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The adoption of silvopastoral systems promotes the recovery of ecological processes regulated by dung beetles in the Colombian Andes

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Abstract 1. Conventional cattle ranching with low plant diversity and a high dependence on chemical fertilisers and herbicides, simplifies ecosystems and negatively affects their functioning. In tropical regions, the cattle ranching systems that use fodder trees and shrubs along with grasses offer a useful landscape management tool that may contribute to the conservation of biodiversity and the stability of ecological processes.

2. Given the functional importance of dung beetles in natural and anthropogenic ecosystems, this study evaluates the recovery of some of the ecological services in which these insects play a role by comparing treeless improved pastures (IP) with those that have been converted into silvopastoral systems (SPS: two species of grass, *Cynodon plectostachyus* and *Pannicum maximum*, in association with *Leucaena leucocephala* trees) in a cattle ranching landscape of the Colombian Andes.

3. The results reveal an increment in the abundance of dung beetles in SPS and, as a consequence, an increase in dung, soil and seed removal, as well as a reduction in the number of adult flies and their larvae compared with IP.

4. This suggests that SPS offer suitable refuges for the dung beetle fauna that complement the role of protected forest remnants, riparian forests and live fences in conserving the integrity of key ecological processes in cattle ranching landscapes.

Key words. Biodiversity–function relationship, cattle ranching, ecological integrity, human-dominated landscapes, Scarabaeinae.

Introduction

One of the main factors responsible for the loss of world's biodiversity is the transformation of natural ecosystems driven by the increasing demand for food and other natural products (Dirzo & Raven, 2003). More than half of the land surface of the planet is used for agriculture (12%), livestock (33%) and the cultivation of exotic trees (15%) (Steinfeld *et al*., 2006). During the last decades, the expansion of livestock production has been a key factor in deforestation, especially in Latin America (Wassenaar *et al*., 2007). In this context, silvopastoral and agroforestry systems that combine trees with pastures and crops, respectively, play a key role in reducing the negative impacts of agriculture on biodiversity conservation (Schroth *et al*., 2004) given that they retain a substantial part of the species present in the original vegetation remnants within landscapes dominated by human activity (Bhagwat *et al*., 2008). However, we know little about the potential of these biodiversity friendly production systems with respect to the recovery and maintenance of ecological processes in tropical ecosystems (Harvey & Sáenz, 2008).

Conventional cattle ranching simplifies ecosystems by promoting grass monoculture as the main food source. This simplification results in the loss of species and changes in the dynamics of several ecological processes that are key to the

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functioning of the ecosystem, including decomposition of organic matter, nutrient recycling, regulation of potential pest populations and pollination, among others (Giller & O'Donovan, 2002; Kremen, 2005).The most important impacts of conventional cattle ranching are soil degradation, mainly compaction and erosion, and the contamination of water bodies with sediments, animal faeces and chemicals from fertilisers, herbicides and insecticides (Steinfeld *et al*., 2006).

The conversion of conventional cattle ranching to silvopastoral systems (SPS) is a landscape management strategy that combines the protection of forest remnants and areas of secondary succession with live fences, riparian corridors and diversified crops. This is done with the aim of contributing to the recovery of biological diversity and maintaining the integrity of several ecological processes that are vital to the function of areas used for cattle ranching, resulting not only in environmental benefits, but also in increased productivity and financial returns to the farmers (Murgueitio *et al*., 2008).

Dung beetles are well known for their role in ecosystem function because of their strong dependence on vertebrate excrement, particularly that of mammals, for feeding and reproduction (Halffter & Matthews, 1966). Recently, dung beetles have been receiving a fair bit of attention as indicators of land-use change (Spector, 2006) and pasture health (Davis *et al*., 2004). The activities of these beetles are linked to a wide variety of ecological processes, including the incorporation of organic matter into the soil, bioturbation (i.e. the displacement and mixing of sediment particles by animals and plants), the control of haematophagous flies and gastrointestinal parasites that breed in manure and affect domestic animals and humans, and secondary seed dispersal (see Nichols *et al*., 2008 and references therein). Vegetation structure, along with the spatial and temporal variation in dung availability, shapes dung beetle assemblages (Hanski & Cambefort, 1991). It is also known that the intensification of crop and livestock farming in tropical and subtropical regions modify dung beetle assemblages (Nichols *et al*., 2007), although to date there is no knowledge about the impact of this change on the ecological processes mediated by these beetles in the ecosystems (Nichols *et al*., 2008).

