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Running title: Land clearing and Australian dung beetles.

The Effects of Land Use Change on Native Dung Beetle Diversity and Function in Australia's Wet Tropics

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ABSTRACT

The impacts of land use change on biodiversity and ecosystem functions are variable, particularly in fragmented tropical rainforest systems with high diversity. Dung beetles (Scarabaeinae) are an ideal group to investigate the relationship between land use change, diversity and ecosystem function as they are easily surveyed, sensitive to habitat modification, and perform many ecosystem functions. Though this relationship has been investigated for dung beetles in some tropical regions, there has been no study assessing how native dung beetles in Australia's tropical rainforests respond to deforestation, and what the corresponding consequences are for dung removal (a key ecosystem function fulfilled by dung beetles). In this study we investigated the relationship between dung beetle community attributes (determined through trapping) and function (using dung removal experiments that allowed different dung beetle functional groups to access the dung) in rainforest and cleared pasture in a tropical landscape in Australia's Wet Tropics. Species richness, abundance and biomass were higher in rainforest compared to adjacent pasture, and species composition between these land use types differed significantly. However, average body size and evenness in body size were higher in pasture than in rainforest. Dung removal was higher in rainforest than in pasture when both functional groups or tunnelers only could access the dung. Increased dung removal in the rainforest was explained by higher biodiversity and dominance of a small number of species with distinct body sizes, as dung removal was best predicted by the evenness in body size of the community. Our findings suggest that functional traits (including body size and dung relocation behaviour) present in a dung beetle community are key drivers of dung removal. Overall, our results show that deforestation has reduced native dung beetle diversity in Australian tropical

landscapes, which negatively impacts on the capacity for dung removal by dung beetles in this region.

Keywords: dung removal; ecosystem function; land use change; Scarabaeinae; tropical rainforest.

INTRODUCTION

Many of the world's tropical and subtropical forests have been heavily cleared, modified or fragmented for agricultural expansion (Laurance *et al.* 2013). Such land use changes across the tropics have been shown to lead to declines in tropical forest biodiversity (Foley *et al.* 2005, Gibson *et al.* 2011).

In Australia, it is estimated that 50% of the wet tropical forests of Northern Queensland have been extensively cleared for agricultural production since European settlement (Woinarski 2010). Clearing for pasture in this region has mostly impacted level areas with fertile soils such as the Atherton Tableland, and has resulted in mosaic landscapes of agricultural land uses and remants of tropical forests (Catterall *et al.* 2004). It is known that land clearing has led to declines in the biodiversity of vertebrates, including mammals and birds in the Australian tropics (Catterall *et al.* 2004, Ford 2011, Woinarski *et al.* 2011), yet few studies have examined how invertebrates are impacted by land use changes (Nakamura *et al.* 2007, Leach *et al.* 2013).

Further, while these studies have explored the links between land use change and biodiversity in Australia, few have assessed how changes in biodiversity affect ecosystem functioning in deforested and/or degraded areas of Australia (Gollan *et al.* 2013). Biodiversity assessments coupled with an understanding of the relationship between biodiversity and ecosystem function can provide insights into the efficiency of ecological functioning across disturbance gradients in tropical forests (Lewis 2009).

Biodiversity metrics including species richness, abundance and biomass positively correlate with ecosystem function in some tropical systems (Horgan 2005, Slade *et al.* 2011, Braga *et al*. 2013, Gollan *et al.* 2013), though the main driver of this relationship varies by system. This variation relates to which functions are being examined, and which processes and mechanisms are mediating functional trait diversity and overall assembly in different regions and environments (Mayfield *et al.* 2010).

Dung beetles (Scarabaeinae) are an ideal group for studying biodiversity-function relationships in highly modified landscapes as they are easily surveyed, sensitive to habitat modification, and perform many ecosystem functions including nutrient cycling, secondary seed dispersal and dung removal (involving the relocation of dung into underground chambers for feeding and breeding) (Cambefort & Hanski 1991, Nichols *et al*. 2008). As a result dung beetles have been extensively used as bioindicator species of forest degradation in tropical regions around the world (Nichols *et al.* 2007).

In Australia, however, dung beetle research has primarily been tied to agricultural interests since the commencement of the CSIRO Australian Dung Beetle Project in 1964, which involved the introduction of 41 exotic dung beetle species adapted to cattle dung, 22 of which became established (Edwards 2007). Exotic species were used because most native species prefer marsupial dung rather than more moist cattle dung (Doube *et al.* 1991, Geoff Monteith pers. comm. 2015). Therefore, assessment of dung beetle ecosystem function has focused on removal rates of cattle dung to reduce forage fouling of pastures and to control pest fly populations (Ridsdill-Smith & Edwards 2011). There have been comparatively fewer studies on native species in the context of ecosystem function (Gollan *et al*. 2013), especially in tropical forests.

The aim of this study was to determine how land use change (specifically deforestation for cattle grazing) impacts native dung beetle communities and ecosystem function (in particular dung removal) in the Wet Tropics of Australia. We examined several community attributes (species composition, richness, abundance, and biomass and body size) as well as function of native dung beetles in forested and deforested (cattle pasture) land use types in a heavily fragmented tropical landscape of the Atherton Tableland, Queensland, Australia.

Dung beetles were subdivided into two functional groups (sets of species with similar effects on ecosystem processes) based on nesting behaviour. In tropical regions, studies investigating function typically subdivide dung beetles into: tunnelers, which bury dung directly beneath dung deposits, and rollers, which transport and bury dung some distance away from the collection site (Cambefort & Hanski 1991). The type and number of dung beetle functional groups present in an environment may affect the level of ecosystem functioning through complementarity or resource partitioning to achieve greater function (Slade *et al*. 2007). For example, Slade *et al.* (2007) found that tunnelers were greater contributors to dung removal than rollers, but also found complementarity between them, indicating that dung removal was driven by functional group richness.

