J Insect Conserv
DOI 10.1007/s10841-014-9645-5

ORIGINAL PAPER

Response of a dung beetle assemblage along a reforestation gradient in *Restinga* forest

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Received: 22 August 2013 / Accepted: 16 June 2014
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Abstract Scarabaeinae dung beetles are indicator insects used in the evaluation of the ecological effects caused by changes in habitat structure and ecosystem integrity resulting from environmental degradation. We compared dung beetle diversity in conserved *restinga* forests (coastal tropical moist broadleaf forest) and in reforested areas of various ages during the rainy and dry seasons, on the coast of Paraíba State, Brazil. A total of 3,634 individuals comprising 14 species were collected. In the reforested areas there was a gradual increase in species abundance relative to the area's age, but in the conserved *restinga* the abundance of individuals was 10–20 times higher than that recorded in areas of recent reforestation. The highest species richness was found in the conserved *restinga* and in the oldest reforested area (16 years old) during the rainy season. During the dry season, when environmental conditions do not seem to favor adult survival, most of the species were found in the conserved *restinga* forest. The dung beetle community structure was related to the increases in habitat heterogeneity in the successional processes of the reforested areas. Our results suggest that reforested areas act as a source of and refuge for dung beetle species.

Keywords Fragmentation · Diversity · Ecological succession · Scarabaeinae

Introduction

The Atlantic Forest or Mata Atlântica extends along the Atlantic coast of Brazil, from the Rio Grande do Norte to the Rio Grande do Sul, and is made up of different forests, including low forests which grow on stabilized coastal dunes known as *restinga* (coastal plain usually covered with tropical moist broadleaf forest) (ISA 2008). *Restinga*, like other ecosystems in the Mata Atlântica, has been strongly threatened by activities associated with human occupation, and small isolated forest fragments with high levels of disturbance are frequently found in this region (Ranta et al. 1998; Morellato and Haddad 2000).

The current devastation and loss of diversity in the Atlantic forest has resulted in many strategies for its recovery, and one of these is the reforestation of degraded areas. The process of reforestation includes phases closely related to ecological succession, such as colonization and establishment of new species. To evaluate changes in the richness, abundance and distribution of species during each phase, it is recommended that bioindicator groups be monitored (Brown 1997; Freitas et al. 2004; Uehara-Prado et al. 2009).

Scarabaeinae dung beetles (Coleoptera: Scarabaeidae) function as decomposers in tropical and temperate ecosystems, using decaying organic material as food for both

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Published online: 17 July 2014

larvae and adults. Dung beetles are considered good indicators of environmental degradation (Halffter and Favila 1993; Favila and Halffter 1997; Spector 2006) because they rapidly respond to the effects of destruction, fragmentation and isolation of tropical forests, and under such conditions their communities have distinct organizational patterns compared to those found in original forests (Howden and Nealis 1975; Janzen 1983; Klein 1989; Halffter et al. 1992; Davis et al. 2001; Halffter and Arellano 2002; Nichols et al. 2007; Gardner et al. 2008a, b; Hernández and Vaz-de-Mello 2009, Barlow et al. 2010). The mammal excrement is the main component of their diet (Halffter and Edmonds 1982), and both the decrease in mammal population size and the extinction of some mammals can result in an ecological cascade effect, provoking a decrease in dung beetle species richness and abundance, as well as in their biomass when the ecosystems are modified by human activities (Estrada et al. 1999; Scheffler 2005; Gardner et al. 2008b; Nichols et al. 2009; Barlow et al. 2010). Another advantage of using dung beetles to evaluate the ecological consequences of anthropic disturbances is the ease and low cost of sampling, in addition to the fact that the taxonomy of the group is well known, which allows, in general, for the identification of species (Halffter and Favila 1993; Gardner et al. 2008a).

The objective of the present study was to evaluate the changes in the structure and diversity of dung beetle assemblages during the rainy and dry seasons in relation to the complexity of the vegetation in reforested areas of *restinga* that varied in age and that were originally subjected to mining. This was compared with a conserved area of *restinga* forest. We expected that the abundance and species richness of dung beetles would be greater during the rainy season than during the dry season, and that remnant areas of *restinga* forest, with their more complex vegetation structure, would sustain greater species richness and abundance of dung beetles than reforested areas.

