

# Replacing low-intensity cattle pasture with oil palm conserves dung beetle functional diversity when paired with forest protection

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## Abstract

Meeting rising demand for oil palm whilst minimizing the loss of tropical biodiversity and associated ecosystem functions is a core conservation challenge. One potential solution is focusing the expansion of high-yielding crops on presently low-yielding farmlands whilst  
25 protecting nearby tropical forests that can enhance provision of ecosystem functions. A key question is how this solution would impact invertebrate functional diversity. We focus on oil palm in the Colombian Llanos, where plantations are replacing improved cattle pastures and forest fragments, and on dung beetles, which play key functional roles in dung removal. We show that functional richness (FRic) and functional diversity (FD) is greater in oil palm than in  
30 cattle pasture, and that all functional metrics are comparable between oil palm and remnant forest. The abundance-size class profile of dung beetles in oil palm was more similar to forest than to pasture, which had lower abundances of the smallest and largest dung beetles. The abundance of tunneling and rolling dung beetles did not differ between oil palm and forest, while higher forest cover increased the abundance of tunneling and diurnal beetles in oil palm  
35 landscapes. This suggests that prioritizing agricultural development on low-yielding cattle pasture will have minimal effects on functional diversity and highlights the need for forest protection to maintain ecosystem functioning within agricultural landscapes.

## Keywords

40 Dung beetles, Colombia, Llanos, oil palm, functional diversity, landscape configuration

## Introduction

Land-use change, driven primarily by agricultural expansion, poses an existential threat to tropical forests (Laurance *et al.*, 2007). Conversion of natural habitats to farmland causes major declines in taxonomic richness (Gibson *et al.*, 2011), a proliferation of habitat generalist species at the expense of forest specialists (Clavel *et al.*, 2010; Newbold *et al.*, 2018), and is thus a key driver of the global extinction crisis. Of particular concern in the Neotropics is the predicted increase in the production of oil palm (Butler & Laurance 2009). Previous expansion of oil palm cultivation in Southeast Asia has occurred largely at the expense of tropical forest (Gunarso *et al.*, 2013). Conversion to oil palm drives wholesale reductions in species richness (Foster *et al.*, 2011; Gray *et al.*, 2014), and functional (Edwards *et al.*, 2013; Edwards *et al.*, 2014b) and phylogenetic diversity (Chapman *et al.*, 2018).

Despite the environmental risks, the potential socio-economic benefits of oil palm development have led Latin American governments to incentivize the expansion of oil palm (Castiblanco *et al.*, 2013). For instance, Brazilian forest legislation has been revised to allow oil palm in Amazonia to be considered a low-impact crop (Mendes-Oliviera *et al.*, 2017), while the majority of Peruvian oil palm expansion has occurred at the expense of forest, partly driven by tax exemptions for oil palm investments (Gutiérrez-Vélez *et al.*, 2011). Elsewhere, Colombia's western Llanos, a region largely comprised of cattle pasture with fragmented patches of forest (Etter *et al.*, 2008), has been identified as a priority area for future oil palm plantations (García-Ulloa *et al.*, 2012). Previous studies show that expanding oil palm cultivation at the expense of forest in the Neotropics drives biodiversity losses across several taxa (Gilroy *et al.*, 2015; Lees *et al.*, 2015). However, expanding on improved pasture in the Llanos would conserve species richness (Gilroy *et al.*, 2015), and the phylogenetic and

65 functional diversity of birds (Prescott *et al.*, 2016a; 2016b), especially when forests are retained nearby.

A key knowledge gap is whether promoting the expansion of Neotropical oil palm cultivation at the expense of low-yield farmland is effective at conserving invertebrate functional diversity. Retaining a diversity of species' functional traits and life histories is vital  
70 in preserving ecosystem functions and bolstering resilience (Cadotte *et al.*, 2011). Functional diversity (FD) quantifies the range of functional traits and roles present in a community (Petchey & Gaston 2002). Land-use change can lead to environmental filtering, altering community composition and reducing functional diversity (Flynn *et al.*, 2009). Declines in FD can cause ecosystem destabilisation and lead to losses of ecosystem service provision  
75 (Cardinale *et al.*, 2012). Deforestation for oil palm drives reductions in the FD of dung beetles in Borneo (Edwards *et al.*, 2014b) and orchid bees in the Brazilian Amazon (Brito *et al.*, 2018), while forest conversion to cattle pasture in the Colombian Andes also decreases the FD of dung beetles (Davies *et al.*, 2020). Yet how oil palm replacement of low-yield farmland affects invertebrate functional diversity and composition is unknown.

