

Assessing the Ecological Response of Dung Beetles in an Agricultural Landscape Using Number of Individuals and Biomass in Diversity Measures

C. A. Cultid-Medina^{1,2} and F. Escobar^{3,4}

¹Investigador Asociado, Wildlife Conservation Society–Colombia Program, Calle 2 No. 42–23, Cali, Colombia (carlos.cultid@gmail.com), ²Grupo de Investigación en Biología, Ecología y Manejo de Hormigas, Departamento de Biología, Universidad del Valle, Calle 13 No. 100–00, Cali, Colombia, ³Instituto de Ecología, A. C., Apartado Postal 63, Xalapa, Veracruz, México (federico.escobarf@gmail.com), and ⁴Corresponding author, e-mail: federico.escobarf@gmail.com

Received 20 July 2015; Accepted 30 November 2015

Abstract

The global increase in demand for productive land requires us to increase our knowledge of the value of agricultural landscapes for the management and conservation of biodiversity, particularly in tropical regions. Thus, comparative studies of how different community attributes respond to changes in land use under different levels of deforestation intensity would be useful. We analyzed patterns of dung beetle diversity in an Andean region dominated by sun-grown coffee. Diversity was estimated using two measures of species abundance (the number of individuals and biomass) and was compared among four types of vegetation cover (forest, riparian forest, sun-grown coffee, and pastures) in three landscape plots with different degrees of deforestation intensity (low, intermediate, and high). We found that dung beetle diversity patterns differed between types of vegetation cover and degree of deforestation, depending on whether the number of individuals or biomass was used. Based on biomass, inequality in the dung beetle community was lowest in the forest, and increased in the sun-grown coffee and pastures across all levels of deforestation, particularly for the increasing dominance of large species. The number of beetles and biomass indicate that the spatial dominance of sun-grown coffee does not necessarily imply the drastic impoverishment of dung beetle diversity. In fact, for these beetles, it would seem that the landscape studied has not yet crossed “a point of no return.” This system offers a starting point for exploring biodiversity management and conservation options in the sun-grown coffee landscapes of the Colombian Andes.

Key words: tropical montane cloud forest, agricultural landscape, sun-grown coffee, Hill numbers, inequality

The change in vegetation cover associated with the expansion and intensification of agriculture is the most visible indicator of human activity and the main cause of the decrease in biodiversity across the planet (Phalan et al. 2014). As such, it is obvious that agricultural landscapes will continue to be key elements in the successful conservation and management of biodiversity and the ecological processes that depend upon it (Chazdon et al. 2009). Agricultural landscapes can be very heterogeneous, with a diversity of types of vegetation cover providing habitats and resources that can be complementary and beneficial for both biodiversity and agricultural systems (Bawa et al. 2004). This is why it is of utmost importance to evaluate the potential of these landscapes as conservation targets.

In Latin America, fully exposed or sun crops have replaced other ways of growing coffee such as shade coffee plantations (Perfecto et al. 2009). The proportion of shade-grown coffee has fallen by nearly 20% since 1996, resulting in the modification of tracts of native vegetation at the regional scale and decreasing its conservation

value (Jha et al. 2014). In Colombia, coffee is an emblematic agricultural product and 25% of the rural population of the country depends on it for their income (Federación Nacional de Cafeteros–CENICAFÉ [FNC] 2013a). It is also one of the most controversial crops in environmental terms owing to the high use of agrochemicals (Perfecto et al. 2009). Of the area in the country where coffee is grown (975,000 ha), ~90% is sun-grown coffee (FNC 2013b) and a large part of it is produced at elevations of 1,300 to 2,000 m above sea level (a.s.l.) (Guhl 2004), where tropical montane forest—known for its high degree of diversity and concentration of endemics—can be found (e.g., Young et al. 2002).

Several studies have shown that replacing tropical montane forest at intermediate elevations with sun-grown coffee impoverishes the taxonomic and functional diversity of ants, birds, amphibians, and soil arthropods (Perfecto and Armbrrecht 2003, Rivera and Armbrrecht 2005, Philpott et al. 2008). Others, however, have not detected any negative response of diversity in landscapes dominated

by sun-grown coffee (Numa et al. 2005, Muriel and Kattan 2009, De la Mora et al. 2013, Zabala et al. 2013). This discrepancy partly results from that fact that the response of diversity depends not only on the sensitivity of the taxonomic group studied to habitat disturbance, but also on factors operating beyond the local scale. These can include the history of regional management and the heterogeneity (structure and composition) of the landscape (Tscharntke et al. 2005, Fahrig et al. 2010), as well as the attributes of the community that are being evaluated (i.e., richness, the number of individuals or their biomass, trophic guild).

Dung beetles are traditionally used to evaluate the impact of human activity on biodiversity (Nichols et al. 2007). In general, elimination of the forest canopy modifies the community structure of these beetles, affecting the efficiency of several ecological processes that are important to ecosystem functioning, such as the removal of organic matter and nutrient recycling (see Nichols et al. 2008). Our knowledge of the response of dung beetles in coffee-growing landscapes is limited and most of the studies have only been carried out at the local scale. In fact, much of the information comes from Mexico (Estrada et al. 1998, Pineda et al. 2005), where shade coffee plantations dominate. To date, there have been no studies evaluating the impact of intensifying sun-grown coffee cultivation on the diversity of dung beetles in the landscapes of the Andes.

Most of the studies that evaluate the changes in diversity on agricultural landscapes are based on species incidence and the number of individuals. Over the last two decades, there has been an increase in the use of species biomass in ecological studies of dung beetle ecology (Scholtz et al. 2009). In general, the modification of natural habitats appears to have a more drastic and obvious effect on the distribution of biomass in the dung beetle community (Horgan 2005, Gardner et al. 2008, Larsen et al. 2008, Rös et al. 2012). However, the use of biomass to assess the response of dung beetle diversity to different levels of human disturbance is still limited. Biomass is considered a key variable in community ecology, particularly in terms of energy flow and the productivity and dynamics of the food webs (Brown et al. 2004), and can be an alternative indicator to describe the structure of the community (Magurran 2004). This is because not all of the species of a community are functionally equivalent and thus the number of individuals of one species does not necessarily predict its contribution in relative terms of biomass or concentrated energy (Saint-Germain et al. 2007).

We evaluate the changes in dung beetle community through diversity measures using number of individuals and biomass in an Andean landscape in Colombia dominated by sun-grown coffee. The following questions were addressed: 1) How does dung beetle diversity differ among four types of vegetation cover (forest, riparian forest, sun-grown coffee, and pasture)? 2) How do any differences detected differ for landscapes with different degrees of deforestation intensity (low, intermediate, and high)? In Figure 1A, the expected patterns for the number of beetles, beetle biomass, and diversity with respect to vegetation cover and degree of landscape deforestation are shown.

