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Dung beetles and their ecological functions in three agroforestry systems in the Lacandona rainforest of Mexico

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Abstract   There is growing interest in evaluating the impact that management intensity of agroecosystems has on animal communities and their ecological functions. Dung beetles are a highly used focal taxon for assessing the effects of anthropogenic disturbances and management practices on biodiversity. In the Lacandona rainforest region in southern Mexico, we quantified several metrics of the dung beetle community (number of species, number of individuals, total biomass, mean beetle size) and four of their ecological functions (dung removal, soil excavation, seed dispersal, seed exhumation) in conserved rainforest and three agroforestry systems with different management intensities: rustic cocoa, polyculture cocoa, and rubber monoculture. We also assessed the correlation between dung removal and the other functions, as well as the relationships between functions and community metrics. Land-use type affected the dung beetle communities as well as their functions, with negative effects on response variables in the most intensely managed agroecosystems (polyculture cocoa and rubber). Rustic cocoa had values similar to those of

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the conserved forest for all functions and community metrics, except the mean number of species per trap. Dung removal was correlated with the other ecological functions. The mean number of species per trap was significantly associated with all four functions. In our study region rustic cocoa plantations favor the maintenance of a high proportion of dung beetle species and maintain their ecological functions. Our findings corroborate that agroecosystems with less intense management may contribute to buffering the effects of landscape homogenization caused by more intensely managed agroecosystems, such as rubber plantations.

Keywords   Agroecosystem · Anthropogenic landscape · Biodiversity conservation · Rubber · Scarabaeinae · Shade cocoa

Introduction

Over one quarter of our planet's terrestrial surface is covered by ecosystems modified because of agricultural activities (Altieri 2004). The speed and extent of the transformation of natural landscapes have tremendous consequences on biotic communities (Alkorta et al. 2003). In human-dominated landscapes, though, some types of agroecosystems may serve as complementary and/or supplementary habitats for native species, thus contributing to biodiversity conservation and ecosystem function (Vandermeer et al. 2008; Tscharntke et al. 2011; Häger et al. 2015). In regions of tropical forests, agroforestry systems that maintain a complex structure and composition of the vegetation, often have a higher value for the conservation of biodiversity (Vandermeer and Perfecto 2007; Perfecto and Vandermeer 2008; Tscharntke et al. 2011). For example, agroforestry systems in which the crop of interest is grown underneath a tree canopy (e.g., shade coffee and cocoa) can be important habitats for different types of organisms (e.g., Pineda et al. 2005; Estrada et al. 2012). In addition, these types of agroecosystems may constitute a type of anthropogenic matrix that buffers the effects of forest fragmentation by increasing connectivity (Perfecto and Vandermeer 2008), thus contributing to the functional dynamics at the landscape level.

Not many studies have evaluated the relationship between the attributes of animal communities living in tropical agroecosystems and the amount of ecological function they perform (e.g., Johnson et al. 2010; Williams-Guillén and Perfecto 2010; Zárate et al. 2014). In this context, dung beetles (Scarabaeinae) constitute an insect group that is abundant, diverse, and functionally important in tropical forests, and that is commonly used in applied biodiversity studies (Nichols and Gardner 2011). Most tropical dung beetles remove and bury vertebrate dung in underground tunnels dug through soil excavation (Halffter and Edmonds 1982). As a consequence of this behavior, dung beetles play crucial roles in a variety of ecological processes (Nichols et al. 2008). Several of these processes are related to seed dynamics, including both secondary dispersal of seeds defecated by mammals, as well as upward movement and exhumation of seeds buried in the soil (Santos-Heredia and Andresen 2014).

Dung beetles are negatively affected by anthropogenic disturbances of the tropical forest (Nichols et al. 2007; Culot et al. 2013; Edwards et al. 2017), but certain agroforestry systems can harbor communities very similar to those found in forest (Arellano et al. 2005; Giraldo et al. 2011; Neita and Escobar 2012). Not all agroforestry systems have the same value for biodiversity conservation, though; this value greatly depends on management type and intensity (Williams-Guillén and Perfecto 2010; Tisovec et al. 2014).

Even though dung beetles are very frequently used as a focal taxon in studies that assess the effects of forest disturbance on biodiversity (Nichols and Gardner 2011; Nichols et al. 2013; França et al. 2016; Edwards et al. 2017), the functional consequences for the ecosystem are generally inferred indirectly through the quantification of dung beetle community parameters (Noriega et al. 2017). However, the relationships between community parameters and community functions are not always straightforward (Slade et al. 2011; Dangles et al. 2012; Kudavidanage et al. 2012; Braga et al. 2013; Hosaka et al. 2014) and may even be contrary to what is expected (e.g., Griffiths et al. 2016). Furthermore, when function is directly quantified, in most cases only dung removal is determined (Horgan 2005; Slade et al. 2011; Dangles et al. 2012; Kudavidanage et al. 2012). Dung removal is then used as a proxy variable to infer changes in other functions. The relationships between dung removal and other ecological functions, however, may not necessarily be strong and/or linear (Braga et al. 2013; Nichols et al. 2013; Hosaka et al. 2014).

