, less than half of the world's tropical forests remain and much of these are degraded (Brancalion et al. 2019). Ecological restoration is urgently needed to increase ecosystem services, reverse biodiversity loss, and mitigate climate change impacts (Brancalion et al. 2019).

Despite increasing rainforest restoration efforts, the efficacy of different reforestation styles (including the importance of planting diversity and density) to contribute to biodiversity conservation is still largely untested and many restoration attempts have failed to deliver the desirable outcomes in a relevant time scale (Meli et al. 2017). Previous studies report that specialist animals may take some considerable time to colonize even

Authors contribution: all authors contributed to the conception and design of the research; RM, GBM carried out the data collection; GBM did the species identification; RM analyzed the data and wrote the first draft; all authors contributed to the editing of the manuscript.

[1]Lancaster Environment Centre, Lancaster University, Lancaster LA1 4YQ, U.K.
[2]Address correspondence to R. Menéndez, email r.menendez@lancaster.ac.uk
[3]Queensland Museum, Brisbane, PO Box 3300, South Brisbane BC, Queensland 4101, Australia
[4]College of Science and Engineering, Centre for Tropical Environmental and Sustainability Science, James Cook University, Cairns, Queensland 4811, Australia
[5]Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin, Northwest Territories 0909, Australia

doi: 10.1111/rec.14104
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.14104/suppinfo

diverse restoration plantings even though many rainforest faunal species are likely to colonize fairly quickly (Whitehead et al. 2014; Catterall 2018; Derhé et al. 2018).

Most studies use chronosequences (*space for time* substitution approach, Pickett 1989) in order to assess recovery (e.g. Lennox et al. 2018). While useful in assessing the time required for restoration plots to become similar to the original rainforest, it remains difficult to disentangle the key drivers of recovery which are fundamental in guiding recovery efforts. This is because habitat structure and forest age are correlated, and for most studies, starting points and planting methods are uncertain. Understanding key drivers of recovery is crucial for providing guidelines for successfully restoring rainforests that are both highly diverse and fully functioning ecosystems, in the most efficient way. As a result, long-term reforestation experiments controlling the starting point of restoration and testing different restoration approaches (e.g. active vs. passive) have begun in the last two decades (Hector et al. 2011; Holl & Aide 2011; Marshall et al. 2023). This study was carried out in one of these restoration experiments, the Thiaki rainforest restoration project (TRRP), established in 2010 in the Australian Wet Tropics (https://www.biome5.com.au/thiaki).

Monitoring the success of ecological restorations has tended to focus on assessing the recovery of plant diversity and forest structure. Recovery of faunal diversity, particularly the recovery of invertebrate groups and their associated ecosystem functions, has also begun to be considered in recent years (Sant'Anna et al. 2014; Derhé et al. 2016; Lawes et al. 2017;). Dung beetles are an excellent indicator group to assess forest recovery, as they are highly sensitive to forest disturbance (Nichols et al. 2013; Fuzessy et al. 2021; Noble et al. 2023) and play key roles in nutrient cycling, seed dispersal, and seedling establishment (Slade et al. 2007; Nichols et al. 2008; deCastro-Arrazola et al. 2023). As dung beetles rely on dung from other fauna their recovery provides insight on the likely recovery of this fauna (including birds, mammals, reptiles, and amphibians). Previous studies assessing the recovery of dung beetles and their associated function in reforestation plots have shown that native forests have higher dung beetle diversity compared to monoculture plantations, particularly of exotic tree species (López-Bedoya et al. 2022). Dung beetles can also reveal transition stages from a "pasture-like" to a "rainforest-like" dung beetle community in ecological restoration (Audino et al. 2014; Derhé et al. 2016).

Here, we investigated the efficacy of different reforestation approaches in delivering both diversity and functional recovery of dung beetle communities. We tested for differences in dung beetle species richness, diversity, abundance, and biomass as well as in two ecological functions performed by this group of insects (dung removal and secondary seed dispersal) between experimental rainforest reforestation plots that vary in tree species diversity and density, after 6 years since the planting was undertaken. We anticipated that close-spaced diverse plantings would more quickly develop a closed canopy. This would allow for faster colonization by rainforest specialist dung beetles resulting in a more diverse and rainforest-like dung beetle community. Due to the known relationship between diversity and ecosystem functions in dung beetles (deCastro-Arrazola et al. 2023), we expected that functional recovery would follow a similar pattern to diversity, but with the speed of recovery depending on the function and the traits of the species colonizing the plots.

Methods

Study Area and Experimental Design

The study was conducted in the TRRP, located in the southern Atherton Tablelands of far north Queensland, Australia (17.43°S, 145.51°E), at elevations between 900 and 1000 m Above sea level (ASL). The region has a humid tropical climate with mean winter and summer temperatures of 15.6 and 25.3°C, respectively. Median annual rainfall is 1234 mm and is seasonal with peak rainfall months from December through April (Bureau of Meteorology, http://www.bom.gov.au/climate/; accessed 15 Apr 2022). Rainforest was the predominant original vegetation of the site but most of the study site was cleared in the mid-1940s, with some cleared in the late 1980s (Preece et al. 2017) for beef cattle. Grazing ceased in 2010—the year before establishing the reforestation experimental plots. Except along the northern boundary, most of the cleared areas of Thiaki are directly contiguous with intact original rainforest (Fig. S1). There is thus the potential for dung beetles to move directly from one habitat to the other.

TRRP comprises 50 ha of non-native pasture of which 14 ha was planted in 2011 in 64 experimental plots, each of 0.25 ha (50 × 50 m), using native tree species in a factorial randomized block design testing tree species diversity (1 species, 6 species, and 24 species, plus controls with no planting) and with two planting spacings (1.75 and 3 m) resulting in plots with high and low density of trees, respectively (Fig. S1). Native saplings were grown from seeds of native rainforest species sourced from local forests and grown in forestry tubes to around 30 cm tall and sun-hardened before planting (details about the experiment are provided in Preece et al. 2023). The saplings were planted in eight blocks with one replicate for each of the six treatments and two control replicates in each block.

The Thiaki Dung Beetle Fauna

There are almost 500 species of native dung beetles in Australia, of which about 100 have yet to be described. The nomenclature and literature for the described species is summarized by Gunter et al. (2019). The undescribed species are designated within each genus by an alpha-numeric code used by Australian dung beetle workers (Gunter & Weir 2019). In addition, 25 species of non-native dung beetles have been introduced to Australia to disperse cattle dung and are now widespread. The nomenclature of these is summarized by Edwards et al. (2015).

Table 1 provides an annotated, benchmark list of the 34 species of dung beetles (31 native, 3 introduced) that have been recorded from all environments on Thiaki property since 2010. Table 1 documents habitat occurrence of each species based on all collections from all Thiaki habitats (21,622 specimens) on a simple presence/absence basis (rainforest vs. open, including reforestation plots and surrounding grassland area).

Full taxonomic citations are given for all. Some undescribed species cited by code number in earlier Thiaki studies (Derhé et al. 2016; Kenyon et al. 2016) have since been described and the list enables these to be linked. Faunistically, the list can be assumed to be quite complete since only one extra species (1 specimen of *Digitonthophagus gazella*) has been recorded since the first (2010) of four major surveys recorded 33 species.

Dung Beetle Sampling in the Experimental Plots 6 Years After Planting

In the present study, we examine the patterns of the 18 species recorded in the reforestation plots in 2017. For the analysis, we classified these species into two groups based on their habitat preference: rainforest species (>80% abundance found in rainforest compared to grasslands in 2010) and open-habitat species (<20% abundance found in rainforest compared to grasslands in 2010), with abundance data taken from Kenyon et al. (2016). We also classified the species into functional groups based on their nesting behavior: "tunnelers" species that dig tunnels under the dung deposit where they relocate dung masses and "rollers" species that construct a brood ball of dung, roll, and bury it away from the dung deposit.

Dung beetle sampling took place during the rainy season in January–February 2017, when most dung beetle species were active. This was 6 years since the planting of the experimental plots. Dung beetles were collected using baited pitfall traps. In each experimental plot, four traps were placed 25 m apart and baited alternately with fresh wallaby dung (50 g) and rotting mushrooms to attract a wider range of native dung beetle species (Ebert et al. 2019). Traps were open for 5 days and specimens were collected and preserved in 70% ethanol. All specimens collected were identified to species level by G. B. Monteith.