The relationship between dung beetle biodiversity and dung removal is variable among study regions, with some studies showing that certain biodiversity metrics and/or certain functional traits are better predictors of dung removal than others (Horgan 2005, Larsen *et al*. 2005, Slade *et al*. 2011, Braga *et al*. 2013, Barnes *et al.* 2014). In particular, beetle body size is important for determining species responses to land use change, as large species have been found to be more sensitive to disturbance (Larsen *et al.* 2005). This may have an impact on function as body size is known to affect dung removal (Nervo *et al.* 2014).

Through field manipulation experiments and surveys in both rainforest and (cleared) pasture plots, we investigated: (1) whether land use change affects dung beetle community attributes (species composition, species richness, abundance, biomass and body size) overall and for each functional group; (2) whether land use change and/or the absence of certain functional groups (controlled by exclusion treatments) affects the extent of the ecosystem function of dung removal; and (3) whether there is a relationship between any of the community attributes measured and levels of dung removal.

METHODS

STUDY SITE

This study was conducted during the wet season of 2010 (January) on the privately-owned Thiaki Creek Nature Refuge ('Thiaki') on the Atherton Tableland of north-east Queensland (145°51′ E, 17°43′ S; Elevation: 900-1000 m above sea level). Mean and maximum January rainfall in the study area is 288.5 mm and 1379.6 mm (average for 1992-2009), respectively. The average maximum and minimum temperatures are 27.4°C and 18.3°C (average for 1994-2008), respectively (Bureau of Meterology 2014). The property contains 130 ha of rainforest classified as Endangered Regional Ecosystem 7.8.4, Upper Barron complex notophyll vine forest (Bell *et al.* 1987) and 51 ha of pasture. Pasture areas within the property were largely cleared of original rainforest approximately 60 years ago, with the most recent clearing occurring in 1978 (Barry Pember pers. comm. 2015). Cattle grazing in all pasture areas occurred until late 2010. The rainforest portion was selectively logged between the 1960's and 2000's using snigging, a method consisting of lifting and dragging single logs (Noel Preece pers. comm. 2010). Cattle entered the forest understory near forest edges until they were removed from the property in late 2010. Since 2008 the forest has been protected as a Nature Refuge (Department of Environment and Resource Management 2009).

The study area included five 2-ha rainforest blocks and five 2-ha pasture blocks, each divided into eight 50 x 50-m plots. Five plots in each block were randomly selected as locations for dung beetle sampling and dung removal experiments (Fig. 1). Rainforest blocks were at least 50 m to 200 m from the forest edge to reduce edge effects and increase the probability of trapping 'interior' rainforest species (Hill 1995). Ambient and soil temperature dataloggers (Thermochron iButtons®) were operational in three pasture and three rainforest plots from the commencement to the end of the study.

DUNG BEETLE SAMPLING

Dung beetles were collected using baited pitfall traps to assess community attributes for each plot. Traps were baited with macropod dung (a mixture of kangaroo and wallaby dung) in order to attract native species which are believed to inadequately utilize cattle dung (Doube *et al.* 1991, Geoff Monteith pers. comm. 2015). Nevertheless, sampling trials using cattle dung-baited traps were also conducted in the same plots following collection of the macropod dung-baited traps to ensure that the bait type used did not lead to an underestimation of native species richness (see Table S1).

Each trap comprised a 450-ml plastic cup, buried flush with the ground and containing a 100-ml solution of propylene glycol, water and detergent. Dung was collected fresh from free-ranging kangaroos and wallabies at the Lone Pine Koala Sanctuary reserve in Brisbane, Australia. All dung was mixed together in a bucket and formed into balls of approximately 50 g wet weight, wrapped in porous cloth and tied with a suspension wire. The bait was suspended inside the cup from a wire grid (2-cm^2 grid size) pegged over the cup, which reduced vertebrate by-catch and interference. A polycarbonate cover dug in at an angle over the trap acted as a roof.

Two traps, 35 m apart, were installed within three of the five 50 x 50-m selected plots from each block (Fig. 1). Traps were installed following collection of the dung removal experiments (Section 2.3) in an attempt to collect a similar array of dung beetle species in each plot to those attracted to the exclusion treatments.

After five days, specimens were collected and preserved in 70 percent ethanol. Dataloggers were collected after 12-14 days. All dung beetles were identified to species level (Table 1). Species were classified into functional groups (tunnelers or rollers) based on leg morphology, behavioural observations by G. B. Monteith and R. Menéndez, and taxonomy (Matthews 1974). Voucher specimens of species caught were deposited at the Queensland Museum. To calculate mean dry weight for each species and subsequently average body size, evenness in body size and biomass per plot, one to twenty individuals (mean: 16.6 ±6.6) of each species were oven-dried to a constant weight. Using the 'FD' package in 'R' (Laliberté *et al.* 2014), we calculated per plot: average body size as the community weighted mean (CWM) for body size, which is species mean dry weight weighted by their abundance; and body size evenness (FEve), which measures the degree to which abundances are equally distributed across different body sizes. Biomass per plot was the sum of each species mean dry weight multiplied by their abundance. Catches for the two macropod dung traps within each plot were pooled for analysis.

