



Edge effects on dung beetle assemblages in an Andean mosaic of forest and coffee plantations

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ABSTRACT

In landscapes dominated by agriculture, conspicuous edges often occur between landscape elements. However, there is disagreement about the existence and intensity of edge effects, and information about species-specific responses remains scarce. Studying such edge effects can help elucidate functional landscape connectivity and contribute to agricultural management. We, therefore, assessed whether sun-grown coffee represents a barrier to dung beetles in an Andean agricultural landscape. We also evaluated whether the response to edge effects differs among species. We found that diversity and abundance tend to decrease from forest to sun-grown coffee and that there are sharp increases in species turnover at the forest–coffee edge. We detected several different species-specific responses to the forest–coffee edge, suggesting differences in the mobility of the species (or spillover) and in the degree of penetration that takes place from forest patches to sun-grown coffee plantations. This study demonstrates that the sun-grown coffee matrix constitutes a barrier to forest species and suggests that the forest–coffee ecotone is more complex than expected. Our results support the notion that the conservation value of native forest patches in agricultural scenarios depends on the functional connectivity of forest units in the landscape to maximize the opportunities species have to disperse through the agricultural matrix.

Key words: Andean cloud forest; beta diversity; Colombia; effective number of species; non-linear models; Scarabaeinae; sun-grown coffee.

IN AGRICULTURAL LANDSCAPES WHERE THERE ARE CONSPICUOUS EDGES OR ECOLOGICAL TRANSITIONS between modified habitats and the remnants of natural vegetation (Forman 1995), it is crucial to understand how ecotone characteristics modulate functional connectivity and habitat quality for different species (Fischer & Lindenmayer 2007). These edges are presumed to have deleterious effects on organisms that inhabit natural vegetation, leading to changes in population or community structure (Murcia 1995). In addition to the intrinsic traits of the taxa (*i.e.*, habitat preference, body size), the magnitude and extent of edge effects depend on the degree of contrast in structure and composition between adjacent habitats (Ries *et al.* 2004). However, given the scarcity of species-specific information, the edge effect is still debated among conservation scientists (Ries *et al.* 2004).

In the Colombian Andes, coffee crops are a dominant component of the agricultural landscape at medium elevations (1300–2000 m asl) (Perfecto *et al.* 2009). Within the coffee growing area in Colombia, approximately 90 percent (975,000 ha) of the crop is sun-grown (FNC 2013). This agricultural practice is considered

one of the main causes of diversity loss, largely because of the transformation and fragmentation of the cloud forest (Perfecto *et al.* 2009), of which <10 percent of the original area remains (Etter & Wyngaarden 2000, Armenteras *et al.* 2003). In this agricultural landscape, hard boundaries exist between sun-grown coffee and adjacent forest fragments, which may be exacerbated by the heavy input of agrochemicals in the plantations. These boundaries are maintained by the constant clearing of pioneer plants from the edge of the forest. Since the boundaries between forest patches and sun-grown coffee plantations are abrupt, the effects of abiotic conditions (*i.e.*, solar radiation, wind, soil, and air humidity) and associated biotic changes (*i.e.*, tree mortality, loss of foraging habitats, and invasion of exotic species) usually penetrate more deeply into the contiguous habitats (Perfecto *et al.* 2007). The physical limit between contrasting habitats may have a low degree of ecological permeability and thus act as a barrier to several groups of organisms (Perfecto & Armbrrecht 2003, Perfecto *et al.* 2009).

Dung beetles are a diverse and abundant group of insects that perform many key ecological functions in tropical forests (Nichols *et al.* 2008). Given that they are relatively short lived, their life cycle is dependent on ephemeral resources (dung or carrion) and populations are sensitive to environmental alterations,

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dung beetles can respond rapidly to changes in the landscape resulting from human activities (Halffter & Favila 1993, Quintero & Roslin 2005, Larsen *et al.* 2008). Neotropical assemblages of dung beetles are often species rich in forest habitats but poor in open areas (Horgan 2005, Escobar *et al.* 2007). Edge effects between contrasting habitats (*e.g.*, forest–savannah) generally affect dung beetles in two ways (*sensu* Feer 2008): (1) species richness and abundance decrease from the preferred habitat toward the edge and into the non-preferred habitat (Hill 1996, Spector & Ayzama 2003); and (2) species richness and abundance are higher in the ecotone than in the adjacent habitats (Escobar 1997, Durães *et al.* 2005). In both cases, rapid species turnover occurs on the physical border, indicating that due to the contrasting ecotone, the edge itself is not a suitable habitat for many dung beetle species (Feer 2008). In some species, a common response to the presence of a hard edge is a sigmoid pattern, where abundance decreases from the preferred toward the non-preferred habitat and penetration distance into the non-preferred habitat is <60 m (Peyras *et al.* 2013, Barnes *et al.* 2014).

Most information on the spatial distribution of dung beetle diversity in agricultural mosaics with grown coffee comes from shade-coffee plantations in Mexico (Morón 1987, Estrada *et al.* 1998, Arellano *et al.* 2005, Pineda *et al.* 2005), while little is known about the Andean landscape dominated by sun-grown coffee plantations (Noriega *et al.* 2012, Cultid-Medina & Escobar 2016). The aim of this study was to assess how the diversity of dung beetles responds across the forest–sun-grown coffee ecotone in the Colombian Andes. We addressed the following questions: (1) how do the species richness and abundance of dung beetles change across the ecotone in the two sites? (2) How do the magnitude and extent of edge effects differ between species and sites? And (3) is sun-grown coffee an absolute barrier to dung beetles in the study landscape? Assuming that sun-grown coffee represents a low-quality habitat for dung beetle species, we expect the edge effects to be large in both magnitude and extent in all cases, *i.e.*, the dung beetle species will tend to avoid the physical boundary between the forest and sun-grown coffee.