In this study, we determined dung beetle community parameters and measured four of their ecological functions in three types of agroforestry systems, comparing values to those observed in the conserved rainforest. The three agroecosystems had different levels of management intensity, from the lowest intensity in rustic cocoa plantations, to intermediate intensity in polyculture cocoa plantations, and the highest intensity in rubber monocultures. We had the following specific objectives: (i) to determine the effects of land use on four dung beetle community parameters (number of species, number of individuals, total biomass and mean beetle size); (ii) to determine the effects of land use on four ecological functions of dung beetles (dung removal, soil excavation, secondary seed dispersal and seed exhumation); and, (iii) to assess the relationship between dung removal and other functions, as well as the relationships between community parameters and ecological functions.

Methods

Study system

We carried out our study in the Lacandona rainforest region in the Mexican state of Chiapas. This region is one of the few large remaining areas of humid tropical forest in Mesoamerica and the last one in Mexico (Cuarón 2000). Mean annual temperature is 22 °C, and mean annual precipitation is 3000 mm, with most of the rainfall (~90%) occurring between June and November. Tropical rainforest is the dominant vegetation type (Holdridge 1967). Detailed information about the study region can be found elsewhere (De Jong et al. 2000; Zermeño-Hernández et al. 2016).

The conserved rainforest was in the Montes Azules Biosphere Reserve. The three agroforestry systems were located in three municipalities (Marqués de Comillas, Ocosingo and Benemérito de las Américas) in an anthropogenic landscape constituted by a mosaic of land uses, such as large forest areas (> 1000 ha), forest fragments, human settlements, successional vegetation and different types of agroecosystems. We performed our study in a period of 17 months (October 2011–February 2013) in 12 study sites (three per land use).

(i) *Conserved rainforest* The three sites were within the biosphere reserve, approximately 800 m from the Lacantún River (16°07′18.3″N, 90°56′23.7″W), with a distance of 5–11 km between sites.

(ii) *Rustic cocoa* (*Theobroma cacao*) The three rustic cocoa fields were in Ejido Playón de la Gloria. Cocoa trees were planted in the 1980 decade by inserting them into the understory and leaving most of the canopy intact (16°08′46.2″N, 90°52′54.8″W). At the time of our research, the three fields had low levels of cocoa harvest, and additional management only included some pruning or removal of a few shade trees. Cocoa fields had an area of 4–7 ha, were 1–1.5 km apart, and were surrounded by other shade cocoa fields, which all together constituted an area of approximately 120 ha of shade cocoa.

(iii) *Polyculture cocoa* These three fields were in Ejido Loma Bonita. Cocoa trees were planted in the 1980 decade in clear-cut areas (16°05′49.6″N, 90°58′34″W). Shade in these fields was provided by few native tree species that were planted along with the cocoa trees. At the time of our research, fields were actively managed by harvesting cocoa fruits, manually removing vegetation between 30 and 300 cm of height, and applying fertilizers. Cocoa fields had an area of 1.8–2.2 ha, were 2–5 km apart, and were surrounded by pastures and/or annual crops.

(iv) *Rubber monoculture* (*Hevea brasiliensis*) The three rubber fields were in Ejido Francisco J. Grajales; they were planted in the 1990 decade in clear-cut areas (16°04′56.0″N, 90°44′13.4″W). At the time of our research, the rubber trees had an average height of 12 m; management included constant removal of all other vegetation and the use of fertilizers. Rubber fields had an area of 0.5–0.7 ha, were 0.8–1 km apart, and were surrounded by other rubber fields, all together constituting an area of approximately 240 ha of rubber.

Dung beetles

We used pitfall traps baited with 30 g of fresh howler monkey dung (*Alouatta pigra*) to capture dung beetles. Howler monkey dung was readily obtained as a parallel study was being conducted that entailed following monkey groups (Zárate et al. 2014). Also, howler monkey dung is believed to be very important in supporting dung beetle communities in Neotropical forests (e.g., Gill 1991). Traps were plastic containers (11 cm tall and 9 cm opening diameter), filled to one-third of their volume with soapy water and buried with the rim at ground level. We placed a plastic plate 20 cm above the trap to protect it from rain.

In each of the 12 study site we placed four traps, one in each corner of a 50×50 m^2. Traps were baited and opened in the late afternoon (16:00–18:00 h), and beetles were collected after 48 h. During the study period, we sampled on three occasions (t_1, October 2011; t_2, February 2012; t_3, October 2012) using the same trap locations. Captured beetles were identified to species with the help of Fernando Escobar at Instituto de Ecología A.C., Xalapa, Veracruz, Mexico.