DUNG REMOVAL EXPERIMENTS

Dung removal experiments tested the individual and combined effects of different dung beetle functional groups (tunnelers and rollers) on dung removal in rainforest and pasture plots. Experiments were undertaken three days prior to dung beetle sampling to avoid potential effects on dung removal rates as a result of temporary localised depletion of dung beetle communities. The experiment was exclusion based and included three treatments: rollers only (excluding tunnelers), tunnelers only (excluding rollers) and combined (no beetle exclusion). Enclosures were constructed using a wire mesh cylinder (2-cm^2 grid size; 10-cm height; 11-cm diameter) containing a macropod dung ball and topped with a plastic plate roof. In the roller-only treatment, tunnelers were prevented from burying dung pieces by pegging a 20-cm^2 piece of wire mosquito mesh (1-mm^2 mesh size) beneath the dung (Fig. 2). In the tunneler-only treatment, rollers were prevented from burying dung by encircling the cylinder with an open-topped wire and shade cloth cylindrical enclosure (10-cm height; 30-cm diameter) (Fig. 2). This structure prevented rollers from transporting dung pieces far from the resource, causing them to abandon rather than bury them (Peck & Forsyth 1982). Abandoned dung pieces were considered as remaining dung in order to measure the amount of dung removed by tunnelers only. Leaf litter inside enclosures was cleared in order to easily remove abandoned dung pieces to be weighed later. The wet weight of each dung ball was recorded prior to deployment. The original dry weight of each dung ball was estimated from a linear regression (dung dry weight = 1.22 + 0.27*dung wet weight, $R^2 = 0.65$, $F = 92.64$, $df = 50$, $p < 0.001$) of 52 dung balls not used in the experiment. Wet weights of these dung balls were recorded before being oven-dried to a constant weight.

The experiment followed a nested block design, with each exclusion treatment replicated once within each of the five selected plots across 10 blocks, totalling 50 replicates per treatment. Exclusion treatments within plots were separated by a distance of 25-35 m. They were deployed during daylight and left for 72 hours, and all treatments within a plot were set and collected at the same time. Remaining dung was collected and oven-dried to a constant weight. The dry weight of the remaining dung was subtracted from the estimated original dry weight to determine the amount of dung removed, expressed as proportion of dung lost.

Data analysis

Species accumulation curves were created using the EstimateS software version 9.1.0 (Colwell 2013) to assess the adequacy of the traps in collecting the full complement of dung beetle species present in the study area. One of the native species collected, *Demarziella interrupta*, was excluded from analyses because it utilises dung buried by other dung beetles (kleptocoprid) and therefore does not contribute to dung removal (Slade *et al*. 2007, Cambefort & Hanski 1991). Despite being found in low abundances, exotic species were included in analyses as they form part of the dung beetle fauna in the pasture and can contribute to dung removal.

To test whether dung beetle community attributes (species richness, abundance, biomass, average body size and evenness in body size) differed between rainforest and pasture plots, the 'R' (R Core Team 2014) package 'lme4' (Bates *et al.* 2014) was used to fit linear generalised mixed-effects models that included land use as the fixed effect and block as the random effect. The poisson distribution was specified for models describing species richness and abundance as they are count data, biomass was square root transformed, and average body size was log transformed to achieve normality of residuals. The significance of the fixed effect was tested by assessing changes in deviance between models with and without the individual terms using chi-squared (χ^2) tests.

To determine whether land use type and functional group affected the proportion of dung removed, we used a linear mixed-effects model with block as a random factor and dung beetle exclusion treatment and land use type as fixed factors. The significance of fixed effects and interactions was assessed by changes in deviance as described above. The 'R' package 'effects' (Fox *et al.* 2014) was used to calculate upper and lower 95% confidence intervals (CI) to determine significant differences for all two-way comparisons among levels of fixed effects. Following Warton & Hui (2011), the response variable (proportion of dung removed) was logit-transformed to achieve normality in the residuals. Logit-transformation does not work for zero values and thus we excluded samples for which no dung was removed. Thus, our analysis assesses which factors influence the amount of dung removed, once dung has been removed at all. In other words, we asked the question - if dung is removed, how important is dung beetle functional group and land use to the amount of dung removal. We assessed the robustness of this method by repeating the analysis and including all samples but adjusting zero values to 0.001 proportion of dung removed.

To assess the effect of each community attribute (species richness, abundance, biomass, average body size and body size evenness) on dung removal we used an information-theory approach. We performed separated linear mixed-effects models with proportion of dung removed (logit-transformed) as the response variable and each of the community attributes as an explanatory variable; block was included in each model as a random effect. To rank and select the best model, we used Akaike Information Criterion corrected for small sample size (AIC_c) as recommend by Burnham & Anderson (2002). We compared the differences in AIC_c for each model with respect to the AIC_c of the best candidate model (the one with the lowest AIC_c). We also calculated the AIC_c weight (w_i) for each model, which indicates the probability that model i is the best model in the set of candidate models. The 'MuMIn' package in 'R' was used for the analyses (Bartoń 2014). The significance of each community attribute was also tested by assessing changes in deviance between the null model (including block as a random effect) and the models with each of the community attributes using chi-squared (χ^2) tests.

RESULTS

Air and soil temperatures in the pasture (air mean: 22.23°C; 95% CI: 21.95, 22.50 and soil mean: 22.62°C; 95% CI: 22.48, 22.77) were significantly higher than those in the rainforest (air mean: 20.88°C; 95% CI: 20.78, 20.98 and soil mean: 20.27°C; 95% CI: 20.22, 20.32) (air $t = -8.90$, $df = 1054.96$, $p < 0.001$ and soil $t = -29.92$, $df = 1040.86$, $p < 0.001$).

In total, 5484 dung beetles were collected from 27 species of which 25 were native and 2 were exotic (Table 1). Twenty-two species (12 tunnelers and 10 rollers) were collected in rainforest and nine species (7 tunnelers and 2 rollers) were collected in the pasture (Table 1 and see Fig. S1 for species accumulation curves for each land use type). The only two exotic species found in our survey were caught in pasture plots at very low abundances (11 individuals), equal to 0.2% of all trapped beetles in macropod dung-baited traps (Table 1). Exotics also only accounted for 0.5% of individuals collected when cattle dung was used in baited-traps (trials not included in our main analysis but presented in Table S1). Combined, these results suggest that exotic species were not common in the study area, and that the macropod bait type was not under-sampling these beetles.

