

# Movement and population size of two dung beetle species in an Andean agricultural landscape dominated by sun-grown coffee

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**Abstract** Understanding how species use and persist in agricultural areas is useful for planning conservation efforts at the landscape scale. Information at the population level is scarce, even for organisms, such as dung beetles, that are traditionally used in biodiversity studies to evaluate the effects of anthropic disturbance. Based on multiple mark–recapture events, the description of movement patterns and three population parameters (population size, survival and recruitment) were compared for two dung beetle species (*Dichotomius* cf. *alyattes* and *Oxysternon conspicillatum*) in a fragmented Andean landscape dominated by sun-grown coffee crops. Interspecific differences were detected in movement patterns and in the minimum distance moved across the landscape, with the latter associated with wing loading and species habitat preferences. *D.* cf. *alyattes* was captured in both the forest and in sun-grown coffee plots, but tended to limit its movement to patches of forest, while *O. conspicillatum* covered large distances in short periods of time across the sun-grown

coffee crops (ca. 1.7 km/24 h). The population of each species increased during the months of greatest precipitation, prior to the recruitment of new beetles. Given their great capacity for movement, habitat preference and their differential use of the landscape, the species studied can be used as models to evaluate the functional connectivity of Andean landscapes under high anthropic demand. Our results support the idea of the differential response of species to land-use changes, an aspect that should be considered for effective biodiversity conservation and ecosystem functioning in human-dominated landscapes.

**Keywords** Scarabaeinae · Colombian Andes · Mark–recapture · Jolly–Seber · Population size

## Introduction

The population-level study of insects is an important source of information for the design of monitoring and conservation strategies for landscapes where the demand for agricultural land is high (Samways et al. 2005). Insects represent a considerable portion of the biomass of ecosystems and participate in a large number of processes that are key to ecological functioning (see Didham et al. 1996). Additionally, insects have relatively short life cycles and quickly respond to the intensification of land use (Brown 1991), characteristics that make them the ideal model for evaluating, in a reasonable amount of time, the effects of human activities. However, population-based studies in tropical agricultural landscapes are scarce owing largely to three kinds of limitations: taxonomic (i.e. high diversity), conceptual (i.e. the definition of a landscape) and methodological (i.e. sampling design and specimen marking techniques).

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It has been documented that the movement of species and the permanence of their populations is, in part, determined by the spatial arrangement of the elements that make up the landscape, i.e., the types of vegetation cover and degree of isolation of patches of habitat, along with the life history traits of species (i.e. body size, habitat preference and flight capability; the latter a variable related to an organism's dispersal ability at local, landscape and regional scales), and the demographic characteristics of populations (i.e. population size, survival and the rate of addition of new individuals to the population or recruitment rate) (Hagen et al. 2012). However, quantitative evidence of these aspects is still limited for most dung beetle species (Roslin and Viljanen 2011) and in the Neotropics, only two studies offer concrete data. The study by Arellano et al. (2008) in a deciduous tropical forest in southern Mexico, found that although *Canthon cyanellus* is preferentially associated with patches of native forest it can move through a highly fragmented forest as long as there are corridors (such as living fences) that increase the functional connectivity of the landscape. The other study, by Larsen et al. (2008), revealed that the degree to which dung beetles are prone to extinction when fragmentation (in Venezuela) is intensified depends on the interaction of the ecological traits of species, such as body size, wing loading, flight strategy, habitat preferences, body size and the population density of the species in the forest fragments, and notes that some dung beetles, in particular large species, require relatively large tracts of forests for their survival.

In conservation terms, sun-grown coffee is considered a low quality habitat for biodiversity (Perfecto and Armbrrecht 2003; Rivera and Armbrrecht 2005; Philpott et al. 2008). However, at the landscape level the response of the communities and populations are not only modulated by the presence of sun-grown coffee, but also by the spatial context and the management context in which these crops are immersed (De La Mora et al. 2013; Muriel and Kattan 2009). In the Colombian Andes, the appearance of sun-grown coffee plantations has not been uniform in space or time (Guhl 2004) and so these crops are immersed in environmental mosaics with differing degrees of spatial heterogeneity (complexity), some of which favors the persistence in the landscape of species tolerant to the agricultural matrix (Muriel and Kattan 2009). For example, in the Central Andes of Colombia Muriel and Kattan (2009) found that the sun-grown coffee matrix was not impenetrable to butterflies belonging to the Ithomiinae family. Their flight in sun-grown coffee plantations was fast and directional, while in shaded areas such as the forest and shade-grown coffee these butterflies fly slowly, suggesting that there are also behavioral changes in their habitat use and a high degree of mobility in the sun-grown coffee matrix.