Acknowledged for their high biodiversity, the Andes are the Colombian region most negatively affected by human activities. Seventy per cent of the country's population lives there, and the pressure of unsustainable agricultural practices and rapid livestock expansion puts enormous stress on natural ecosystems (Kattan & Alvarez-López, 1996). Currently, pastures cover around 10 million ha within the region, a large part of which are degraded and thus unsuitable for grazing. This has motivated the development of programmes for sustainable cattle ranching based on the adoption of SPS (Murgueitio, 1999).

In this study, using a relatively simple experimental protocol, we simultaneously evaluate the impact of the conversion of improved treeless pastures into intensive (high tree and shrub density) SPS on four ecological processes that are regulated by dung beetles in a cattle ranching landscape of the Central Cordillera in the Colombian Andes. Specifically, the following questions were addressed: (i) How does dung beetle abundance change when treeless pastures are transformed into intensive silvopastoral systems? (ii) How does dung beetle abundance affect the quantity of dung and soil that is removed, and the number of seeds that are buried by the beetles? and (iii) How is the abundance of the hematophagous horn fly (*Haematobia irritans*) affected by the conversion of treeless pastures into silvopastoral systems?

Materials and methods

Study area

The study was carried out in a cattle ranching landscape located on the western slope of the Central Cordillera in the Colombian Andes between 1140 and 1200 m a.s.l. in the middle basin of the La Vieja River, on the border of the departments of Quindío and Valle del Cauca (4°26′–4°44′N; 75°38′–75°52′W). Mean annual precipitation and temperature in the region are 1750 mm and 21 °C, respectively. The vegetation is characteristic of the transition zone between low montane humid forest (bh-MB) and pre-montane humid forest (bh-PM) (Espinal, 1977). The intensification of agricultural activities in the region over the last 30 years has resulted in a marked loss of the original forest cover and its biodiversity (Murgueitio, 1999).

The replacement of conventional pastures with SPS took place between 2003 and 2008 in the context of the *Integrated silvopastoral approaches for ecosystem management* regional project, funded by the Global Environmental Facility, the World Bank, and the Livestock and Environment Initiative. The project included 104 farms with a combined area of 3536 ha. An evaluation of the most important land-use changes in the project area between 2003 and 2006 revealed a 21% reduction of treeless pastures and a 10.4% increment in pastures with trees. In addition, the intensive SPS planted throughout the project covered 3.3% of the total area by 2006. These management practices appear to have reduced the pressure on the well-preserved forest remnants and secondary succession areas, resulting in a slight increment (0.4%) in the total forest cover (Zapata *et al*., 2007).

Improved pastures (IP) in this region have star grass *Cynodon plectostachyus* monocultures and a tree and shrub cover below 5% or completely absent (Fig. 1a). Herbicides are commonly used during land preparation. IP are heavily fertilised (0.01 kg of urea m^{-2} every 35 days) and chemical weed control is applied after the second year when pasture quality and productivity decline. The mean lifespan of this pasture system is 6 years, after which it must be renewed.

Silvopastoral systems combine one or more tree and shrub species with grasses, legumes and other spontaneous or cultivated herbs that serve as cattle forage. The SPS evaluated in this study includes two grass species, *C. plectostachyus* and *Pannicum maximum*, associated with *Leucaena leucocephala* trees (Fig. 1b) planted at a density above 10 000 plants ha^{-1}. *Leucaena leucocephala* (height between 3 and 7 m) is a fast growing leguminous, nitrogen-fixing tree that has been successfully used in tropical