Dung Beetle Ecosystem Functions

Two dung beetle functions (dung removal and secondary seed dispersal) were measured using experimental dung baits set up in each plot. Bait consisted of 50 g of wallaby dung (two baits per plot) and left on the ground for 48 hours before the dung beetle sampling. Thirty round plastic beads (3 mm) were dispersed through the dung of each dung bait, to act as seed mimics. Any soil or dung beetles in the remaining dung were removed and all seed mimics present in the dung were removed and counted. The remaining dung was oven dried at 80°C until a constant weight was achieved. Dung ball controls (50 g wet mass; $n = 5$) were used to calculate the ratio of wet to dry dung mass to assess dry mass loss.

Data Analysis

All statistical analyses were performed in R (R Core Team 2021) and results graphically represented using the *ggplot2* package (Wickham 2016).

Differences in dung beetle species richness and diversity between controls and the tree diversity treatments were assessed using accumulation curves with bootstrapping-derived 95% CIs and by calculating Chao estimators (asymptotic diversity estimate) using the *iNEXT* package (Hsieh et al. 2016).

Generalized linear mixed effect models (GLMMs), performed in the *lme4* package (Bates et al. 2015), were used to assess the effect of tree diversity treatment on dung beetle abundance (total, open-habitat species, and rainforest species), biomass (total, tunnelers, and rollers) and ecological functions (dung removal and seed dispersal). Separate analyses were performed for plots with low and high tree density. The fixed factor consisted of four levels: the control (initial pasture) and three tree diversity treatments (plots planted with 1, 6, and 24 species of trees), with block included as a random factor in each model. The statistical significance of the fixed factor in each model was tested with analysis of variance by comparing each model with the null model without the fixed factor, differences between levels of the fixed factor were tested with post hoc Tukey test using the *mulcomp* package (Hothorn et al. 2008). Poisson error structure was used for abundance data, Gaussian for log-transformed biomass and dung removal, and negative binomial for seed dispersal, using the *DHARMa* package (Harting 2022) to assess the appropriate error structure for each dependent variable.

We also used GLMM to assess the influence of different dung beetle community attributes on explaining ecosystem functions (dung removal and seed dispersal). For this analysis, we excluded plots for which diversity or function were zero and our assumption here is that if some function was measured in a plot, then the beetles collected in the traps a few days later were likely responsible for that function. Plots in which no beetles or function was recorded (zero values) provide no relevant information to assess the relationship between diversity and function. Gaussian error structure was specified for dung removal and negative binomial for seed dispersal, with the *step* function used to select significant predictors. All predictors were standardized using z-scores and block was included as random effect.

Community attributes included: species richness, biomass (separate for tunnelers and rollers), community weighting mean for body mass (CWM_body) and a measure of functional diversity, Rao's quadratic entropy (RaoQ), which measures how even the community is in terms of trait's abundance (Finke & Snyder 2008). CWM_body and RaoQ were calculated using the *FD* package (Laliberté et al. 2014) using abundance data and two species traits: body mass (average dry body weight per species) and functional group (tunnelers or rollers). Trait data were obtained from Kenyon et al. (2016) and Derhé et al. (2016).

Results

A total of 297 dung beetles belonging to 18 species were collected in the experimental plots during the study in 2017, of which 9 were classified as rainforest species, 7 were open-habitat species, and 2 were non-native species (Table 1). The most abundant species was *Onthophagus cuniculus*, an open-habitat species, representing around 55% of all individuals. All open-habitat species were tunnelers (species belonging to the genus *Onthophagus*) while rainforest species included both tunnelers (*Coptodactyla depressa*) and rollers (*Temnoplectron politulum* and several species belonging to the genus *Amphistomus*).

Table 1. List of scarabaeine dung beetle species (alphabetic order), with taxonomic authorities, which have been detected in the cumulative total of 21,622 specimens collected in intact original rainforest, open pasture, and young reforestation plots on Thiaki during all surveys (2010, 2012, 2014, and 2017) that have been conducted. Undescribed species have code numbers as used in Australia, with their closest species relationship indicated in parentheses. Species described since the Thiaki study commenced have their former code number in parentheses. Introduced species are preceded by (*). For each species their presence in rainforest (RF) and in the reforestation plots or surrounding open pasture (OH) is provided. Vouchers of all species are in the Queensland Museum, Brisbane. For the species recorded in the Thiaki experimental plots in 2017 and used in the analysis in this paper we also provide their body size, functional group, habitat preference, and their abundance in 2017. Body size is taken from Kenyon et al. (2016) and Derhé et al. (2016). Habitat preferences are based on abundance data in 2010 before the experiment began (Kenyon et al. 2016) and are as follow: rainforest species (>80% abundance found in rainforest compared to grasslands) and open-habitat species (<20% abundance found in rainforest compared to grasslands in 2010).

	Presence					
Species name	*RF*	*OH*	*Body size (mg)*	*Functional group*	*Habitat preference*	*Number of individuals*
Amphistomus complanatus (Matthews 1974)	x	x	9.60	Roller	Rainforest species	5
Amphistomus NQ3 (new sp. near *A. calcaratus*; Macleay 1871)	x					
Amphistomus NQ4 (new sp. near *A. pygmaeus* (Matthews 1974)	x	x	3.21	Roller	Rainforest species	1
Amphistomus NQ5 (new sp. near *A. pygmaeus* (Matthews 1974)	x	x	1.55	Roller	Rainforest species	8
Boletoscapter cornutus (Macleay 1887)	x	x	8.50	Tunneler	Rainforest species	3
Coptodactyla depressa (Paulian 1933)	x	x	51.25	Tunneler	Rainforest species	6
C. onitoides (Gillet 1925)	x					
Demarziella interrupta (Carter 1936)		x	2.95	NA	Open-habitat species	1
Lepanus globulus (Macleay 1887)	x					
L. dichrous (Gillet 1925) (formerly *Lepanus nitidus-S*)	x	x	1.40	Roller	Rainforest species	1
L. vangerweni (Gunter & Weir, 2021; formerly *Lepanus nitidus*-L or *NQ9*)	x	x				
L. reidi (Gunter & Weir 2019; formerly *Lepanus NQ5*)	x					
L. pisoniae (Lea 1923)	x					
**Onitis vanderkelleni* (Lansberge, 1886)		x				
Onthophagus bornemisszanus (Matthews 1972)		x	20.00	Tunneler	Open-habitat species	22
O. bundara (Storey & Weir, 1990)	x	x				
O. capella (Kirby, 1818)	x	x	52.95	Tunneler	Open-habitat species	30
O. capelliformis (Gillet, 1925)	x	x				
O. cuniculus (Macleay, 1864)		x	19.70	Tunneler	Open-habitat species	165
O. darlingtoni (Matthews 1972)	x					
O. dicranocerus (Gillet, 1925)	x	x	31.04	Tunneler	Rainforest species	4
**Digitonthophagus gazella* (Fabricius, 1787)		x	58.57	Tunneler	Open-habitat species	1
O. millamilla (Matthews 1972)	x					
**O. nigriventris* (d'Orbigny, 1902)		x	38.31	Tunneler	Open-habitat species	1
O. paluma (Matthews 1972)		x	28.50	Tunneler	Open-habitat species	41
O. pillara (Matthews 1972)	x	x	4.04	Tunneler	Open-habitat species	1
O. rubicundulus (Macleay, 1871)	x	x				
O. thoreyi (Harold, 1868)		x	23.10	Tunneler	Open-habitat species	1
O. wagamen (Matthews 1972)	x					
O. waminda (Matthews 1972)	x					
O. wilgi (Matthews 1972)	x	x	1.08	Tunneler	Rainforest species	1
Temnoplectron aeneopiceum (Matthews 1974)	x					
T. bornemisszai (Matthews 1974)	x					
T. politulum (Macleay, 1887)	x	x	18.56	Roller	Rainforest species	5

Dung Beetle Diversity, Abundance, and Biomass

For all dung beetles and open-habitat species, estimated species richness did not differ between diversity treatments either calculated as rarefaction or Chao estimators but species diversity (both Shannon and Simpson) was higher in plots with 24 tree species planted compared to both the control plots and the other tree diversity treatments (Table S1; Fig. 1A & 1B). For rainforest species, there were significant differences between treatments on both species richness and diversity, with plots with 6 and 24 tree species planted