We measured body size (length from head to pygidium) and dry weight based on ten individuals per species when ≥ 10 individuals were captured, or based on all individuals captured for those species with < 10 captures. For each trap, we obtained the following: the number of individuals, the number of species, total biomass and mean beetle size. The total biomass was the dry weight of all beetles captured in a trap; it was estimated by using the mean dry weights of each species, multiplied by the number of individuals of that species and added over all species captured in a trap. Mean beetle size is a weighted average that yields a representative size of the beetles captured in a trap. For each trap, this variable was calculated as [Σ(size sp $i \times$ abundance sp i)/Σ abundance sp i], where $i = 1, 2 \ldots n$ and n is the number of species captured in that trap.

Ecological functions

We quantified dung removal, soil excavation, secondary seed dispersal and seed exhumation through a field experiment by using four stations per site. Each station was located next to a pitfall trap (see above) and consisted of a circular area on the soil surface, with a radius of ~ 70 cm from which we removed the leaf litter. We did not use a physical barrier to delimit the outer border of the station; thus it is possible that some beetles moved some of the dung beyond the area cleared of litter. However, in a study carried out in the study region in which movements by dung beetles were measured, the maximum reported distance was 60 cm (Ponce Santizo 2008). One week before opening the pitfall traps, we placed in the center of each station 50 g of fresh howler monkey dung and measured ecological functions after 48 h. In each site, we also placed a control dung pile (50 g of dung covered with a fine wire mesh) to estimate weight loss caused by evaporation. We used a plastic roof to protect dung piles from rain.

To quantify dung removal, we collected the fecal material remaining on the surface, weighed it, and calculated the percentage of dung removed (correcting for evaporation). To estimate soil excavation, we collected with a spoon all the loose soil visibly recognizable as having been excavated by dung beetles; we dried and weighed the collected soil. Our values of soil excavation represent conservative estimates, as some dung might have been buried by beetles, and thus soil excavated, beyond the area of the stations. To determine seed dispersal and exhumation, we placed round plastic beads (hereafter referred to as seeds) of three sizes, used as seed mimics, inside the 50 g of dung (Andresen 2002). Each dung pile contained 50 small seeds (4 mm), 20 medium seeds (8 mm) and ten large seeds (12 mm), following Braga et al. (2013). To quantify seed dispersal, we counted the seeds (with or without dung) visible on the soil surface and then calculated the percentage of seeds that had been buried by beetles. Dung beetles disperse seeds present in the dung both vertically and/or horizontally (Andresen 2002). As dung beetles in our study site generally move seeds to maximum distances of 60 cm (Ponce Santizo 2008), we assume that in the present study, our measure of seed dispersal reflects mostly vertical dispersal (seed burial) that occurred within the litter-cleared area encompassed by each station. However, it is possible that our measure also included some horizontal seed dispersal (with seeds either buried or remaining on the surface) when dung beetles moved seeds beyond the 70 cm radius. To quantify seed exhumation, which occurs when dung beetles move to the surface some of the seeds that had been buried in the soil (Santos-Heredia and Andresen 2014), we calculated the percentage of seeds found again on the soil surface, from the accumulated number of seeds that had been previously buried by beetles. Ecological functions were also measured three times during the study period (t_1, t_2, t_3; see above). Dung removal, excavated soil and seed dispersal were measured during t_1, t_2 and t_3. We used experimental seeds of different colors each time. We could not quantify exhumation during t_1 as the first experimental seeds were buried by beetles during this time. Thus, to be able to have a third temporal replicate for seed exhumation, four months after t_3 we again placed 50 g of dung in each station (t_4, February 2013), but without beads. Thus, seed exhumation was measured during t_2, t_3 and t_4.

Data analyses

To evaluate inventory completeness, the sample coverage ($\hat{C}n$) was calculated at the habitat scale using the 'iNEXT' package for R (Hsieh et al. 2016), which applies the formula

$$\hat{C}n = 1 - \frac{f_1}{n} \left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2} \right],$$

where $f1$ and $f2$ are the number of *singletons* and *doubletons* in the sample and n is the total number of beetles. $\hat{C}n$ indicates the proportion of the 'total community' represented by the captured species; when $\hat{C}n \approx 100\%$, sampling is complete in terms of the effort and capture technique used (Chao and Jost 2012).

To analyze community composition in the four land uses we performed an ordination of the 12 sites by using non-metric multidimensional scaling (NMDS) with a Sørensen (Bray–Curtis) distance measure based on abundances. We report the *stress* (a measure of how well the real multivariate distance between samples is represented in a reduced-dimensional space) and the *linear fit* value (the correlation between fitted values and ordination distances). In addition we used a multi-response permutation procedure (MRPP) to assess differences among groups. Analyses were carried out in R version 2.15.3 (R Development Core Team 2013) using the 'vegan' package (Oksanen et al. 2007).