Materials and Methods

Study Area

This study was conducted on the eastern face of the Western Range of the Colombian Andes, Risaralda Department (5° 1'17.33"–5° 0'28.27" N and 76° 1'51.71" W; 76° 57'29.43" W). The landscape spans elevations of 1,300 to 2,000 m a.s.l. (Fig. 1B), where sun-grown coffee is dominant (Wildlife Conservation Society–Colombia [WCS] 2013), and corresponds to the transition zone between the

Lower Montane Wet Forest and the Premontane Moist Forest (Espinal 1977). Mean annual rainfall is 2,500 mm and mean annual temperature is 18°C. The region is a mosaic of vegetation types dominated by patches of native vegetation that differ in size (located at the top of the mountains and in glens), sun-grown coffee annual crops, stover, and pasture (WCS 2013).

The forests on the mountain tops are relicts of tropical cloud forest with typical mid-elevation floral diversity; for practical purposes, we refer to this type of vegetation cover as forest. Riparian forest comprises remnants of native vegetation associated with rivers and streams, surrounded by sun-grown coffee and pastures (Fig. 1B). Riparian forests are located in areas with steep slopes that limit access for agriculture and to livestock, and the persistence of riparian forest on the landscape can also be attributed to the protection of water sources. Hereafter, we refer to the forest plus the riparian forest as native vegetation.

Most of the area where coffee (*Coffea arabica*) is grown has sun-grown coffee, mainly of two varieties: Caturra and Colombia. The coffee matrix is managed by smallholders (farms of 3 to 10 ha) and coffee plants range from 15 mo to 9 yr in age. Where the coffee is grown, there are trees such as *Cordia alliodora*, *Inga* sp., and *Psidium guajava*, along with seasonal crops such as banana and cassava trees. Pastures are used for a few head of cattle (one to ten animals) and cover less than 10% of the landscape. We included pasture because it represents the most extreme level of disturbance to dung beetles (Nichols et al. 2007). Hereafter, we refer to sun-grown coffee plus pasture as anthropic cover.

Degree of Deforestation Intensity

We set up three landscape plots, each with an area of ~500 ha (2.3 by 2.3 km) and representing different degrees of deforestation intensity or percentage of native vegetation cover (forest + riparian forest) relative to the area used for sun coffee (Fig. 1B) and set up over a similar range of elevation: low (LD: 57%; elevation average: 1,698 m a.s.l.; range: 1,450–1,900 m a.s.l.), intermediate (ID: 29%; 1,750 m a.s.l.; 1,580–1,950 m a.s.l.), and high (HD: 18%; 1,740 m a.s.l.; 1,580–1,893 m a.s.l.; Fig. 1B). Each landscape was characterized in spatial terms using cartographic information from the Federación Nacional de Cafeteros (1:100,000) and the Corporación Autónoma de Risaralda (CARDER: 2007 land cover maps 1:25,000). Vegetation cover types were verified in the field between 2008 and 2009, and the information was processed using ArcGIS 9.3 (ESRI Inc. 1999–2008).

Sampling Design

In each landscape plot, four types of vegetation were chosen: forest, riparian forest, sun-grown coffee, and pasture. Given that large (> 50-ha) patches of forest are scarce in the study region (WCS 2013), it was only possible to include a single patch of forest in each landscape plot (Fig. 1B). In each vegetation type, two or three sites were set up, separated by more than 250 m (34 sites in total: 12 LD, 11 ID, and 11 HD). In each site, a transect was set up with six non-lethal pitfall traps (Cultid et al. 2012) at 30-m intervals. The traps consisted of a 0.5-liter container buried flush with the soil and baited with 35 g of excrement (a 7:3 mixture of human and pig excrement), located in the top part of the container. There were a total of 204 traps: 72 LD, 66 ID, and 66 HD. Sampling was conducted monthly between March and August 2008, covering the first rainy season and the beginning of the second dry season. At each site, the traps were active for 48 h for a total effort of 58,752 h/trap. Due to the steep topography and landscape plot size, sampling was not