Methods

The study was conducted in areas of *restinga* on land worked by the Millennium Inorganic Chemicals mining company, located in the municipality of Mataraca, Paraíba (6°29′S; 34°56′W). The company washes and screens titanium-bearing minerals (ilmenite, zirconite, rutile and kyanite) found in the sand dunes of the area. During mining, the original *restinga* vegetation is completely removed and the sand is used during mineral separation. The Brazilian Institute of Environmental and Renewable Resources (IBAMA) authorizes this deforestation. After the washing process, the waste is pumped out and forms new dunes, which are later reforested. This has been underway since 1988.

The region's climate is tropical and rainy, with a short dry season. Average annual precipitation is 1,755 mm and the rain mainly falls between February and August, with April and July the rainiest months (250–300 mm/month). December is the driest month (20 mm/month). The average annual temperature is 26.0 °C, with a narrow range of fluctuation from 23.7 °C in April to 27.2 °C in November (Santos et al. 2000).

Four areas for which reforestation time is known were selected to analyze the changes in dung beetle communities: 2, 4, 8, and 16 years old (which we refer to as Ref-2, Ref-4, Ref-8, Ref-16, respectively). A natural low *restinga* forest (RF) remnant was used as the control. In each reforested area, and in the control, three sites separated from each other by at least 250 m were selected to ensure that we were sampling relatively homogeneous internal conditions, but far enough apart to ensure their independence (Gotelli and Ellison 2004). In each site four pitfall traps were installed along transects 25 m away from each other, for a total sampling effort of 60 traps per sampling period (5 areas × 3 sites × 4 traps per site). Each pitfall trap consisted of a plastic bowl (12 cm high and 15 cm in diameter) about two-thirds full of a 2 % solution of water and neutral detergent. A cup with 10 g of human dung as bait was suspended ca 5 cm over the plastic bowl of the trap. Traps were left for two consecutive days every sampling period. Dung beetles were collected in each area during the dry season in November 2005 and 2006, and during the rainy season in May 2006 and 2007. The beetles caught were identified to species level with the help of the available literature, and the reference collection belonging to the Entomology Laboratory of the Systematics and Ecology Department at the Federal University of Paraíba, where they were deposited.

The species richness data was pooled for each reforested area and for the *restinga* forest and sampling efficiency was evaluated using species accumulation curves. Chao 1 and Chao 2 estimators were used because they are the most appropriate for small sample sizes (Colwell and Coddington 1994). Inventory completeness was measured as the percentage of observed species with respect to the number of species predicted by the estimators.

Species richness and Shannon diversity were determined to analyze alpha, beta and gamma diversity in the study area. These form part of the so-called true diversities ^{q}D because they represent the number of species of a community (Hill 1973), and are named numbers equivalents of the diversity indexes (Jost 2007). According to Jost et al. (2010), the numbers equivalent of a diversity index is the number of equally likely species needed to produce the given value of the diversity index. Species richness is the diversity of order $q = 0$, while the exponential of Shannon's index, called Shannon diversity, is the diversity of order q = 1. Species richness (^{0}D) is not sensitive to frequency, and this assigns excessive weight to rare species (Jost 2007; Tuomisto 2010). In contrast, Shannon diversity (^{1}D) weights each species according to its frequency in the community, without favoring rare or abundant species (Jost 2007). When the weights of the communities analyzed are not equal—a situation common to real data—^{0}D and ^{1}D are the only measures of true diversity that can be partitioned into independent alpha and beta diversities (Jost 2007). According to Jost, true beta diversity is the effective number of different communities in a given landscape or region, and the unequal sizes of the different communities affects the outcome. Beta diversity is lowest when one community dominates the landscape, so minimal species turnover between sampling units is expected, with beta diversity increasing as the communities share an increasing number of species in the landscape (Jost 2007).

True alpha and beta diversity were obtained using the following formulas:

$$^0D_\gamma = S$$

$$^0D_\alpha = (1/N)\left(S_1 + S_2 + \cdots + S_{\mathrm{j}}\right)$$

$$^0D_\beta =^0 D_\gamma/^0D_\alpha$$

where S_{j} is the number of species per sampling unit, and N is the number of sampling units, in our case each area analyzed. $^0D_\gamma$ is the total number of species in the entire set of sampling units, i.e. our whole landscape including all of the reforested areas and the *restinga* forest.