The most abundant species in the rainforest was the small roller species, *Amphistomus NQ5*, accounting for 45% of the dung beetles trapped in the rainforest. The most abundant species in pasture were large native tunnelers *Onthophagus capella* and *Onthophagus cuniculus*, which accounted for approximately 50% and 20% of the dung beetles trapped in pasture, respectively. The dominant species in terms of biomass were *Coptodactyla depressa* in the rainforest (a large tunneler accounting for approximately 34% of total biomass in rainforest) and *O. capella* in pasture (accounting for 68% of total biomass in pasture).

EFFECT OF LAND USE TYPE ON DUNG BEETLE COMMUNITY ATTRIBUTES

Rainforest and pasture plots had distinct species compositions, with only four of the 27 dung beetle species shared by the two land use types (Table 1). Total species richness ($\chi^2 = 26.94$, $p < 0.001$, Fig. 3A), abundance ($\chi^2 = 34.87$, $p < 0.001$, Fig. 3B) and biomass ($\chi^2 = 24.21$, $p < 0.001$, Fig.3C) were significantly higher in rainforest than pasture plots, but the opposite trend was found for average body size ($\chi^2 = 32.23$, $p < 0.001$, Fig. 3D) and body size evenness ($\chi^2 = 8.82$, $p = 0.003$, Fig. 3E). In the pasture, the abundances of species were evenly spread across a variety of body sizes. This was not the case in the rainforest, where a small number of species of certain body sizes dominated.

Tunneler species richness ($\chi^2 = 18.94$, $p < 0.001$, Fig. 3A), abundance ($\chi^2 = 23.14$, $p < 0.001$, Fig. 3B) and biomass ($\chi^2 = 9.19$, $p = 0.002$, Fig.3C) was significantly higher in rainforest than pasture plots, but average body size was significantly lower in rainforest than in pasture plots ($\chi^2 = 35.36$, $p = 0.001$, Fig. 3D) and no significant differences were found in body size evenness between land use types ($\chi^2 = 2.39$, $p = 0.122$, Fig. 3E).

Roller species richness ($\chi^2 = 31.72$, $p < 0.001$, Fig. 3A), abundance ($\chi^2 = 36.31$, $p < 0.001$, Fig. 3B), biomass ($\chi^2 = 32.78$, $p < 0.001$, Fig.3C) and average body size ($\chi^2 = 5.46$, $p = 0.019$, Fig. 3D) were all significantly higher in rainforest than pasture plots. No data were available to calculate body size evenness in pasture for this group because at least three species are needed to calculate this metric.

EFFECT OF LAND USE TYPE AND DUNG BEETLE FUNCTIONAL GROUPS ON DUNG REMOVAL

Dung removal was significantly affected by land use type ($\chi^2 = 11.77$, $p < 0.001$), by dung beetle exclusion treatment ($\chi^2 = 12.64$, $p = 0.002$) and by the interaction between the two factors ($\chi^2 = 24.47$, $p < 0.001$). Results remained the same when all samples were included in the analysis (see Table S2). In the rainforest, the proportion of dung removed was higher when both rollers and tunnelers were allowed to access the dung, following by tunnelers only and finally by rollers only, though differences were only significant between the rollers only treatment and combined treatment (Fig. 4). In the pasture, no significant differences were found between any beetle exclusion treatments (Fig. 4). Lower proportions of dung were removed in the pasture than the rainforest plots, though this difference was not significant when only rollers were allowed access to the dung (Fig. 4).

RELATIONSHIP BETWEEN DUNG BEETLE COMMUNITY ATTRIBUTES AND DUNG REMOVAL

For all beetles combined, the global model including all community attributes explained 78% of the variation in the proportion of dung removed from a plot. Significantly more dung was removed in plots with higher species richness, abundance and biomass and in plots where body size was less even and beetles were smaller in size (Table 2, Fig. S2). Despite all community attributes contributing to explain dung removal, body size evenness was the best predictor of all, with strong evidence (Akaike weight = 0.61) that the model using body size evenness as a predictor was the best model among those tested (Table 2).

For rollers only, the global model explained 58% of the variation in the proportion of dung removed. Abundance was the only significant variable (Table 2), having a positive effect on the proportion of dung removed by rollers only (Fig. S2) and there was strong support for abundance as the best predictor (Akaike weight = 0.68, Table 2). Dung removal by tunnelers was not significantly explained by any of the community attributes analysed (Table 2).

DISCUSSION

Effect of land use type on dung beetle community attributes

We found a marked decrease in species richness, abundance and biomass of dung beetles in the degraded pasture compared to adjacent rainforest plots, in accordance with previous studies on beetles in general (including some dung beetle species) conducted in similar vegetation types on the Atherton Tableland region (Grimbacher *et al*. 2006, 2008) and with studies conducted in tropical regions in the Americas and Southeast Asia (Horgan 2005, Larsen *et al.* 2005, Braga *et al*. 2013, Edwards *et al.* 2013, Korasaki *et al.* 2013). Differences in community attributes between land use types are likely to be driven by differences in micro-climatic conditions rather than resource limitation, as kangaroos, wallabies and pademelons regularly visit the pastures, so macropod dung is likely to be available in both pasture and rainforest plots. Land use modification can alter micro-climatic conditions by changing characteristics such as canopy height, temperature and precipitation retention, which have been found to affect dung beetle species composition and positively correlate with dung beetle species richness and abundance (Davis *et al.* 2002, Korasaki *et al.* 2013). During the time of our study, air and soil temperatures were around 2°C higher in the pasture plots than in the adjacent rainforest plots, which could affect both adult activity and larval survival (Chown & Klok 2011).