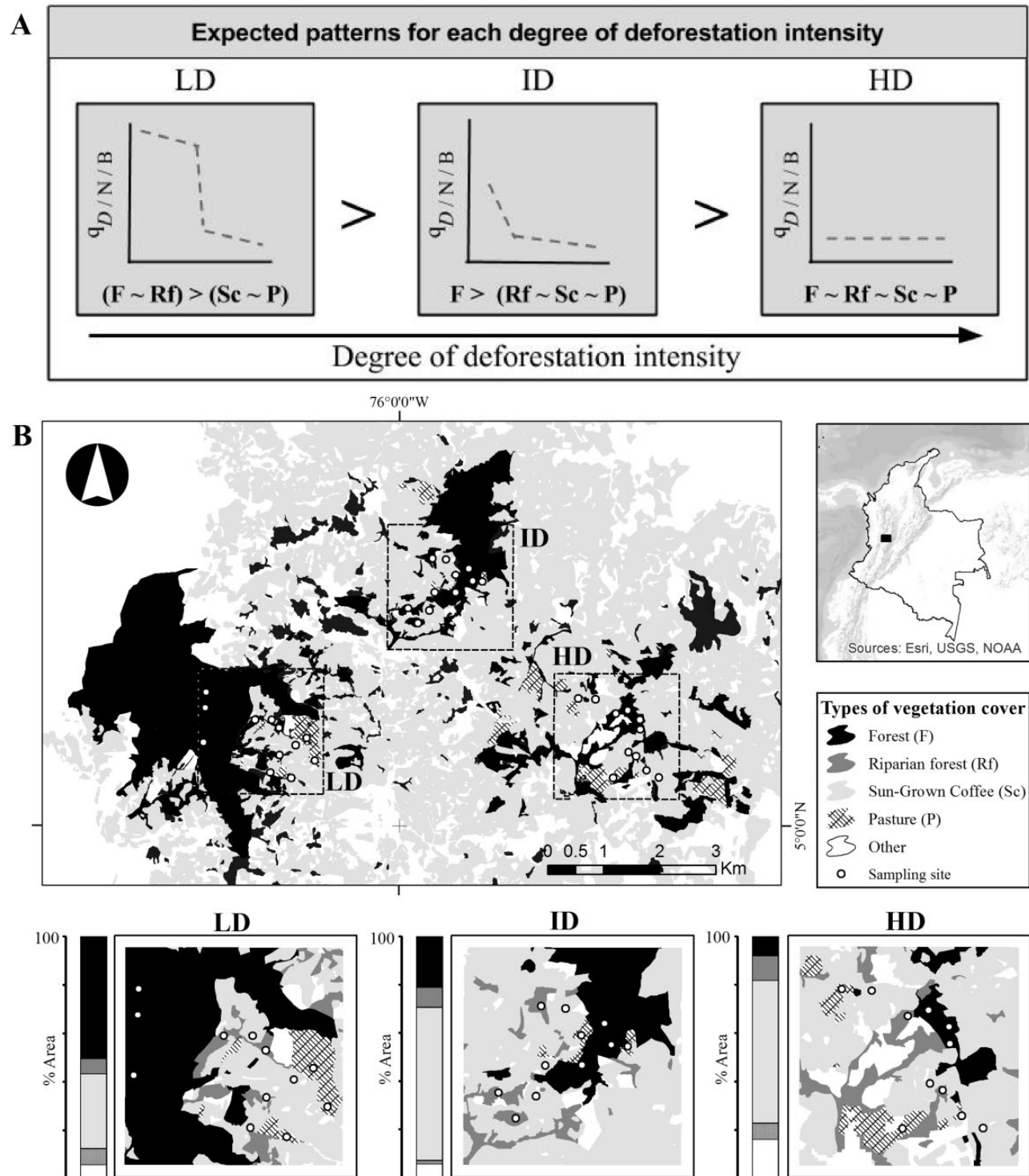


Fig. 1. (A) Expected patterns for the response variables number of beetles (N), beetle biomass (B), and diversity (qD) related to types of vegetation cover (F, forest; Rf, riparian forest; Sc, sun-grown coffee; P, pasture) for each landscape plot (deforestation intensity: LD, low; ID, intermediate; HD, high). ~ indicates there are no differences. Under the hypothesis that sun-grown coffee at the landscape scale is a low-quality habitat for dung beetles, we expect forest dung beetle diversity to decrease as the dominance of sun-grown coffee increased, such that under extreme deforestation (HD) diversity would be lower and similar among the different types of vegetation cover. (B) Study area. The Western Andes of Colombia, showing the landscape plots. For each landscape our sampling sites are indicated by the type of vegetation cover. Bars to the left of each landscape plot indicate the proportion (%) of the area covered by each type of vegetation cover.

performed simultaneously at all the sites; rather, sampling in each landscape plot was completed over a period of ~6 d per month.

Response Variables

We used the following response variables: number of beetles (N), beetle biomass (B), diversity weighted by number of beetles (${}^qD_{(N)}$), and beetle diversity weighted by biomass (${}^qD_{(B)}$). These variables were analyzed at two levels: between types of vegetation cover for each degree of deforestation intensity and between landscape plots. Biomass was calculated as the product of the mean dry weight of each species and its abundance per trap. To obtain the dry weight and depending on the number of individuals caught for each species, 1 to 32 specimens were dried at 60°C for 48 h, after which each specimen was weighed on a precision digital balance (Ohaus Adventure ± 0.0001 g).

Diversity was evaluated in terms of “effective numbers of species” (qD) (Jost 2006; see below)—an approach that is equivalent to Hill’s numbers (Hill 1973):

$${}^qD = \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)},$$

where qD only depends on the proportional abundance (numbers of individuals or biomass) per species (p_i) and the exponent q (Jost 2006). qD is an ecologically intuitive measure for describing and comparing diversity because it is expressed in biologically interpretable units (i.e., effective number of species; Jost 2006, 2010). The exponent q determines the influence of species abundance on diversity values and ranges from 0 to infinity (Jost 2006). We used three q values: order 0 (0D , species richness), 1 (1D , exponential of Shannon’s entropy), and 2 (2D , inverse Simpson concentration). 0D is not sensitive to species abundance and thus gives disproportionate weight to rare species (Jost 2006). 1D weights each species according to its abundance in the community; hence, it can be interpreted as typical diversity or the number of common species in the community (Jost 2006). Finally, 2D can be interpreted as the number of “very abundant” or “dominant” species in the community (Jost 2006).

Analysis of Numbers of Individuals, Mass, and Biomass of Dung Beetle Species

Following the recommendation of Saint-Germain et al. (2007), we evaluated two relationships: 1) average body dry mass (g) with total of number of individuals and 2) biomass with total of number of individuals for both levels of comparison (i.e., types of vegetation cover in each landscape and between landscape plots). We did not expect the first relationship to be significant, but did expect the second to be significant. In the latter case, both variables can order species in a similar manner (i.e., a species that is dominant in terms of the numbers of individual would also be dominant in terms of biomass), so species ranking was examined visually using rank-abundance curves (also known as dominance–diversity curves; Feinsinger 2003). Simple linear regressions were used to test for any relationships among the variables ($\alpha = 0.05$), with $\log_{10}$ transformed data. The number of individuals and biomass between types of vegetation cover in a given landscape plot and between landscape plots were compared using a Kruskal–Wallis test. For both, an *a posteriori* comparison was carried out using Dunn’s test (Zar 1999).

Sampling Completeness and Diversity Analysis

The comparison of diversity (qD) among assemblages is only ecologically appropriate under the same sample coverage (Chao and Jost 2012). For each type of vegetation cover and landscape plot, sample

coverage ($\hat{Cm}$) was calculated—a value that indicates the proportion of the statistical population that is represented by the species captured (Good 1953, Chao and Jost 2012):

$$\hat{Cm} = \left(1 - \frac{f_1}{n} \left[\frac{(n-1)f_1}{(n-1)f_1 + 2f_2} \right] \right) * 100,$$

where n is the abundance of the sample and f_1 and f_2 are the number of singletons and doubletons, respectively. $\hat{Cm}$ has values from 0 (minimal completeness) to 100 (maximum completeness). When completeness is close to 100% and similar between assemblages, diversity values (qD) can be compared directly (Chao and Jost 2012). For comparisons of diversity using the number of individuals (${}^qD_{(N)}$) and biomass (${}^qD_{(B)}$), the 95% CI were used and differences were determined following the recommendations of Cumming et al. (2007), where no overlap between CI values indicates significant differences. Sample coverage values, qD , and their respective confidence intervals were obtained using the iNEXT package for R (Hsieh et al. 2015).

Magnitude of the Difference in Diversity (MD)

On expressing diversity as the effective number of species and making comparisons under the same sample coverage, the replication principle is met and it is possible to calculate the magnitude of the difference in diversity (MD) among communities (Jost 2006). That is, it is possible to determine how many times a type of vegetation cover or landscape is more or less diverse than another. The magnitude of the difference was expressed as a percentage: %MD = $100 - [({}^qD_{\text{sample 2}} \times 100) / {}^qD_{\text{sample 1}}]$ (modified from Moreno et al. 2011). Thus, when sample 1 is more diverse than sample 2, MD will be positive (+%MD); otherwise, it will be negative (–%MD). Therefore, %MD will vary from 0 (no change in the diversity of a given pair of samples) to ($\pm$) 100% (completely different diversity). Values of %MD were compared visually and the interpretation of the comparisons is complementary to those of the 95% CI.

Relative Logarithmic Inequality (RLI) Profiles

To examine the loss of diversity across types of vegetation and the three degrees of deforestation inequality profiles based on number of individuals and biomass were used. RLI is a logarithmic transformation of the inequality factor (IF) proposed by Jost (2010):

$$RLI = \frac{(\ln IF_{0,q})}{(\ln S)},$$

where S is the total species richness for a given type of vegetation cover and landscape plot and $IF_{0,q}$ is the inequality factor, which is the rate of change of magnitude between species richness values (0D) and qD ($q > 1$): $IF_{0,q} = {}^0D / {}^qD$ (Jost 2010). Values of RLI range from 0 (minimum inequality) to 1 (maximum inequality) (Jost 2010).