To analyze results at the trap/station level, we first averaged the three temporal samples and obtained one datum per trap/station for each response variable. Dung beetle community variables were as follows: number of species, number of individuals, total biomass and mean beetle size (all expressed per trap). Ecological function variables were the following: percentage of dung removed, dry weight of excavated soil, percentage of dispersed seeds, and percentage of exhumed seeds (all expressed per station). To assess the effect of land use we analyzed each of the above variables (except exhumed seeds, for which no model adequately fit the data due to many zeroes) with mixed-effects models, with land use as the fixed factor and site as the random factor (traps and stations were nested within sites; sites are the replicates). To explore the relationship between dung removal and the three other ecological functions we calculated Spearman correlation coefficients. Finally, to assess the relationship between ecological functions and community metrics we performed a mixed-effects model for each of the ecological functions (response variables), including all the community metrics as explanatory variables and site as random factor. The significance of explanatory variables was determined through backward sequential deletion. For all mixed-effects models we used the function *glmer.nb* (i.e., negative binomial error structure) to model response variables that consisted of percentage and count data with overdispersion (dung removal, seed dispersal, number of individuals, number of species) and we used *lmer* (i.e., normal error structure) for all other response variables (total biomass, mean beetle size, excavated soil). Adequacy of models was verified by examining the standardized residuals vs the fitted values, in addition to the graphical distribution of errors. For the analyses of deviance and the tests of contrasts, we used the Type II Wald Chi square test. For the adjustment of the values of P in the constrasts, we used the Holm method. Analyses were carried out using the 'lme4' (Bates et al. 2017), 'glmmML' (Broström 2017), 'multcomp' (Hothorn et al. 2017), 'car' (Fox et al. 2013), 'phia' (De Rosario-Martinez et al. 2015), and 'MASS' (Ripley et al. 2017) packages in R.

Results

Dung beetles

We captured a total of 8785 individuals of 40 species (Appendix I in Online Resource 1). In particular, we captured 37 species (3832 individuals) in conserved forest, 28 species (3528 individuals) in rustic cocoa, 27 species (1248 individuals) in polyculture cocoa, and 16 species (177 individuals) in rubber. Sample coverage was very high in all habitats (> 97% of the species recorded; Appendix I in Online Resource 1), indicating that our sampling effort was adequate for comparing among them.

Three species accounted for 63% of all individuals (Appendix I in Online Resource 1): *Eurysternus caribaeus* (2976 individuals), *Copris laeviceps* (1471 individuals) and *Onthophagus batesi* (1090 individuals). In general, most dung beetle species found in the agroecosystems were subgroups of species found in the conserved forest (Appendix I in Online Resource 1). Only two of all registered species were absent from the conserved forest: *Bdelyropsis bowditchi*, which was only found (> 400 individuals) in the rustic cocoa sites, and *Onthophagus yucatanus*, which was only found (50 individuals) in the polyculture cocoa. No dung beetle species was found exclusively in the rubber plantations, or had higher abundance in this agroecosystem (Appendix I in Online Resource 1). A two-dimensional ordination showed three distinct groups of sites, with conserved forest and rustic cocoa sites in the same group, polyculture cocoa sites in a second group and rubber sites in a third (NMDS: stress = 0.051, linear fit $r^2 = 0.992$; MRPP: $P = 0.001$; Fig. 1).

Considering beetle captures at the trap level, we found that the effect of land use was significant for all response variables: number of species ($\chi^2 = 285.8$, df = 3, $P < 0.001$), number of individuals ($\chi^2 = 1066.2$, df = 3, $P < 0.001$), total biomass ($\chi^2 = 393.77$, df = 3, $P < 0.001$), mean beetle size ($\chi^2 = 98.6$, df = 3, $P < 0.001$). For the number of species captured per trap all pairwise comparisons were significant (Fig. 2a). The number of individuals captured and the total biomass per trap were similar in conserved forest and rustic cocoa, but lower in polyculture cocoa and even lower in rubber (Fig. 2b, c). Mean beetle size was similarly high in conserved forest and rustic cocoa, and similarly low in polyculture cocoa and rubber (Fig. 2d).