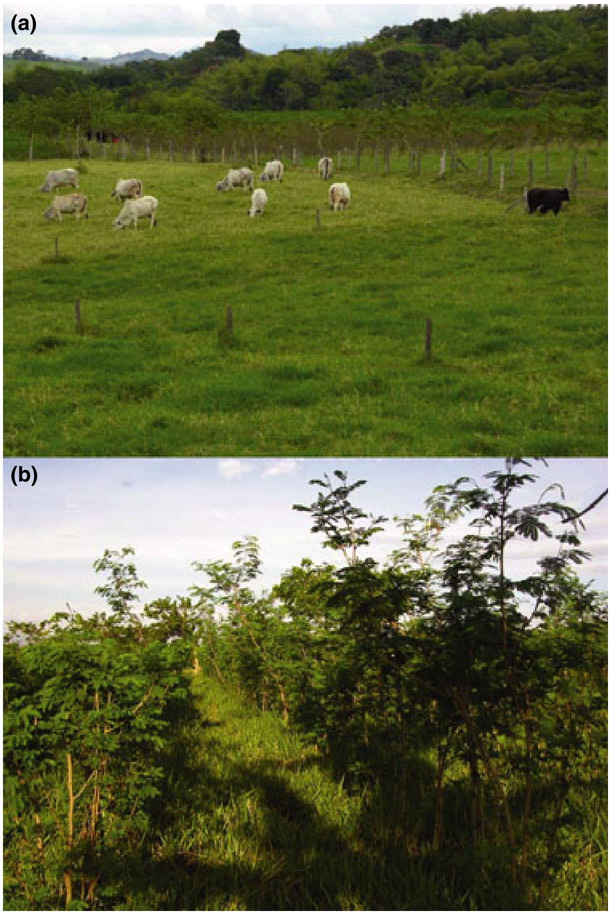

Fig. 1. (a) An improved pasture without trees (IP) and (b) a silvopastoral system (SPS) at Asturias farm, Central Cordillera, Colombian Andes (August 2008).

and subtropical regions to rehabilitate deteriorated lands while providing forage, firewood and green manure (Parrotta, 1992). Owing to these characteristics, fewer chemicals are needed to establish and manage SPS that include *L. leucocephala* (Espinel *et al*., 2004).

Even though *Leucaena* is native from Mexico, it has become a valuable species for land rehabilitation in Colombia. Planted at a high density and managed as a fodder shrub within intensive SPS, *Leucaena* reduces the need for weeding and herbicides while eliminating the dependence on synthetic nitrogen fertilisers and allowing stocking rate increments between 200% and 500%. No known native tree or shrub can tolerate the grazing regime of intensive SPS and sustain the biomass production and fodder quality of *Leucaena* (Murgueitio *et al*., 2008).

Experimental design

Three farms were chosen for this study: Asturias, La Ramada and Lusitania (Table 1). In each farm, two areas (designated as treatments) were selected: a treeless IP and an intensive SPS. Within each area, we set up two sites at least 250 m apart and without cattle grazing activity roughly 10 days before the experiment was performed. In each site, the following variables were simultaneously measured twice (August and October 2008): dung removal, soil removal, seed removal, number of horn fly larvae and adults, and abundance and richness of dung beetles. To quantify dung removal, soil removal and seed removal, we used dung balls of known weight (70 g, prepared using a mixture of cattle and pig dung in 1:1 proportion), to which 140 artificial seeds (coloured beads in three diameters: 0.5, 0.8 and 1.0 cm) were added. Pig manure was used to enhance dung attractiveness to increase the chances of sampling the complete diversity of the dung beetle fauna of SPS. Experimentation balls were covered with a plastic plate to avoid dehydration. Earlier surveys had shown that balls covered in this way lose $<5\%$ of their weight.

At each site, we set up a linear transect with three dung balls separated by 30 m and after leaving them in place for 24 h, we estimated the following: (i) amount of excrement removed (*g*), expressed as the difference between the fresh initial and final weights ($W_{\text{initial}} - W_{\text{final}}$), (ii) amount of soil removed (*g*) from around each dung ball as a result of dung being incorporated into the soil; this was scraped from the soil surface and weighed *in situ*, and (iii) the number of seeds remaining in each dung ball.

To estimate the abundance of adult horn flies and their larvae (larvae that are produced only in the absence of dung beetles), three freely accessible fly traps were set up at each site 1 m above the soil surface and baited with 50 g of dung (a mixture of cattle and pig dung in similar proportions). Each trap was made out of

Table 1. General characteristics of each of the farms evaluated.