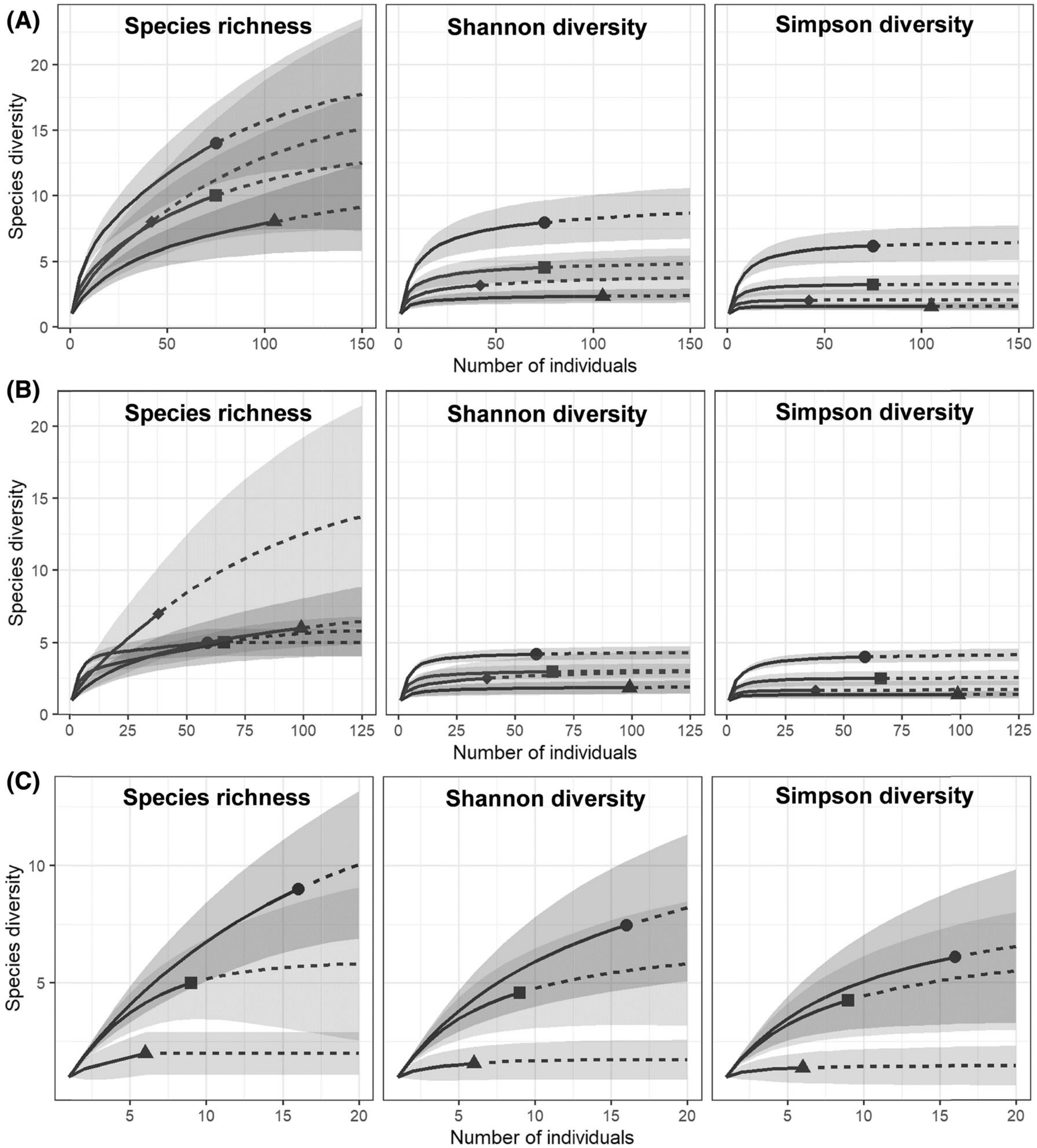

Figure 1. Individual-based rarefaction curves for three measures of species diversity (species richness, Shannon, and Simpson diversity) for all dung beetles (A), open-habitat species (B), and rainforest species (C) recorded in control plots (diamond) and plots with 1 species (triangle), 6 species (square), and 24 species (circle) of planted trees. Continuous lines are rarefaction, dashed lines extrapolation, and shaded areas bootstrapping-derived 95% CIs.

showing higher species richness than controls and monocultures (Table S1; Fig. 1C).

Total dung beetle abundance differed significantly between diversity treatments, but the differences were dependent on the density of trees in the plot (Table 2). In plots with low density of trees, total number of beetles was significantly lower in the six tree species treatment and control compared to the other two treatments (Fig. 2A). However, in plots with high density of trees, total number of beetles was significantly lower in the 24 tree species treatment and control (Fig. 2B). The abundance of open-habitat species showed a similar pattern as for total abundance (Table 2; Fig. 2C & 2D). For rainforest species, significant differences were also observed between tree diversity treatments (Table 2), but in this case abundance was significantly higher in the 24 tree species treatment compared to the control plots when tree density was low (Fig. 2E) and marginally significant when tree density was high (Fig. 2F).

In plots with low density of trees, biomass did not differ between tree diversity treatments either for all beetles, tunnelers only, or rollers only (Table 2; Fig. 3A, 3C, & 3E). For plots with high density of trees, biomass was significantly lower in the

Table 2. Differences in dung beetle abundance and functions between plots with different tree diversity treatments (control, 1 species, 6 species, and 24 species of trees) based on GLMMs with tree diversity as fixed factor and block as a random factor. Results are presented separately for plots with low and high density of trees. Significant differences are highlighted in bold.

Dependent variable	*Tree density*	*Chi-squared*	p *Value*
Total abundance	Low	30.467	**<0.001**
	High	47.045	**<0.001**
Open-habitat species abundance	Low	23.701	**<0.001**
	High	48.733	**<0.001**
Rainforest species abundance	Low	16.398	**<0.001**
	High	9.135	**0.028**
Total biomass	Low	1.357	0.716
	High	11.117	**0.011**
Tunneler's biomass	Low	0.399	0.941
	High	12.740	**0.005**
Roller's biomass	Low	3.660	0.301
	High	2.223	0.527
Dung removal	Low	9.726	**0.021**
	High	7.558	0.056
Seed dispersal	Low	8.950	**0.030**
	High	2.265	0.519

24 tree species treatment for all beetles and tunnelers only, but roller's biomass did not significantly differ between tree diversity treatments (Table 2; Fig. 3B, 3D, & 3F).

Dung Removal and Secondary Seed Dispersal

Seed dispersal was positively correlated with dung removal (for all plots: $r = 0.82$, $p < 0.001$; and excluding plots with zeros: $r = 0.67$, $p < 0.001$; Fig. S2). This is to be expected as the former is a direct consequence of the latter because the seed mimics were placed within the dung, and so the number of seeds not found in the remaining dung or in the soil surface after 48 hours were likely dispersed by the dung beetles when using the dung.

Dung removal significantly differed between tree diversity treatments in plots with low density of trees (Table 2), being higher in the 24 tree species treatment compared to the control and the single and six tree species treatments (Fig. 4A). In plots with high density of trees, there were only marginally significant differences in dung removal between tree diversity treatments (Table 2; Fig. 4B).

Seed dispersal was also significantly higher in the 24 tree species treatment compared to the control and the single tree species treatments (Table 2; Fig. 4C) in plots with low density of trees, but no differences were observed between treatments in plots with high density of trees (Table 2; Fig. 4D).

Dung removal was best explained by species richness and biomass (Fig. 5; Table S2), increasing significantly with species richness ($r^2 = 0.10$, $F = 5.046$, $df = 1$; 40.78, $p = 0.030$) and with both roller's biomass ($r^2 = 0.33$, $F = 22.463$, $df = 1$; 40.95, $p < 0.001$) and tunneler's biomass ($r^2 = 0.27$, $F = 12.258$, $df = 1$; 30.28, $p = 0.002$). However, seed dispersal was not explained by any of the community attributes analyzed (Table S2).