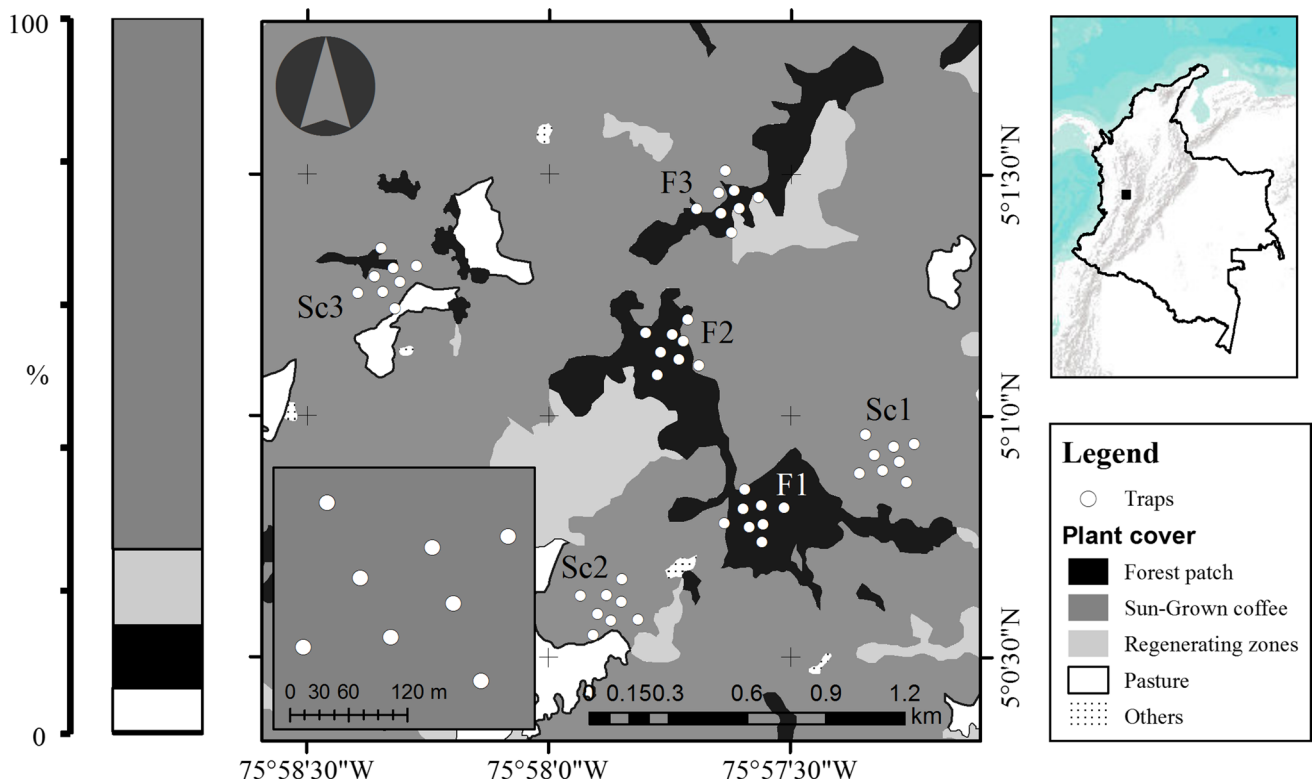
Native species that can tolerate the agricultural matrix can be of great value in the maintenance and integrity of ecological processes for the functioning of agroecosystems (e.g. predation, seed dispersal, pollination; Tscharntke et al. 2008). Thus, beetles have an important role in the removal of dung and recycling of nutrients, improving the condition of the soil and contributing to the biological control of flies and parasites that are disease vectors (Nichols et al. 2008). Given that dung beetle assemblages in sun-grown coffee plantations in the Andes are dominated by large species that account for much of the beetle community's biomass in these systems (Escobar 2004; Cultid et al. 2012), and considering the ephemeral nature of the resource these beetles use to feed and nest (excrement, carrion), they are expected to have a relatively high degree of mobility and therefore large foraging areas (Cambefort and Hanski 1991). That being said, the population ecology of these species and our knowledge of their functional impact on agricultural landscapes is in its infancy.

In this study, we compared the population parameters and evaluated the pattern and degree of mobility of two species of dung beetle (*Oxysternon conspicillatum* and *Dichotomius cf. alyattes*) that are large (>10 mm) and relatively abundant in the agricultural landscapes of the Western Andes of Colombia (Cultid et al. 2012) in order to address the following questions: What is the population size and what is the probability of survival and recruitment (i.e. adding new individuals to a population) for these two species? How do their patterns of movement in the landscape differ; and, are any differences in movement pattern associated with interspecific differences in wing loading? In the Colombian Andes, *O. conspicillatum* is a dominant species where there is cover of anthropic origin such as sun-grown coffee crops and appears to avoid entering large patches of forest (Escobar 2004; Cultid et al. 2012). In contrast, *D. cf. alyattes* has been caught in both forest and sun-grown coffee plantations (Cultid et al. 2012). Thus, a comparative study of the movement patterns of species with different habitat requirements, can provide ecologically relevant information for designing landscape mosaics of natural and anthropogenic land use for effective biodiversity conservation and ecosystem functioning.

## Materials and methods

### Study area

This study was done in a fragmented agricultural landscape of about 760 ha in the foothills of Alto de Plumas hill (1450–1900 m a.s.l.) between the municipalities of La Celia and Santuario, in the Department of Risaralda, Colombia (5°00'58.55"N–75°57'29.33"W; Fig. 1). Three-



**Fig. 1** Agricultural landscape studied in the Western Andes of Colombia dominated by sun-grown coffee. The landscape is approximately 760 ha in area. The spatial arrangement of the sampling sites

in the forest (F1–F3) and in the sun-grown coffee (Sc1–Sc3) is shown. The inset map shows the setup of the traps at each sampling site. The sidebar on the left shows the cover (%) of each type of vegetation

quarters of the landscape’s area is covered by sun-grown coffee plantations (74.4 % of total area), dotted with forest remnants, abandoned areas that are regenerating and pastures (Fig. 1). Most of the area under cultivation has coffee grown in full sun (for classification details see Moguel and Toledo 1999). In the study area coffee plantations are relatively small (3–10 ha) and coffee plants range from 15 months to 9 years in age. Where coffee is grown there are scattered trees such as *Cordia alliodora*, *Psidium guajava* and *Inga* sp., along with seasonal crops such as banana and cassava trees, especially at the limits between plots of coffee. The forest remnants are mainly located on the mountaintops and in the valleys (Fig. 1), and still have the floristic elements characteristic of the Wet Forest Lower Montane and Moist Forest Premontane life zones (Espinal 1967). The patches of forest are small (5–30 ha), with predominantly pioneer species and a high degree of human activity (e.g. logging for different purposes). The coffee crops are located on the sides of the mountain and have been there for 1–10 years. Pastures are located on the flat parts of the landscape and have a low livestock load (1–15 head of cattle; pasture size range 0.7–26.4 ha) and represent <6 % of the area. The regenerating zones (10.6 % of the study area) are plots of sun-grown coffee or

abandoned pastures on the hillsides, in the valleys, and in areas adjacent to the forest remnants (Fig. 1).