80 Preserving invertebrate functional diversity within agricultural land may be achieved by retaining natural habitats adjacent to farmland, but this remains untested across the tropics. In Malaysia, oil palm plantations show similar dung beetle and ant community composition and dung removal rates irrespective of the presence of riparian reserves, although taxonomic diversity declines with increasing distance from riparian strips (Gray *et al.*, 2016). For Colombian birds in oil palm and pasture, the proportion of forest within 250 m  
85 had a positive effect on functional diversity (Prescott *et al.*, 2016b). These studies point to the potential for beneficial spill-over of species and their associated functions.

In this study, we assess the impacts of oil palm expansion in the Colombian Llanos on the functional diversity of dung beetles. Dung beetles represent an ideal study taxon as they perform important ecosystem functions, including secondary seed dispersal, soil aeration and nutrient cycling (Nichols *et al.*, 2008; Manning *et al.*, 2016). They are also sensitive to environmental change (Larsen *et al.*, 2005), are indicators of other taxonomic groups, especially mammals (Nichols *et al.*, 2009; Edwards *et al.* 2014a), and are taxonomically well-described and cost-effective to sample (Gardner *et al.*, 2008). Firstly, we compare the functional diversity and functional trait composition of dung beetles in oil palm, cattle pasture, and remnant forest in the Colombian Llanos, where oil palm is expanding (Garcia-Ulloa *et al.*, 2012). Secondly, we assess the extent to which landscape composition and configuration of remnant forest influences functional diversity and trait composition in oil palm plantations.

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## **Methods**

### ***Study area***

We worked at three sites across the Colombian Llanos in the departments of Meta and Cundinamarca, over an altitudinal range of 180-320 m.a.s.l. The Llanos is a semi-natural system of grassland, interspersed with patches of wet and dry forest. The study areas were dominated by low-intensity cattle grazing on improved pasture and large oil palm plantations (Romero-Ruiz *et al.*, 2010). 'Improvement' of grassland via the introduction of non-native grass species for cattle grazing is widespread throughout the Llanos, although cattle yields remain low (Etter *et al.*, 2008). Remnant forests in the region, including our study areas, are mostly composed of riparian strips and isolated forest fragments. Sampled oil palm

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plantations were all within plots where palms were of fruit bearing age (between 5 and 28 years old).

### ***Dung beetle sampling***

115 Sampling was conducted between January and May 2013, coinciding with the relative dry season in the region. Dung beetles were sampled using a total of 159 pitfall traps placed in randomly allocated clusters within each of the three habitat types: oil palm plantations (54 traps), cattle pasture (54 traps) and remnant forest patches (51 traps). Six pitfall traps were placed within each cluster, with 150 m spacing between traps. Given the small size of some remnant forest patches, full cluster samples were not always possible; in these instances, 120 traps were placed randomly in the habitat whilst retaining 150 m spacing between sample points. Traps were baited with fresh human dung, known to attract the majority of dung-feeding species (Davis & Philips 2005), with samples collected every 24 hours for four consecutive days, and traps were rebaited after 48 hours. The rim of the trap was buried level to the ground and the trap was partially filled with a mix of scent-free washing up liquid and 125 water to immobilize trapped beetles. Species identifications were made by J. S. Cardenas, A. González and C. A. Medina-Urbe using the Instituto Alexander von Humboldt reference dung beetle collection, and where specimens are deposited.