The composition of dung beetle species in rainforest and pasture differed substantially, which is consistent with the idea of environmental filtering. Most native Australian dung beetle species are associated with forested areas (Matthews 1972, 1974, 1976) and specialist rainforest species are likely to have low tolerance of elevated temperatures associated with disturbed areas including plantation forest and open areas (Andresen 2008, Gardner *et al.* 2008). Dominant species present in the study pasture, *O. capella* and *O. cuniculus*, are normally associated with open forest (Matthews 1972) and likely to be well adapted to drier, hotter conditions. In addition, the almost total absence of roller species in pastures could be associated with reduced larval survival under higher soil temperatures. Roller species make burrows in the soil that are shallower than those made by tunneler species (Gregory *et al.* 2015), which could decrease larval survival by increasing desiccation risk (Sowig 1995).

The low diversity of native dung beetle fauna in pasture was not compensated for by an increase in the number and abundance of exotic species, as we only recorded two exotic species in pasture (which were at low abundance). This is in contrast to a study undertaken by Gollan *et al.* (2011) in temperate Australia which found exotic dung beetles to be abundant in cleared riparian areas, and the exotic-to-native species ratio to increase with increasing disturbance. Our results likely reflect a low abundance of exotic species in this region, a finding consistent with previous observations indicating that exotic dung beetle species did not establish as well in the Atherton Tablelands compared to other areas of Australia (Edwards 2007).

Finally, we found that although other community metrics decreased in the pastures, there was an increase in beetle body size. Pasture plots also had dung beetle communities with higher evenness in body size (less dominance of a particular body size or body sizes). This may be the result of reduced competition between species when overall beetle numbers are low. There have been mixed findings about body size responses to land use change, with some studies reporting that large species are more sensitive to disturbance (Larsen *et al.* 2005) and other studies finding increases in the abundance of larger beetles with increasing tropical forest conversion (Nichols *et al.* 2013). In our case the larger body size in the pasture was driven by higher numbers of tunneler species (both native and exotic species). Tunnelers were larger in the pasture than in the rainforest, while roller species showed the opposite trend. Large body size is likely to be advantageous in dry open land use types like the Thiaki pasture, as water evaporation rates decrease with body size, reducing desiccation risk (Chown & Gaston 2010). This finding, in relation to the broader literature, suggests that microclimate conditions are very important in determining the traits of dung beetles that are and are not successful in different types of degraded tropical landscapes.

Effect of land use type and dung beetle functional groups on dung removal

Like most community attributes, we found a marked decrease in dung removal in the degraded pasture plots compared to adjacent rainforest plots. Less than 10% of the dung was removed over three days in the pasture compared to more than 60% in the rainforest plots. This is consistent with previous studies in other tropical regions showing that deforestation not only negatively affects dung beetle biodiversity but also their ecosystem functioning (Horgan 2005, Braga *et al.* 2013, Gollan *et al.* 2013). In our case the effect depended on which dung beetle functional groups were allowed to access the dung. There was a significant decline in the amount of dung removed by all beetles and by tunnelers only in pasture compared to rainforest plots, but no significant difference between land use types when only rollers were allowed to access the dung.

In the rainforest, a greater proportion of dung was removed when both rollers and tunnelers were allowed to access the dung. Although the result was not significant between all beetles and tunnelers only, this does suggest that both functional groups are needed to achieve maximum function. A possible mechanism for this relationship is a reduction in interspecific competition due to niche partitioning (Hooper *et al*. 2005), although our experimental design did not allow for distinction between an additive effect or complementarity. However, Slade *et al.* (2007) found complementarity between tunnelers and rollers in a rainforest in Borneo, and the driving mechanism was temporal (diurnal vs. nocturnal) segregation of this resource by different species. Our results are more likely to be due to differences in dung relocation behaviour between tunnelers and rollers. For example, high densities of tunnelers can constrain dung removal due to physical interference and competition for space beneath dung deposits (Ridsdill-Smith *et al*. 1982), while rollers do not compete for this space as they move portions of dung away. Differences in body size between rollers and tunnelers may also be important - we have observed that the activity of large tunnelers breaking down a dung deposit facilitates small rollers to take advantage of small pieces of dung that are inadequate for larger beetles.

Rainforest tunnelers and rollers did not remove significantly different proportions of dung from each other, despite the high abundance of small to medium-sized roller species in the rainforest compared to tunnelers. The most dominant species in terms of biomass was *C. depressa*, a large nocturnal tunneler with a mean body mass of 51.25 ± 13 mg (mean ± SD). Body size has been found to be a reliable indicator of a beetle’s functional efficiency (Horgan 2001, Nervo *et al*. 2014) and large dung beetle species are known to remove disproportionately large amounts of dung in short periods of time (Doube 1990, Larsen *et al.* 2005). It is possible that *C. depressa* functionally compensated for lower overall tunneler abundance in the rainforest with its large body size.

In the pasture, there were no differences in dung removal between dung beetle exclusion treatments, with no evidence of a facilitative relationship between functional groups. The selection effect, when one or two species has a large impact on ecosystem functioning (Hooper *et al.* 2005), may be operating in Thiaki pastures. A single species, *O. capella*, made up 50% of all individuals collected in the pasture and has been reported to be able to remove large amounts of dung (Doube *et al*. 1991). Previous studies have found functional dominance of certain dung beetle species to increase with disturbance (Nichols *et al.* 2007, Korasaki *et al.* 2013), but how this will affect function is likely to depend on the functional traits of the dominant species and other species in the community (Nichols *et al.* 2007; Korasaki *et al*. 2013).

RELATIONSHIP BETWEEN COMMUNITY ATTRIBUTES AND DUNG REMOVAL

It is pertinent to mention that a major assumption of this study was that dung was removed in the exclusion treatments by the same beetles as those caught in our traps. This is considered a reasonable assumption because the non-lethal dung removal experiment was carried out three days *prior* to trapping, allowing the full complement of species present at the commencement of the study to access the traps. This approach is commonly used by studies assessing the relationship between dung beetle diversity and function, making our data comparable with previous studies.