**Species, marking technique and sampling design**

*Oxysternon conspicillatum* and *Dichotomius* cf. *alyattes* are typical species of the northern Andes and were selected for the following reasons: (1) they are large species (body length: 10–35 and 16–24 mm, respectively), which facilitates marking them, (2) their abundance is relatively high and constant throughout the year (Cultid unpubl. information), and (3) the two species differ in their habitat preferences and daily activity rhythms. *D.* cf. *alyattes* is a nocturnal species that is caught in both the forest and sun-grown coffee plantations, while *O. conspicillatum* is diurnal (Escobar 2004; Cultid et al. 2012). Differences in the way these species use the landscape could be of great value to conservation planning in areas dominated by human activities, in agricultural Andean landscapes.

To capture beetles of both species nonlethal pitfall traps were used. The trap consists of a 0.5 L container with a plastic cone at the entrance to prevent the beetles from escaping (see Cultid et al. 2012). Traps were baited with a mix of human and pig excrement in a 7:3 ratio. The bait was

suspended 15 cm above the trap. The traps were set up at six sites: three in the forest (F1–3) and three in sun-grown coffee plantations (Sc1–3; Fig. 1). At each site, two quadrats of traps differing in size (one inside the other) were set up, with a trap at each corner for a total of eight traps per site and 24 traps per vegetation type (48 traps altogether; Fig. 1). The traps in the inner quadrat were separated by at least 50 m and those in the outer quadrat, by 130–160 m. Based on the position of the outer traps, sampling sites were separated by a distance of 370–1300 m (Fig. 1).

The technique proposed by Martínez-Quintero et al. (2013) was used to mark the beetles: using a Mototool (DREMEL STYLUS 1100®), a number was tattooed on the surface of the pronotum or the elytra of each beetle. This way, for each beetle it was possible to assign a consecutive number associated with the following variables: sex, site, type of vegetation cover (where marked, and if applicable where recaptured), as well as complementary information about the state of maturity of the beetles (recently emerged or teneral). Previous trials indicated that marking the beetles this way neither affects their behavior nor kills them, at least not during the trials using beetles of both species kept in terrariums under field conditions (Martínez-Quintero et al. 2013). From March to August 2012, beetles were marked and recaptured over periods of 5 days, with three 24-h-long capture events each month, each of which was, separated by a period of 24 h when the traps were not baited. That is, the capture and marking of beetles in each month was performed at 24, 72 and 120 h. In total there were 16 sampling events (including the initial capture and marking) per vegetation type (forest, sun-grown coffee) and for each sampling event, all of the individuals captured were marked and released.

Wing loading is an aerodynamic parameter for flying animals that is based on the relationship between body weight (mg, dry weight in this study) and wing area (mm<sup>2</sup>). This parameter is associated with aspects of the aerodynamic behavior of organisms (i.e. speed, turning and maneuvering; Norberg 1994). To calculate wing loading 57 unmarked *O. conspicillatum* and 59 unmarked *D. cf. alyattes* were caught. After each beetle was dried at 60 °C for 48 h, it was weighed on an analytical balance (Ohaus Adventure ± 0.0001 g). Wing area was calculated based on a photograph of the extended right wing of each beetle, which was processed using *imageJ* software (<http://rsbweb.nih.gov/ij/>).

## Data analysis

### Abundance patterns, wing loading and movement

Beetle species abundance was compared between vegetation types (forest, sun-grown coffee) and sampling sites

using a nonparametric repeated measures test (Friedman's test;  $\alpha = 0.05$ ) and specific differences were identified with an a posteriori paired Wilcoxon's test with Bonferroni corrections. For this, net abundance ( $N_{net}$ ) from each sampling event was used, which is equal to the number of beetles caught minus the number recaptured per sampling event. This was done to avoid overestimating the number of individuals that are effectively captured, allowing for a more realistic comparison. The comparison did not include data from the first sampling event because only two (F1 and Sc1) of the six sampling sites were sampled.

Wing loading capacity and body weight (dry) were normally distributed (Shapiro test,  $p > 0.05$ ), so these variables were compared between species and sexes using Student's *t* test (independent pairs of samples). All of the comparisons were made using R v. 3.0.3 (R Core Team 2015).

We used ArcGIS 9.3 (ESRI Inc. 1999–2008) to obtain the distances moved for each species. Distance was calculated as the linear distance between the marking trap and the recapture trap. To compare the distances moved by the two species, we concentrated on the distance covered by the beetles marked between sampling events within a given month of sampling, i.e. the distance marked individuals covered 24–120 h after being marked (these were considered the minimum distances moved and we refer to this as the type I distance). It is important to remember that these minimum distances are an approximation that underestimates the organism's capacity for movement, given that beetles do not necessarily move in a straight line. To examine how beetles of each species might move around the landscape, all distances moved were visually inspected, including for the beetles that were caught 2, 3, 4 and 5 months after being marked (which we call type II distance).