METHODS

STUDY AREA.—This study was carried out at two localities between the municipalities of La Celia and Santuario (Verdum: 5°2'34.8" N, 75°59'27" W and El Brillante: 5°0'47.9" N, 76°1'29.7" W), in the Department of Risaralda, Colombia (Fig. S1). The elevation range of the sites was 1720–1920 m asl. at the transition between two life zones: the wet low montane forest and wet pre-montane forest (Espinal 1977). According to Escobar *et al.* (2005, 2007), in the Colombian Andes, the difference in elevation among sites (≤ 250 m) has no significant effect on the diversity and composition of dung beetle species. Temperature ranges from 15 to 20°C and annual rainfall is 2140–2900 mm. More than 60 percent of the landscape is covered by sun-grown coffee interspersed with forest patches of different sizes and disturbance levels, as well as areas featuring other types of land use (*e.g.*, pastures, riparian forest, annual crops, and human settlements) (Fig. S1; Table S1). The

management of sun-grown coffee includes the deliberate removal of the pioneer vegetation in areas adjacent to forest patches. At both sites, therefore, the forest–sun-grown coffee edge is considered to be abrupt (Fig. S2).

SAMPLING DESIGN.—Sampling was conducted monthly from August 2010 to February 2011, which includes two seasons: the dry season (August–September 2010 and January–February, 2011) and the rainy season of 2010 from October to December (FNC 2012). We selected two of the largest forest fragments (~196 ha and ~515 ha, Table S1) in the study area (WCS 2013) to minimize any interaction between edge effects and forest area (Gardner *et al.* 2008, Banks-Leite *et al.* 2010). At each site, we established three transects, each 420 m in length, perpendicular to the forest fragment–coffee plantation edge (Fig. S1). The three transects at each site were situated at least 600 m apart, and along each transect, we set 15 non-lethal pitfall traps at 30-m intervals. Thus, there were seven traps in each habitat (forest and coffee plantation) along each transect and one trap directly on the edge (physical limit between habitats) for a total of 45 traps per site.

Each trap consisted of a 0.5-L container buried at ground level with a plastic funnel at the top to keep the trapped beetles alive while preventing their escape (see Cultid *et al.* 2012). Human excrement is known to be excellent bait with which to accurately sample dung beetles; however, due to short supply in the field and the large quantities necessary for such extensive studies, a mixture of pig and human dung (with at least 10% of the latter) has recently been proposed as a suitable alternative (Marsh *et al.* 2013). Traps were, therefore, baited with 30 g of mixed human and pig excrement (7:3) set for 48 h each month and checked twice every 24 h, when we collected dung beetles and put fresh bait in the traps.

The beetles, most of which were easily identified in the field, were released unharmed after each monthly sampling campaign (we did not release individuals right on the sampling transect), thereby minimizing the impact on the Scarabaeinae community (Cultid *et al.* 2012). When identification was not possible in the field, specimens were assigned to morphospecies based on their external morphology and characteristics of the male genitalia (*e.g.*, Medina *et al.* 2003). Representative individuals of each morphospecies were taken and incorporated into the collection of the Museum of Entomology of the Universidad del Valle (MUSE-NUV; Cali, Valle del Cauca, Colombia). For identification, we used keys and descriptions of the genera and species of the Colombian Andes (See Table 1).

ANALYSIS OF ASSEMBLAGE DIVERSITY.—We evaluated the diversity and abundance patterns of the dung beetle assemblages across the forest–sun-grown coffee ecotone at each site and examined the response of the most abundant species to the edge. We compared Scarabaeinae diversity between ecotone components (forest, edge, and sun-grown coffee) in terms of the effective number of species (qD) under the same sample completeness between habitats, following Chao *et al.* (2014). Sample completeness (\hat{C}_n) indicates the proportion of the total community represented by the trapped species (Chao & Jost 2012). When $\hat{C}_n \approx 100$ percent,

TABLE 1. Species and number of individuals of dung beetles recorded in each site and component of the forest–sun-grown coffee ecotone. The table shows q -order diversity in effective number of species and their respective 95% CI.

| Species* | Body size | Verdum | | | El Brillante | | | Total |
|---|-----------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|--------------------------------|-------|
| | | Forest | Edge | Sun-grown coffee | Forest | Edge | Sun-grown coffee | |
| <i>Canthidium</i> (<i>Canthidium</i>) <i>convexifrons</i> Balthasar, 1939 | S | 17 | 1 | 7 | 19 | 8 | 4 | 56 |
| <i>Canthidium</i> (<i>Canthidium</i>) sp1 | S | | | 22 | 3 | 2 | | 27 |
| <i>Canthidium</i> (<i>Eucanthidium</i>) sp1 [†] | S | 516 | 2 | 7 | 1430 | 28 | 3 | 1986 |
| <i>Canthon</i> cf. <i>aberrans</i> | L | 1 | | 16 | | | | 17 |
| <i>Canthon politus</i> [†] Harold, 1868 | L | 110 | 1 | | 3420 | 58 | 4 | 3593 |
| <i>Deltochilum</i> (<i>Deltohyboma</i>) sp1 [†] | L | 87 | 2 | | 255 | 19 | 1 | 364 |
| <i>Deltochilum mexicanum</i> Burmeister, 1848 | L | 16 | 2 | | 26 | | | 44 |
| <i>Dicotomius</i> cf. <i>satanas</i> sp1 [†] | L | 126 | 5 | 9 | 446 | 14 | 6 | 606 |
| <i>Dicotomius</i> cf. <i>abyattes</i> [†] | L | 167 | 19 | 181 | 545 | 116 | 243 | 1271 |
| <i>Eurysternus foedus</i> Guérin-Ménéville, 1830 | L | | 1 | 1 | | | | 2 |
| <i>Eurysternus marmoreus</i> Castelnau, 1840 | L | | 1 | | 5 | 3 | 2 | 11 |
| <i>Genieridium medinae</i> [†] (Gill & Vaz de Mello, 2003) | S | 1 | | | 147 | 5 | | 153 |
| <i>Ontherus lunicollis</i> [†] Génier 1996 | L | 98 | 4 | 8 | 357 | 20 | 41 | 528 |
| <i>Ontherus</i> cf. <i>azteca</i> | L | 8 | 1 | | 16 | 10 | 1 | 36 |
| <i>Onthophagus curvicornis</i> [†] Latreille, 1811 | S | 6 | 3 | 53 | 10 | 18 | 208 | 298 |
| <i>Onthophagus</i> sp01H | S | | | | | | 3 | 3 |
| <i>Onthophagus mirabilis</i> Bates, 1887 | S | | | | 2 | | | 2 |
| <i>Onthophagus nasutus</i> [†] Guérin-Ménéville, 1855 | S | 2 | | 52 | 1 | 8 | 90 | 153 |
| <i>Oxycysternon conspicillatum</i> [†] (Weber, 1801) | L | 5 | 10 | 141 | 9 | 3 | 189 | 357 |
| <i>Uroxys boneti</i> [†] Pereira & Halffter, 1961 | S | 3 | | | 63 | 1 | 1 | 68 |
| <i>Uroxys nebulinus</i> [†] Howden & Gill, 1987 | S | 254 | 9 | 4 | 1078 | 21 | 9 | 1375 |
| <i>Uroxys pauliani</i> [†] Balthasar, 1940 | S | 179 | 2 | 4 | 1398 | 45 | 4 | 1632 |
| Number of individuals | | 1596 | 63 | 505 | 9230 | 379 | 809 | 12582 |
| Species richness (⁰ D) | | 17 (± 2) ^a | 15 (± 3) ^a | 13 (± 1.25) ^a | 19 (± 1.5) ^a | 17 (± 1.7) ^a | 16 (± 2.9) ^a | 22 |
| Typical diversity (¹ D) | | 7.7 (± 0.4) ^a | 9.2 (± 2.3) ^a | 6 (± 0.5) ^b | 6.7 (± 0.1) ^a | 9.6 (± 1.0) ^b | 5.4 (± 0.3) ^c | 8.9 |
| Dominant species diversity (² D) | | 5.8 (± 0.4) ^a | 6.5 (± 2.1) ^a | 4.3 (± 0.4) ^b | 4.8 (± 0.1) ^a | 6.6 (± 1.0) ^b | 4.4 (± 0.2) ^a | 6.6 |
| Completeness (\hat{C}_n) % | | 100 | 92 | 100 | 100 | 100 | 100 | 100 |