Discussion

We investigated how methods of actively restoring rainforest (diversity and density of planted trees) in pasture sites influence the recovery of dung beetle communities and their ecological functions. Our aim was to identify the methods that best delivered the recovery of biodiversity and function at the early stages of restoration. We recorded 18 species of dung beetles in the experimental plots, doubling the number of species recorded in the plots before planting in 2010 (Kenyon et al. 2016). In terms of rainforest species, nine species were recorded in the plots, representing around 41% of the species found in the adjacent rainforest (Kenyon et al. 2016). This indicates that after only 6 years since planting a native dung beetle community has colonized the planted plots, likely resulting from an increase in tree cover which provides the right environmental conditions as well as a potential increase in resource availability. The composition of the dung beetle community in the planted plots is on a trajectory to become a more rainforest-like community, with the methods used for reforestation significantly speeding up this process. We found that planting a higher diversity of trees appears to be the best method for restoring dung beetle communities and their functions and this is particularly important when the density of planted trees is low, which has important implications for future reforestation project design.

Recovery of Dung Beetle Diversity and Shift in Community Composition

We found that total species richness was not significantly different between the control and any of the diversity treatments. This was due to the fact that dung beetle communities in the planted plots were dominated by native dung beetle species that are associated with open-habitats, which are able to tolerate drier and hotter conditions in both controls and plots with low canopy cover. These species are also able to colonize pastures in the region, but they are not present in the remnant natural rainforest (Derhé et al. 2016). When canopy cover increases in the restoration plots, the open-habitat species are replaced by rainforest species which are better adapted to the humid conditions characteristic of the rainforest. We observed that species richness of rainforest species was significantly higher in plots planted with many species of trees, particularly the 24 tree species treatment. These results are consistent with previous studies on dung beetle communities comparing diverse restoration plantings of similar ages both in the region (Derhé et al. 2016) and in other regions (Davis et al. 2002; Audino et al. 2014). In our previous work, using a chronosequence (2–17 years since planting) of ecological rainforest restoration sites in the Atherton Tablelands, we found no significant differences in total species richness between pastures and young restorations (<5 years) but higher species richness after 9 years since planting (Derhé et al. 2016). Studies in the same region assessing ant diversity show similar results, where ant communities in restoration sites older than 5–10 years converged toward those of mature rainforest (Lawes et al. 2017).

Although the replacement of open-habitat by rainforest species is not yet completed in our plots after 6 years, the abundance data already shows a clear trend toward the transition.

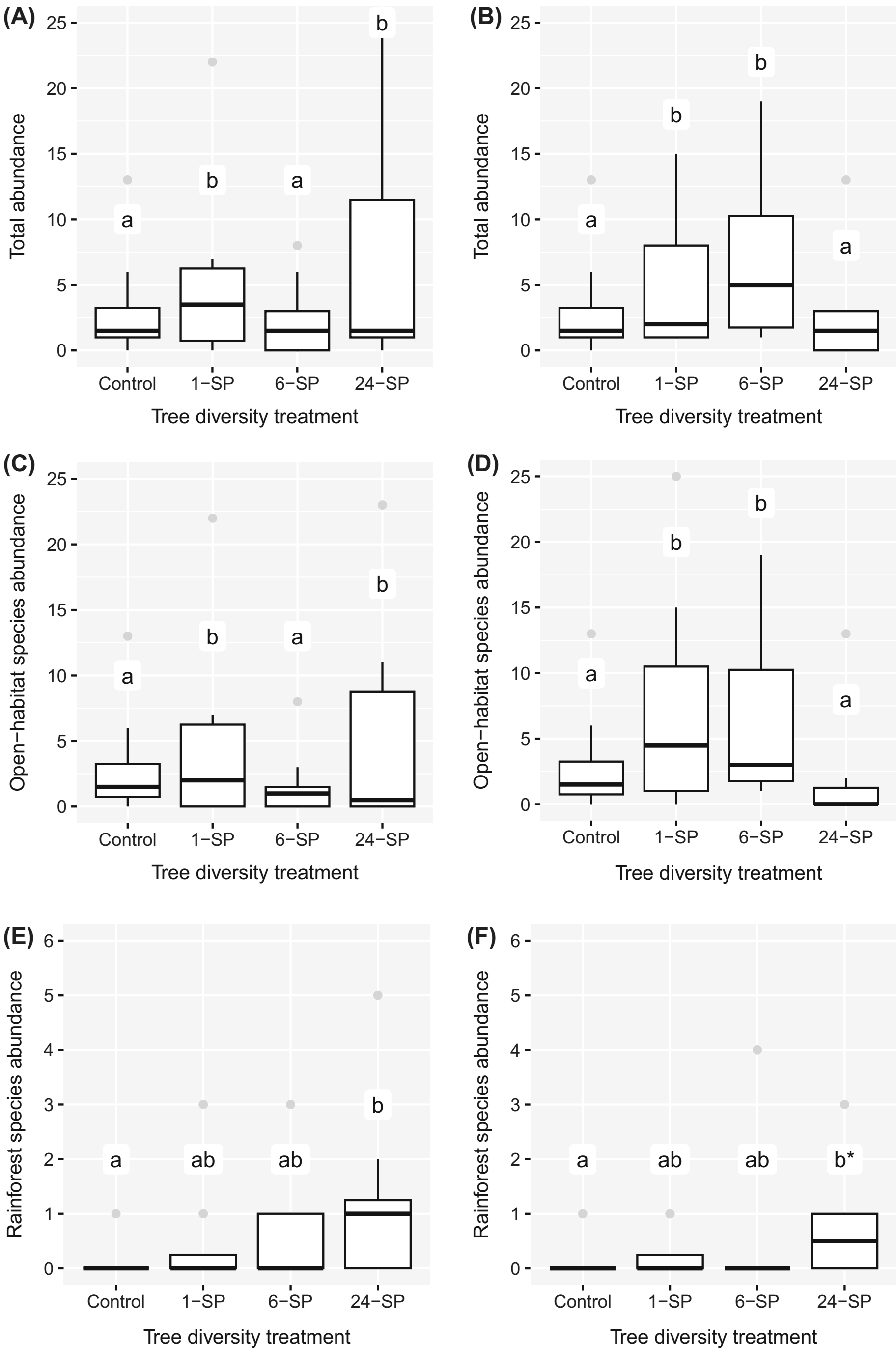

Figure 2. Abundance of all dung beetles, open-habitat species, and rainforest species in relation to tree diversity treatments and separately for plots with low (A, C, E) and high (B, D, F) density of trees. Different letters above bars indicate significant differences between treatments at p less than 0.05 (* indicates $p < 0.1$).

Open-habitat species were more abundant in plots planted with one or six species of trees, particularly in plots with high density of trees whereas the opposite result was observed for rainforest species. This change in the dung beetle community from species that prefer open-habitat to species that prefer rainforest may be driven by canopy development, as dung beetle community composition is known to be closely related to vegetation structure, particularly canopy cover (Nichols et al. 2007; Filgueiras et al. 2011; Lennox et al. 2018). In our study region, active plantings with relatively high density of native trees can develop a closed canopy within 5 years and promote rainforest conditions (Kanowski & Catterall 2010), reflected in the Thiaki reforestation where canopy closure in many plots occurred around 3–5 years after planting.