### Population structure and size

For each species, the proportion of beetles recaptured throughout the sampling period was determined. Using the Jolly–Seber method (Jolly 1965, Seber 1965), three population parameters were estimated for each species and sampling event: population size ( $N_t$ ), new beetles ( $B_i$ : from recruitment and immigration) and survival rate ( $\Phi$ ) (Southwood and Henderson 2000). According to Jolly–Seber for open populations the survival rate is calculated assuming that migration and mortality of individuals are equal. Fluctuations in population size were examined in detail ( $N_t \pm SE$ ) throughout the sampling period, without taking vegetation type into account. The 16 sampling events were used to estimate percent recapture, but to estimate population size the last event was not included because no new beetles were marked at that time. Changes

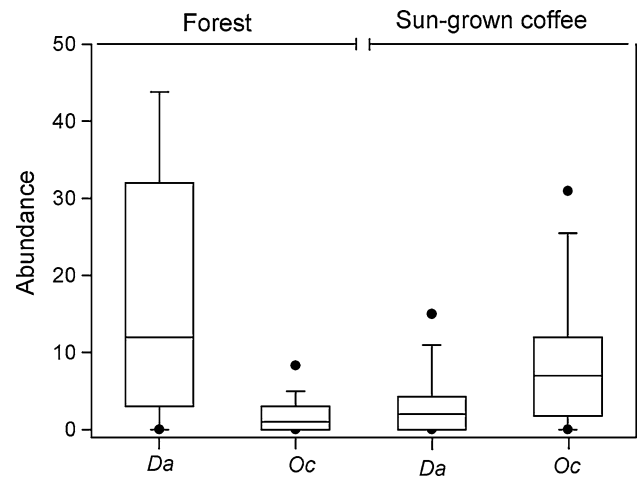
in the population parameters are discussed with respect to the minimum distance moved and historical mean monthly precipitation in the study area (FEDECAFE 2013).

## Results

### Abundance, movement and wing load

A total of 2102 beetles were marked, 1470 *D. cf. alyattes* and 632 *O. conspicillatum* (Table 1). There were significant differences in the net abundance ( $N_{net}$ ) of species depending on vegetation type ( $\chi^2 = 36.84$ ;  $df = 3$ ;  $p < 0.0001$ ). *D. cf. alyattes* was more abundant in the forest, and *O. conspicillatum* in sun-grown coffee plantations (Fig. 2). In detail, species abundance differed between sampling sites (*D. cf. alyattes*:  $\chi^2 = 43.36$ ;  $df = 5$ ;  $p < 0.0001$  and *O. conspicillatum*:  $\chi^2 = 31.35$ ;  $df = 5$ ;  $p < 0.0001$ ; Table 1). For *D. cf. alyattes* site F1 was different from the other sites sampled ( $p < 0.01$ ) with 62.3 % of this species recorded in the forest and 53.1 % at the landscape scale (Table 1). The abundance of *O. conspicillatum* was significantly higher in all of the sun-grown coffee sites and these were not different from F1 (Table 1).

For both species, a similar number of movements was observed (*D. cf. alyattes* = 37; *O. conspicillatum* = 32). For *D. cf. alyattes* 56 % of the events occurred between forest sites, 41 % between coffee crop and forest sites, and only 3 % between coffee sites. In contrast, 89.2 % of *O. conspicillatum* movement took place between coffee crop and forest sites, 10.8 % between coffee sites and none between forest sites. The longest distance moved was 1700 m (type I) covered in 24 h by a male *O. conspicillatum* captured in the forest (F3) and recaptured in sun-grown coffee (Sc2; Fig. 3b). Type I distances moved by *O. conspicillatum* were 479–1700 m, while the range was more limited for *D. cf. alyattes* at 456–717 m (Fig. 3a). On observing all flights by both species at the same time



**Fig. 2** Comparison of the medians of net abundance ( $N_{net}$ : total number of beetles captured minus the number of individuals recaptured) between species and type of vegetation cover. Boxes indicate the 25–75 % quartiles and the whiskers are the minimum and maximum values. Black dots are atypical values. Da, *Dichotomius cf. alyattes*; Oc, *Oxysternon conspicillatum*

(Fig. 3c, d; type I + type II distance), one can see tendencies in the way the beetles moved around the landscape. In general terms, *D. cf. alyattes* tended to move within and between forested areas (Fig. 3c), while *O. conspicillatum* tended to move through the sun-grown coffee crops and around the largest patch of forest on the landscape (Fig. 3d). Body weight and wing loading were significantly greater for *O. conspicillatum* than for *D. cf. alyattes* ( $t_{112(0.05)} = -13.447$ ;  $p < 0.001$  and  $t_{112(0.05)} = -21.015$ ;  $p < 0.001$ , respectively) and there were no differences between sexes (Table 2).

### Population structure and size

Net recapture was 379 beetles, equivalent to 18 % of all the beetles marked (Table S1). The majority (87.3 %) were of beetles recaptured once, with 11 % recaptured twice and