Different letters indicate significant differences in ^q D among ecotone components.

*References used for taxonomic identification: Génier (1996), Edmonds and Zidek (2004), González *et al.* (2009); Génier (2009), Vaz-de-Mello (2008), Vaz de Mello *et al.* (2011).

[†]The species were used to assess the edge response models. Body size follows Hanski and Cambefort (1991): S = small (<10 mm); L = large (>10 mm).

sampling is complete in terms of the effort and capture technique used (Chao & Jost 2012).

Diversity was calculated as follows:

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

where p_i is the proportional abundance of each species and the q -order determines the influence of species abundance on diversity values (Jost 2006). We used three q values: order 0 (⁰ D , species richness), 1 (¹ D , the exponential of Shannon's entropy), and 2 (² D , the inverse of Simpson's concentration). ⁰ D is not sensitive to species abundance and thus gives disproportionate weight to

rare species (Jost 2006). ¹ D weights each species according to its abundance in the community and therefore can be interpreted as the typical diversity in the community (Jost 2006). Finally, ² D can be interpreted as the number of very abundant or dominant species in the community (Jost 2006). Diversity (^q D) was compared based on 95% confidence intervals (CI) through 100 bootstrap iterations (Chao *et al.* 2014), where no overlap between 95% CI values indicates significant differences between the estimated values of ^q D (Cunningham *et al.* 2007). This analysis was performed with the R code published by Chao *et al.* (2014).

EDGE EFFECTS AT THE ASSEMBLAGE LEVEL.—We employed a Friedman nonparametric repeated-measures test to assess richness

0D) and abundance patterns of beetle assemblages across the forest–sun-grown coffee ecotone at each site (Zar 2010). In our case, both variables were compared among distances to the edge (traps), using the monthly sampling data as repeated measures ($N = 6$). We employed a Nemenyi *post-hoc* test, included in BioEstat (Ayres *et al.* 2004) at $\alpha = 0.05$, to identify where the differences between distances occurred.

To assess whether sun-grown coffee represents an environmental barrier for Scarabaeinae species, we quantified species turnover between pairs of consecutive distances across the ecotone and between all pairs of ecotone components (from forest to coffee). We measured turnover as ${}^qT_\beta = 100 * [({}^qD_\beta - 1) / (N - 1)]$, where N is equal to two samples and ${}^qD_\beta = {}^qD_\gamma / {}^qD_x$ (Jost 2007) (Appendix S1); ${}^qT_\beta$ ranges from 0 (minimum turnover) to 100 percent (maximum turnover) (Jost 2007). For this analysis, we used the same q values that were employed to compare diversity (Appendix S1).

EDGE EFFECTS AT THE SPECIES LEVEL.—We used the protocol of Ewers and Didham (2006), modified by Zurita *et al.* (2012), to assess the edge effects and penetration distances of the species per site. The protocol consists of fitting observed abundance ($y_i = \text{total number of individuals} * \text{distance at edge} * \text{sites}$) across the ecotone to five functions or models that increase in complexity: mean (or null), linear, exponential, sigmoid, and unimodal (Table S2). A mean function indicates that there is no change in abundance across the ecotone (*i.e.*, no edge response). A linear or exponential fit suggests an incomplete response to edge effects (*i.e.*, edge effects extend beyond the sampled distances). The sigmoid and unimodal functions represent a complete response to edge effects; in the former, the species decreases in abundance toward the edge and exhibits a preference for one habitat over the other; in the latter, the species exhibits a preference for the edge. In addition, we fitted models to the number of individuals (N) and species richness (0D) for distance to the edge in each site. In all cases, the best model was that which met the following statistical criteria: normal distribution of residuals ($\alpha = 0.05$), smallest AICc (second-order of the Akaike information criterion for small samples sizes), and a high regression coefficient (R^2) (Burnham & Anderson 2002). Two models will be equally parsimonious when $|\Delta\text{AICc}| \leq 6$ (Richards 2015); in this case, we used R^2 for model selection.