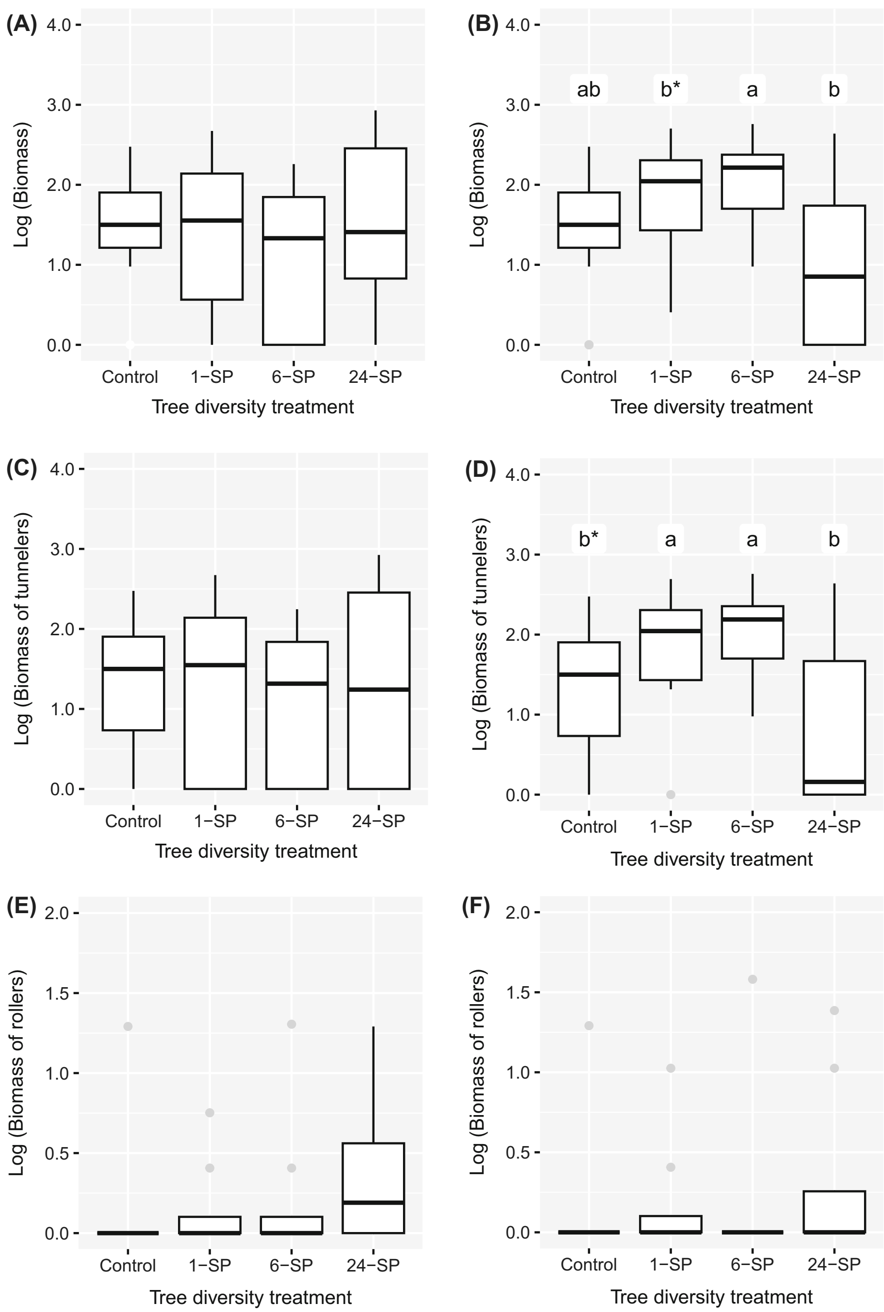

Figure 3. Biomass of all dung beetles (A, B), tunnelers (C and D) and rollers (E, F) in relation to tree diversity treatments and separately for plots with low (A, C, E) and high (B, D, F) density of trees. Different letters above bars indicate significant differences between treatments at p less than 0.05 (* indicates $p < 0.1$).

The abundance of rainforest species increased with increasing tree diversity within the plots, showing significantly higher values than the control plots that have no trees, likely due to environmental conditions inside these plots having become more favorable to rainforest species (Audino et al. 2014; Díaz-García et al. 2020). Increase in canopy cover is accompanied by an increase in leaf litter, leading to shading and higher humidity as well as more stable microclimatic conditions in the forest floor (Davis et al. 2002; Gómez-Cifuentes et al. 2019; Díaz-García et al. 2020), which may increase adult beetle activity and larval survival. Most of the rainforest species collected in our plots were rollers, species which transport dung for nesting across the forest floor before burying it where humid conditions prevent dung ball desiccation. Moreover, rollers have been reported to dig shallower nests than tunnelers (Gregory et al. 2015), so the hotter and drier conditions experienced in pastures and open canopy forest are likely to increase the risk of larval mortality in shallow nests (Mamantov & Sheldon 2020). Despite the increase in rainforest species in the experimental plots, their abundance is still very low compared

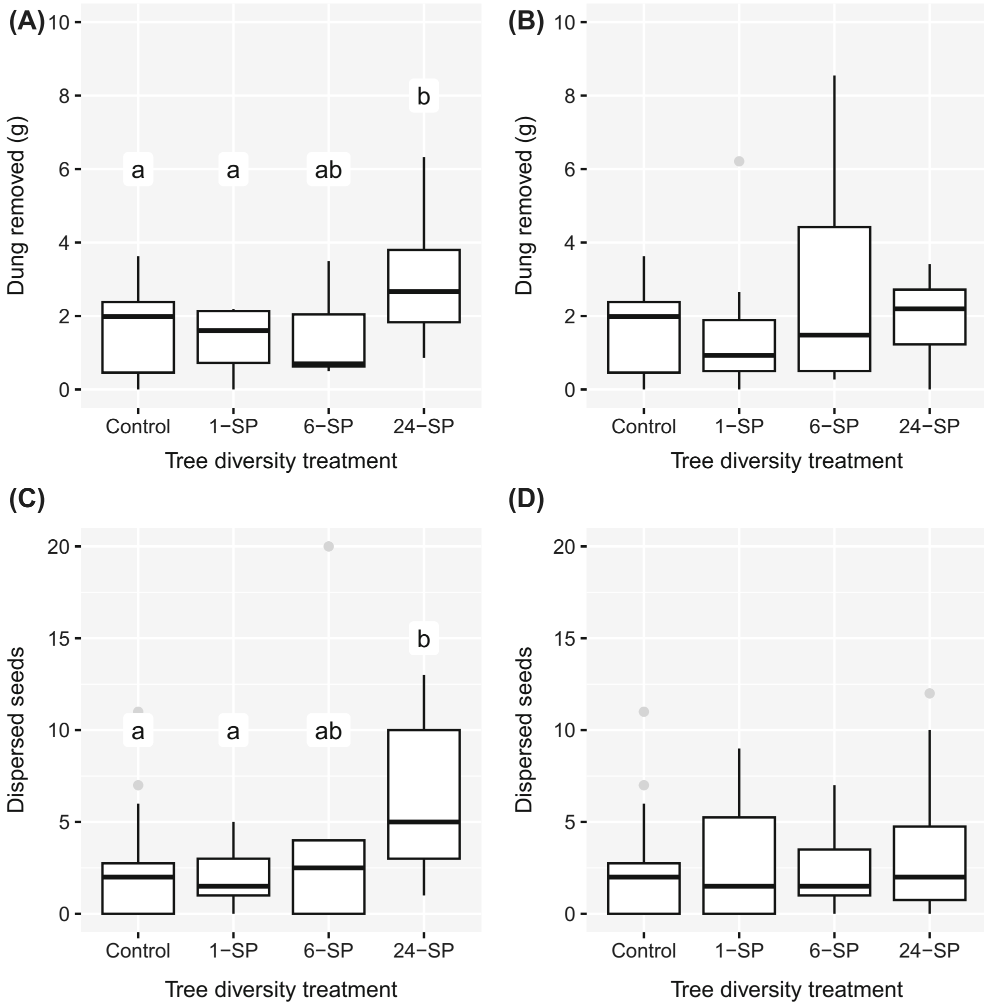

Figure 4. Dung removal and seed dispersal in relation to tree diversity treatments and separately for plots with low (A, C) and high (B, D) density of trees. Different letters above bars indicate significant differences between treatments at $p < 0.05$.

to the numbers recorded in the rainforest (Kenyon et al. 2016), which could indicate individuals moving to and from the nearby rainforest rather than there being resident populations.

Another potential explanation for the higher species richness and abundance of rainforest species toward more diverse plantings is that plots with high diversity of trees provide higher diversity of resources for dung beetles, both in terms of diversity of dung types (mammal and other vertebrate species) and other resources (fruits, carrion, and fungi). Our previous research has shown that the transition from pasture-like to rainforest-like small mammal communities in diverse reforestation plantings in our study region occurs progressively over the years after planting, with total biomass and abundance increasing with time since planting (Derhé et al. 2018). So, it is possible that more dung could be available in plots planted with 6 and 24 tree species compared to control and monoculture plots. Moreover, many of the rainforest dung beetles in Australia belong to endemic genera with many species having a diverse diet, being attracted to rotten fruit, fungi, carrion as well as dung (Ebert et al. 2019). Plots with a higher diversity of trees could provide a wider range of these other resources.