For all beetles combined, species richness, abundance and biomass were all positively related to dung removal, consistent with findings of other studies in Central and South America and in Australia (Larsen *et al.* 2005, Braga *et al.* 2013, Gollan *et al.* 2013, Barnes *et al.* 2014). We found, however, that evenness in body size was the best predictor of dung removal, with more dung removed by communities in which species abundances were not evenly distributed across body sizes. These communities were dominated, in terms of abundance, by a small number of species each with distinct body sizes. This further supports the idea that larger beetles are facilitating function by smaller beetles. It also suggests that a small number of dominant species with particular body sizes carry out most of the function in terms of dung removal. Slade *et al.* (2011) found a significant positive relationship between dung removal and biomass of large-bodied nocturnal beetles. However, we found no effect of body size evenness on dung removal when each functional group was analysed separately, indicating that several functional traits, not just body size, are important for function. This is consistent with the growing body of evidence purporting that trait diversity is more important to ecosystem function than traditional taxonomically-based biodiversity measurements (Cadotte *et al.* 2011).

When functional groups were analysed separately, there was a positive relationship between the amount of dung removed by rollers and their abundance but no relationship was found for dung removed by tunnelers. This may be explained by differences in intra-functional group competition. For example, a high abundance of small rollers is likely to result in greater dung removal, but this may not be the case for a high abundance of large tunnelers due to physical interference and competition as previously explained (Ridsdall-Smith *et al.* 1982). The lack of significant diversity-function relationships for separate functional groups provides further evidence for some degree of facilitative behaviour between rollers and tunnelers, suggesting that both functional groups are required to maximize ecosystem functioning in this system. Conducting additional dung removal experiments with further division of functional groups (according to body size, diel activity and burrowing rate), as well as incorporating a wider range of species functional traits into the analysis, may further reveal the underlying mechanisms driving the observed patterns.

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TABLES

Table 1 Total abundance of each species trapped in rainforest and pasture plots in macropod dung-baited traps. Each species is assigned to a functional group (either tunneler or roller based on taxonomy, leg morphology and behavioural observations by G.B. Monteith & R. Menéndez). Average body size (dry weight) is provided for each species. Species not native to Australia are indicated with an asterisk. Undescribed species are given standardized code names (e.g. NQ3) as devised by G. B. Monteith and T. A. Weir for the purpose of databasing Australian dung beetles.

Species	**Abundance**		**Functional Group**	**Average Body Size (mg)**
	Rainforest	**Pasture**		
Amphistomus complanatus Matthews 1974	134	0	Roller	9.60
Amphistomus NQ3	601	0	Roller	18.31
Amphistomus NQ4	78	0	Roller	3.21
Amphistomus NQ5	2446	8	Roller	1.55
Lepanus dichrous Gillet 1925	81	0	Roller	1.40
Lepanus NQ9	17	0	Roller	3.50
Lepanus NQ5	1	0	Roller	0.87
Temnoplectron bornemisszai Matthews 1974	1	0	Roller	63.50
Temnoplectron aeneopiceum Matthews 1974	27	0	Roller	4.56
Temnoplectron politulum Macleay	667	1	Roller	18.56

Species	Abundance		Functional Group	Average Body Size (mg)
	Rainforest	Pasture		
1887				
Coptodactyla depressa Paulian 1933	345	1	Tunneler	51.25
Coptodactyla onitoides Gillet 1925	2	0	Tunneler	76.80
Onthophagus bundara Storey & Weir 1990	12	1	Tunneler	1.29
Onthophagus capella Kirby 1818	0	42	Tunneler	52.95
Onthophagus capelliformis Gillet 1925	13	0	Tunneler	25.47
Onthophagus cuniculus Macleay 1864	0	17	Tunneler	19.70
Onthophagus darlingtoni Matthews 1972	16	0	Tunneler	15.62
Onthophagus dicranocerus Gillet 1925	11	0	Tunneler	31.04
Onthophagus millamilla Matthews 1972	517	0	Tunneler	4.38
Onthophagus nigriventris d'Orbigney 1902*	0	10	Tunneler	38.31
Onthophagus pillara Matthews 1972	7	0	Tunneler	4.04
Onthophagus rubicundulus Macleay 1871	225	0	Tunneler	1.86
Onthophagus thoreyi Harold 1868	0	3	Tunneler	23.10

Species	Abundance		Functional Group	Average Body Size (mg)
	Rainforest	Pasture		
Onthophagus wagamen Matthews 1972	131	0	Tunneler	5.70
Onthophagus waminda Matthews 1972	50	0	Tunneler	1.93
Onthophagus wilgi Matthews 1972	18	0	Tunneler	1.08
Onitis vanderkelleni Lansberge 1886*	0	1	Tunneler	173.46
Total	**5400**	**84**		