Fig. 1 Ordination (NMDS) of the 12 study sites where dung beetles were captured in four land uses: conserved forest (triangles), rustic cocoa (squares), polyculture cocoa (diamonds) and rubber monoculture (circles)
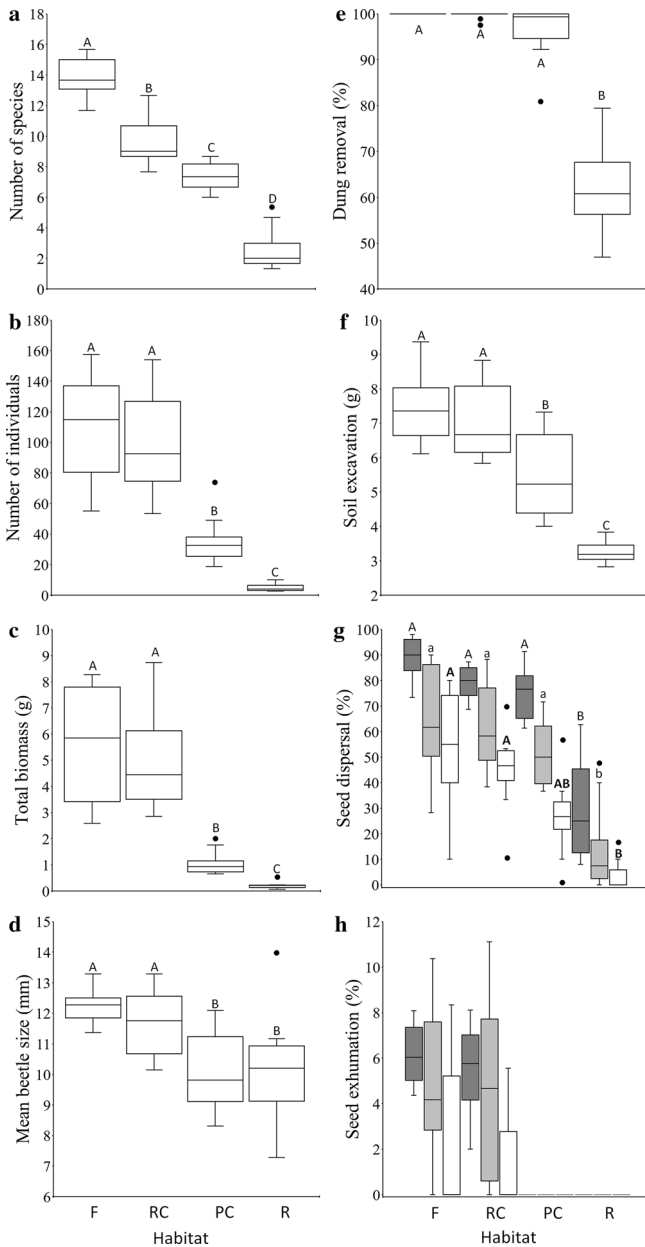
Linear fit, $r^2 = 0.992$
Stress = 0.051

Axis 2

Axis 1
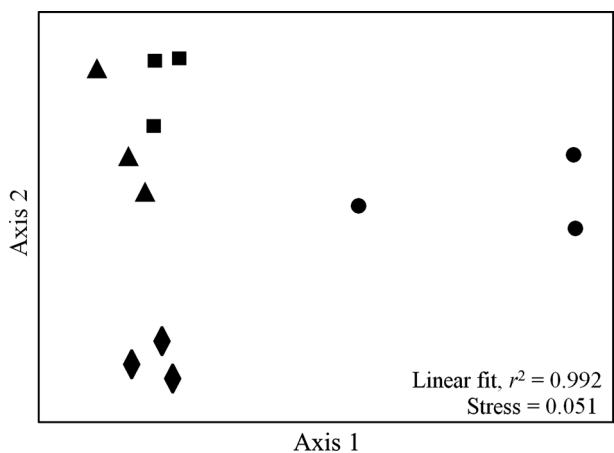
Fig. 2 Box-plot graphs comparing dung beetle community metrics per trap (**a–d**) and ecological functions per experimental station (**e–h**), quantified in four land uses: conserved forest (F), rustic cocoa (RC), polyculture cocoa (PC) and rubber monoculture (R). Panels (**g**) and (**h**) show results for the three artificial seed sizes used in the experiments: small (4 mm, black bars), medium (8 mm, gray bars) and large (12 mm, white bars). The bottom and top lines of the box are the first (q1) and third quartiles (q3), respectively; the middle line inside the box is the median value; the upper error bar represents $q3 + 1.5(q3 - q1)$, while the lower error bar represents $q1 - 1.5(q3 - q1)$; the circles represent outliers. Different letters above the bars indicate statistical differences (with the function *testInteractions* using R package 'phia'). In panel (**g**) upper case letters, lower case letters, and bold letters correspond to tests for small, medium and large seeds, respectively. Seed exhumation (**h**) only occurred in the conserved forest and rustic cocoa, and adequate statistical modeling could not be carried out

Ecological functions

The four functions evaluated were affected by land use (Fig. 2e–h). Dung beetles removed more dung in conserved forest and both types of cocoa agroecosystems (>97%) than in rubber (62%; $\chi^2 = 15.83$, df = 3, $P = 0.001$; Fig. 2e). In addition, dung beetles excavated more soil in conserved forest and rustic cocoa than in polyculture cocoa; in the rubber agroecosystem, the amount of soil excavated was lowest ($\chi^2 = 453.23$, df = 3, $P < 0.001$; Fig. 2f). Similarly, land use had an effect on seed dispersal for all seed sizes (small: $\chi^2 = 15.11$, df = 3, $P = 0.002$; medium: $\chi^2 = 18.39$, df = 3, $P < 0.001$; large: $\chi^2 = 10.94$, df = 3, $P = 0.012$). Seed dispersal showed a very high variability such that statistical differences were only detected between the rubber (with lower percentages) and the other land uses (Fig. 2g). Finally, seed exhumation, which also showed large variability, was infrequent: 1–6% of buried seeds were brought back to the soil surface. In addition, it only occurred in conserved forest and rustic cocoa (Fig. 2h).