### ***Functional traits***

130 We analysed six functional traits: body size, front leg area, front-to-rear leg ratio, behavioural guild, diel activity, and diet range. We measured body size (length [base of head to elytra base] x width [of elytra]), front leg area (front femur area + front tibia area), and front to rear leg ratio ((front femur length + front tibia length)/(rear tibia length + rear femur length + rear spur length)) using photos, taken against a standardised scale in ImageJ. A subset of

individuals for each species were measured depending on occurrence ( $n = 1-36$ ). Mean values  
135 of each of these three traits were calculated for each species. Information on species'  
behavioural guild, diel activity, and diet range were obtained from the literature (Table S1).  
For species for which trait information was unavailable, we assumed that traits were common  
across a genus.

### ***Landscape configuration and composition***

140 We took metrics of both landscape composition and configuration in a circular buffer of 100  
m radius around each of our oil palm points. We used maps of forest cover and gain from  
Hansen *et al.* 2013 to determine patches of forest within our landscapes. However, these  
maps do not differentiate between native tree cover and plantation tree cover, so we  
manually designated oil palm plantations within the landscape using Google Earth v 7.3.3  
145 (Landsat imagery from 2010). These maps were then used to generate rasters of 30 m spatial  
resolution, distinguishing between forest and non-forest matrix vegetation.

We subsequently calculated indices of landscape configuration and composition in  
FRAGSTATS v 4.2 (McGarigal, Cushman & Ene 2012) using 100 m source radius and eight-cell  
neighbourhood rule. We analysed three metrics of landscape configuration and composition:  
150 (i) percentage forest cover, (ii) edge density – which totals the length of all forest edges in the  
buffer area divided by the total buffer area (m/ha), with a lower number indicating less edge  
effect, and (iii) distance to the nearest forest edge – which was measured manually using  
Google Earth v 7.1.2. (Landsat imagery from 2010).

## Statistical analyses

### **Functional diversity**

We calculated four metrics of functional diversity: functional richness (FRic), functional evenness (FEve), functional diversity (FD), and the standard effect size of FD (sesFD), using *FD* (Laliberté *et al.*, 2014) and the *picante* (Kembel *et al.*, 2010) packages in R (R Core Team). FRic and FEve are based on the hypervolume concept in which traits act as coordinates in functional space, identifying a species' functional niche (Villéger *et al.*, 2008). FRic is a measure of the volume of space occupied by constituent species and FEve describes the distribution of species' abundances within occupied functional space (Villéger *et al.*, 2008).

165 All traits were equally weighted, with species weighted by abundance.

FD and sesFD are derived from a functional dendrogram drawn connecting all constituent species of a community, with FD calculated by summing all branch lengths of the dendrogram (Petchey & Gaston 2002). FD is closely correlated to species richness (Petchey & Gaston 2002; Villéger *et al.*, 2008) and so sesFD was also calculated to control for this relationship. To calculate sesFD we compared the FD of each community to 999 null communities for which species richness is held constant, but species identity is randomly drawn from the species pool. Positive values of sesFD indicate that the FD of a community is greater than would be expected by chance, with negative values indicating the opposite.

To calculate hypervolume-based functional diversity metrics (FRic and FEve), the number of species in a community needs to be greater than the number of axes (in this case  $S > 2$ ). At the trap level, this condition was not met by 31 points (29 pasture and 2 oil palm points), and so these points were not included in the calculation of functional diversity.

### ***Comparing functional diversity between habitats***

All functional diversity metrics were compared between habitats using linear mixed-effect models (LME) with maximum likelihood estimation in the *lme4* package (Bates *et al.*, 2014). All models contained site and cluster as random effects to control for potential spatial autocorrelation. Likelihood ratio tests (LRT) were used to compare full models to null models (with the fixed effect of habitat removed). In cases where the full model was a better fit (i.e., the full model had a lower AIC value than the null model; Table S2), post hoc Tukey tests were performed using the *multcomp* package (Hothorn *et al.*, 2008).

For comparisons of trait composition, we used the model framework described above to compare dung beetle body size and the abundance of dung beetles from each feeding guild (tunneller, roller, and dweller) and diel activity (diurnal, nocturnal) between habitats (see SOM for analysis of additional functional traits). For body size, we placed beetles into five size classes (0 to 25 mm<sup>2</sup>, 25 to 100 mm<sup>2</sup>, 100 to 200 mm<sup>2</sup>, 200 to 300 mm<sup>2</sup>, >300 mm<sup>2</sup>) and compared the abundance within each class between habitats using LME.