Results

Sampling Completeness, Number of Beetles, and Beetle Biomass

A total of 20,697 beetles belonging to 28 species and 11 genera were caught (Supp Table 1 [online only]). In all cases, the sampling deficit was $\leq 5\%$ (Supp Table 1), and so the comparisons of diversity (qD) were made directly by visual inspection of the overlap of the 95% CI.

The relationship between species body mass and total number of individuals was not significant, but a statistically significant relationship was detected between species biomass and the number of

individuals in each degree of deforestation intensity, as well as for types of vegetation cover in landscape plots (Supp Figs. 1 and 2 [online only]). Also, we observed that some abundant species were not dominant in biomass (Supp Figs. 1 and 2 [online only]).

There were no differences among landscape plots in the number of individuals, but there were differences in biomass, with HD accounting for nearly 50% of the total biomass and differing significantly from the other landscape plots (Table 1; Supp Table 1 [online only]). In general, both the number of individuals and biomass decreased from forest to pasture, although, in the LD, biomass in sun-grown coffee was significantly greater than in the other vegetation cover types, with no significant differences among the latter (Table 1; Supp Table 1 [online only]).

Diversity Patterns (^qD)

Species richness (⁰D) in LD was significantly higher than in the other two landscape plots (Fig. 2A). Using the number of individuals, typical diversity (¹D_(N)) differentiated and ranked the landscapes as expected with respect to the decrease in the area of native vegetation (LD > ID > HD; Fig. 2A). However, the number of dominant species (²D_(N)) in LD was not different from that in ID, and both landscape plots were more diverse than HD (Fig. 2A). In contrast, using diversity weighted by biomass (¹D_(B) and ²D_(B)), landscape plots were similar, but differed from the expected pattern because the intermediate degree of deforestation was the most diverse (Fig. 2A). All expressions of diversity (⁰D, ¹D, and ²D) were lowest in HD (Fig. 2A).

Diversity patterns in vegetation cover types changed with the intensification of deforestation of the landscape, and these differences depended on whether the number of individuals or the biomass had been used to calculate diversity. In general, for the three landscape plots and for all measures of diversity, forest tended to be more diverse than the other types of vegetation cover (Fig. 2B, C, and D). That being said, in HD, species richness (⁰D) was similar among cover types, coinciding with the expected pattern (Fig. 2D). For diversity weighted by the number of individuals (¹D_(N) and ²D_(N)), sun-grown coffee in HD was significantly more diverse than forest for both measures of diversity (Fig. 2D), whereas, in LD using biomass and only for the number of dominant species (²D_(B)), sun-grown coffee was more diverse than the other types of vegetation cover (Fig. 2B).

Changes in Diversity (MD)

The magnitude and direction of the change between pairs of cover vegetation types and landscape plots became evident in typical diversity values (¹D) and in the number of dominant species (²D). The

decrease in diversity when calculated based on the number of individuals does not necessarily imply a significant reduction (or one with the same direction) in terms of biomass (e.g., ^qD for LD vs. ID, Fig. 2B and C). These discrepancies were more evident in HD, for which sun-grown coffee was more diverse than forest in terms of the number of individuals (– %MD), but, with respect to biomass, the loss of diversity occurred in the opposite direction, from forest to sun-grown coffee (+ %MD; Fig. 2D).

Inequality Profiles (RLI)

Inequality based on biomass has a marked pattern of increasing dominance that varies between 50% and values close to 100%, while, with the number of individuals, it only varies between 25 and 66% (Fig. 3). Forest had the lowest inequality in LD using the number of individuals, while the other types of vegetation cover had similar inequality values that were higher than those of the forest. This differed from that observed in biomass, for which inequality increased notably from forest to pasture (Fig. 3). For the other landscape plots, the pattern was different owing to changes in the inequality values for forest: in HD, for the number of individuals and for both measures of diversity (¹D and ²D), inequality for the forest was high and similar to that of the pasture (Fig. 3). In contrast, for LD and ID, inequality values for the forest were lower and more similar to each other (Fig. 3). In terms of biomass, inequality was observed to be accentuated in pasture (range: 64–96%), while riparian forest and sun-grown coffee in the three landscape plots tended to have inequality values more similar to those observed for forest (Fig. 3).

Discussion

None of the variables we used (number of beetles, beetle biomass, diversity weighted by number of beetles or biomass) to evaluate the response of the dung beetle community followed the expected response patterns for vegetation cover across differing degrees of deforestation intensity (Fig. 1A). In general, for the agricultural landscape we studied, it was obvious that the forest was more diverse than the other types of vegetation cover, although the pattern varied with the expression of diversity that was used (⁰D, ¹D, and ²D) and whether the number of individuals or biomass was used to estimate diversity. Thus, our results show that the use of biomass was not necessarily redundant, but rather provided complementary ecological information about the impact of land use on the structure of the dung beetle community and its functional role in ecosystems.

Table 1. Observed response patterns for number of beetles (*N*) and their biomass (*B*) related to the degree of deforestation intensity in the landscape plots (LD, low; ID, intermediate; HD, high) and vegetation cover type for each landscape plot (F, forest; Rf, riparian forest; Sc, sun-grown coffee; P, pasture)

Variable	Landscape plots: LD > ID > HD	Vegetation cover types in landscape plots		
		LD: (F ~ Rf) > (Sc ~ P)	ID: F > (Rf ~ Sc ~ P)	HD: F ~ Rf ~ Sc ~ P
Number of individuals (<i>N</i>)	ID ~ HD ~ LD (6.45; 0.039)	F > (Sc ~ Rf ~ P) (44.69; 0.0001)	(F > Rf) > (Sc ~ P) (60.02; 0.0001)	(F ~ Rf) > (Sc ~ P) (38.18; 0.0001)
Beetle biomass (<i>B</i>)	HD > (ID ~ LD) (49.86; 0.0001)	Sc > (F ~ Rf ~ P) (13.35; 0.004)	(F ~ Rf) > (Sc ~ P) (48.21; 0.0001)	F ~ Rf; F > (Sc ~ P); Rf ~ Sc ~ P (16.15; 0.001)

Expected patterns are above and in bold (see Fig. 1A). Below each observed pattern are the Kruskal–Wallis test values (H and *p* values). Specific differences were detected with a multiple comparisons test (Dunn test). > indicates a statistically significant and higher value, ~ indicates there are no significant differences. Median abundance and biomass per trap are given in Supp Table 1 (online only).