Dung beetle biomass was lower in plots planted with 24 tree species where the density of trees was high. This can be explained by both a lower abundance of open-habitat species on these plots and by the smaller body size of species found on those plots. In most tropical regions, rainforests contain large-bodied species, that are lost in degraded forest and plantations, leading to a reduction in beetle biomass (Larsen et al. 2008; Hidayat et al. 2010; Filgueiras et al. 2011). However, in our study region, rainforest dung beetle species are of small to medium body size (Kenyon et al. 2016), with only a few exceptions such as *Coptodactyla depressa*. Although we recorded this large species in our experimental plots, numbers were very low compared to those in mature rainforest where it is a dominant species.

Finally, although total species richness did not differ significantly between experimental plots, species diversity was highest in the plots planted with 24 tree species, indicating that the dung beetle community in these plots is becoming less dominated by a few species and evidencing the shift from a pasture/open-forest to a rainforest dung beetle community.

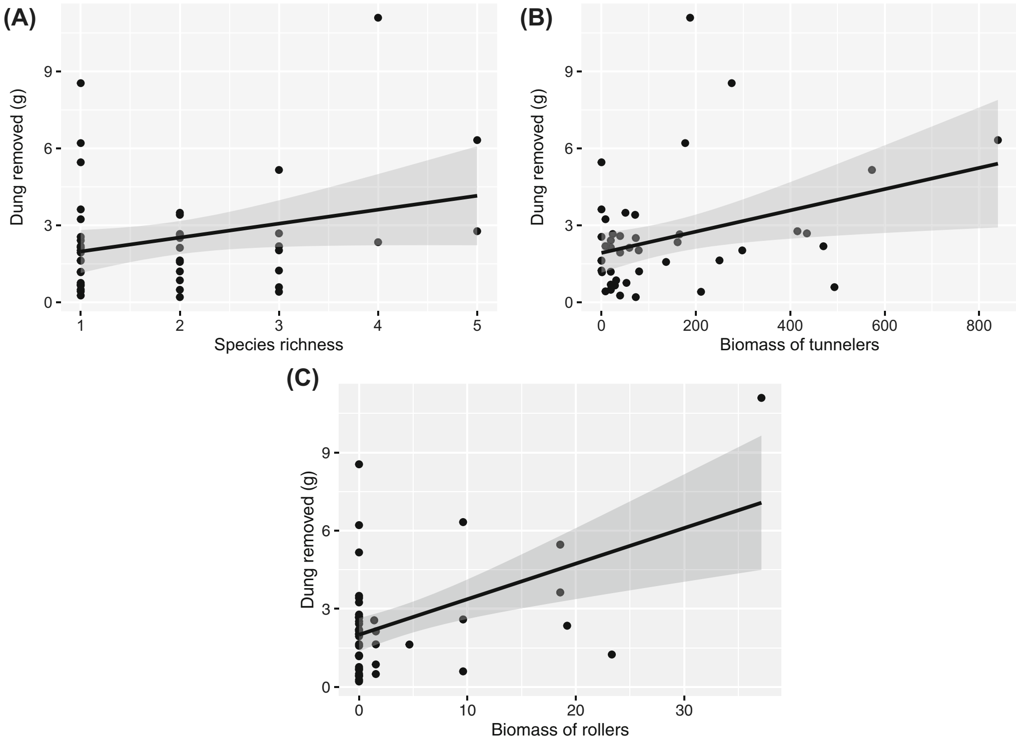

Figure 5. Relationship between dung removal and dung beetle diversity metrics: species richness (A), tunneler's biomass (B) and roller's biomass (C). Raw data (dots) and GLMM best model fit (solid line) and 95% CIs (shadow) are presented.

Interaction Between Tree Diversity and Density Determines the Recovery of Dung Beetle Functions

We found that both dung removal and secondary seed dispersal were significantly different between tree diversity treatments, but the effect was dependent on the density of trees in the plot. Higher function was achieved in plots planted with 24 tree species compared to controls, monocultures, and six species, but only when tree density was low, whereas no differences were observed between tree diversity treatments with high tree density. Several studies have reported a decline in dung beetle functions (dung removal and/or seed dispersal) with rainforest modification and degradation (Braga et al. 2013; Santos-Heredia et al. 2018; Noriega et al. 2021). Moreover, dung beetle functions appear to be better explained by measures of functional diversity (Derhé et al. 2016; Milotić et al. 2019), with several species' traits driving function (deCastro-Arrazola et al. 2020). In particular, dung relocation strategy (rollers vs. tunnelers), body size, and other morphological traits associated with digging have been reported to directly influence function (deCastro-Arrazola et al. 2023).

We found that dung removal was best explained by species richness and biomass rather than functional diversity metrics, such as functional evenness or mean body size. This apparent contradiction with previous studies may be due to the fact that in early stages of rainforest restoration when the number of species is still low and the most functionally efficient species are missing, similar levels of dung removal could be achieved by more species being present or by higher numbers of one or a few species with particular traits (tunnelers vs. rollers). In northern temperate regions, tunnelers have been recorded to burrow more dung than dwellers (dung beetles that lay their eggs in dung or at the dung–soil interface), at least in the first month after dung deposition but this difference disappeared after 1 year (Nervo et al. 2017; Buse & Entling 2020). Complementarity between functional groups and species of different body size has been shown to also lead to greater dung removal (Slade et al. 2007; Kenyon et al. 2016; Menéndez et al. 2016), with large tunnelers having a disproportionate (large) effect on dung removal in the tropics (Slade et al. 2007).

In our experimental plots, it appears that higher dung removal was achieved in different plots by alternative mechanisms, complementary effects (higher species richness), or dominance effect (higher biomass of a particular functional group). Seed dispersal was also higher in the 24 tree species plots and positively correlated with dung removal, but was not significantly explained by any of the diversity metrics analyzed. Tunnelers have been reported to disperse more seeds than rollers (Slade et al. 2007), but as seeds are a contaminant, dung beetles have been reported to clean the dung before burying it, with large seeds more often discarded than small seeds (Andresen & Levey 2004; Braga et al. 2017; Pedersen & Blüthgen 2022). As the size of our mimic seeds (3 mm) is relatively large compared to the size of the beetles present in the plots (body length ranges from 3.3 to 13.5 mm, with an average body length of 9.8 mm for the most abundant species; sizes taken from Matthews 1972, 1974, 1976), this could explain the lack of relationship between diversity metrics and seed dispersal in our case. The mechanism driving high ecosystem functioning levels are dependent on the traits, functions, and taxa considered (Gagic et al. 2015; Slade et al. 2017) but also the environmental context (Griffiths et al. 2015).

In conclusion, we found that at early stages of reforestation, diverse tree plantings accelerate the recovery of both dung beetle communities and their functions, more so when the density of trees in the plots was low. This is important as many reforestation projects suffer from high tree mortality in the first years (Evans & Turnbull 2004; Engert et al. 2020; Banin et al. 2022), including our experimental plots in which up to 19% tree loss was recorded in the first 4 months after planting, and we found that increasing tree diversity could buffer against tree loss and improve the success of restoration in the long term (Preece et al. 2023). We found that some functionality can be recovered even before differences in dung beetle species richness are detected, with different mechanisms potentially involved in delivering function.

Acknowledgments

This work contributes to Australian Research Council Linkage project LP0989161 *Cost-effective reforestation for biodiversity and carbon in the wet tropics*; funding was provided to establish the experiment, maintain all the plantings and undertake some research. Funding for the 2017 sampling was provided by the British Ecological Society (Research Grant SR16/1297). We are grateful to E. Kruck for hosting R.M. and G.B.M. in her home during the fieldwork and looking after us so well. We thank Lancaster University, James Cook University, and Charles Darwin University for continuing support. We acknowledge the Traditional Custodians of the Ngadjon lands where this work was conducted.