### ***Effect of landscape configuration and composition on the functional diversity and trait composition of oil palm communities***

We assessed the effect of each landscape variable on all four functional indices in our oil palm points using LME with maximum likelihood estimation. LRT were employed to assess the influence of landscape metrics on diversity, with site and cluster retained as random effects in all models. Full models with all the landscape variables included were compared to null models with the landscape variable of interest removed. We also used LME to assess the effect of landscape variables on dung beetle size-class distribution, and the abundance of beetles from each feeding guild and diel activity.

## Results

### *Effect of habitat on functional diversity and trait composition*

The model that best fit the data contained habitat as a fixed effect for all functional metrics, except FEve. FRic and FD were significantly greater in forest than in both oil palm and pasture, but the FRic and FD of oil palm was greater than pasture (LME; Figure 1A, C; FRic,  $X^2 = 22.644$ , d.f. = 2,  $P < 0.001$ ; FD,  $X^2 = 45.416$ , d.f. = 2,  $P < 0.001$ ). Pasture had greater sesFD than both forest and oil palm, which did not differ from one another (Figure 1D;  $X^2 = 7.787$ , d.f. = 2,  $P < 0.05$ ). FEve did not differ between any of the three habitats (Figure 1B;  $P > 0.05$  in all cases).

The hyper-abundance of dung beetles in the smallest size class (0-25 mm<sup>2</sup>), as well as the abundance of the largest dung beetles (>300 mm<sup>2</sup>), did not differ between oil palm and forest, whilst their abundance in pasture was significantly less than in forest (Figure 2; 0-25 mm<sup>2</sup>,  $X^2 = 12.723$ , d.f. = 2,  $P < 0.005$ ; >300 mm<sup>2</sup>,  $X^2 = 10.491$ , d.f. = 2,  $P < 0.01$ ). The abundance of small-medium beetles (26-100 mm<sup>2</sup>) was greater in forest than in both oil palm and pasture, which did not differ from one another (Figure 2;  $X^2 = 9.741$ , d.f. = 2,  $P < 0.01$ ). Both medium (101-200 mm<sup>2</sup>) and medium-large (201-300 mm<sup>2</sup>) sized beetles did not differ in abundance between any of the habitats (Figure 2; 101-200 mm<sup>2</sup>,  $X^2 = 3.886$ , d.f. = 2,  $P > 0.05$ ; 201-300 mm<sup>2</sup>,  $X^2 = 1.966$ , d.f. = 2,  $P > 0.05$ ).

Forest had a significantly greater abundance of tunneling dung beetles than pasture, but their abundance in oil palm did not differ from forest or pasture (Figure 3B;  $X^2 = 9.632$ , d.f. = 2,  $P < 0.005$ ). The abundance of rolling and dwelling dung beetles did not differ between any of the three habitats (Figure 3A, C; Rollers,  $X^2 = 5.980$ , d.f. = 2,  $P > 0.05$ ; Dwellers,  $X^2 = 4.372$ , d.f. = 2,  $P > 0.05$ ). Both diurnal and nocturnal dung beetles were more abundant in

forest than pasture, but their abundance in oil palm did not differ from either forest or pasture (Nocturnal,  $\chi^2 = 8.261$ , d.f. = 2,  $P < 0.05$ ; Diurnal,  $\chi^2 = 11.403$ , d.f. = 2,  $P < 0.005$ ).

#### 225 ***Effect of landscape configuration and composition on dung beetle communities in oil palm***

Increasing the distance to the nearest forest edge had no effect on any of the functional metrics ( $P > 0.05$  in all cases). Similarly, the percentage of forest cover and edge density had no effect on any functional metrics ( $P > 0.05$  in all cases).