We estimated the magnitude and extent of edge effects for species that exhibited sigmoid or unimodal behavior (Ewers & Didham 2006). Magnitude corresponded to the difference between the upper and lower asymptotes of the function and was expressed as a percentage ($100 * (Y_{\text{max.}} - Y_{\text{min.}}) / Y_{\text{max.}}$). For a sigmoid response, $Y_{\text{max.}}$ and $Y_{\text{min.}}$ came directly from the function. For a unimodal response, $Y_{\text{max.}}$ corresponds to the inflection point of the first derivative (Ewers & Didham 2006). We calculated the extent of the edge effect on a sigmoid response as the distance between the maximum and minimum of the second derivative of the function and for a unimodal function as the distance between the two peaks of the second derivative (Ewers & Didham 2006). In addition, we calculated penetration distances and edge avoidance.

Penetration was expressed as the maximum distance at which it was possible to capture at least one individual of a species in its non-preferred habitat. Species that avoid the edge will have an inflection point at ≥ 30 m from the edge, which is the minimum possible distance that can be evaluated according to the sampling design employed. This point corresponds to the negative or positive peak of the first derivative. We fitted the functions with the *nls2* package version 0.2 for R 3.0.3 (R Core Team, 2014).

Finally, after fitting and selecting the most appropriate model for each species, as well as for richness and total abundance per site, we evaluated the spatial structure of the residuals using semi-variograms and three theoretical models (spherical, exponential, and Gaussian) with two estimation approaches (weighted least square and maximum likelihood) (Negrete-Yankelevich & Fox 2015) in the *geoR* package for R 3.0.3 (R Core Team 2014). As can be seen in Table S3, in neither case was it possible to detect a significant spatial structure for the residuals. Therefore, we based the analysis of the response patterns, the estimation of the coefficients of each model, and the subsequent estimation of the magnitude and extent of the edge effect (when possible for sigmoidal and unimodal models) on a statistically supported modeling process that meets all the assumptions required for the critical and statistical selection of models, including spatial independence of errors.

RESULTS

DIVERSITY PATTERNS.—We collected 12,582 beetles belonging to 22 species. In Verdum, there were 2164 beetles belonging to 20 species and in El Brillante, 10,418 beetles belonged to 21 species (Table 1). We directly compared diversities (qD) among ecotone components, since completeness was close to 100 percent in virtually all cases (Table 1). Species richness (0D) was similar among ecotone components (forest, edge and coffee) at both sites, while 1D and 2D diversities tended to be higher on the edge, intermediate in the forest, and lower in sun-grown coffee (Table 1).

EDGE EFFECTS AT THE ASSEMBLAGE LEVEL.—The Friedman test showed that median species richness and number of individuals differed significantly among distances to the edge at each site (Fig. 1). The Nemenyi test indicated that traps recorded higher dung beetle richness and abundance in the forest than in the sun-grown coffee plantations. However, the *post-hoc* test showed that the richness in Verdum was significantly lower only at three distances from the edge in the sun-grown coffee (30, 90, and 120 m; Fig. 1). In fact, the edge response patterns differed between the two sites. At Verdum, species richness and abundance decreased exponentially from the forest interior into the sun-grown coffee plantation, while at El Brillante, both variables presented sigmoid behavior (Table 2). Moreover, at El Brillante, there was a more marked edge effect on abundance (magnitude: 98%; extent: 3.3 m) than on species richness (magnitude: 48%; extent: 26.3 m) (Table 2).

We detected a sharp increase in species turnover at the forest–coffee edge (Fig. 2). Specifically, ${}^0T_\beta$ tended to be higher

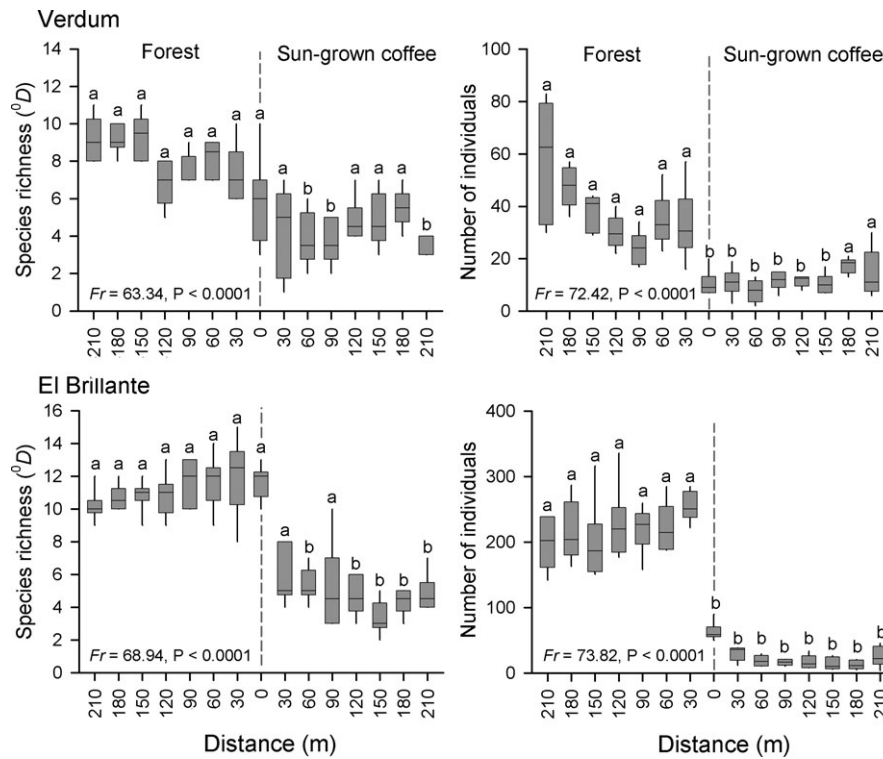


FIGURE 1. Species richness and number of dung beetle individuals across the forest–sun-grown coffee ecotone at both localities. The line within each box represents the median, the height of each box represents the first and third quartiles, and the whiskers represent the maximum and minimum values. Different letters indicate significant differences according to the Nemenyi test ($\alpha = 0.05$). Fr = Friedman test.