LITERATURE CITED

Andresen E, Levey DJ (2004) Effects of dung and seed size on secondary dispersal, seed predation, and seedling establishment of rain forest trees. Oecologia 139:45–54. https://doi.org/10.1007/s00442-003-1480-4

Audino LD, Louzada J, Comita L (2014) Dung beetles as indicators of tropical forest restoration success: is it possible to recover species and functional diversity? Biological Conservation 169:248–257. https://doi.org/10.1016/j.biocon.2013.11.023

Banin LF, Raine EH, Rowland LM, Chazdon RL, Smith SW, Rahman NEB, et al. (2022) The road to recovery: a synthesis of outcomes from ecosystem restoration in tropical and sub-tropical Asian forests. Philosophical Transactions of the Royal Society B 378:20210090. https://doi.org/10.1098/rstb.2021.0090

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models Usinglme4. Journal of Statistical Software 67:1–48. https://doi.org/10.18637/jss.v067.i01

Braga RF, Carvalho R, Andresen E, Anjos DV, Alves-Silva E, Louzada J (2017) Quantification of four different post-dispersal seed deposition patterns after dung beetle activity. Journal of Tropical Ecology 33:407–410. https://doi.org/10.1017/S0266467417000335

Braga RF, Korasaki V, Andresen E, Louzada J (2013) Dung beetle community and functions along a habitat-disturbance gradient in the Amazon: a rapid assessment of ecological functions associated to biodiversity. PLoS One 8:e57786. https://doi.org/10.1371/journal.pone.0057786

Brancalion PHS, Niamir A, Broadbent E, Crouzeilles R, Barros FSM, Almeyda Zambrano AM, et al. (2019) Global restoration opportunities in tropical rainforest landscapes. Science Advances 5:eaav3223. https://doi.org/10.1126/sciadv.aav3223

Buse J, Entling MH (2020) Stronger dung removal in forests compared with grassland is driven by trait composition and biomass of dung beetles. Ecological Entomology 45:223–231. https://doi.org/10.1111/een.12793

Catterall CP (2018) Fauna as passengers and drivers in vegetation restoration: a synthesis of processes and evidence. Ecological Management and Restoration 19:54–62. https://doi.org/10.1111/emr.12306

Davis AL, Van Aarde RJ, Scholtz CH, Delport JH (2002) Increasing representation of localized dung beetles across a chronosequence of regenerating vegetation and natural dune forest in South Africa. Global Ecology and Biogeography 11:191–209. https://doi.org/10.1046/j.1466-822X.2002.00283.x

de Castro-Arrazola I, Andrew NR, Berg MP, Curtsdotter A, Lumaret JP, Menéndez R, et al. (2023) A trait-based framework for dung beetle functional ecology. Journal of Animal Ecology 92:44–65. https://doi.org/10.1111/1365-2656.13829

de Castro-Arrazola I, Hortal J, Noriega JA, Sánchez-Piñero F (2020) Assessing the functional relationship between dung beetle traits and dung removal, burial, and seedling emergence. Ecology 101:e03138. https://doi.org/10.1002/ecy.3138

Derhé MA, Murphy H, Monteith GB, Menéndez R (2016) Measuring the success of reforestation for restoring biodiversity and ecosystem functioning. Journal of Applied Ecology 53:1714–1724. https://doi.org/10.1111/1365-2664.12728

Derhé MA, Murphy HT, Preece ND, Lawes MJ, Menéndez R (2018) Recovery of mammal diversity in tropical forests: a functional approach to measuring restoration. Restoration Ecology 26:778–786. https://doi.org/10.1111/rec.12582

Díaz-García JM, López-Barrera F, Pineda E, Toledo-Aceves T, Andresen E (2020) Comparing the success of active and passive restoration in a tropical cloud forest landscape: a multi-taxa fauna approach. PLoS One 15:e0242020. https://doi.org/10.1371/journal.pone.0242020

Dirzo R, Raven PH (2003) Global state of biodiversity and loss. Annual Review of Environment and Resources 28:137–167. https://doi.org/10.1146/annurev.energy.28.050302.105532

Ebert KM, Monteith GB, Menéndez R, Merritt DJ (2019) Bait preferences of Australian dung beetles (Coleoptera: Scarabaeidae) in tropical and subtropical Queensland forests. Austral Entomology 58:772–782. https://doi.org/10.1111/aen.12396

Edwards PB, Wilson P, Wright J (2015) Pages 3169. Introduced dung beetles in Australia. 3rd ed. CSIRO Publishing, Clayton South, Victoria, Australia. https://doi.org/10.1071/9781486300709

Engert JE, Vogado NO, Freebody K, Byrne B, Murphy J, Sheather G, Snodgrass P, Nugent L, Lloyd D, Laurance SGW (2020) Functional trait representation differs between restoration plantings and mature tropical rainforest. Forest Ecology and Management 473:118304. https://doi.org/10.1016/j.foreco.2020.118304

Evans J, Turnbull J (2004) Plantation forestry in the tropics. 3rd ed. Oxford University Press, Oxford, United Kingdom. https://doi.org/10.1093/oso/9780198529941.001.0001

Filgueiras BKC, Iannuzzi L, Leal IR (2011) Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biological Conservation 144:362–369. https://doi.org/10.1016/j.biocon.2010.09.013

Finke DL, Snyder WE (2008) Niche partitioning increases resource exploitation by diverse communities. Science 321:1488–1490. https://doi.org/10.1126/science.1160854

Fuzessy LF, Benítez-López A, Slade EM, Bufalo FS, Magro-de-Souza GC, Pereira LA, Culot L (2021) Identifying the anthropogenic drivers of declines in tropical dung beetle communities and functions. Biological Conservation 256:109063. https://doi.org/10.1016/j.biocon.2021.109063

Gagic V, Bartomeus I, Jonsson T, Taylor A, Winqvist C, Fischer C, et al. (2015) Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proceedings of the Royal Society of London B: Biological Sciences 282:142620. https://doi.org/10.1098/rspb.2014.2620

Gómez-Cifuentes A, Giménez Gómez VC, Moreno CE, Zurita GA (2019) Tree retention in cattle ranching systems partially preserves dung beetle diversity and functional groups in the semideciduous Atlantic forest: the role of microclimate and soil conditions. Basic and Applied Ecology 34:64–74. https://doi.org/10.1016/j.baae.2018.10.002

Gregory N, Gómez A, Oliveira TMF, Nichols E (2015) Big dung beetles dig deeper: trait-based consequences for faecal parasite transmission. International Journal for Parasitology 45:101–105. https://doi.org/10.1016/j.ijpara.2014.10.006

Griffiths HM, Louzada J, Bardgett RD, Beiroz W, França F, Tregidgo D, Barlow J (2015) Biodiversity and environmental context predict dung beetle-mediated seed dispersal in a tropical forest field experiment. Ecology 96:1607–1619. https://doi.org/10.1890/14-1211.1

Gunter NL, Lemann K, Weir TA (2019) Scarabaeidae: Scarabeinae Latreille, 1802. Pages 443–466. In: Ślipiński A, Lawrence JF (eds) Australian beetles: Archostemata, Myxophaga, Adephaga, Polyphaga (part). Vol 3169. CSIRO Publishing, Clayton South, Victoria, Australia

Gunter NL, Weir TA (2019) Revision of Australian species of the dung beetle genus Lepanus (Coleoptera: Scarabaeidae: Scarabaeinae): key to species groups and description of 14 new species from the L. pygmaeus species group. Zootaxa 4564:41–80. https://doi.org/10.11646/zootaxa.4564.1.2

Harting F (2022) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.6. https://cran.r-project.org/web/packages/DHARMa/index.html (accessed 2 October 2023)

Hector A, Philipson C, Saner P, Chamagne J, Dzulkifli D, O'Brien M, et al. (2011) The Sabah biodiversity experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning. Philosophical Transactions of the Royal Society B 366:3303–3315. https://doi.org/10.1098/rstb.2011.0094

Hidayat P, Manuwoto S, Noerdjito WA, Tscharntke T, Schulze CH (2010) Diversity and body size of dung beetles attracted to different dung types along a tropical land-use gradient in Sulawesi, Indonesia. Journal of Tropical Ecology 26:53–65. https://doi.org/10.1017/S0266467409990423

Holl KD, Aide TM (2011) When and where to actively restore ecosystems? Forest Ecology and Management 261:1558–1563. https://doi.org/10.1016/j.foreco.2010.07.004

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical Journal 50:346–363. https://doi.org/10.1002/bimj.200810425

Hsieh TC, Ma KH, Chao A (2016) iNEXT: a R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451–1456. https://doi.org/10.1111/2041-210X.12613