The abundance of both the smallest (0-25 mm<sup>2</sup>) and largest (>300 mm<sup>2</sup>) beetles  
230 increased with greater forest cover (Figure 4A, B; 0-25 mm<sup>2</sup>,  $\chi^2 = 4.180$ , d.f. = 2,  $P < 0.05$ ; >300 mm<sup>2</sup>,  $\chi^2 = 14.071$ , d.f. = 2,  $P < 0.001$ ). Likewise, the abundance of tunneling and diurnal beetles increased with forest cover (Figure 4C, D; Tunnellers,  $\chi^2 = 3.913$ , d.f. = 1,  $P < 0.05$ ; Diurnal,  $\chi^2 = 3.992$ , d.f. = 1,  $P < 0.05$ ). The abundance of rollers increased with increasing edge density (Figure 4E;  $\chi^2 = 3.902$ , d.f. = 1,  $P < 0.05$ ), whereas tunnellers decreased with greater edge  
235 density (Figure 4F;  $\chi^2 = 4.015$ , d.f. = 1,  $P < 0.05$ ). Distance to the nearest forest edge had no effect on the abundance of any of our measured traits ( $P > 0.05$  in all cases).

## **Discussion**

With oil palm cultivation expected to grow throughout the Neotropics (Butler & Laurance  
240 2009; Garcia-Ulloa *et al.*, 2012), minimizing the effects of expansion on functional diversity is vital to maintain ecosystem function and service provision. Our study shows that allowing future oil palm development at the expense of cattle pasture, as opposed to remnant forest, conserves dung beetle functional diversity in the Colombian Llanos, especially with increasing forest cover in the landscape. Expanding oil palm on low-intensity pasture is thus biodiversity-

245 friendly and combined with the retention of forest patches within oil palm landscapes would  
conserve functional diversity that likely bolsters ecosystem functioning and services.

***Functional diversity and trait composition in remnant forest, oil palm, and pasture***

Oil palm plantations retain a greater diversity of functional traits than improved cattle pasture  
in the Colombian Llanos, mirroring results previously found for birds (Prescott *et al.*, 2016b).

250 Remnant forest had greater FRic and FD than both oil palm and pasture, reflecting trends seen  
in South America (Brito *et al.*, 2018) and Southeast Asia (Edwards *et al.*, 2014b), and further  
demonstrating the potential for oil palm to severely diminish functional diversity when  
expansion is allowed at the expense of forest. Hence, forest protection should be the  
foremost concern of future oil palm expansion across South America (Gilroy *et al.*, 2015; Lees  
255 *et al.*, 2015).

The sesFD of both forest and oil palm was significantly lower than cattle pasture,  
suggesting higher levels of functional redundancy in these habitats (Pavoine & Bonsall 2011).  
This could be beneficial to the long-term functioning of forest and oil palm as species  
extinctions are less likely to lead to losses of unique functional traits, with functions provided  
260 by remnant species. Functional evenness (FEve) did not change across any of the three  
habitats, suggesting that resource utilization efficiency is equal across habitats (Mason *et al.*,  
2005). This agrees with evidence from Southeast Asia showing conversion of forest to oil palm  
does not affect the FEve of dung beetle assemblages (Edwards *et al.*, 2014b).

Of eleven functional traits, only three differed significantly between forest and oil  
265 palm, whereas six differ between pasture and forest (see SOM). Similar abundance of  
tunneling and rolling dung beetle species between forest and oil palm contrasts with findings  
from Sabah, Malaysian Borneo, where oil palm lacked dung-rolling species (Edwards *et al.*,

2014b), which has been attributed to roller larvae experiencing reduced survival due to increased soil temperature (Larsen 2012). Dung beetle assemblages are extremely sensitive to microclimatic conditions (Larsen *et al.*, 2005). The lack of a difference in body size and guild abundances between forest and oil palm thus suggests that oil palm in the Llanos provides microclimatic conditions similar to that of forest (Senior *et al.*, 2017). This has important functional implications, as tunneling species are important in cycling nutrients through the soil column and have the highest dung removal rates (Slade *et al.*, 2007), while dung-rollers are pivotal in moving seeds and nutrients away from concentrated piles of dung (Nichols *et al.*, 2008).