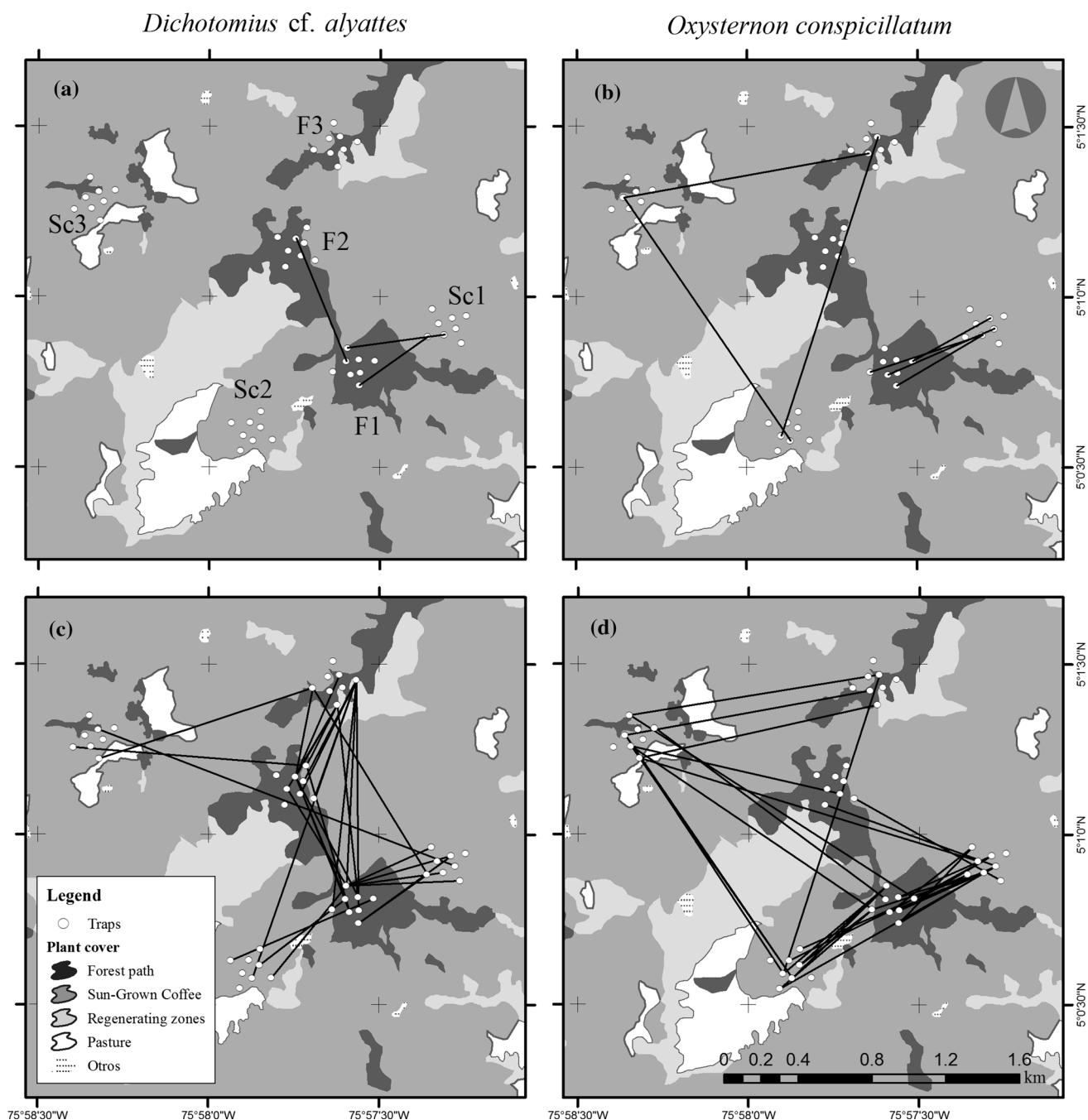
**Table 1** Number of marked individuals with net abundance ( $N_{net}$ ) in parenthesis per species (i.e. total number of beetles captured minus the number of beetles recaptured per sampling event)

Species	Forest			Sun-grown coffee			Total
	F1	F2	F3	Sc1	Sc2	Sc3	
<i>D. cf. alyattes</i>	840 (579) <sup>a</sup>	245 (197) <sup>b</sup>	181 (154) <sup>b</sup>	78 (51) <sup>c</sup>	74 (66) <sup>c</sup>	52 (43) <sup>c</sup>	1470 (1090)
♀	456	144	97	29	30	25	781
♂	384	101	84	49	44	27	689
<i>O. conspicillatum</i>	89 (59) <sup>a</sup>	12 (12) <sup>b</sup>	19 (18) <sup>b</sup>	275 (206) <sup>d</sup>	128 (101) <sup>de</sup>	109 (95) <sup>e</sup>	632 (491)
♀	35	2	7	103	49	45	241
♂	54	10	12	172	79	64	391

Comparisons were made between groups of traps per species; different letters indicate significant differences ( $\alpha = 0.05$ )

F1–3, forest sites; Sc1–3, sun-grown coffee sites





**Fig. 3** a, b Movement (linear distance) during the first month of sampling (type I distance, see Table S1) for *Dichotomius cf. alyattes* and *Oxysternon conspicillatum*, respectively. c, d Total movement

(linear distance) recorded over the entire sampling time (5 months) for each species (type II distance). Sampling sites in the forest (F1–F3) and in the sun-grown coffee crops (Sc1–Sc3) are shown

1.3 % three times. Only one beetle was recaptured throughout the 5 months of sampling (beetle number 1, a male *D. cf. alyattes*; Table S1). Of the total net recapture, 65.4 % was *D. cf. alyattes* (Table S1). It is also important to mention that 186 teneral *D. cf. alyattes* and 151 teneral *O. conspicillatum* were marked, of which 7 (3.8 %) and 22 (14.6 %) were recaptured, respectively.

Population size was highest for both species at the first sampling event in June, with 25,592 *D. cf. alyattes* and 30,932 *O. conspicillatum* (Fig. 4a). Prior to and after June, estimated population size for *D. cf. alyattes* did not exceed 3800 beetles, and for *O. conspicillatum* did not exceed 8000 (Fig. 4a). Changes in the probability of survival ( $\Phi$ ) and the recruitment, or the addition of new beetles to the

**Table 2** Comparison of body weight (dry) and wing load between species and sex by species (mean ± SE)

Species	Body weight (mg)	Wing loading (g/mm <sup>2</sup> )
<i>D. cf. alyattes</i>	729.82 ± 186.70 <sup>a</sup>	1.81 ± 0.29 <sup>a</sup>
♀	738.21 ± 183.47 <sup>a</sup>	1.86 ± 0.30 <sup>a</sup>
♂	721.72 ± 192.65 <sup>a</sup>	1.77 ± 0.27 <sup>a</sup>
<i>O. conspicillatum</i>	1692.13 ± 491.81 <sup>b</sup>	4.06 ± 0.75 <sup>b</sup>
♀	1818.62 ± 400.85 <sup>a</sup>	4.19 ± 0.73 <sup>a</sup>
♂	1577.50 ± 542.67 <sup>a</sup>	3.93 ± 0.76 <sup>a</sup>