Relationships between dung removal and the other functions, and between dung beetle community metrics and ecological functions

We found that the percentage of dung removal was positively correlated with three other ecological functions measured, i.e., the amount of soil excavated, and the percentages of seeds dispersed and exhumed (Fig. 3). Regarding the association between the ecological functions and the dung beetle community metrics, we found that all metrics significantly explained the variation of at least one ecological function (Table 1). The two metrics related to dung beetle abundance per trap, i.e., number of individuals and biomass, only had significant positive effects on seed dispersal. The metric indicative of the average size of beetles captured in a trap (mean beetle size) had a significant positive effect on dung removal, seed dispersal and seed exhumation. Finally, the best predictor variable, as it was significantly associated (positively) with all four ecological functions, was the mean number of species per trap (Table 1).

Discussion

Management intensity in tropical agroforestry systems: dung beetle communities and their ecological functions

Dung beetles play important roles in many ecological functions, providing crucial and highly valued ecosystem services, particularly in agricultural settings (Noriega et al. 2017; Nichols et al. 2008). However, agricultural landscapes are highly diverse and the effects of management practices on biodiversity and its functions are context-specific (Frank et al. 2017). Our study revealed that in the Lacandona rainforest region of Mexico, rustic cocoa plantations maintained dung beetle communities similar to those found in the forest, with a consequent similarity in their functionality. More intensively managed cocoa plantations, the polyculture cocoa, had diminished community metrics and functions, while the values of the variables measured were very low in the rubber plantation. This finding is in general accordance with previous studies that also measured both community metrics and

Fig. 3 Spearman correlations between the ecological function of dung removal and the other ecological functions measured: soil excavation (**a**), seed dispersal (**b**), and seed exhumation (**c**)
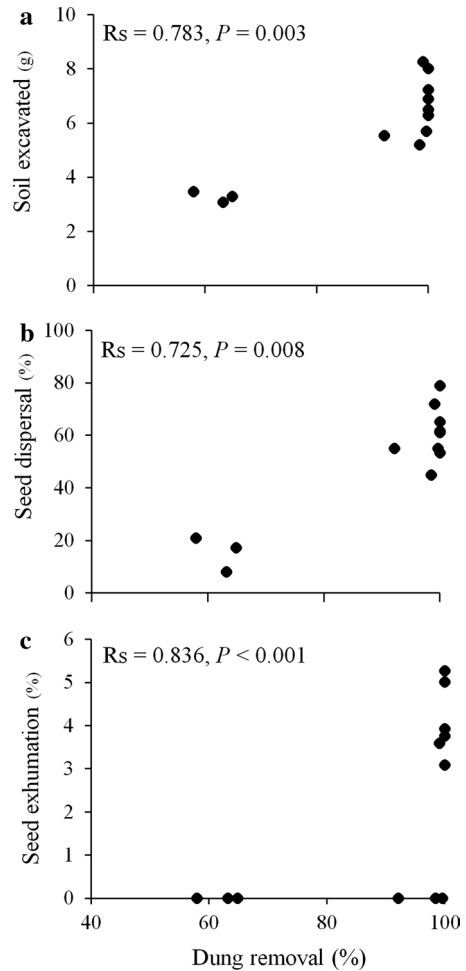
functions of dung beetles and found strong negative effects in intensively managed agro-ecosystems such as pasture and annual crops (e.g., Giraldo et al. 2011; Braga et al. 2013; Frank et al. 2017).

In the studied agroecosystems, we found subgroups of species present in the conserved forest (except for two species that were exclusively found in high numbers, one in the rustic cocoa and one in the polyculture cocoa; Appendix I in Online Resource 1). Rubber plantations, the agroecosystem with the highest management intensity, harbored only 43% of the dung beetle species and 4.6% of the abundance found in the conserved forest, and the ecological functions of the community were accordingly greatly diminished. Strongly impoverished dung beetle communities have also been reported in other homogeneous agroforestry systems (Gardner et al. 2008; Gray et al. 2014). Native rainforest dung beetles are often habitat specialists that depend on a complex vegetation structure and respond negatively to canopy openness (Halffter and Arellano 2002). Furthermore, dung beetle communities are also negatively affected when the populations of native herbivorous mammals decline (Culot et al. 2013). In this regard, the rubber