Dung beetles in pasture had a greater mean body size than beetles in either oil palm or forest (Figure S1), which appears to be driven by a severe depression in the abundance of smaller-bodied species in pasture (Figure 2). Several small beetle species—*Uroxys sp.04H*, *Onthophagus sp.2J*, *Onthophagus sp.01H*, and *Canthidium sp.16H*—found in particularly high abundances in both forest and oil palm were in extremely low abundances or entirely absent from pasture points. The absence of the largest dung beetle species in pasture (*Phanaeus haroldi*, *Deltochilum guildingii*, and *Dichotomius sp.08H*) may be due to the lower thermal tolerances of large-bodied beetle species (Larsen *et al.*, 2008), which makes them less likely to persist in open, hotter pastures (Senior *et al.*, 2017).

The average body size of dung beetles increased with forest cover (Figure S2), driven by an increase in the abundance of the largest species (Figure 4B), which has important functional consequences as larger beetles remove more dung at faster rates (Slade *et al.*, 2007). Evidence suggests that retaining forest cover and understory vegetation in oil palm plantations in the Llanos increases both diurnal and nocturnal mammal occupancy (Pardo *et*

*al.*, 2019), which may explain the positive association between diurnal beetle abundance and forest cover. The abundance of rollers within oil palm plantations also increased with higher edge density, suggesting spillover from forest refuges and enhanced dung removal and dispersal at the forest-oil palm interface (Nichols *et al.*, 2008; Gray *et al.*, 2016).

295 Our study has two key caveats. In our study, 31 traps (29 in pasture) did not have sufficient species for functional diversity analysis (see Methods). Consequently, we may have overstated the true functional diversity of pasture since the least taxonomically diverse traps were not included in the calculation of functional diversity. Even so, our results still demonstrate the severely diminished functional diversity of dung beetle communities found  
300 in pasture. Secondly, we only focused on dung beetles, indicating that further research is required to understand how conversion of low-intensity farmland and retention of forest within the landscape impact the functional diversity of other invertebrate taxa. However, dung beetles are good indicators of patterns in other invertebrate groups (Nichols *et al.*, 2009; Edwards *et al.*, 2014a).

### 305 ***Management of oil palm landscapes***

This study indicates that oil palm expansion in the Colombian Llanos can be achieved with minimal effects on biodiversity and related ecosystem function by replacing improved, low-intensity cattle pasture (Gilroy *et al.*, 2015; Prescott *et al.*, 2016a; 2016b). It also indicates an important role of remnant forest patches in protection and spillover of ecosystem functions,  
310 underscoring the need for forest protection in this region. Uptake of Roundtable for Sustainable Oil Palm (RSPO) membership, which requires protection of forest patches with high conservation value, in combination with regional landscape planning, provides impetus for such sustainable expansion.

Adopting a land-neutral management plan is necessary to provide protection for  
315 remnant forest patches and riparian strips in the region, whilst ensuring that cattle production  
is not displaced to regions with lesser protection, termed 'leakage' (Lataweic *et al.*, 2015).  
Thus, intensification of cattle production will be necessary to assure a land-neutral outcome,  
with relatively minor changes in husbandry predicted to meet such yield gaps (Garcia-Ulloa *et*  
*al.*, 2012). Cattle integration within oil palm plantations is a mixed farming land management  
320 approach, whereby cattle are grazed under mature palms, which may reduce problems  
associated with leakage, whilst also boosting beetle abundance and dung removal rates (Slade  
*et al.*, 2014). Additionally, maintenance of understory vegetation within oil palm plantations  
could bolster dung beetle communities, by increasing habitat heterogeneity (Azhar *et al.*,  
2014) and providing microclimatic conditions beneficial to dung beetles at no yield cost (Luke  
325 *et al.*, 2019).

Finally, while forests seemingly protect functional diversity and wider biodiversity  
(Gilroy *et al.* 2015), current riparian corridor widths may not be sufficient to maximise  
biodiversity protection (Mitchell *et al.*, 2018; Harada *et al.*, 2020). Future management of oil  
palm landscapes should therefore seek to mandate minimum widths for riparian strips,  
330 maximizing the potential for these remnant habitats to provide a refuge for the most  
vulnerable species, whilst also boosting intra-farmland biodiversity and ecosystem function.