FIGURES

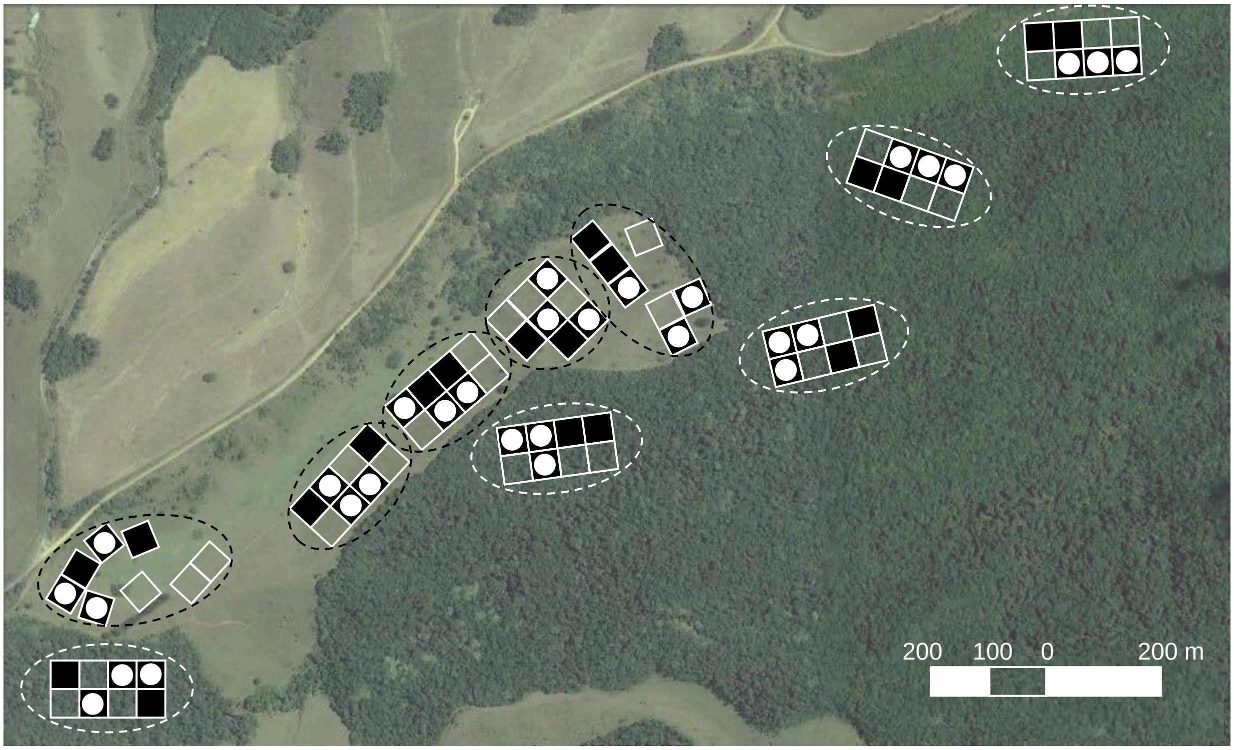

Fig. 1 Map showing the five rainforest blocks and five pasture blocks used in this study; terrain image from Map data: Google © 2009 (accessed 25 February 2010). Dotted lines encircle eight plots within each block (white dotted line in rainforest and black dotted line in pasture). Plots in which dung removal experiments were conducted are coloured black. White circles indicate plots in which traps were also installed (two traps per plot).

Fig. 2 Dung removal experiment apparatus for: rollers only exclusion treatment (left) which excluded tunnelers; and tunnelers only exclusion treatment (right) which excluded rollers. The combined treatment included only the wire mesh cylinder topped with plastic plate roof.

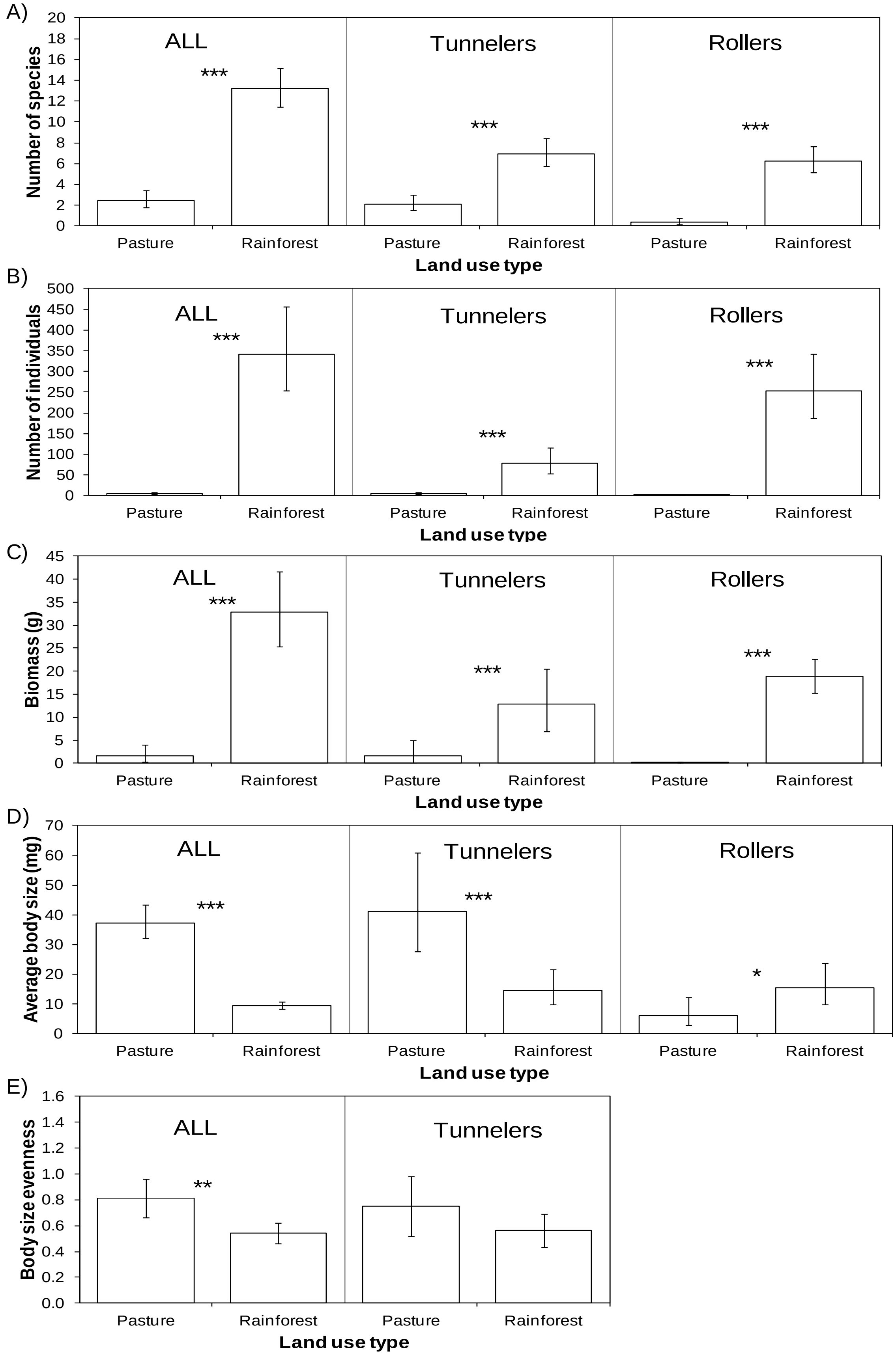
A)
Number of species
ALL
Tunnelers
Rollers
***
***
***
Pasture
Rainforest
Land use type
B)
Number of individuals
ALL
Tunnelers
Rollers
***
***
***
Pasture
Rainforest
Land use type
C)
Biomass (g)
ALL
Tunnelers
Rollers
***
***
***
Pasture
Rainforest
Land use type
D)
Average body size (mg)
ALL
Tunnelers
Rollers
***
***
*
Pasture
Rainforest
Land use type
E)
Body size evenness
ALL
Tunnelers
**
Pasture
Rainforest
Land use type