Table 1 Results of the mixed-effects models to assess the relationships between ecological functions and community metrics

Ecological function	Dung beetle community metrics			
	Number of species	Number of individuals	Mean body size	Total biomass
Dung removal	$\chi^2 = 5.706$	$\chi^2 = 2.852$	$\chi^2 = 5.897$	$\chi^2 = 2.494$
	$P = 0.017$	$P = 0.091$	$P = 0.015$	$P = 0.114$
Soil excavation	$\chi^2 = 9.274$	$\chi^2 = 0.146$	$\chi^2 = 0.088$	$\chi^2 = 0.001$
	$P < 0.001$	$P = 0.702$	$P = 0.767$	$P = 0.973$
Seed dispersal	$\chi^2 = 13.114$	$\chi^2 = 8.914$	$\chi^2 = 6.564$	$\chi^2 = 6.382$
	$P < 0.001$	$P = 0.003$	$P = 0.010$	$P = 0.012$
Seed exhumation	$\chi^2 = 5.384$	$\chi^2 = 2.159$	$\chi^2 = 12.741$	$\chi^2 = 2.495$
	$P = 0.020$	$P = 0.142$	$P < 0.001$	$P = 0.114$

We performed a model for each of the ecological functions (response variables), including all the community metrics as explanatory variables and site as random factor. The significance of the explanatory variables was determined through backward sequential deletion and the Type II Wald Chi square test

plantations studied had a relatively open and low canopy (ca. 12 m), and they were not being used by diurnal herbivorous mammals (CS-H and DAZ, personal observation). This shows that not all agroecosystems that include a continuous tree layer have the same value in terms of biodiversity conservation and ecological functions. Thus, studies should be carried out to assess a system's suitability as an alternative or complementary habitat for animals and its ability to maintain ecosystem functions, prior to proposing it as a conservation option.

The rustic cocoa, which was the agroecosystem with the lowest management intensity, had values similar to the conserved forest for all variables measured at the trap/station level, except for the number of species, which was significantly lower. Previous studies have stressed the importance of low-intensity management agroecosystems in maintaining diverse and abundant dung beetle communities, similar to those found in conserved forest (Arellano et al. 2005; Giraldo et al. 2011; Braga et al. 2013). However, the fact that the number of species captured per trap was lower than in conserved forest, may suggest that while rustic cocoa seems to be maintaining most community attributes and functions, it is possible that differences between rustic cocoa and conserved forest could increase with time. Long-term monitoring will be necessary to assess this.

Finally, the polyculture cocoa agroecosystem harbored 68% of all species recorded, but only 14 and 9% of the number of individuals and total biomass, respectively (Appendix I in Online Resource 1). For some response variables, this agroecosystem showed values similar to conserved forest and rustic cocoa; for others, the values were as low as in rubber, and yet for others the values were intermediate. Not only management intensity but also landscape composition and configuration in which the polyculture cocoa plantations were inserted could have affected the dung beetle communities, as suggested by the results of a previous study in the same region (Sánchez-de-Jesús et al. 2016). Polyculture cocoa sites were surrounded by pasture and/or annual crops, while the rustic cocoa sites were surrounded by more rustic cocoa. Generally, agroecosystems with higher management intensity are immersed in landscapes in which other types of anthropogenic disturbance occur simultaneously (e.g., higher fragmentation, higher loss of forest cover, higher loss of connectivity, more hostile matrices, higher

loss of other organisms), with potentially additive or synergistic negative effects on biodiversity (Laurance and Useche 2009; Otieno et al. 2011).

In terms of the dung beetle communities of the Lacandona rainforest region, our results suggest that agroforestry systems with less intense management, such as the rustic cocoa plantations, may compensate against some of the negative effects of homogenization caused by monocultures in anthropic landscapes. However, several other land uses occur in this landscape (e.g., forest fragments, riparian forest, successional vegetation, cattle pastures, annual crops) and it would be very valuable for future studies to include increased sampling in all dominant landscape elements and determine how the diversity of dung beetles is partitioned within and between land uses at large spatial scales.

Relationships between dung removal and other functions, and between community metrics and functions

Studies in forest ecosystems that use dung beetles as a focal taxon to assess the effects of habitat changes on the functions performed by these insects often measure only dung removal. This is due to methodological simplicity, as well as the fact that most other functions are a consequence of dung removal and burial. However, not all studies have found an agreement between dung removal and other functions. In particular for seed dispersal, while some studies have found a strong relationship with dung removal (Slade et al. 2007), others have not (Braga et al. 2013). In our study, we did find significant relationships between dung removal and the other ecological functions measured, including seed dispersal. However, we want to point out that our methodology for quantifying dung removal did probably not yield good precision in terms of removal rates in the different land uses. We measured dung removal after 48 h; in the conserved forest and both types of cocoa plantations, most dung had been removed after that time period. It could be that, if we had measured dung removal in shorter time intervals (e.g., every 6 h), we could have detected differences in the removal rate of dung in these three habitats. This is something that future studies must consider in order to have good precision when estimating dung removal. However, this lack of precision for the estimation of dung removal, does not affect our precision in the estimation of the other ecological functions.