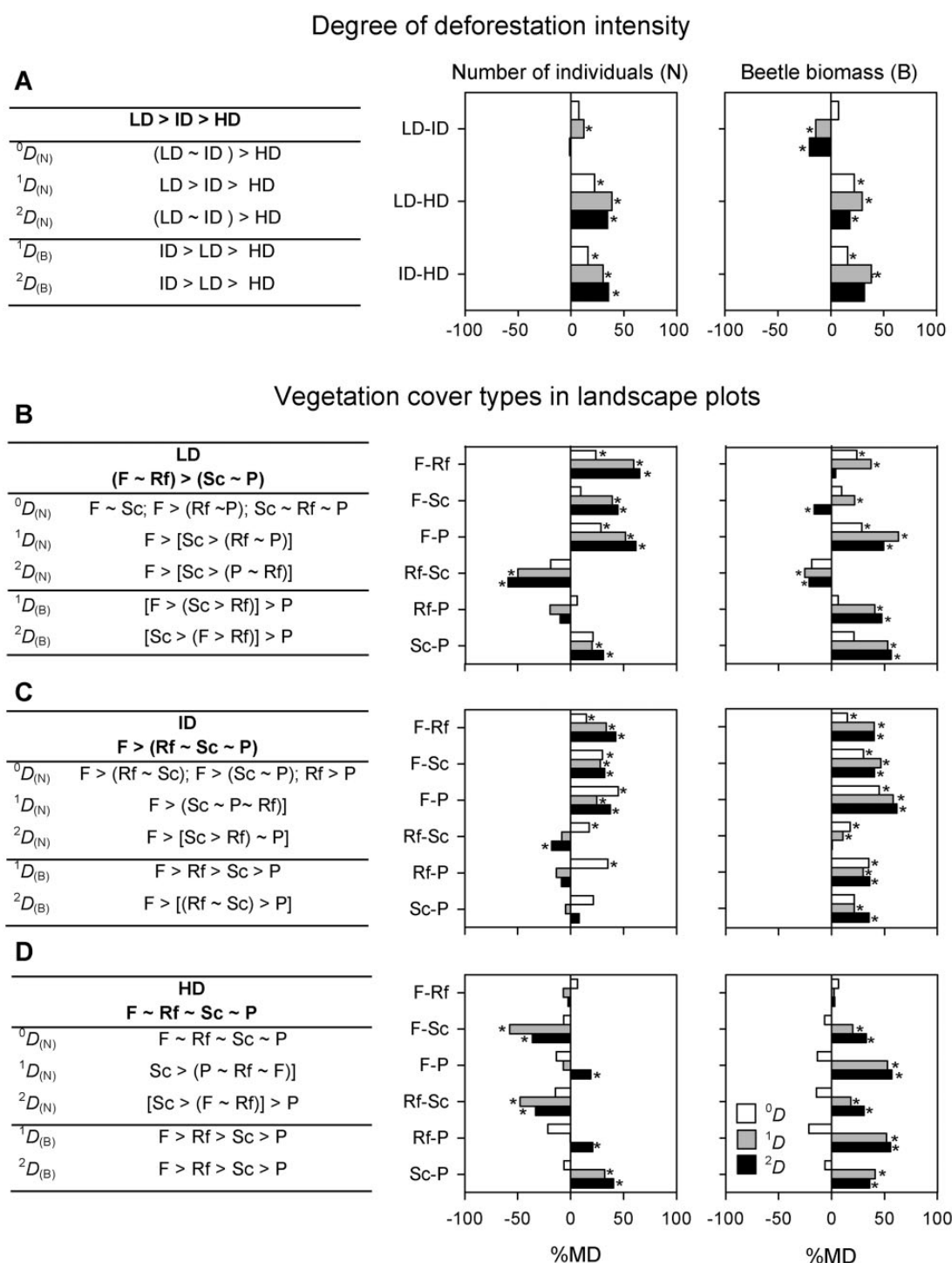


Fig. 2. (A–D) Panels on the left side correspond to observed patterns of clustering for diversity comparisons among types of vegetation cover and across degrees of deforestation intensity on the overlap of the 95% CI (expected response pattern is in bold as shown in Fig. 1A) and panels on the right side correspond to %MD between pairs of vegetation cover types and landscape plots using number of beetles or beetle biomass (right side). On each bar with an asterisk (*) the %MD associated with statistically significant differences in diversity for each pair of comparisons is given. $^0D_{(N)}$ = number of beetles–based data; $^1D_{(N)}$ = biomass–based data; F, forest; Rf, riparian forest; Sc, sun-grown coffee; P, pasture. Vegetation cover and landscape plots are arranged from highest to lowest values (see Supp Table 1 [only online]).