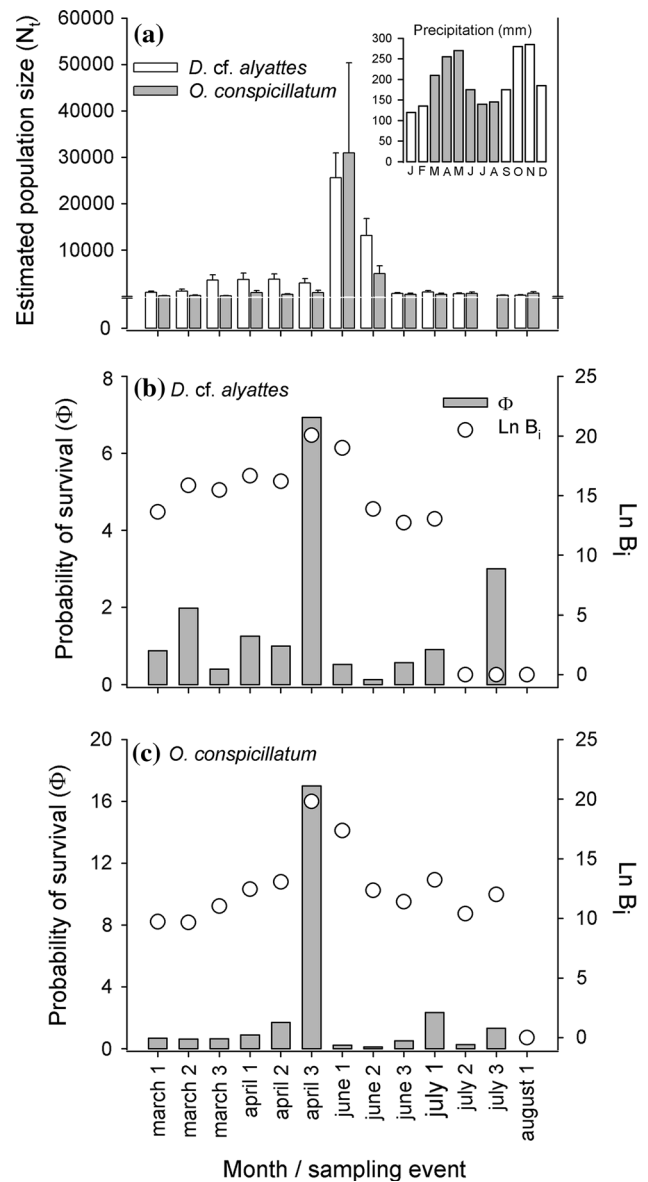
Different letters indicate significant differences ( $p < 0.001$ )

population, (Bi) were similar for both species, with the highest values during the third sampling event of April, the rainiest month of the year (Fig. 4b, c).

### Discussion

The proportion of recaptures reported in our study (18 %) is higher than that reported by similar studies carried out over periods longer than 6 months: 2.25 % ( $N_{total} = 931$ ; Escobar and Chacón 2000) and 5 % ( $N_{total} = 2460$ ; Arellano et al. 2008). This is probably the result of four factors: (1) we used a permanent form of marking that was always legible and did not alter the behavior or integrity of the beetles, (2) we used two large species (>10 mm), which made marking the beetles much easier (Martínez-Quintero et al. 2013), (3) both species are important in abundance and biomass in the agricultural landscapes of the Colombian Andes (Cultid et al. 2012), and (4) the species chosen for the study can be captured throughout the year, unlike the other species selected for mark–recapture studies in regions with marked seasonality (e.g. *Canthon cyanellus*, Arellano et al. 2008).

We found that *D. cf. alyattes* does not use the entire landscape, but rather appears to move preferentially between forest patches (Fig. 3a, c). In contrast, *O. conspicillatum* is more abundant in sun-grown coffee, and moves over much of the landscape, crossing or occasionally using small forested areas (Fig. 3b, d). This species seems to avoid entering large forest remnants (Escobar 2004; Escobar et al. 2007), but we found that the forest patches in the landscape studied do not appear to be an effective barrier to the movement of *O. conspicillatum*, owing perhaps to their elongated shape and small area (<30 ha). These results highlight the need for future studies that quantify how the area, shape and position of forest patches in a landscape affect the movement patterns of the Scarabaeinae species to develop strategies for the preservation of their populations.



**Fig. 4** a Estimated population size (Nt) for each species, *Dichotomius cf. alyattes* and *Oxysternon conspicillatum*, over the course of monthly sampling (see Table S1). Lines are standard error, the inset graph shows historical mean monthly precipitation (mm) (>5 years) in the study region with the sampling period bars in gray. b, c Changes in the probability of survival ( $\Phi$ ) and the number of beetles gained by the population (Bi); in Ln to make the comparison easier) throughout the study period for each species

The abundance of *O. conspicillatum* tended to be lower at the sampling site scale and was not significantly different from that of *D. cf. alyattes* in the sun-grown coffee crops (Fig. 2); however, the evaluation of estimated population size indicates that *O. conspicillatum* does not necessarily have smaller populations at the landscape scale. Maximum estimated population size did not differ between species (note overlap of error bars, Fig. 4a), but compared to that

of *D. alyattes*, the population of *O. conspicillatum* could at any given moment have more than 50,000 beetles, almost twice as much as the maximum population size of *D. cf. alyattes*. In our study, it is possible that the relatively low abundance of *O. conspicillatum* at the scale of the sampling sites is a result of its being a species with a high capacity for movement, able to cover large areas during the day in its search for resources. Thus the population of *O. conspicillatum* could be more spread out on the landscape than *D. cf. alyattes* is. This is consistent with the differences detected between species with respect to wing loading (significantly greater in *O. conspicillatum*) and in the minimum distances moved (lower in *D. cf. alyattes*).