Shannon diversity was partitioned into true alpha and beta diversities using the following formulas (Jost 2007):

$$^1D\gamma = exp\left[-\sum_{n=1}^{s}(pi\ln pi)\right]$$

$$^1D\alpha = exp\left[-w1\sum_{n=1}^{s}(pi\ln pi) + -w2\sum_{n=1}^{s}(pi\ln pi) + \cdots\right]$$

$$w_j = \mathrm{ind}_j/\mathrm{ind}_{\mathrm{tot}}$$

$$^1D_\beta =^1 D^1_{\gamma/}D_\alpha$$

where w is the statistical weight of each area, expressed as the number of individuals in area j divided by the total number of individuals in the landscape or region.

A nested ANOVA was used to analyze the effect of the following independent variables on abundance (number of individuals): season (dry and rainy), and age of the area with five levels: 2, 4, 8, 16 years, and *restinga* forest, with age nested in season. Data were log transformed, and homoscedasticity and normality of the residuals were satisfied. A nested generalized linear model with a Poisson distribution was used to analyze the effect of the independent variables on richness. The Akaike Information Criterion (AIC) was used to obtain the optimal model. The best supported model has the lowest AIC compared to the other models (Crawley 2007). Statistical analyses were carried out using R 2.9.0 software (R development Core Team 2006).

To determine habitat heterogeneity across the succession, a phytosociological survey was conducted in 5 × 20 m plots in each reforested area during October 2005. Trees were identified to the species level with the help of the available literature. For all trees species measuring 3 cm or more in diameter, at a height of 10 cm above ground, the following were measured: diameter at 10 cm above the ground, height, largest width of the crown, and smallest width of the crown. A Pearson's correlation test was used to test collinearity between all pairs of variables. When two variables were correlated ($p > 0.7$, Dormann et al. 2013), only one of the variables was included in the analysis. The statistical analysis was done using Statistica (StatSoft Inc 2004).

Results

A total of 3,634 specimens of Scarabaeinae dung beetles belonging to 14 species and 9 genera, included in 5 tribes were captured in all the areas studied (Table 1).

Chao 1 and Chao 2 estimators showed that the species record was complete for two of the reforested areas (Ref-4 and Ref-8), and nearly complete in the *restinga* forest used as the control (Table 2). Species inventory completeness was lower than predicted by both estimators in Ref-2 and Ref-16 (70 and 77 % of the expected species, respectively).

In terms of true alpha diversity values, Ref-2, Ref-4, and Ref-8 had the lowest diversity values for richness (^0D), and the highest was recorded for Ref-16 and in the *restinga* forest (Table 3). However, Shannon alpha diversity behaved differently, because the youngest reforested area had the lowest value, while the highest was calculated for Ref-4, and then decreased with the age of the reforested areas (Table 3). For all of the fragments analyzed mean alpha diversity was nearly 8 species and gamma diversity, 14 species. The true beta diversity for richness (order 0) was nearly 2, indicating that there are almost two completely distinct groups of reforested areas, with the first group clearly formed by Ref-2, Ref-4 and Ref-8, and the second group by Ref-16 and the conserved *restinga*, confirming our previous results. Shannon's beta diversity was 1.01, indicating that there are only 1.01 communities in our data set. According to this measure of diversity all the areas are almost truly identical. However, Shannon's beta diversity was lower than the beta diversity from species richness, suggesting that the differences between the areas were due to the rare species, but that the most abundant species were the same (Table 3).