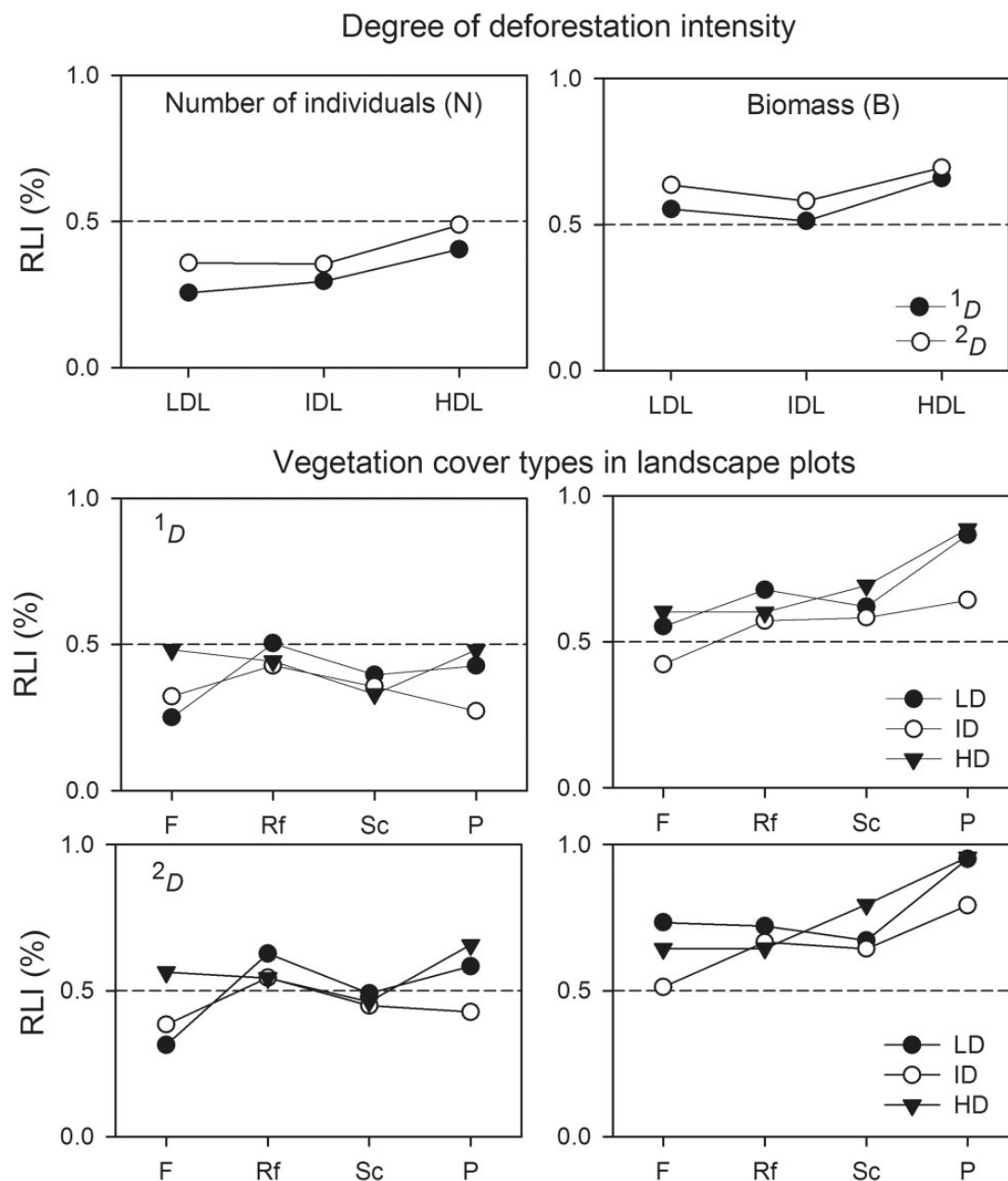


Fig. 3. Relative logarithmic inequality profiles (RLI) based on number of individuals and biomass across types of vegetation cover at both levels of analysis: landscape plots with different degree of deforestation intensity. RLI values equal to or greater than 50% indicate that half or fewer than half of the species account for most of the number of individuals or biomass (i.e., dominant species). F, forest; Rf, riparian forest; Sc, sun-grown coffee; P, pasture.

According to Saint-Germain et al. (2007), there is a strong and significant relationship between the number of individuals and the biomass of invertebrates when sampling methods that depend on the activity of species rather than their density are used (e.g., baited pit-fall traps). Those authors conclude that, in those cases, biomass is not informative. Contrary to this, we found that the relationship was significant and even higher (R^2 between 0.69 and 0.95; Supp Figs. 1 and 2 [online only]) with respect to that reported by Gardner et al. (2008; R^2 varied between 0.32 and 0.39) for the dung beetles of an agroforestry landscape in the Amazon. In contrast to the findings of Gardner et al. (2008), we did not detect any discrepancies in patterns of species rank, regardless of whether the number of individuals or the biomass was used. In spite of potential bias resulting from the use of baited traps, a short sampling time, and few samples,

we think that, because our study was carried out over six months, it provides an appropriate estimate of the relative abundance of the scarabs that prefer dung as substrate for feeding and reproduction. Therefore, our results show that biomass can provide useful information when it is used to evaluate diversity from the perspective of Hill numbers—an analytical approach that has not been explored using biomass and was not included in the review by Saint-Germain et al. (2007) or in the study by Gardner et al. (2008).

Using the biomass data made it possible to examine, in a different way, the response of typical diversity (1D) and the number of dominant species (2D) to the intensification of agriculture on the landscape (i.e., homogenization of the matrix). In general, for the three landscapes studied, the magnitude of the difference between the forest and the other vegetation types tended to be greater in

terms of biomass. In fact, from the native vegetation cover (forest + riparian forest) to anthropic vegetation (sun-grown coffee + pastures), the values of %MD for diversity weighted biomass (i.e. $^1D_{(B)}$ and $^2D_{(B)}$) were positive and considerably higher than those obtained using the number of individuals (Fig. 2).

Diversity calculated using biomass revealed a remarkable increase in inequality that was not detected using the number of individuals and this pattern varied between types of vegetation cover (Fig. 3). For the number of individuals, the beetle communities in the riparian forest, sun-grown coffee, and pasture had similar inequality values but, when biomass was used, inequality was higher in sun-grown coffee and pasture. In other words, there were no changes observed in the distribution of the number of individuals among species, but changes were observed for biomass. Additionally, the shape of the RLI profiles based on biomass varied with respect to the degree of deforestation intensity; in fact, for sun-grown coffee and pasture, inequality was high for the landscape plot with the HD, while, in LD and ID, the inequality of sun-grown coffee was only slightly higher than or equal to that of the forest. So the use of biomass to estimate diversity not only highlighted the loss of diversity from the beetle assemblage owing to the increase in deforestation intensity; it also suggests a more complex scenario regarding the effect of sun-grown coffee on dung beetle diversity and species composition under certain circumstances of loss of native vegetation at the landscape scale.

Although sun-grown coffee is considered a lower-quality habitat for diversity (Perfecto et al. 2009), in the landscape we studied, its species richness was quite high (14 to 19 species) and it had 30 to 50% of the diversity (1D and 2D) observed for native vegetation. In addition, in sun-grown coffee, diversity was practically constant across the three degrees of deforestation intensity. Because of this and taking into account our analysis method, it is not possible to state that the spatial dominance of sun-grown coffee in the matrix is associated per se with an impoverished dung beetle community at the landscape scale. Furthermore, coffee crops house a relatively distinct fauna that can represent up to 50% of the total species (see Supp Table 1 [online only]). It is important to mention that, at intermediate elevations, mountain dung beetle faunas are made up of tolerant species adapted to recurring disturbance on the landscape and able to use environments associated with human activity. This has been documented for other sites in the Colombian Andes (Escobar 2004) and for tropical cloud forest in Mexico (Rös et al. 2012, Barragán et al. 2014).

Although riparian forest tended to be less diverse than sun-grown coffee, these remnants of vegetation may facilitate the movement of some species across the landscape, allowing them to reach core areas (forest patches). In the riparian forest of LD, species typical of large, well-preserved forest patches were occasionally recorded (e.g., *Canthidium convexifrons*, *Deltochilum* (*Deltohyboma*) sp. 1, *Uroxys brachialis*, and *U. boneti*). Also, in HD, riparian vegetation represents nearly 50% of the area of native forest and, in terms of biomass, was more diverse than sun-grown coffee. As such, in parts of the highly transformed landscape, riparian vegetation can also act as a refuge for some species; in our study, this was the case for the two largest species on the landscape: *D. cf. alyattes* and *D. gr. satanas* sp. 1. According to Cultid-Medina et al. (2015), *D. cf. alyattes* prefers to move using forest patches, avoiding sun-grown coffee. Thus, riparian vegetation, which is one of the most common types of native vegetation in the agricultural landscapes of the Neotropics, turns out to be a key element for maintaining the functional connectivity of these landscapes, as has been confirmed for several other taxonomic groups (Harvey et al. 2006, Gray et al. 2014).

The relatively high values of biomass and the population size of some species in sun-grown coffee might lead us to assume that, at the landscape scale, coprophagous species have access to a considerable amount of resource. However, this does not necessarily mean that there is a high diversity of mammals. In the Colombian Andes, the dung beetle community associated with anthropic types of vegetation cover is dominated by *Oxysternon conspiciatum* (740 mg), a large species that is apparently favored by the supply of human excrement and domestic animals on cropland and human settlements, playing a critical role in the removal of excrement (Escobar 2004, Cultid et al. 2012).