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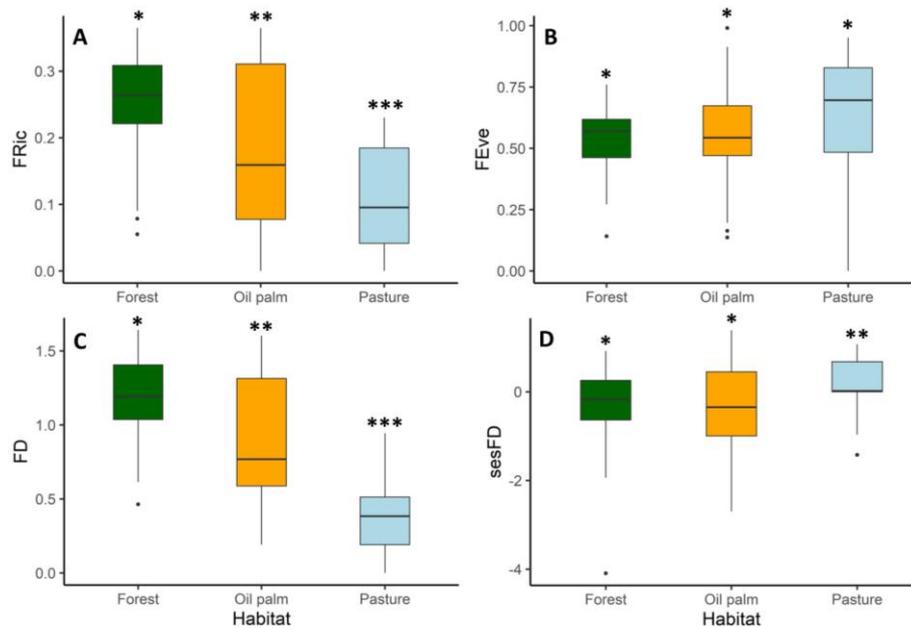
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## Figures



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Figure 1. A) functional richness (FRic), B) functional evenness (FEve), C) functional diversity (FD), D) standard effect size of functional diversity (sesFD) in remnant forest (green), oil palm (orange) and cattle pasture (blue). Box whisker plots show median, interquartile and 1.5 x interquartile ranges, and outliers. Different symbols (\*, \*\*, \*\*\*) indicate significant differences between habitats, tested at the  $P < 0.05$  level.

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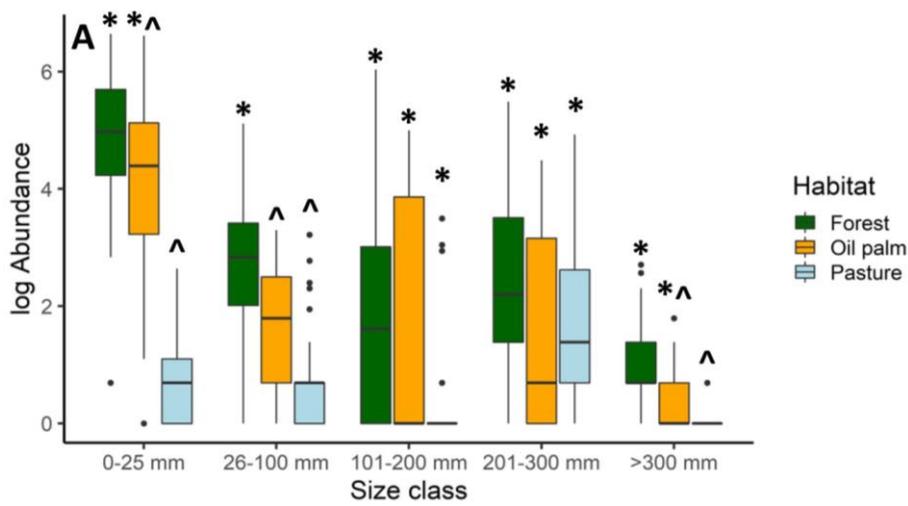
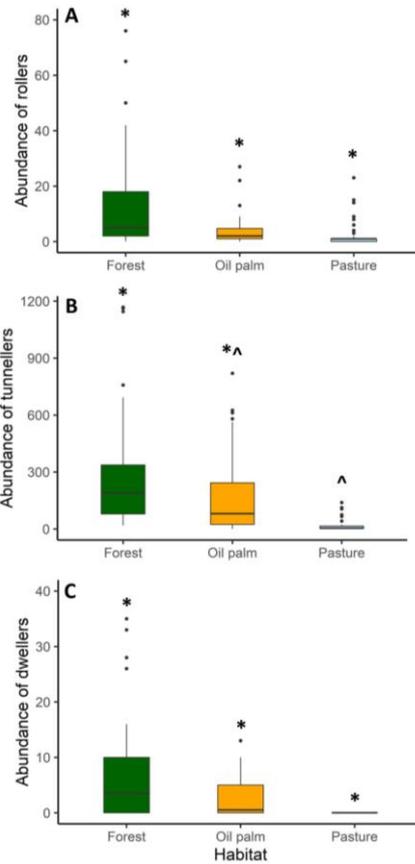