Table 1 Species abundance of Scarabaeinae dung beetles sampled in reforested areas of different ages (2, 4, 8, and 16 years old), and one conserved area of *restinga* forest (RF), between 2005 and 2007, in the municipality of Mataraca, Paraíba, Brazil

Species	2 years	4 years	8 years	16 years	RF	Total
Dichotomius aff. irinus	148	58	116	599	2,061	2,982
Canthidium manni	–	2	7	41	281	331
Canthon chalybaeus	1	26	50	27	2	106
Canthon staigi	–	–	–	1	104	105
Canthidium sp.1	11	–	–	–	21	32
Ateuchus semicribratus	3	11	7	6	1	28
Eurysternus hirtellus	–	–	–	18	2	20
Uroxys sp.	1	–	–	–	11	12
Canthidium sp.2	5	–	–	2	–	7
Canthon sp.	–	2	2	–	1	5
Onthophagus aff. hirculus	–	1	–	1	–	2
Ontherus azteca	1	–	–	1	–	2
Deltochilum pseudoicarus	–	–	1	–	–	1
Dichotomius semisquamosus	–	–	–	1	–	1
Abundance	170	100	183	697	2,484	3,634

Table 2 Observed (S) and estimated richness of Scarabaeinae using Chao 1 and Chao 2, with completeness in brackets for each estimator in reforested areas of different ages and in a conserved *restinga* forest (RF) in Paraíba, Brazil

	S	Chao 1	Chao 2
2 years	7	10 (70.0 %)	9.94 (70.4 %)
4 years	6	6 (100 %)	6.49 (92.4 %)
8 years	6	6 (100 %)	6.00 (100 %)
16 years	10	13 (76.9 %)	12.94 (77.3 %)
RF	9	9.3 (96.4 %)	9.33 (96.5 %)

The nested ANOVA showed significant differences in abundance between season ($F_{(1,10)} = 44.47$; $p < 0.001$), or between successional age of vegetation nested in each season ($F_{(8,10)} = 24.49$; $p < 0.001$). Abundance was higher during the rainy season than during the dry season (Fig. 1). During the dry season abundance was higher in the *restinga* forest than in Ref-2, Ref-4, Ref-8, and Ref-16 (Fig. 2a). During the rainy season, only in Ref-4 was abundance significantly lower than in the conserved *restinga* (Fig. 2b).

The nested GLM revealed significant differences in richness among successional stages for each season (dry and wet) ($p = 0.016$). During the dry season Ref-2 had the lowest species number, and the *restinga* forest had more species than all the reforested areas ($p = 0.011$) (Fig. 3). There were no significant differences in richness during the rainy season in any of the areas studied ($p = 0.852$).

Dichotomius aff. irinus was the most abundant species in all sites sampled, representing 82 % of the total abundance, followed by *Canthidium manni* at 9.1 % of the total abundance and found in all sites sampled except for Ref-2. *Canthon chalybaeus* and *Canthon staigi* were the other two most abundant species, each representing 2.9 % of the total abundance. *Canthon chalybaeus* was present in all sampled sites, but *Canthon staigi* was collected in the *restinga* forest in 99 % of the samples during the four sampling excursions (n = 104), with only one individual found in Ref-16 (Table 1). Rare species included only one individual of *Deltochilum pseudoicarus*, which was collected in Ref-8, and one of *Dichotomius semisquamosus* in Ref-16. One individual of *Onthophagus aff. hirculus* was collected in Ref-4 and one in Ref-16, and one of *Ontherus azteca* in Ref-2 and in Ref-16 (Table 1). Applying the criteria used

Table 3 Multiplicative diversity partitioning for reforested areas of *restinga* of different ages and for a conserved *restinga* forest (RF) in Paraíba, Brazil

	Age of reforested area					Components of diversity		
	2 years	4 years	8 years	16 years	RF	γ	α	β
^{0}D	7	6	6	10	9	14	7.6	1.84
^{1}D	1.75	3.04	2.64	1.89	1.85	1.94	1.91	1.01

The components of diversity are: gamma diversity (γ), mean alpha diversity (α), and beta diversity (β) for richness (^{0}D) and Shannon diversity (^{1}D)

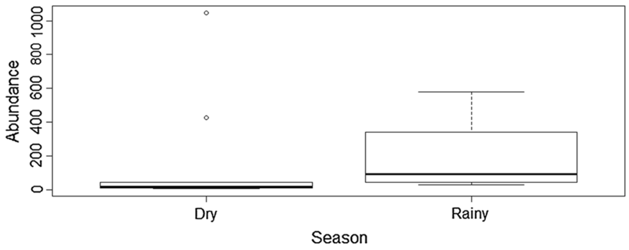

Fig. 1 Abundance of Scarabaeinae dung beetles in 2005 and 2007, in the municipality of Mataraca, Paraíba, Brazil during the dry and rainy seasons. Median (*black line*), 25–75 % quartiles (*boxes*) and extreme values (*whiskers*) are represented