Of the four large species in the landscape (biomass > 110 mg), only *Deltochilum mexicanum* is limited to forest patches in LD and ID (Supp Table 1 [online only]); this species is considered an indicator of highly conserved montane cloud forest (González et al. 2009, Rös et al. 2012), while other large species such as *D. cf. alyattes* (310 mg) and *D. gr. satanas* sp. 1 (430 mg) dominate riparian vegetation and relatively small forest patches (area < 30 ha) in HD. Differences in habitat selection by dung beetles has been related to variables such as microclimate, soil type, and, in particular, food preferences: *O. conspiciatum* in the Andes is a diurnal, highly vagile competitor that feeds on different types of excrement (e.g., dog, human, bovine), while *D. mexicanum* is a nocturnal species that prefers carrion (Cultid et al. 2012). This could explain changes in abundance between types of vegetation cover.

The disappearance of the forests in Andean sites has a greater impact on the species of genera that are small or medium-sized and limited to mature forest (e.g., *Genieridium medinae*, *Ontherus lunicollis*), as this decrease is characterized by reduced populations of mammals. Some species that inhabit the mountain forests are dung-specialized or use other resources, such as decaying fruit and invertebrate cadavers, as reported for species of *Canthon*, *Canthidium*, *Deltochilum*, and *Uroxys* (Escobar 2003, González et al. 2009). Precisely in the Andean region that we studied, small species became rare in or disappeared from sun-grown coffee and pasture, and this was most obvious in the landscape plot with the HD (Supp Table 1 [online only]). Its disappearance explains, to a large extent, the decrease in diversity from LD to HD.

Although biomass revealed an impoverishment of the dung beetle community from the forest to the pastures (i.e., inequality increased), it is worth noting the functional relevance of some species associated with anthropogenic cover. This is the case of *O. conspiciatum*, a flagship species in sun-grown coffee with a great capacity for movement at the landscape scale in the Central-Western and Southern Andes of Colombia (Escobar 2004, Cultid et al. 2015). The persistence of large species in agricultural landscapes can have direct implications for soil nutrient dynamics and soil fertility—an aspect that has been poorly studied (Nichols et al. 2008). While the recommendations for the conservation of biodiversity derived from the study of dung beetle focus on native forests (mature and secondary), our results indicate that management and conservation at the landscape scale must take into account the diversity of this group of insects that is so very closely associated with the agricultural matrix.

Our results suggest that sun-grown coffee are not necessarily an inhospitable environment, nor one of low quality for dung beetles, in particular for large body size species. These findings also show that dung beetle diversity depends to a considerable extent on the specific characteristics of the types of vegetation cover on the landscape, namely, the rough topography of the landscape and the heterogeneity of the agricultural mosaic, along with differences in the age of the crops, planting density, type of agricultural management (hedges, trees, and associated crops), and the amount of remaining

tree cover. Thus, the results of this study support the idea that the medium- and long-term viability of agricultural landscapes dominated by sun-grown coffee for conservation in the Colombian Andes not only requires that agricultural management be improved at the local level, but also that a management strategy that ensures environmental heterogeneity continues to be a characteristic of these landscapes.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

Acknowledgments

This project was funded by WCS–Programa Colombia and by the Catherine MacArthur Foundation. We thank P. Franco by management to finance the project. Thanks to C. Medina and A. González for identifying the species, and G. Halffter, C. Moreno, and S. Muriel for their comments on an earlier version of the manuscript. We are grateful to N. Betancur, B. Martínez, S. Villada, and G. Copete for help with lab and field work. This study forms part of the doctoral thesis of C. A. Cultid-Medina, funded by COLCIENCIAS, WCS–Colombia and Universidad del Valle (Colombia) Project No. 110652128706, “Analysis of spatial the heterogeneity and diversity of ants and dung beetles in coffee growing landscapes.”