in sun-grown coffee, while ${}^1T_\beta$ and ${}^2T_\beta$ increased abruptly between 0 and 60 m from the edge into the sun-grown coffee (maximum turnover: 20% in Verдум and 35% in El Brillante); both below and above these distances, ${}^1T_\beta$ and ${}^2T_\beta$ did not exceed 10 percent (Fig. 2). Patterns of species turnover among ecotone components differed between sites. At both sites, taking into account ${}^1T_\beta$ and ${}^2T_\beta$, the highest turnover occurred between forest and sun-grown coffee (Fig. 2); however, at El Brillante, the ${}^1T_\beta$ and ${}^2T_\beta$ between the edge and sun-grown coffee were higher than at Verдум (Fig. 2). Notably, turnover mostly occurred in the very abundant species (${}^2T_\beta$) (Fig. 2).

EDGE EFFECTS AT THE SPECIES LEVEL.—We performed an edge effect evaluation for 13 of the 22 species, which represented ~98 percent of the total abundance (Table 1). As the abundance of the remaining species was <30 individuals per site, it was not possible to properly fit any of the models (Table 1). At both sites, the most common edge response was the sigmoid pattern (Verдум: six species; El Brillante: seven species), followed by the unimodal pattern (Verдум: two species; El Brillante: four species), while the remaining species had the linear or exponential pattern (Table 2).

For seven of the 13 species, the pattern of response to the edge differed between sites, and these species were distributed equally between the categories of body size (four small, four large) (Table 2). For instance, *Canthon politus* and *Dichotomius cf.*

alyattes had an exponential response in Verдум but a sigmoid response in El Brillante (Table 2; Fig. 3). Both *Ontherus lunicolis* and *Onthophagus nasutus* had a unimodal response in El Brillante, while in Verдум, the patterns were sigmoid and linear, respectively (Table 2; Fig. 3). Among the species analyzed, the magnitude of the edge effects ranged from 64 to 100 percent (Table 2), in which *D. cf. alyattes* and *O. lunicolis* had the lowest magnitudes at 64 and 78 percent, respectively (Table 2). The extent of the edge effects varied between species and sites, ranging from <30 m to 420 m. In Verдум, *Canthidium (Eucanthidium) sp1* and *Deltochilum (Deltochyboma) sp1* had the highest edge effect extent values: 420 m and 264 m, respectively (in both cases, magnitudes = 100%).

Regarding penetration, we trapped beetles from most species up to 210 m from the edge; however, in most cases, these represented occasional records in the non-preferred habitat (maximum three individuals; Table 2; Fig. 3). *Canthidium (Eucanthidium) sp1*, *C. politus*, *Dichotomius cf. satanas sp1*, *Genieridium medinae* and *Uroxya pauliani* at El Brillante, and *D. (Deltochyboma) sp1* at Verдум had the most dramatic response to the edge, with zero penetration into the non-preferred habitat (Table 2). Finally, we found that four species avoided the edge and, for the remaining species with sigmoid response, the decrease in abundance occurred at <30 m from the edge, *i.e.*, these individuals were trapped up to the edge (Table 2).

TABLE 2. Response models to the forest-sun-groam coffee ecotone evaluated for the most abundant species.

| Species | Verdum | | | | | | | | | | El Brillante | | | | | | | | | |
|--------------------------------------|--------|---------|----------------|-------|--------|---------|---------|---------|------|---------|----------------|-------|--------|---------|---------|---------|--|--|--|--|
| | N | Mo | R ² | AICc | P(s) | Ext (m) | Mag (%) | Pen (m) | N | Mo | R ² | AICc | P(s) | Ext (m) | Mag (%) | Pen (m) | | | | |
| <i>Canthidium (Eucanthidium) sp1</i> | 525 | Uni | 0.93 | 118.5 | 0.1024 | 420 | 100 | 0-180 | 1460 | Uni | 0.81 | 169.8 | 0.3677 | 246 | 100 | 0 | | | | |
| <i>Carthou politus</i> | 111 | Exp [-] | 0.88 | 85.3 | 0.3136 | | | 0 | 3482 | Sig | 0.95 | 169.7 | 0.0555 | 3.28 | 100 | 0 | | | | |
| <i>Delochitum (Deltolyboma) sp1</i> | 89 | Uni | 0.71 | 98.3 | 0.4083 | 264.5 | 100 | 0 | 275 | Sig | 0.70 | 121.2 | 0.5440 | 98.4 | 100 | 120 | | | | |
| <i>Dichotomis cf. satanas sp1</i> | 140 | Sig | 0.91 | 78.6 | 0.3618 | 22.97 | 93 | 0-150 | 466 | Sig | 0.92 | 115.2 | 0.2550 | 16.4 | 97.3 | 0 | | | | |
| <i>Dichotomis cf. alyattes</i> | 367 | Exp [+] | 0.81 | 109.6 | 0.2014 | | | 0-210 | 904 | Sig | 0.76 | 132.9 | 0.464 | 1.64 | 63.8 | 0-210 | | | | |
| <i>Genieridium medinae</i> | 1 | | | | | | | | 152 | Sig | 0.85 | 89.8 | 0.1843 | 11.5 | 100 | 0 | | | | |
| <i>Ontberus laticollis</i> | 110 | Sig | 0.81 | 86.5 | 0.3428 | 9.9 | 96 | 0-120 | 418 | Uni | 0.72 | 134.8 | 0.2381 | 98.4 | 78.1 | 0-210 | | | | |
| <i>Ontboplogus curvicornis</i> | 62 | Sig | 0.43 | 80.3 | 0.0563 | 118.7 | 100 | 0-90 | 236 | Uni | 0.84 | 115.6 | 0.2537 | 149.3 | 92.9 | 110 | | | | |
| <i>Ontboplogus nasutus</i> | 54 | Lin [+] | 0.52 | 81.8 | 1.000 | | | 120 | 99 | Uni | 0.81 | 104.1 | 0.062 | 77.11 | 95.8 | 90 | | | | |
| <i>Oxysternon conspiciatum</i> | 156 | Sig | 0.91 | 88.7 | 0.569 | 3.28 | 95.3 | 0-180 | 201 | Exp [+] | 0.76 | 108.5 | 0.0247 | | | 0-120 | | | | |
| <i>Uroexys boneti</i> | 3 | | | | | | | | 64 | Lin [-] | 0.83 | 68.0 | 0.167 | | | 90 | | | | |
| <i>Uroexys nebulinus</i> | 267 | Sig | 0.65 | 125.7 | 0.104 | 3.29 | 100 | 0-180 | 1108 | Sig | 0.90 | 154.4 | 0.6717 | 103.4 | 100 | 0-210 | | | | |
| <i>Uroexys pauliani</i> | 185 | Sig | 0.88 | 100.7 | 0.1993 | 127.9 | 99.8 | 0-180 | 1447 | Sig | 0.96 | 139.6 | 0.4663 | 61.2 | 99.9 | 0 | | | | |
| Number of individuals (N) | | Exp [-] | 0.84 | 155.4 | 0.3774 | | | | | Sig | 0.96 | 202.1 | 0.1269 | 3.3 | 98.3 | | | | | |
| Species richness (⁰ D) | | Exp [-] | 0.22 | 67.0 | 0.8010 | | | | | Sig | 0.76 | 68.3 | 0.6904 | 26.3 | 48.0 | | | | | |