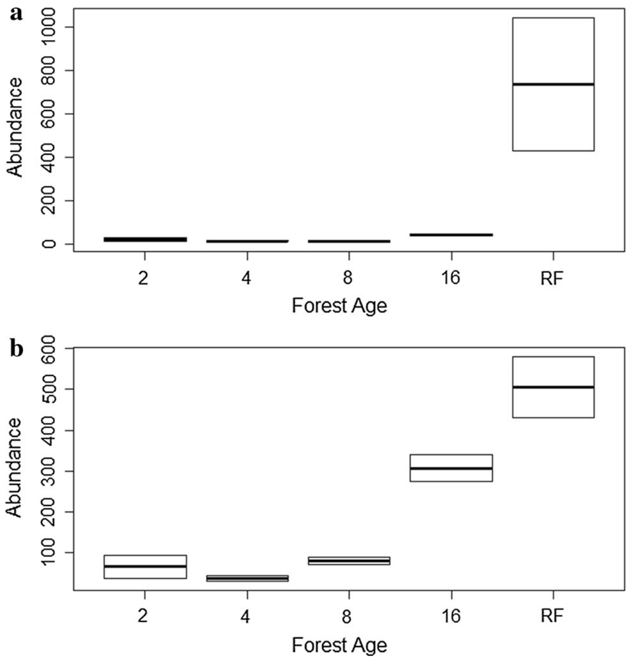

Fig. 2 Abundance of Scarabaeinae dung beetles in reforested areas of different ages (2, 4, 8, and 16 years old), and in a conserved area of *restinga* forest (RF), during the dry season (**a**) and rainy season (**b**). Median (*black line*), 25–75 % quartiles (*boxes*) and extreme values (*whiskers*) are represented

by Collwell to identify rare species (<10 individuals), 43 % of all the species found in our *restingas* can be considered rare.

The number of tree species was correlated with the number of trees (r = 0.86), and with tree height (r = 0.85), and the latter was correlated with tree crown diameter (0.73). Tree diameter at 10 cm above ground was correlated with tree crown diameter (r = 0.83) (Table 4). To accurately represent the vegetation structure and diversity of the gradient studied, we used tree species richness and tree diameter at 10 cm above ground level in this section. The successional age of reforested areas was strongly correlated with tree species richness (r = 0.97), so the latter is explained by the successional age of the reforested areas studied. Tree diameter at 10 cm above ground was not, however, related to the age of the reforested areas, but that is because some of the tree species planted in the reforested areas are fast growing, such as for example "caju" (*Anacardium occidentale*) (unpublished data).

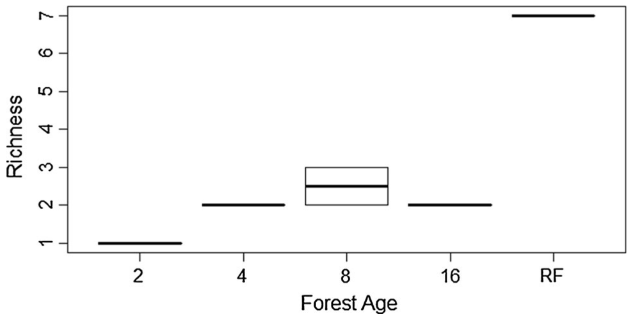

Fig. 3 Richness of Scarabaeinae dung beetles in reforested areas of different ages (2, 4, 8, and 16 years old), and in a conserved area of *restinga* forest (RF), during the dry season. Median (*black line*), 25–75 % quartiles (*boxes*) and extreme values (*whiskers*) are represented