*Oxysternon conspicillatum* has been listed as a species that is clumsy in flight (Peck and Forsyth 1982). This may be due to its having very fast, directed flight with little maneuverability when it suddenly changes direction, however some observations suggest that it flies with a high degree of precision and efficiency when locating excrement (Medina et al. 1990; T. Larsen pers. comm.). This notable capacity for flight could be associated with the need to cover large distances to find food. During sampling several *O. conspicillatum* were observed using the excrement of different domestic animals (dog, horse, cow and pig) as well as human excrement. In general these types of excrement dehydrate quickly and at the same time are highly sought after by other species of diurnal coprophagous beetles that are abundant in sun-grown coffee (e.g. *Onthophagus curvicornis* and *Onthophagus marginicollis*, Cultid et al. 2012). Moreover, it is important to keep two things in mind: (1) the species we studied have a wing loading associated with highly mobile species of Scarabaeinae and with populations that appear to require large tracts of habitat and (2) the results do not suggest a lower capacity for movement in relatively small individuals or significant differences in wing loading between sexes. Therefore, for both species all of the members of the population (including the teneral) appear to have a similar capacity for movement.

The abrupt increase in population size estimated for both species during the first two sampling events of June could be related to the climate and to species phenology. The increase occurred after the two rainiest months in the study region (April and May; Fig. 4a). Although no marked seasonality has been detected in the behavior of the dung beetles of the Colombian Andes (Escobar 2000), the number of some species tends to increase toward the beginning and the end of the rainy season (Escobar and Chacón 2000). It is possible that this phenomenon is a result of recruitment, which occurs in some Scarabaeinae species during the rainy season with the emergence of new beetles (Cambefort and Hanski 1991). Evidence of this is that the number of marked *D. alyattes* teneral beetles was

recorded during April (55 individuals). This explains the sudden increase in the recruitment parameter ( $B_1$ ) prior to the increase in population size (Fig. 4c, d). That said, it is important to mention that the detection of teneral beetles is rather low because after they emerge they remain buried for much of the time while undergoing chitinization and physiological maturation (Halffter and Matthews 1966).

In terms of body size and abundance, *O. conspicillatum* and *D. cf. alyattes* are important components of the Andean landscape studied and their populations probably play a critical role in the removal of excrement at spatial scales greater than 700 ha. For example, according to Medina et al. (1990), *O. conspicillatum* can move up to 40 times its own body weight and this beetle can move more than 60 g of excrement in a very short time (0.44 cm/s on average). As such, based on the minimum estimated population size in this study (126 beetles; Fig. 4a) and assuming that all the beetles find food at the same time, this number of *O. conspicillatum* beetles can remove about 7.5 kg of excrement in less than half an hour. So, over the course of a month, the maximum estimated population of this species could contribute by removing approximately two tons of excrement.

Field observations during this study indicate that both beetle species are eaten by vertebrates. In the forest and in the burrow of a small mammal (perhaps, a nine-banded armadillo: *Dasybus novemcinctus*) we found the remains of a male *D. cf. alyattes*, which had been marked 10 days prior. On other occasions, *Momotus aequatorialis* was observed to follow and hunt *O. conspicillatum* beetles. Similarly, the pronotum of a marked female *O. conspicillatum* was found on a trunk possibly used as an anvil by some species of bird.

This study presents new information about some aspects of the populations of two Scarabaeinae species with different habitat preferences and movement capabilities that are dominant in the agricultural landscapes of the Colombian Andes. Our results support the idea of the differential response of species to land use changes, and this could be of great importance for designing landscape mosaics of both natural land and land used by people to effectively conserve biodiversity and ecosystem functioning. Conservation efforts will also require multiple but interdependent management actions at the landscape level (both forest and crop areas), in order to ensure the effective conservation of dung beetles. Similarly, our results support the idea that some species of Scarabaeinae (mainly large species) require areas larger than those traditionally used for studying them at the landscape scale (400–500 ha, e.g. Numa et al. 2009; Larsen et al. 2008; Rös et al. 2012). In this sense, while *O. conspicillatum* and *D. cf. alyattes* are associated with intermediate and high levels of anthropic disturbance, both species are ideal models for evaluating



two critical aspects of the management and conservation of biodiversity in situations where the demand for agricultural land is high as occurs in the northern Andes: (1) changes in functional connectivity relative to the area and spatial arrangement of forest patches and sun-grown coffee on the landscape scale, particularly for different spatial arrangements of both vegetation types and levels of disturbance and (2) the functional impact of these native dung beetle species on the ecological processes occurring in and on the soil and their potential benefits to agriculture.

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**Conflict of interest** The authors of this manuscript declare that there is no conflict of interest.