	Lusitania	La Ramada	Asturias
Coordinates	4°41′48″N; 75°50′19.9″W	4°54′52.6″N; 75°49′42.5″W	4°27′33.2 N; 75°48′19.6″W
Elevation (m a.s.l.)	1142	1200	1173
Year SPS was established	2004	2003	2003
Total area of the farm (ha)	61.3	51.1	78.6
Area of the silvopastoral system (ha)*	12.0 (19.6%)	17.2 (33.6%)	43.27 (55.0%)
Management practices prior to conversion to SPS	Herbicides and burning	Fertilisers and herbicides	Fertilisers, herbicides and feed supplements for cattle

*The percentage of the area of each farm that has been converted in to a silvopastoral system (SPS) is given in parentheses.

a 350-ml plastic cup with a 1-cm^2 opening on the side; the bait was placed in the bottom and a lid on the top to prevent the trapped flies from escaping. After 24 h, the contents of each trap were placed in a 70% alcohol solution to later quantify the number of adult flies and larvae. Dung beetle abundance at each site was estimated by using three pitfall traps (250 ml capacity), buried flush with the ground 30 m apart and baited with a mixture of 25 g of cattle and pig dung. These traps were left in place for 24 h. Both the balls and capture traps were placed at the same time of the day and for equal time intervals.

Data analysis

Data from both sampling periods were pooled together for analysis. To control for effects associated with the differences in the management history or spatial arrangement of the different types of land use in the three farms, a nested ANOVA (Model III) with two levels was used (k = 2, treatments nested within farms) through generalised linear models. For all of the variables quantified, the model applied was $Y = \mu + \text{farm} + \text{treatment (farm)} + \varepsilon$. To compare the quantity of dung removed, the error structure was defined as following a normal distribution. The weight of soil removed was $\log_{10}$-transformed to obtain constant variance (Crawley, 2007). When the response variable was a proportion (seeds removed), a binomial error distribution was used (logit link function). For the response variables consisting of counts (number of beetles, number of adults and horn fly larvae), the error structure was defined as having a Poisson distribution (log link function). In all cases, the fit to the model was verified by examining the standardised vs. fit values, in addition to visual inspection of the distribution of the residuals against the fitted values to verify homoscedasticity and residuals against the quantiles of the standard normal distribution to check normality (Crawley, 2007). For those variables where the analyses indicated an overdispersion of the model >2, we used F as the test statistic and χ^2 when overdispersion was <2 (Crawley, 2007). *Post hoc* comparisons were performed to determine the differences among farms according to recommendations of Crawley (2007) for each type of variable. All the analyses were performed using the freely available R software (R Development Core Team 2008).

Results

A total of 418 individuals belonging to five species and four genera of two subfamilies were captured: Scarabaeinae (three species) and Aphodiinae (two species). In the IP, 143 individuals were caught belonging to three species (*Ontherus lunicollis*, *Aphodius brasiliensis* and *Aphodius* sp. 1) and there were 275 individuals belonging to five species in the SPS, the same three found in the IP as well as *Onthophagus curvicornis* and *Dichotomius satanas*. For all three farms, the number of beetles caught per trap was significantly larger in SPS than in IP ($F_{3,66}$ = 14.29, $P < 0.001$; Fig. 2a) and the analysis reveal no differences in beetle abundance between farms ($F_{2,3}$ = 2.94, $P > 0.05$; Fig. 2a).

The amount of dung removed per ball was greater in the SPS than in the IP ($F_{3,66}$ = 17.13, $P < 0.001$), and this difference was significant for two of the three farms evaluated (Fig. 2b). There were differences between farms ($F_{2,3}$ = 13.09; $P <$ 0.001): dung removal was greater at La Ramada and Asturias than at Lusitania (Fig. 2b).

Consistent with the pattern of dung removal, mean of soil removed tended to be greater in the SPS than in the IP (Fig. 2c). There were only significant differences between treatments in one of the three farms evaluated ($F_{3,66}$ = 3.19, $P < 0.05$). Even though soil removal was greater at La Ramada and Asturias that at Lusitania, there were no differences between farms ($F_{2,3}$ = 4.25, $P > 0.05$, Fig. 2c).

The proportion of seeds buried was greater in the SPS than in the IP ($F_{3,66}$ = 38.53, $P < 0.001$) and the differences were significant for two of the three farms studied (Fig. 2d). There were significant differences between farms ($F_{2,3}$ = 63.82, $P < 0.001$): at La Ramada, the proportion of buried seeds was significantly greater than at Lusitania or Asturias (Fig. 2d).