Figure 2. Dung beetle log abundance-size class distribution in remnant forest (green), oil palm (orange) and cattle pasture (blue). Box whisker plots show median, interquartile and 1.5 x interquartile ranges, and outliers. Different symbols (\*, ^) indicate significant differences between habitats, tested at the  $P < 0.05$  level.

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Figure 3. A) abundance of rollers, B) tunnellers, and C) dwellers in remnant forest (green), oil palm (orange) and cattle pasture (blue). Box whisker plots show median, interquartile and 1.5 x interquartile ranges, and outliers. Different symbols (\*, ^) indicate significant differences between habitats, tested at the  $P < 0.05$  level.

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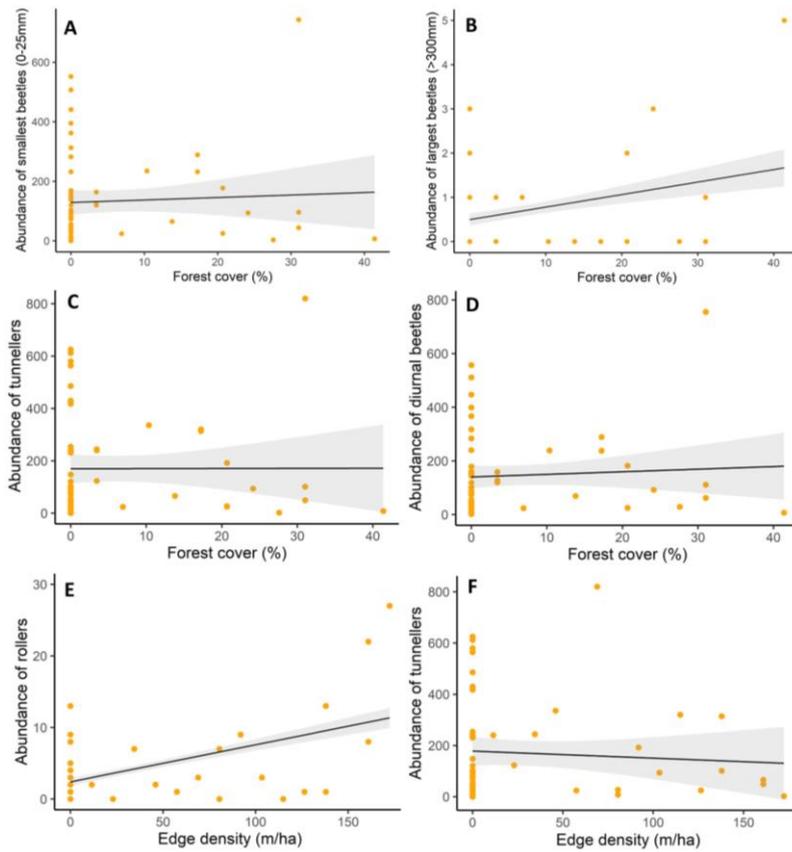


Figure 4. A) Abundance of the smallest (0-25 mm<sup>2</sup>), and B) largest (>300 mm<sup>2</sup>) dung beetles and the C) abundance of tunneling, and D) diurnal dung beetles with increasing forest cover (%); and E) abundance of rolling and F) tunneling dung beetles with increasing edge density. Regression drawn using predictions from model with best fit (model included fixed effect of percentage of forest cover for A, B, C, and D and edge density for E and F), with shaded area indicating 95% confidence interval.