N = number of individuals; Mo = Model (Sig: sigmoid, Uni: unimodal, Lin: linear [+/-]); Exp: exponential [+/-]; P(s) = P-value of Shapiro test; Ext = extension in meters; Mag = magnitude in percentage; Pen = penetration in meters. Also shown is the model selected for the total number of individuals and richness at each locality.

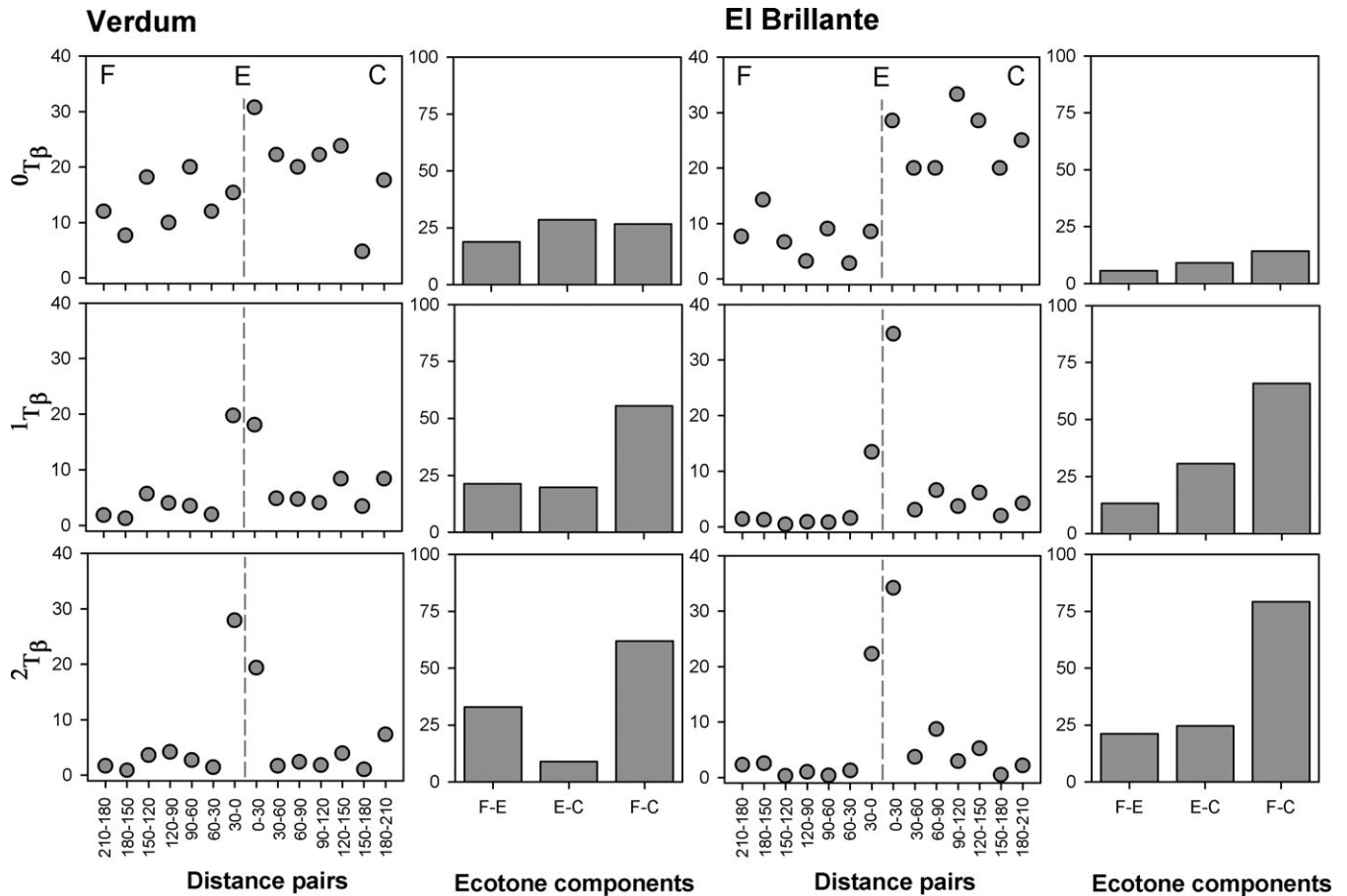


FIGURE 2. Species turnover as a percentage (T_{β}) per site among consecutive pairs of distances to the edge and between pairs of ecotone components. F = Forest, E = Edge, C = Sun-grown coffee.