References Cited

- Bawa, K. S., W. J. Kress, N. M. Nadkarni, S. Lele, P. H. Raven, D. H. Janzen, A. E. Lugo, P. S. Ashton, and T. E. Lovejoy. 2004. Tropical ecosystems into the 21st century. *Science* 36: 227–228.
- Barragán, F., C. E. Moreno, F. Escobar, J. Bueno–Villegas, and G. Halffter. 2014. The impact of grazing areas on dung beetle diversity depends on the biogeographical context. *J. Biogeogr.* 41: 1991–2002.
- Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.
- Chao, A., and L. Jost. 2012. Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. *Ecology* 93: 2533–2547.
- Chazdon, R. L., C. A. Harvey, O. Komar, D. M. Griffith, B. G. Ferguson, M. Martínez–Ramos, H. Morales, R. Nigh, L. Soto–Pinto, M. Van Breugel, et al. 2009. Beyond reserves: A research agenda for conserving biodiversity in human–modified tropical landscapes. *Biotropica* 41: 142–153.
- Cultid, C. A., C. A. Medina, B. Martínez, A. F. Escobar, L. M. Constantino, and N. Betancur. 2012. Escarabajos coprófagos (Scarabaeinae) del Eje Cafetero: guía para el estudio ecológico. WCS–Colombia, CENICAFÉ y la Federación Nacional de Cafeteros. Villa María, Colombia.
- Cultid-Medina, C. A., B. G. Martínez–Quintero, F. Escobar, and P. Chacón de Ulloa. 2015. Movement and population size of two dung beetle species in an Andean agricultural landscape dominated by sun-grown coffee. *J. Insect. Conserv.* 19: 617–626.
- Cumming, G., F. Fidler, and D. L. Vaux. 2007. Error bars in experimental biology. *J. Cell Biol.* 21: 7–11.
- De la Mora, A., C. J. Murnen, and S. M. Philpott. 2013. Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes. *Biodivers. Conserv.* 22: 871–888.
- Escobar, F. 2003. Feeding habits and distributional records of 11 species of Neotropical Scarabaeinae (Coleoptera: Scarabaeidae). *Coleopt. Bull.* 57: 131–132.
- Escobar, F. 2004. Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. *Trop. Zool.* 17: 123–136.
- Estrada, A., R. Coates–Estrada, A. A. Dadda, and P. Cammarano. 1998. Dung and carrion beetles in tropical rain forest fragments and agricultural habitats at Los Tuxtlas, Mexico. *J. Trop. Ecol.* 14: 577–593.
- Espinal, S. 1977. Zonas de Vida y Formaciones Vegetales de Colombia, Vol. XIII, No. 11. Instituto Geográfico Agustín Codazzi–IGAC, Bogotá, Colombia.
- ESRI Inc. (1999–2008) ArcGIS 9.3. License authorized for WCS–Colombia.
- Fahrig, L., J. Baudry, L. Brotons, F. G. Burel, T. O. Crist, R. J. Fuller, C. Sirami, G. M. Siriwardena, and J. L. Martin. 2010. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecol. Lett.* 14: 101–112.
- Feinsinger, P. 2003. El diseño de estudios de campo para la conservación de la biodiversidad. Bolivia, Editorial FAN.
- (FNC) Federación Nacional de Cafeteros–CENICAFÉ. 2013a. Manual del cafetero colombiano. Tomo 1. Colombia.
- (FNC) Federación Nacional de Cafeteros 2013b. Área cultivada en café (http://www.federaciondecafeteros.org/particulares/es/quienes_somos/119_estadisticas_historicas/)
- Gardner, T., M. I. M. Hernández, J. Barlow, and C. A. Peres. 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. *J. Appl. Ecol.* 45: 883–893.
- Gray, C. L., E. M. Slade, D. J. Mann, and O. T. Lewis. 2014. Do riparian reserves support dung beetle biodiversity and ecosystem services in oil palm–dominated tropical landscapes? *Ecol. Evolut.* 4: 1049–1060.
- González, F. A., F. Molano, and C. A. Medina. 2009. Los subgéneros *Calhyboma*, *Hybomidium* y *Telhyboma* (Coleoptera: Scarabaeidae: Scarabaeinae: *Deltochilum*) en Colombia. *Rev. Colombia Entomol.* 35: 253–274.
- Good, I. J. 1953. The population frequencies of species and the estimation of population parameters. *Biometrika* 40: 237–264.
- Guhl, A. 2004. Coffee Production Intensification and Landscape Change in Colombia 1970–2002, pp. 93–115. In A. Millington and W. Jepson (eds.), *Land change science in the tropics: Changing agricultural landscapes*. Springer Science, New York, NY.
- Harvey, C. A., A. Medina, D. M. Sánchez, S. Vilchez, B. Hernández, J. C. Seanz, J. M. Maes, F. Casanoves, and F. L. Sinclair. 2006. Patterns of animal diversity in different forms of tree cover in agricultural landscapes. *Ecol. Appl.* 16: 1986–1999.
- Hill, M. O. 1973. Diversity and evenness: A unifying notation and its consequences. *Ecology* 54: 427–432.
- Horgan, F. 2005. Effects of deforestation on diversity, biomass and function of dung beetles on the eastern slopes of the Peruvian Andes. *For. Ecol. Manag.* 216: 117–133.
- Hsieh, T. C., K. H. Ma, and A. Chao. 2015. Interpolation and extrapolation for species diversity (Version 2.0.5) [Package for R] (<http://chao.stat.nthu.edu.tw/blog/software-download/>)
- Jha, S., C. M. Bacon, S. M. Philpott, V. E. Méndez, P. Läderach, and R. A. Rice. 2014. Shade coffee: Update on a disappearing refuge for biodiversity. *BioScience* 64: 416–428.
- Jost, L. 2006. Entropy and diversity. *Oikos* 113: 363–375.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88: 2427–2439.
- Jost, L. 2010. The relation between evenness and diversity. *Diversity* 2: 207–232.
- Larsen, T. H., A. Lopera, and A. Forsyth. 2008. Understanding trait–dependent community disassembly: Dung beetles, density Functions, and forest fragmentation. *Conserv. Biol.* 22: 1288–1298.
- Magurran, A. 2004. *Measuring biological diversity*. Blackwell Publishing, United Kingdom.
- Moreno, C. E., F. Barragán, E. Pineda, and K. Numa. 2011. Re–análisis de la diversidad alfa: alternativas para interpretar y comparar información sobre comunidades ecológicas. *Rev. Mex. Biodiv.* 82: 1249–1261.
- Muriel, S. B., and G. H. Kattan. 2009. Effects of patch size and type of coffee matrix on Ithomiine butterfly diversity and dispersal in cloud–forest fragments. *Conserv. Biol.* 23: 948–956.
- Nichols, E., T. Larsen, S. Spector, A. L. Davis, F. Escobar, M. Davila, K. Vulinec, and The Scarabaeinae Research Network. 2007. Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta–analysis. *Biol. Conserv.* 137: 1–19.
- Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezcuita, M. E. Favila, and The Scarabaeinae Research Network. 2008. Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. *Biol. Conserv.* 141: 1461–1474.

- Numa, C., J. R. Verdú, and P. Sánchez-Palomino. 2005. Phyllostomid bat diversity in a variegated coffee landscape. *Biol. Conserv.* 122: 151–158.
- Pineda, E., C. Moreno, F. Escobar, and G. Halffter. 2005. Frog, bat, and dung beetle diversity in the cloud forest and coffee agroecosystems of Veracruz, Mexico. *Conserv. Biol.* 19: 400–410.
- Phalan, B., R. Green, and A. Balmford. 2014. Closing yield gaps: perils and possibilities for biodiversity conservation. *Phil. Trans. R. Soc. B.* 369: 20120285.
- Perfecto, I., and I. Armbrrecht. 2003. The Coffee Agroecosystems in the Neotropics: Combining Ecological and Economic Goals. pp. 159–194. *In* J. H. Vandermeer (ed.), *Tropical Agroecosystems*. CRC Press, USA.
- Perfecto, I., J. Vandermeer, and A. Wright. 2009. *Nature's Matrix*. Earthscan, London, United Kingdom.
- Philpott, S. M., W. J. Arendt, I. Armbrrecht, P. Bichier, T. V. Diestch, C. Gordon, R. Greenberg, I. Perfecto, R. Reynoso-Santos, L. Soto-Pinto, et al. 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conserv. Biol.* 22: 1093–1105.
- Rivera, L., and I. Armbrrecht. 2005. Diversidad de tres gremios de hormigas en cafetales de sombra, sol y bosques de Risaralda. *Rev. Colomb. Entomol.* 31: 89–96.
- Rös, M., F. Escobar, and G. Halffter. 2012. How dung beetles respond to a human-modified variegated landscape in Mexican cloud forest: a study of biodiversity integrating ecological and biogeographical perspectives. *Divers. Dist.* 18: 377–389.
- Saint-Germain, M., C. M. Buddle, M. Larrivee, A. Mercado, T. Motchula, E. Reichert, T. E. Sackett, Z. Sylvain, and A. Webb. 2007. Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *J. Appl. Ecol.* 44: 330–339.
- Scholtz, C. H., A. L. V. Davis, and U. Kryger. 2009. *Evolutionary biology and conservation of dung beetles*. Pensoft Publishers, Bulgaria.
- Tscharntke, T., A. M. Klein, A. Ruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.* 8: 857–874.
- (WCS) Wildlife Conservation Society–Colombia. 2013. Conociendo la biodiversidad de nuestro paisaje rural cafetero. La Celia, Balboa y Santuario–Risaralda. Wildlife Conservation Society Colombia–MacArthur Foundation. Santiago de Cali. (<http://colombia.wcs.org/es-es/sobrenosotros/publicaciones.aspx>)
- Young, K. R., C. U. Ulloa, J. L. Luteyn, and S. Knapp. 2002. Plant evolution and endemism in Andean South America: An introduction. *The Botanical Rev.* 68: 4–21.
- Zabala, G., L. M. Arango, and P. Chacón de Ulloa. 2013. Diversidad de hormigas (Hymenoptera: Formicidae) en un paisaje cafetero de Risaralda, Colombia. *Rev. Colomb. Entomol.* 39: 141–149.
- Zar, J. 1999. *Biostatistical analysis*. Fourth edition. Prentice Hall. Upper Saddle River, NJ.