## References

- Arellano L, León-Cortés J, Ovaskainen O (2008) Patterns of abundance and movement in relation to landscape structure: a study of a common scarab (*Canthon cyanellus cyanellus*) in Southern Mexico. *Landsc Ecol* 23:69–78
- Brown KS Jr (1991) Conservation of neotropical environments: insects as indicators. In: Collins NM, Thomas JA (eds) The conservation of insects and their habitats. Royal Entom. Soc. Symposium XV. Academic Press Inc, San Diego, pp 349–404
- Cambefort Y, Hanski I (1991) Dung beetle population biology. In: Hanski I, Cambefort Y (eds) Dung beetle ecology. Princeton University Press, Princeton, New Jersey, pp 36–50
- Cultid CA, Medina CA, Martínez B, Escobar AF, Constantino LM, Betancur N (2012) Escarabajos coprófagos (Scarabaeinae) del Eje Cafetero: guía para el estudio ecológico. WCS-Colombia, CENICAFÉ y la Federación Nacional de Cafeteros. Villa María, Colombia
- De La Mora A, Murnen CJ, Philpott SM (2013) Local and landscape drivers of biodiversity of four groups of ants in coffee landscapes. *Biodivers Conserv* 22:871–888
- Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented habitats. *Trends Ecol Evol* 11:255–260
- Escobar F (2000) Diversidad y distribución de los escarabajos del estiércol (Coleoptera: Scarabaeinae) de Colombia. In: Martín-Piera F, Morrone JJ, Melic A (eds) Hacia un proyecto CYTED para el inventario y estimación de la diversidad entomológica de Iberoamérica PRIBES 2000. Monografías Tercer Milenio, vol 1. Sociedad Entomológica Aragonesa, CYTED, Zaragoza, pp 197–201
- Escobar F (2004) Diversity and composition of dung beetles (Scarabaeinae) assemblages in a heterogeneous Andean landscape. *Trop Zool* 17:123–136
- Escobar F, Chacón P (2000) Distribución espacial y temporal en un gradiente de sucesión de la fauna de coleópteros coprófagos (Scarabaeinae, Aphodiinae) en un bosque tropical montano, Nariño-Colombia. *Rev Biol Trop* 48:961–975
- Escobar F, Halffter G, Arellano L (2007) From forest to pasture: an evaluation of the influence of environment and biogeography on the structure of dung beetle (Scarabaeinae) assemblages along three altitudinal gradients in the Neotropical region. *Ecography* 30:193–208
- Espinal LS (1967) Apuntes sobre ecología colombiana. Universidad del Valle, Cali, Colombia
- ESRI Inc. (1999–2008) ArcGIS 9.3. License authorized for WCS-Colombia (FEDECAFE) Federación Nacional de Cafeteros de Colombia, Centro Nacional de Investigaciones de Café. (2011) Anuario Meteorológico Cafetero. CENICAFÉ, Chinchiná
- FEDECAFE, Federación Nacional de Cafeteros de Colombia, Centro Nacional de Investigaciones de Café (2013) Anuario Meteorológico Cafetero 2012. CENICAFÉ, Chinchiná, Colombia
- Guhl A (2004) Coffee production intensification and landscape change in Colombia 1970–2002. In: Millington A, Jepson W (eds) Land change science in the tropics: changing agricultural landscapes. Springer Science, New York, pp 93–115
- Hagen M, Kissling WD, Rasmussen C, De Aguiar MAM, Brown LE, Carstensen DW, Alves-Dos-Santos I, Dupont YL, Edwards FK, Genini J, Guimarães PR Jr, Jenkins GB, Jordano P, Kaiser-Bunbury CN, Ledger ME, Maia KP, Marquitti FMD, McLaughlin Ó, Morellato LPC, O’Gorman EJ, Trøjelsgaard K, Tylianakis JM, Vidal MM, Woodward G, Olesen JM (2012) Biodiversity, species interactions and ecological networks in a fragmented world. *Adv Ecol Res* 46:89–210
- Halffter G, Matthews EG (1966) The natural history of dung beetles of the subfamily Scarabaeinae. *Folia Entomol Mex* 12–14:1–312
- Jolly GM (1965) Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika* 52:225–247
- Larsen TH, Lopera A, Forsyth A (2008) Understanding trait-dependent community disassembly: dung beetles, density functions, and forest fragmentation. *Conserv Biol* 22:1288–1298
- Martínez-Quintero B, Cultid-Medina C, Rudas-Grajales J (2013) Método para marcar escarabajos coprófagos (Coleoptera: Scarabaeinae) y su implementación en los Andes de Colombia. *Acta Zool Mex* 29:448–451
- Medina C, Escobar F, Rojas M (1990) Aspectos ecológicos y biomecánicos de *Oxysternon conspiciatum* (Col: Scarabaeidae) en el Valle del Cauca. *Rev Colomb Entomol* 6:54–61
- Moguel P, Toledo VM (1999) Biodiversity conservation in traditional coffee systems of Mexico. *Conserv Biol* 13:11–21
- Muriel SB, Kattan GH (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, Spector S, Louzada J, Larsen T, Amezcua S, Favila ME, Network The Scarabaeinae Research (2008) Ecological functions and ecosystems services provided by Scarabaeinae dung beetles. *Biol Conserv* 141:1461–1474
- Norberg UM (1994) Wing, design, flight performance, and habitat use in bats. In: Wainwright P, Reilly SM (eds) Ecological morphology: integrative organismal biology. University of Chicago Press, USA, pp 205–239
- Numa C, Verdú JR, Sánchez A, Galante E (2009) Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. *Divers Distrib* 15:489–501
- Peck SB, Forsyth A (1982) Composition, structure, and competitive behaviour in a guild of Ecuadorian rain forest dung beetles (Coleoptera; Scarabaeidae). *Can J Zool* 60:1624–1634
- Perfecto I, Armbrecht I (2003) The coffee agroecosystems in the neotropical: combining ecological and economic goals. In: Vandermeer JH (ed) Tropical agroecosystems. CRC Press, USA, pp 159–194

- Philpott SM, Arendt WJ, Armbrrecht I, Bichier P, Diestch TV, Gordon C, Greenberg R, Perfecto I, Reynoso-Santos R, Soto-Pinto L, Tejada-Cruz C, Williams-Linera G, Valenzuela J, Zolotoff JM (2008) Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conserv Biol* 22:1093–1105
- R Core Team (2015) R: a language and environment for statistical computing. R foundation for Statistical Computing. Vienna, Austria. <http://www.R-project.org/>
- Rivera L, Armbrrecht I (2005) Diversidad de tres gremios de hormigas en cafetales de sombra, de sol y bosques de Risaralda. *Rev Colomb Entomol* 31:89–96
- Rös M, Escobar F, Halffter G (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 Distrib* 18:377–389
- Roslin LW, Viljanen TJ (2011) Dung beetle populations: structure and consequences. In: Simmons LW, Ridsdill-Smith TJ (eds) *Ecology and evolution of dung beetle*. Wiley-Blackwell, UK, pp 220–224
- Samways MJ, McGeoh M, New TR (2005) *Insect conservation: handbook of approaches and methods*. Oxford University Press, UK
- Seber GAF (1965) A note on the multiple-recapture census. *Biometrika* 52:249–259
- Southwood TRE, Henderson PA (2000) *Ecological methods*. Blackwell Science, UK
- Tscharntke T, Sekercioglu CH, Dietsch TV, Sodhi NS, Hoehn P, Tylianakis JM (2008) Landscape constraints on functional diversity of birds and insects in tropical agroecosystem. *Ecology* 89:944–951