DISCUSSION

Changes in richness, abundance, and species composition across the forest–sun-grown coffee ecotone were determined mainly by habitat type rather than by distance to the edge. Our results indicate that although the sun-grown coffee habitat acts a barrier to forest species, the agricultural matrix has its own assemblage of species, which increases diversity at the landscape scale. This result is consistent with the finding that the boundary between contrasting habitats does not itself represent a habitat for dung beetles (Spector & Ayzama 2003, Durães *et al.* 2005, Feer 2008, Barnes *et al.* 2014). Even though the forest–sun-coffee boundaries at both sites seem very similar, we found evidence that at the species-level, edge responses exhibited a heterogeneous pattern. In contrast to previous studies (Peyras *et al.* 2013), the response patterns of a considerable number of species (7 of the 13 species evaluated) changed according to the site, preventing the occurrence of a general pattern.

At the landscape level, habitat loss and fragmentation may influence the response pattern and magnitude of edge effects based on the area and shape of habitat patches (Ries *et al.* 2004,

Ewers *et al.* 2007). The magnitude of the edge effect may be lower in small patches, while in larger patches, the response of the assemblage may be abrupt and greater (Ewers *et al.* 2007). Although the forest fragment in El Brillante is smaller than that of Verdum (~196 ha vs. ~515 ha respectively), both forest patches were the largest in the studied landscape, and their areas are considerably greater than the 70 ha threshold above which edge effects are reported to be independent of patch size (Ewers *et al.* 2007). It is, therefore, unlikely that the observed differences between sites are due to the different sizes of the forest fragments studied.

In the study area, dung beetle richness in sun-grown coffee adjacent to forest patches was greater than expected for an area dominated by these crops (Estrada *et al.* 1998, Arellano *et al.* 2005). Species richness in sun-grown coffee was similar or equal to that reported by Pineda *et al.* (2005) in shade-grown coffee in a Mexican montane landscape. Moreover, we found that the edge tended to be as diverse as the forest and up to 1.8-times more diverse than sun-grown coffee (1D : El Brillante). We suggest that the increased diversity (1D and 2D) on the edge results from the abundant and very abundant forest and sun-grown coffee species

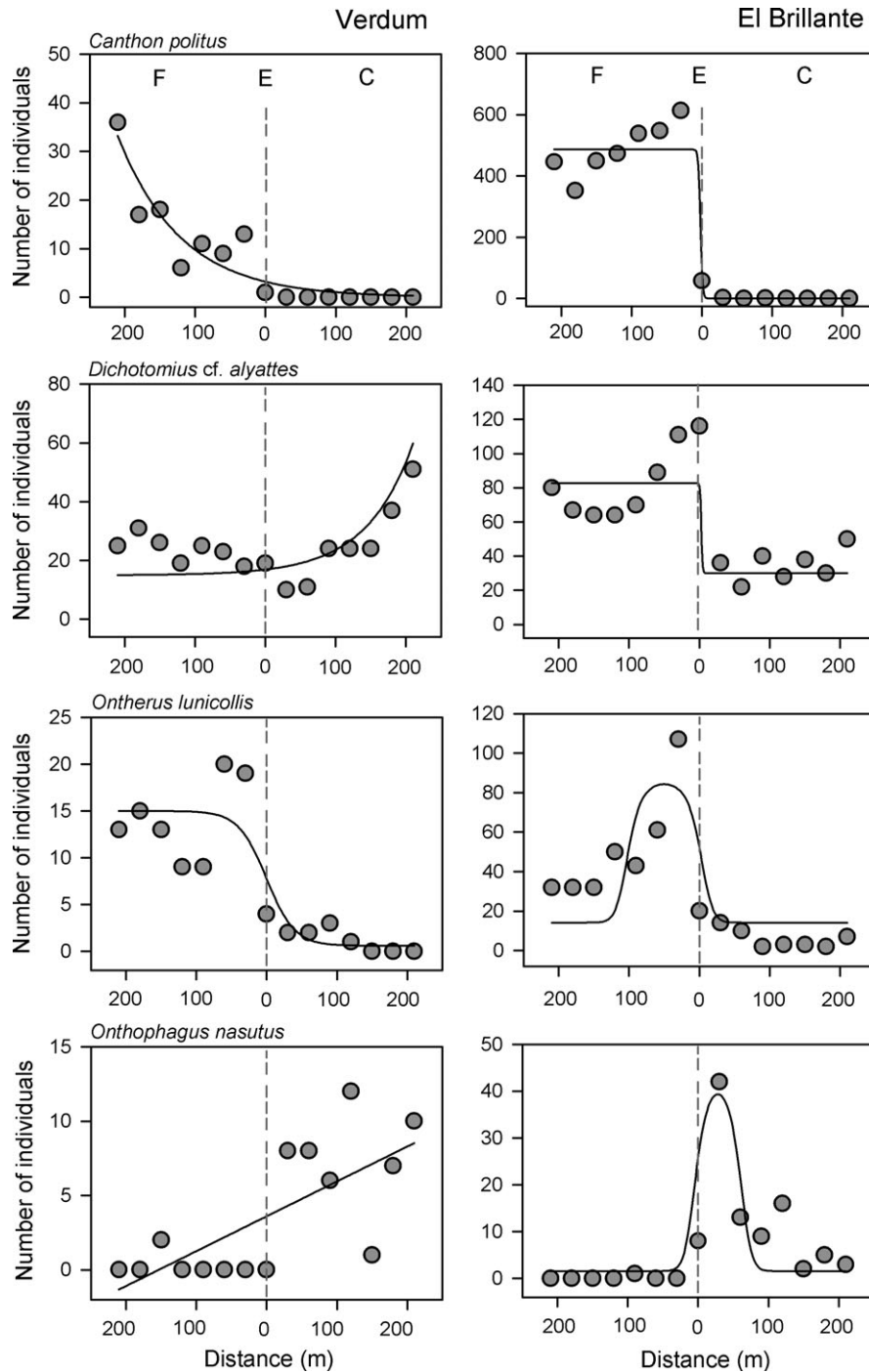


FIGURE 3. Example of edge response differences detected in four species at Verdum and El Brillante (Table 2). The theoretical function of each fitted model (solid line) is shown, as is the edge (E) between forest (F) and sun-grown coffee (C).