Fewer horn flies were captured in the SPS than in the IP (χ^2_2 = 121.53, $P < 0.001$) and the difference between treatments was significant for two of the three farms (Fig. 2e). Adult fly abundance at Lusitania and Asturias were significantly greater than at La Ramada (χ^2_3 = 104.34, $P < 0.001$; Fig. 2e). At all sites, the number of larvae per trap was lower at the SPS than at the IP ($F_{3,64}$ = 574.43, $P < 0.001$; Fig. 2f). Similarly, there were differences between the farms studied ($F_{2,3}$ = 834.14, $P < 0.001$): at Asturias larval abundance was significantly greater than at Lusitania or La Ramada (Fig. 2f).

Discussion

This study suggests that over a relatively short period of time (5 years), the conversion of treeless IP into SPS favours the recovery of dung beetle activity and, in turn, enhances the functioning of several of the ecological processes in which the dung beetles play a role. In spite of the large variation in the response pattern of each of the variables quantified on each farm and between farms, the pattern generally observed was an increase in dung removal and, consequently, greater soil and seed removal in the SPS, whereas the abundance of dung flies and particularly their larvae was lower compared with treeless IP. These results support the idea that livestock practices that include trees and shrubs in the productive system become not only a tool for recovering degraded ranching areas, but also a system for the rational management of livestock (Murgueitio, 1999).

Although beetle species richness is still low in both cattle raising systems, when compared with sites at similar altitudes in the northern Andean forests (mean ± SD = 14.33 ± 3.35, n = 9, alt. 1000–1250 m a.s.l.; Escobar *et al.*, 2005), the results indicate that the tree cover in SPS offers a refuge for different species of dung beetles. Different studies suggest that heterogeneous mountain landscapes where human activity is predominant are home to a dung beetle community that is quite rich in species, as found in Peru (Horgan, 2009), Colombia (Medina *et al.*, 2002; Escobar, 2004) and Mexico (Pineda *et al.*, 2005). However, the limited presence of these beetles in treeless pastures in the Andes