Kanowski J, Catterall CP (2010) Carbon stocks in above-ground biomass of monoculture plantations, mixed species plantations and environmental restoration plantings in north-east Australia. Ecological Management & Restoration 11:119–126. https://doi.org/10.1111/j.1442-8903.2010.00529.x

Kenyon TM, Mayfield M, Monteith GB, Menéndez R (2016) The effects of land use change on native dung beetle diversity and function in Australia's wet tropics. Austral Ecology 41:797–808. https://doi.org/10.1111/aec.12366

Laliberté E, Legendre P, Shipley B (2014) FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.3. https://cran.r-project.org/web/packages/FD/index.html (accessed 14 October 2023)

Larsen T, Lopera A, Forsyth A (2008) Understanding trait-dependent community disassembly: dung density functions, and forest fragmentation. Conservation Biology 22:1288–1298. https://doi.org/10.1111/j.1523-1739.2008.00969.x

Lawes MJ, Moore AM, Andersen AN, Preece ND, Franklin DC (2017) Ants as ecological indicators of rainforest restoration in the Australian wet tropics. Ecology and Evolution 7:8442–8455. https://doi.org/10.1002/ece3.2992

Lennox DG, Gardner TA, Thomson JR, Ferreira J, Berenguer E, Lees AC, et al. (2018) Second rate or a second chance? Assessing biomass and biodiversity recovery in regenerating Amazonian forests. Global Change Biology 24:5680–5694. https://doi.org/10.1111/gcb.14443

López-Bedoya PA, Magura T, Edwards FA, Edwards DP, Rey-Benayas JM, Lövei GL, Noriega JA (2022) What level of native beetle diversity can be supported by forestry plantations? A global synthesis. Insect Conservation and Diversity 14:736–747. https://doi.org/10.1111/icad.12518

Mamantov MA, Sheldon KS (2020) Behavioural responses to warming differentially impact survival in introduced and native dung beetles. Journal of Animal Ecology 90:273–281. https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13366

Marshall AR, Waite CE, Pfeifer M, Banin LF, Rakotonarivo S, Chomba S, Herbohn J, Gilmour DA, Brown M, Chazdon RL (2023) Fifteen essential science advances needed for effective restoration of the world's forest landscapes. Philosophical Transactions of the Royal Society of London B 378:20210065. https://doi.org/10.1098/rstb.2021.0065

Matthews EG (1972) A revision of the scarabaeine dung beetles of Australia. I. Tribe Onthophagini. Australian Journal of Zoology Supplementary Series 9:3–330. https://doi.org/10.1071/AJZS009

Matthews EG (1974) A revision of the scarabaeine dung beetles of Australia. II. Tribe Scarabaeini. Australian Journal of Zoology Supplementary Series 24:1–211. https://doi.org/10.1071/AJZS038

Matthews EG (1976) A revision of the scarabaeine dung beetles of Australia. III. Tribe Coprini. Australian Journal of Zoology Supplementary Series 38:1–53. https://doi.org/10.1071/AJZS038

Meli P, Holl KD, Rey Benayas JM, Jones HP, Jones PC, Montoya D, Moreno Mateos D (2017) A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. PLoS One 12:e0171368. https://doi.org/10.1371/journal.pone.0171368

Menéndez R, Webb P, Orwin KH (2016) Complementarity of dung beetle species with different functional behaviours influence dung–soil carbon cycling. Soil Biology and Biochemistry 92:142–148. https://doi.org/10.1016/j.soilbio.2015.10.004

Milotić T, Baltzinger C, Eichberg C, Eycott AE, Heurich M, Müller J, et al. (2019) Functionally richer communities improve ecosystem functioning: dung removal and secondary seed dispersal by dung beetles in the Western Palaearctic. Journal of Biogeography 46:70–82. https://doi.org/10.1111/jbi.13452

Nervo B, Caprio E, Celi L, Lonati M, Lombardi G, Falsone G, Iussig G, Palestrini C, Said-Pullicino D, Rolando A (2017) Ecological functions provided by dung beetles are interlinked across space and time: evidence from ^{15}N isotope tracing. Ecology 98:433–446. https://doi.org/10.1002/ecy.1653

Nichols E, Larsen T, Spector S, Davis AL, Escobar F, Favila M, Vulinec K (2007) Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. Biological Conservation 137:1–19. https://doi.org/10.1016/j.biocon.2007.01.023

Nichols E, Spector S, Louzada J, Larsen T, Amezquita S, Favila ME (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141:1461–1474. https://doi.org/10.1016/j.biocon.2008.04.011

Nichols E, Uriarte M, Peres CA, Louzada J, Braga RF, Schiffler G, Endo W, Spector SH (2013) Human-induced trophic cascades along the fecal detritus pathway. PLoS One 8:e75819. https://doi.org/10.1371/journal.pone.0075819

Noble CD, Gilroy JJ, Berenguer E, Vaz-de-Mello FZ, Peres CA (2023) Many losers and few winners in dung beetle responses to Amazonian forest fragmentation. Biological Conservation 281:110024. https://doi.org/10.1016/j.biocon.2023.110024

Noriega JA, March-Salas M, Castillo S, García-Q H, Hortal J, Santos AM (2021) Human perturbations reduce dung beetle diversity and dung removal ecosystem function. Biotropica 53:753–766. https://doi.org/10.1111/btp.12953

Pedersen KM, Blüthgen N (2022) Seed size and pubescence facilitate secondary dispersal by dung beetles. Biotropica 54:215–225. https://doi.org/10.1111/btp.13052

Pickett STA (1989) Space-for-time substitution as an alternative to long-term studies. Pages 110–135. In: Likens GE (ed) Long-term studies in ecology. Springer, New York. https://doi.org/10.1007/978-1-4615-7358-6_5

Preece ND, van Oosterzee P, Hidrobo Unda GC, Lawes MJ (2017) National carbon model not sensitive to species, families and site characteristics in a young tropical reforestation project. Forest Ecology and Management 392:115–124. https://doi.org/10.1016/j.foreco.2017.02.052

Preece ND, van Oosterzee P, Lawes MJ (2023) Reforestation success can be enhanced by improving tree planting methods. Journal of Environmental Management 336:117645. https://doi.org/10.1016/j.jenvman.2023.117645

R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria

Sant'Anna CLB, Ribeiro DB, Garcia LC, Freitas AVL (2014) Fruit-feeding butterfly communities are influenced by restoration age in tropical forests. Restoration Ecology 22:480–485. https://doi.org/10.1111/rec.12091

Santos-Heredia C, Andresen E, Zárate DA, Escobar F (2018) Dung beetles and their ecological functions in three agroforestry systems in the Lacandona rainforest of Mexico. Biodiversity and Conservation 27:2379–2394. https://doi.org/10.1007/s10531-018-1542-x

Slade EM, Kirwan L, Bell T, Philipson CD, Lewis OT, Roslin T (2017) The importance of species identity and interactions for multifunctionality depends on how ecosystem functions are valued. Ecology 98:2626–2639. https://doi.org/10.1002/ecy.1954

Slade EM, Mann DJ, Villanueva JF, Lewis OT (2007) Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. Journal of Animal Ecology 76:1094–1104. https://doi.org/10.1111/j.1365-2656.2007.01296.x

Watson JEM, Evans T, Venter O, Williams B, Tulloch A, Stewart C, et al. (2018) The exceptional value of intact forest ecosystems. Nature Ecology & Evolution 2:599–610. https://doi.org/10.1038/s41559-018-0490-x

Whitehead T, Goosem M, Preece ND (2014) Use by small mammals of a chronosequence of tropical rainforest revegetation. Wildlife Research 41: 233–242. https://doi.org/10.1071/WR14082

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer Cham, Switzerland. https://doi.org/10.1007/978-3-319-24277-4

Supporting Information

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

Figure S1. Map of the study site with the location of the experimental planting plots (dotted red lines delimited blocks).

Figure S2. Relationship between seed dispersed and dung removed by dung beetles in the experimental plots, excluding plots with zero values.

Table S1. Observed and Chao asymptotic diversity estimates (Estimators) for the diversity metrics (species richness, Shannon, and Simpson) for each tree diversity treatment.

Table S2. Influence of different dung beetle community attributes on explaining ecosystem functions.

Coordinating Editor: Mia Derhe

Received: 5 November, 2023; First decision: 21 December, 2023; Revised: 3 January, 2024; Accepted: 7 January, 2024