Fig. 3 Effect of land use type on dung beetle species richness (A), abundance (B), biomass (C), average body size (D) and body size evenness (E) per plot for all beetles and for each functional group separately. Bars represent mean ± 95% confident intervals of parameter estimates from glmms (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

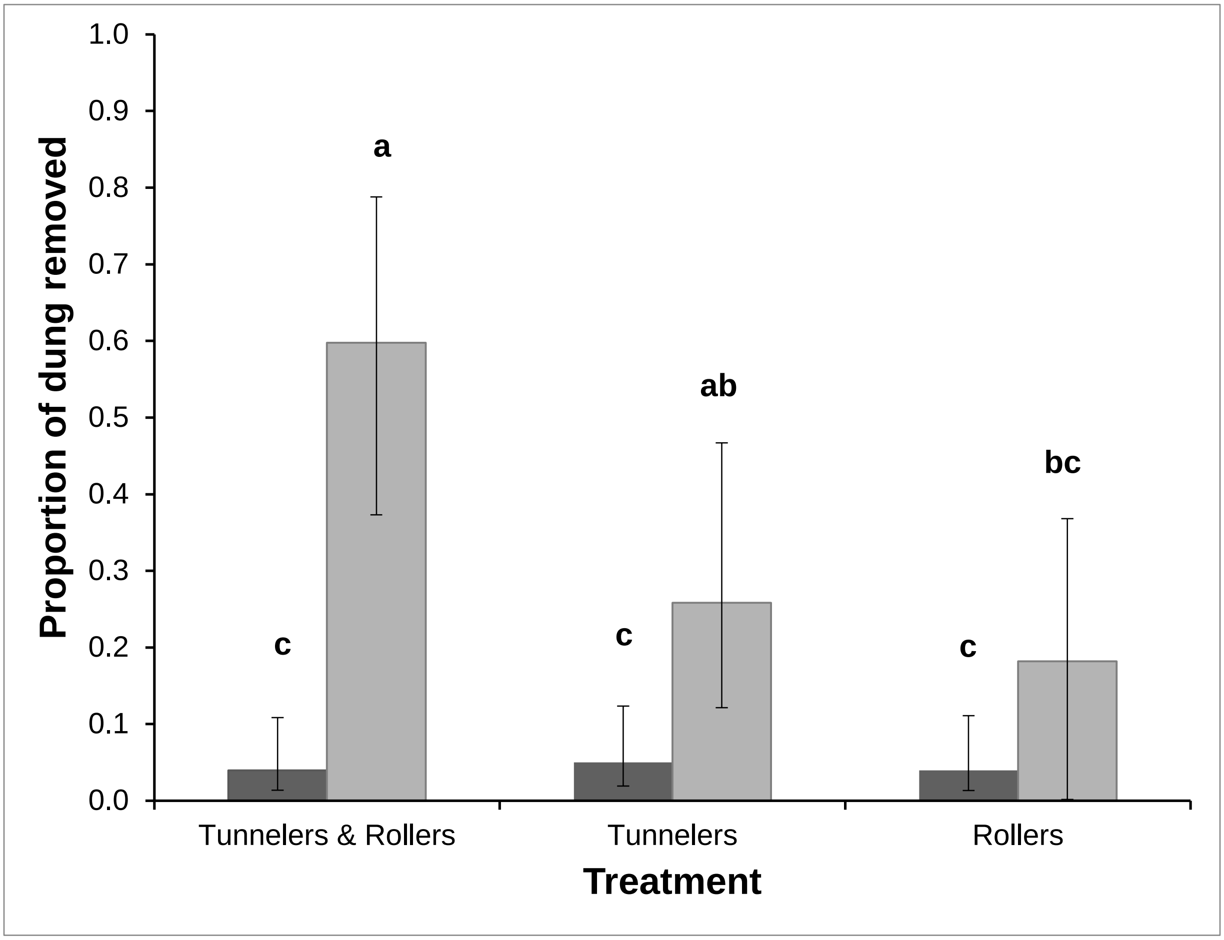

Fig. 4 Effect of land use type (dark grey: pasture plots, light grey: rainforest plots) and dung beetle exclusion treatment (name indicating the functional group that was allowed to access the dung) on the proportion of dung removed. Bars represent back-transformed mean ± 95% confident intervals of the parameter estimated from a linear mixed-effects model (logit-transformed) and significant differences between means are denoted by distinct letters.