(e.g., *U. pauliani*, *D. cf. alyattes*; Table 2). Indeed, Ewers *et al.* (2007) asserted that the confluence of fauna on the edge is more evident when diversity does not differ significantly between the adjacent components of the ecotone.

The response pattern of species across an ecotone may be influenced by the level of fragmentation and matrix type (Ries *et al.* 2004, Reino *et al.* 2009). Specifically, the level of

environmental differentiation (differences in canopy cover, for example) between adjacent habitats can vary because of natural regeneration, crop management, and/or age, which will in turn affect the edge responses of individual species in different ways depending on their physiological constraints, dispersal capacity, and foraging behavior (Peyras *et al.* 2013, Barnes *et al.* 2014). While there were possible differences in the ages of the coffee

plantations, crop management is similar in both sites and the edges are cleared of pioneer plants, producing a marked environmental contrast (or hard edge) between the sun-grown coffee and the forest fragments (Fig. S2) that prevent forest species from moving into the matrix.

The spatial context in which ecotones are immersed may affect the response of the assemblages (Duelli *et al.* 1990, Murcia 1995), which is an aspect of great importance to understanding the spillover or movement of species from forest fragments into an agricultural matrix (Ries *et al.* 2004, Rand *et al.* 2006). The gradual decrease in species richness from the forest to sun-grown coffee in Verdum suggests its border has a higher degree of permeability (or spillover) than that of El Brillante. In fact, in the coffee area at this site, we observed a greater number of forest species, which may explain the increase in ${}^0T_{\beta}$ between pairs of distances close to the edge, as well as the relatively high and consistent species turnover values found among the ecotone elements (Fig. 2). The difference in the degree of permeability between sites indicates that within a relatively small area of the landscape (<40 km²), there may be different intensities of spillover. In general terms, our results demonstrate that there is a limited spillover of dung beetles from the forest to the sun-grown coffee plantations and support the notion that the conservation value of native forest patches in agricultural matrices depends on landscape heterogeneity, the environmental requirements of the organisms, and the intrinsic dynamics of the assemblages involved (Rand *et al.* 2006, Lucey & Hill 2012, Gray *et al.* 2016).

Other nearby forest fragments may offer favorable conditions to species that are normally found in the agricultural matrix (Ricketts 2004); with the proximity of forests patches, it is often possible to find some small- and medium-sized mammal species that can penetrate the crop edge or even move across the matrix (C. Cultid-Medina, pers. obs.). This, along with the excrement of people working in the plantations and that of domestic animals, provides a considerable amount of dung that may contribute to the maintenance of the high dung beetle diversity recorded in coffee plantations (Escobar 2004, Pineda *et al.* 2005) and may explain why abundant species in sun-grown coffee with sigmoid (*Onthophagus curvicornis*) or positive linear (*O. nasutus*) responses in Verdum had a unimodal response in El Brillante. In fact, a unimodal edge response is related to a complementary distribution of the resource (Ries *et al.* 2004), which seems to be promoted in our study by the ecological interaction between forest and adjacent coffee plantations, particularly in El Brillante.

Because dung is a scarce and ephemeral resource in tropical habitats, inter- and intra-specific competitions are common in dung beetle assemblages (Hanski & Cambefort 1991), but the fine-scale coexistence of different species is possible because of ecological segregation through different niche dimensions. These include feeding habits, body size, resource relocation behavior, and daily activity (see Feer & Pinceboure 2005). El Brillante hosts more species than Verdum, while 9 of the 16 species shared between localities were up to 300 percent more abundant in the

El Brillante forest than in Verdum. Consequently, the El Brillante forest harbors a higher density of species and individuals. The latter may impose greater competitive pressure, resulting in a thorough use of the habitat. This may explain why *O. lunicollis* had a unimodal response at El Brillante (Table 2); the species is probably maximizing the use of the resource by concentrating toward the forest edge, which is avoided by other abundant forest species such as *C. politus*, *Uroxys nebulinus*, *U. pauliani*, and *D. (Deltobomboma)* sp1. Nevertheless, the effects of the density of species and individuals on the response of different species to the edge remain to be fully evaluated. For instance, it is unclear why species known as sensitive components of forest assemblages (e.g., *C. politus*, *G. medinae*) are unusually abundant at El Brillante. To determine whether the densities of species and individuals can modify edge responses, a multi-scale approach, including different taxa in different landscape types, is required (Tscharntke *et al.* 2012).

Identifying the specific factors that modulate the expression of edge effects was beyond the scope of this study; however, our results suggest that interactions between species and population dynamics may play an important role. The forest–sun-grown coffee ecotone, at least in the context of the landscape studied, is much more complex than expected for dung beetles. However, this discrepancy may be due to the scarcity of multi-scale data for the spatial distribution of biological diversity in the tropical landscapes where sun-grown coffee is common. While our study had limitations in terms of sampling size, with only three transects used per locality, the high level of sampling completeness ensures that our results represent a valuable starting point for further studies on the connectivity, function, and monitoring of dung beetle diversity in Andean landscapes dominated by sun-grown coffee. This and previous studies in tropical and subtropical areas focusing on the local-scale response of dung beetles to human matrices provide a basis for understanding the processes that drive changes in assemblage composition and species abundance in human-dominated landscapes. Further studies on functional connectivity and population viability are necessary to increase the sustainability of sun-grown coffee production in the Colombian Andes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

FIGURE S1. Location of sampling areas in the Colombian Western Andes.

FIGURE S2. Views of the forest patch, adjacent coffee crops, and the abrupt forest–sun coffee edge studied at Verdum and El Brillante.

TABLE S1. *General characterization of the study area.*

TABLE S2. *Models used for assessing the edge effect across forest–sun-grown coffee ecotones.*

TABLE S3. *Result of the fit of the semi-varigrams by species by site according to the weight least square and maximum likelihood analyses.*

APPENDIX S1. Calculation of ${}^qD_\beta$ for species turnover between pairs of distances and ecotone components.

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