Discussion

Restingas are coastal ecosystems that have developed on Holocene marine sand and cover approximately 80 % of the Brazilian coast with arboreal, shrubby, and herbaceous vegetation. Factors such as the wind, burial by sand, high salinity, nutrient poor soils, excessive heat and insolation, make this ecosystem fragile (Hesp 1991). Similarly, its fauna is composed of a low number of species (Cerqueira 1984), though many of them have an ample distribution and are found in other biomes. The number of species of dung beetles in the *restinga* was low, and they live mainly in Atlantic Forest areas (Endres et al. 2007), but some are able to colonize and adapt to the particular environmental conditions of the *restinga*, in spite of the difficulty building tunnels for their nests (Cambefort and Hanski 1991). Studies conducted in the same area as this study reveal that others insects, such as Nymphalidae butterflies (Lima-Verde and Hernández 2007) and Collembola (Zeppelini et al. 2009) also have a low number of species in the *restinga* areas.

In the area we studied, *restingas* that had undergone mining processes were later reforested, favoring the reestablishment of the vegetation, which has a fundamental role providing protection against the wind and facilitates colonization by the native fauna (Araújo and Lacerda 1987). In our study, of the 14 dung beetle species caught, 9 were collected in the conserved *restinga* that was left intact

Table 4 Average values for arboreal vegetation in 100 m^2 plots, obtained in phytosociological surveys of reforested areas 2, 4, 8, and 16 years in age, and in a conserved area of *restinga* forest, in October 2005, in the municipality of Mataraca, Paraíba, Brazil

Site	Number of trees[a]	Number of tree species[a,b]	Tree height[b,d] (m)	Tree diameter at 10 cm above ground[c] (cm)	Tree crown diameter[c,d] (m)
2 years	6.5	1.3	1.16	14.3	1.0
4 years	12.8	2.5	2.38	21.7	1.9
8 years	13.3	4.2	3.57	33.8	2.8
16 years	17.8	5.0	4.85	34.3	4.1
RF	33.1	8.3	4.71	21.7	2.4

Variables showing collinearity have the same letter

during and it is possible that this area serves as a source for the colonization of adjacent reforested areas. Additionally, our study shows that in the oldest reforested area, which is 16 years old, species richness was similar to that of the conserved *restinga*. Davis et al. (2003) assessed the changes of the dung beetle community composition in a 23-year-old vegetation chronosequence, from disturbed, mined dunes to undisturbed sand dunes, along the Indian Ocean coastline at the southern end of the Maputaland, South Africa. Across this sequence of dune forest restored after mining, they found a sequential tendency toward a recovery of the dung beetle species composition, though species abundance patterns tended to converge with vegetation changes only in the earlier stages of the chronosequence. According to Davis et al. (2003), a decline in the similarity in of older woodland stands suggests that lasting convergence in dung beetles species abundance will only be attained when the *Acacia* woodland, an intermediate stage of regeneration, is replaced by natural secondary natural dune forest. So our results and those of Davis et al. (2003) suggest that in the long term the process of forest restoration has favored the colonization of the reforested area by the dung beetles, and surely by other species as well.

The process of forest degradation reaches alarming levels in northeastern Brazil where less than 5 % of the original area of the Atlantic Forest remains (Silva and Tabarelli 2000). However, it seems that this degradation has not affected the ecological functions of dung beetle species, given that the most abundant species are present in all of the reforested areas we studied. So, for dung beetles at least, in spite of the degradation of the natural environment caused by mining, their functional processes are maintained in the reforested areas, suggesting that reforestation is a good option, not only for preserving species, but also for preserving ecological processes such as nutrient recycling (Halffter and Matthews 1966; Halffter and Edmonds 1982; Hanski 1991; Nichols et al. 2007), vertebrate parasite control, and seed dispersal (Vulinec 2002; Andresen 2003; Larsen et al. 2005). It is important to continue studying the effect of reforestation in *restinga* using other indicator groups that carry out key ecological processes.

The comparison of richness between the dry and rainy seasons showed that although most species were present during the dry periods, many of them were only caught in the *restinga* forest, thus radically decreasing species richness in the reforested areas. This suggests that conserved areas have environmental conditions that are favorable for the dung beetles and facilitate their search for food, a resource that does not seem to be present in the reforested areas. When conditions are unfavorably dry, most dung beetle adults remain dormant in tunnels in the soil (Halffter and Matthews 1966), so it is possible that during the dry season, dung beetles stay dormant in the sand or may even suffer catastrophic mortality in the reforested areas. If so, the species could be dispersing from the oldest reforested areas to younger ones during the rainy season, causing an increase in the richness of these areas. Conserved areas in the *restinga* could therefore be functioning as true refuges (Bierregaard et al. 1992), but that remains to be experimentally tested in future studies.