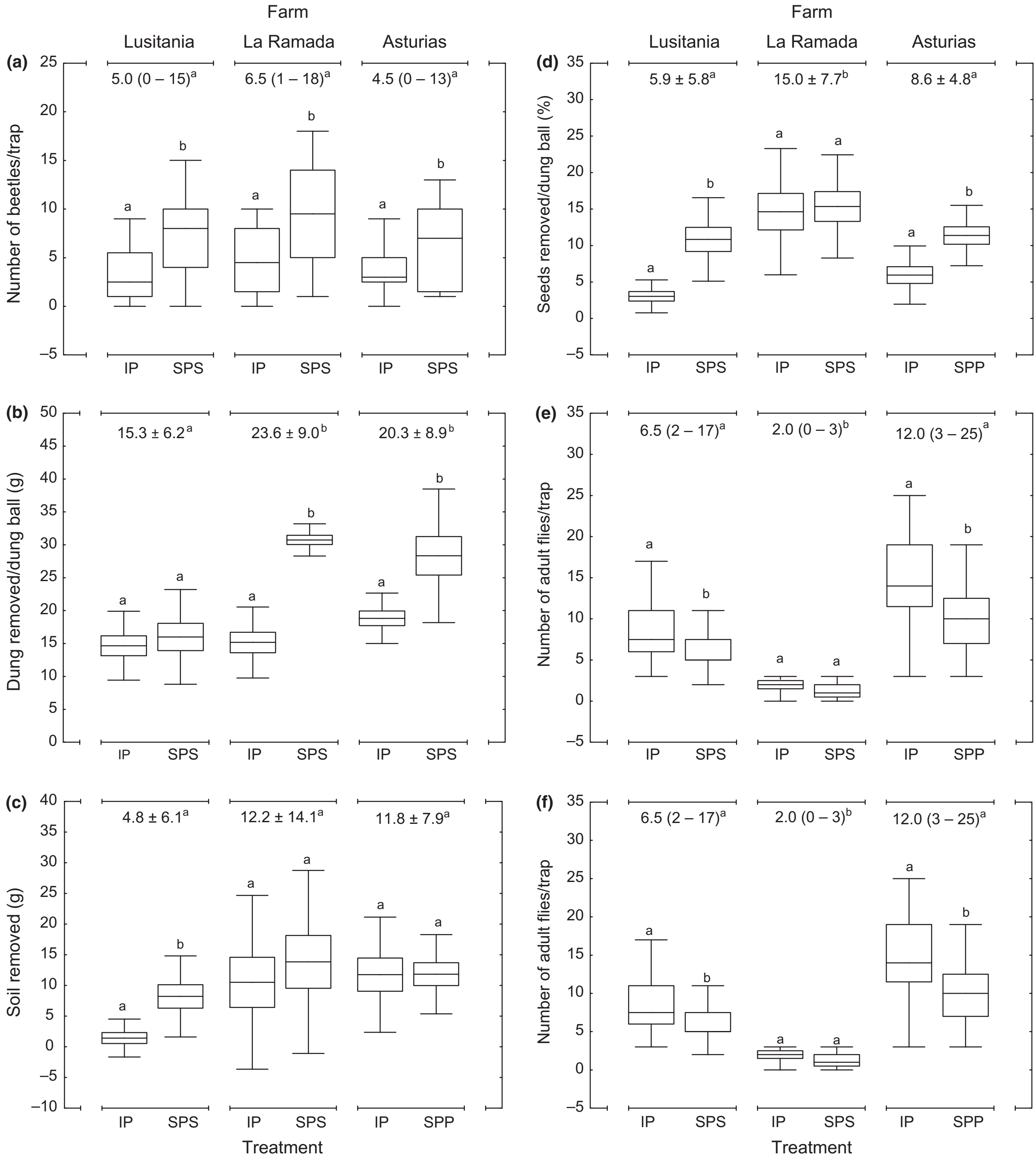

Fig. 2. Comparisons between treeless improved pasture (IP) and the silvopastoral system (SPS) implemented in three cattle farms in the Central Cordillera of the Colombian Andes. (a) Number of dung beetles per trap, (b) amount of dung removed per dung ball (*g*), (c) amount of soil removed (*g*), (d) proportion of seeds removed per dung ball, (e) number of adult flies per trap and (f) number of fly larvae per trap. The values above each of the figures are the comparison between farms. For continuous variables (weight in g) and the percentage of seeds removed, the mean (±SE, SD) is given. For ordinal variables, the median and percentiles are given. Range is given in parentheses in (a, e) and (f). Values of central tendency with different letters indicate statistically significant differences ($P < 0.05$).

(Escobar *et al*., 2007) clearly indicates that in spite of the abundance of food (mainly cow dung) this resource is not adequate for the majority of the native species that live within the forest (Escobar, 2004; Escobar *et al*., 2007; Horgan, 2007). Our results confirm the observation of Halffter (1991) who found that in the Neotropics, the shade provided by trees and shrubs, and its influence on microclimate are more important than food abundance. Hence, the importance for biodiversity conservation in human-dominated tropical landscapes of maintaining and promoting cattle ranching systems in relatively shaded areas that incorporate other vegetation types, such as forest remnants, areas of secondary succession, riparian forests, forest plantations, isolated trees in pastures and live fences.

Although our study was performed on farms with similar environmental characteristics and over a short period of time to reduce the effects of seasonal weather change, it was not possible to control for the factors associated with the history of pasture management (i.e. chemical fertiliser, herbicide and pesticide application), time after system establishment, the size of the area converted to SPS or the spatial arrangement of the different types of vegetation present (i.e. degree of connectivity). The latter is of particular importance with respect to colonisation from more diverse adjacent habitats, such as forest patches that could boost species richness in the SPS. As such, more detailed studies on the species' use of different anthropogenic habitats are needed, especially on the dynamics of beetle movement through landscapes used for raising cattle, to improve the design and establishment of the SPS.

Pasture colonisation by dung beetles depends to a large extent on pasture management practices (Martínez & Lumaret, 2006; Martínez & Cruz, 2009). The differences observed in beetle abundance in this study can also be attributed to differences in the use of agrochemicals in the systems evaluated. In the treeless IP, the farmers of this region apply herbicides, such as 2,4-diclorophenoxiacetic acid (also known as 2,4-D), a highly toxic compound for birds, mammals, aquatic insects, bees and earthworms (Kegley *et al*., 2009). In contrast, the elimination of agrochemicals from the SPS appears to be another of the factors promoting the arrival and permanence of dung beetles and other organisms that are potentially important to the functioning of the SPS. Several studies document that the regular use of herbicides and antiparasitic drugs has a negative effect on beetle survival and decreases the rates of dung removal in pastures (e.g., Martínez *et al*. 2001).