In general, we believe that, to draw stronger conclusions, more than one ecological function of dung beetles should be measured in studies that use this insect group as a focal taxon to assess the effects of habitat disturbance. Additional to dung removal, the amount of soil excavated and seed dispersal are easily measured in the field, and these variables are increasingly being incorporated into project protocols that use dung beetles as a focal taxon (Giraldo et al. 2011; Braga et al. 2013; Hosaka et al. 2014; Griffiths et al. 2016).

Finally, the relationship between biodiversity and ecosystem functioning is a topic that has received much attention and generated many debates in the last few decades (Loreau et al. 2002), and recent assessments are showing that the relationship is consistent across many systems (e.g., Lefcheck et al. 2015). Similar to other studies, we found positive relationships between dung beetle community metrics and function (Bang et al. 2005; Slade et al. 2007, 2011; Dangles et al. 2012; Braga et al. 2013; Gregory et al. 2014; Griffiths et al. 2015, 2016; Manning et al. 2016). There is important variation among and within studies, however, regarding the strength of the relationships between specific community metrics and particular functions. For example, while some studies have found that certain ecological functions are strongly related to total species richness (e.g., Slade et al. 2011; Dangles et al. 2012; Braga et al. 2013, Griffiths et al. 2016), others have found relationships with

functional richness (e.g., Griffiths et al. 2015), others with total biomass (e.g., Griffiths et al. 2016), or with certain functionally efficient groups, such as large beetles (e.g., Slade et al. 2007; Dangles et al. 2012; Braga et al. 2013; Gregory et al. 2014). Furthermore, some studies have found no relationship at all (e.g., Gray et al. 2014). In our study we also found differences. While all community metrics were significantly associated with at least one ecological function, the mean number of species per trap was our most reliable predictor, as it was the only metric that was significantly associated with all four functions measured. In general, while most evidence supports the contention that dung beetle community metrics are associated with their functions, more studies focusing on multiple community variables (Audino et al. 2014) and multiple ecological functions (Manning et al. 2016) are needed to elucidate the specific mechanisms that drive particular relationship patterns for the different functions dung beetles play in ecosystems.

Concluding remarks

Our study showed that an increase in the management intensity of agroforestry systems caused negative effects on the dung beetle community, and consequently also on the amount of functions performed by these insects. It is important to consider, however, that we only compared agroecosystems that include a tree stratum, and that even the rubber plantations may have improved community metrics and functions when compared to less complex agroecosystems such as annual crops or cattle pasture (e.g., Braga et al. 2013). It has been shown that some types of intensive high-yielding agroforestry systems, such as complex silvopastures, can promote dung beetle diversity and function, in comparison to less intensive and low-yielding systems, such as treeless pastures (Montoya-Molina et al. 2016).

We recommend that in addition to dung removal other ecological functions of dung beetles easily measured in the field (in particular soil excavation and seed dispersal) should be quantified in studies that use this insect group as a focal taxon for assessing the effects of habitat disturbances or for assessing the conservation value of particular agroecosystems. It is also highly likely that negative effects on dung beetles will have repercussions for other ecosystem functions such as nutrient cycling, biochemical and physical soil properties, soil-atmosphere gas fluxes, interactions among soil organisms, among others (e.g., Penttilä et al. 2013; Menéndez et al. 2016; Slade et al. 2016a, b). Future studies in the tropics will need to measure these effects in human-modified landscapes. In the tropics some negative effects of land-use change, such as the emission of greenhouse gases associated with cattle production, could have a pronounced global impact, and thus the importance of functioning dung beetle communities in these systems is of utmost importance (Slade et al. 2016a).

Clearly, we need to have a better understanding of all the consequences of altering the communities of this important group of insects for the functioning of tropical ecosystems, both natural and anthropogenic. Such understanding will allow us to propose efficient management strategies that may achieve both production and conservation goals in heterogeneous landscapes (Montoya-Molina et al. 2016). Our study shows that agricultural systems that are managed less intensively, such as the rustic cocoa plantations in our study region, may play a crucial role in buffering the negative effects of the homogenization caused by monocultures, underscoring the importance of diversifying the agricultural matrices in anthropogenic landscapes.

Author contributions   CS-H, EA and FE formulated the research idea. CS-H and EA designed the experiments, with contributions from FE. CS-H and DAZ conducted all fieldwork. CS-H, EA and FE analyzed the data and wrote the manuscript.

Compliance with ethical standards

Conflict of interest   The authors declare that they have no conflict of interest.

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