The analysis of true diversity shows that Shannon beta diversity was lower than beta diversity from species richness, suggesting that the differences between the reforested areas were due to the rare species (see Jost 2007). In conservation, the abundant species are not necessarily the most important, and one of the most pressing questions in biodiversity is the function of rare species (see Halffter and Ezcurra 1992; Favila and Halffter 1997). Lovejoy (1988) suggests two possibilities about the origin and function of rare species: (1) a species that is rare in a community could have been an important species in the past, but was displaced by more competitive species, or (2z) a rare species in a natural community could become important if the community is altered. In this context, our results emphasize the importance of rare species in the process of dung beetle assemblage formation during reforestation. Reforested areas are colonized by species from the *restinga* forest and from open areas, several of these species are rare and do not seem to be well adapted to this kind of environment, but they are crucial to the process of dung beetle assemblage formation after the forest has been disrupted.

The high abundance of *D. aff. irinus* indicates that this is a highly successful generalist species that is able to live even in the least propitious environments such as the 2-year-old reforested area where the vegetation structure is simpler than that of the oldest reforested areas. The ability of *D. aff. irinus* to live in environments with low vegetation cover could be related to its nocturnal habit, which does not expose the species to dehydration from solar incidence, a pattern similar to that observed in many *Caatinga* species (Hernández 2007). Other abundant species that were consistently collected during the 2 years of sampling were *Canthidium manni*, *Canthon chalybaeus* and *Canthon staigi*. The latter is a strictly coprophagous species, and occurs exclusively in conserved forest environments; in fact it was collected 99 % of the time in conserved *restinga* so these ecological and behavioral characteristics allow it to be used as an environmental quality indicator for monitoring sites in the *restinga*. Habitat loyalty was also observed by Endres et al. (2007) for *Canthon staigi*, which represented 17.10 % of the total dung beetle abundance in the Atlantic Forest, but only 0.04 % in the *Tabuleiro Nordestino*, an arboreal savannah, and by Vieira et al. (2008), who reported that all individuals of this species were from the preserved *restinga*.

Trees are considered the ecosystem engineers of the forest (Jones et al. 1994), directly influencing several ecosystem proprieties, such as microclimate, which affect the distribution of ground dwelling arthropods (Aussenac 2000). We found a clear correlation between the richness of arboreal species and the successional age of reforested areas, indicating that the heterogeneity of vegetation increases, as does dung beetle species richness, with the age of reforested areas. This seems to be related to differences in light intensity between the early and late succession that would also play a role in the correlations between dung beetle data and tree species richness. In addition, the greater abundance of vertebrates with increasing habitat complexity in the same reforested areas where this study was done (unpublished data), could be related to the increase in the abundance and richness of dung beetles.

Despite the laws that protect the *restingas*, this fragile ecosystem along the eastern coast of Brazil continues to suffer an ever-increasing impact, mainly due to real estate speculation and the expansion of areas used for agriculture and livestock (Falkenberg 1999). Our results can contribute to the sound environmental management of the region and to the conservation of species in sites undergoing reforestation.

Acknowledgments This study is part of the project "*Ecological Succession and Regeneration of Restingas: Reforestation of Dunes in Mataraca, Paraíba*", financed by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq/Process number 507127/2004-8), in partnership with the Millennium Inorganic Chemicals Company, which provided financial and logistical support for research development through the Federal University of Paraíba. Biology students Pedro Barreto and Valderêz da Costa received ITI/CNPq scholarships (Scientific Initiation). The Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) awarded a PRO-DOC scholarship to Malva I. M. Hernández through the Regional Graduate Program in Development and the Environment of the Federal University of Paraíba. Comments by anonymous reviewers improved the manuscript. Bianca Delfosse revised the final version of the manuscript. We would like to thank Dr. Fernando Z. Vaz-de-Mello, of the Federal University of Mato Grosso, who confirmed the identification of species.

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