The results revealed an increase in dung removal linked to a greater abundance of dung beetles in the SPS. By incorporating dung into the soil, the dung beetles have the potential to improve pasture performance (Bornemissza, 1960; Bertone *et al*., 2006). By digging tunnels and galleries, they contribute to loosening the soil, improving aeration and permeability (Mittal, 1993). In pasture ecosystems, the production of forage depends on the recycling of organic matter, particularly dung. Several experiments link the activities of dung beetles with the return rate of nutrients to the soil (Yokoyama & Kai, 1993; Yamada *et al*., 2007), and with the growth and health of plants (Borghesio, 1999; Bang *et al*., 2005; Bertone *et al*., 2006), all of which could potentially reduce the need to apply fertilisers over time, and decrease production costs. Furthermore, dung beetle activity increases the grazing area by eliminating dung from the soil surface. In pastures in the Andes where dung removal is not efficient, dung pats remain dehydrated on the surface for several months (F. Escobar, pers. obs.). As a consequence, the area available for grazing is reduced and pest insect abundance increases (Martínez & Lumaret, 2006).

Another outcome of greater dung removal in SPS is the increase in the number of seeds buried by the beetles. The spatial relocation of seeds often favours germination and seedling emergence (Andresen & Levey, 2004) by reducing predation and mortality caused by pathogens (Janzen, 1983; Andresen & Feer, 2005). This also could favour the recovery of areas too deteriorated for grazing. Dung beetles transport seeds in two dimensions, horizontally and vertically, relative to where they were deposited in the dung. In tropical regions, the process of dung removal and therefore of the seeds it contains is mainly done by tunnelling species (Larsen *et al*., 2005; Slade *et al*., 2007), such as *O. lunicollis*, the most abundant species, and *D. satanas*, the largest of the Scarabaeinae species found in the study area. The latter can, over a short period of time, bury large chunks of dung in galleries right below the surface where the dung was deposited (C. Giraldo, pers. obs.). Both species are typical of the Andean forests of Colombia (Medina *et al*., 2002; Escobar, 2004) and their presence could be crucial during the start up years of SPS in this region.

The inverse relationship observed between dung beetle and horn fly abundance in the two cattle raising systems could be explained by both plant cover and the contribution of plant litter provided by *L. leucocephala*. The latter favours the establishment not only of the dung beetles, but also of other beneficial fauna that can control pest populations, such as predator beetles of the Staphylinidae family and parasitoid micro-hymenoptera, such as Figitidae, fly pupa parasites and Pteromalidae (C. Giraldo, pers. obs.). In contrast, experimental manipulations in the laboratory and in the field have shown that when dung beetles and horn flies co-occur, fly survival tends to decrease as a consequence of asymmetrical resource competition (Ridsdill-Smith & Hayles, 1987), mechanical damage of eggs by beetles (Ridsdill-Smith & Hayles,1990) and fly predation by phoretic mites (Glida et al., 2003). All this suggests that the complementary action of the dung beetles eliminating dung from the surface and the control of flies by predators and parasitoids can reduce horn fly density in pastures. Preliminary data indicate that the beneficial fauna associated with SPS can reduce the populations of horn flies, *H. irritans* (Muscidae), one of the main threats to cattle health in the study area (Murgueitio & Giraldo, 2009).

Conclusion

Quantifying and interpreting the relationships between biodiversity and functional integrity is of great value for evaluating and predicting the true environmental consequences of the management and use of ecosystems (Kremen, 2005). This is particularly important in simplified tropical landscapes dominated by cattle ranching. Our results show that after 5 years, there is a variable but consistent recovery of several ecological processes controlled by dung beetles associated with the conversion of conventional pastures into SPS in a deteriorated cattle ranching area of the

Colombian Andes. The conversion of pastures as a landscape management strategy contributes to the development of sustainable cattle ranching in both environmental and economic terms. This strategy also offers the opportunity to run experiments to monitor the relationship between diversity and function and understand how communities re-assemble and re-establish ecological processes over time.

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