



Dung beetles as indicators of tropical forest restoration success: Is it possible to recover species and functional diversity?



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ABSTRACT

Tropical forest restoration is becoming increasingly more applied to offset biodiversity loss and maintain ecosystem processes, but knowledge about its efficacy is still limited. We evaluated the success of tropical forest active restoration using dung beetles (Coleoptera: Scarabaeinae) as bioindicators and combining measures of species diversity, composition and functional diversity. We assessed patterns of dung beetles community assembly along a restoration chronosequence and also compared restoration areas with reference (primary and old secondary forest) and degraded (pasture) ecosystems. Species composition in the restoration areas was clearly progressing towards the preserved forests and deviating from the pasture with increasing restoration age. We also found a turnover of open environment specialists and habitat generalists to forest generalists and forest specialist species along the restoration chronosequence. However, the majority of individuals in the older restored habitats were typically forest generalists. Biomass was the only variable that increased with restoration age. Species richness, number of individuals, biomass and functional richness in the restored areas were similar to, or even smaller, than in pastures and substantially lower than forest reference sites. Rarefied richness, functional evenness and functional dispersion did not vary between the habitats. We found that while restored areas have the capacity to host forest-restricted species, 18 years since active restoration has not been long enough to recover a stable and diverse dung beetle assemblage. Our study also demonstrates that measures of composition, species diversity and functional diversity can complement each other and contribute to a better understanding of the efficacy of restoration practices.

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1. Introduction

The maintenance of tropical forest biodiversity and ecosystem processes depends on the development of effective conservation efforts, which remains a great challenge to conservationists (Gardner et al., 2009; Rands et al., 2010). Ecological restoration has been considered one of the major strategies to mitigate the ongoing biodiversity crisis and is being increasingly applied worldwide (Bullcock et al., 2011; Montoya et al., 2012; Rands et al., 2010). Restoration practices are based on intentional activities that aim to recover the physical structure, biodiversity and ecological functions of a degraded ecosystem (Galatowitsch, 2012). However, this

is not an easy task, especially when it comes to restoring complex systems, such as tropical forests (Goosem and Tucker, 1995).

The assessment of restoration progress is a critical step in the application and refinement of restoration strategies, enabling the identification of constraints to success and the prediction of restoration outcomes (Matthews and Spyreas, 2010). The typical approach used is through comparisons of the restored sites with undisturbed reference systems and degraded systems (Matthews and Spyreas, 2010; Rey Benayas et al., 2009). However, most studies taking this approach have focused on plants, largely disregarding faunal recovery (Brudvig, 2011; Majer, 2009). This botanical bias arose because it was assumed that fauna would return with vegetation development (Majer, 2009). However, recent studies investigating faunal recovery have shown that other variables besides vegetation per se can influence its return (e.g. connectivity, composition of the surrounding landscape, regional species pool, biotic factors) (Brudvig, 2011; Grimbacher and Catterall, 2007; Majer, 2009). Even less is known about the recovery of ecological

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functions provided by biological diversity (Brudvig, 2011; Cadotte et al., 2011). Therefore, to truly determine restoration effectiveness and create self-sustainable functioning ecosystems it is critical to monitor not only plants, but also the return of fauna and functions associated with biodiversity (Cadotte et al., 2011; Majer, 2009).

Functional diversity is being increasingly advocated in the literature as a metric by which to evaluate the success of restoration programmes (e.g. Brudvig, 2011; Cadotte et al., 2011; Montoya et al., 2012), because it reflects aspects of the relationship between biological diversity, ecosystem functioning and environmental constraints (Díaz and Cabido, 2001; Mouchet et al., 2010). Indices of functional diversity are based on species traits found in a community and express the extent of functional differences among species in multidimensional space (Mouchet et al., 2010; Petchey and Gaston, 2006; Villéger et al., 2008). High functional diversity can result in greater resilience of the ecosystem to disturbance and higher levels of ecosystem functioning (Cadotte et al., 2011; Montoya et al., 2012). This type of information is not obtained when measuring only species diversity and composition, which are traditionally used to assess recovery in the restoration studies (Mayfield et al., 2010; Mouchet et al., 2010; Mouillot et al., 2013). Therefore, incorporating functional diversity metrics into restoration studies will aid in evaluations of restoration strategy effectiveness and decision-making (Cadotte et al., 2011; Montoya et al., 2012).

Monitoring the species and functional diversity of all fauna in restored areas is typically not logistically feasible, particularly in highly diverse systems like tropical forests. One approach is to select a group of organisms that serve as bioindicators, i.e. taxa that indicate environmental conditions (Gerlach et al., 2013). Dung beetles (Coleoptera: Scarabaeinae) have been widely proposed as cost-effective bioindicators because they are sensitive to ecosystem changes, easily sampled, broadly distributed, and their taxonomy and ecology are relatively well known (Gardner et al., 2008; Halffter and Favila, 1993; McGeoch et al., 2002; Nichols et al., 2007; Spector, 2006). They are also an ideal taxon for biodiversity monitoring because they rely on a large range of resources including rotten fruit, carcasses and feces of other animals (Spector, 2006). In addition, dung beetles are important components of terrestrial ecosystems, providing a set of ecological functions such as nutrient cycling, secondary seed dispersal, soil turbation, fertilization and biological control of vertebrate parasites (Nichols et al., 2008). Thus, dung beetle assemblages can both indicate and influence the success of restoration efforts.

Here we evaluate the efficacy of tropical forest restoration using dung beetles as bioindicators, combining measures of species diversity, composition and functional diversity. To assess restoration progress we evaluated patterns of dung beetle community assembly along a tropical forest restoration chronosequence. Additionally we compared restoration areas with reference (primary and old secondary forest) and degraded (pasture) ecosystems to assess restoration success. Specifically, we asked (1) Does dung beetle species composition shift with increasing time since restoration? (2) Do species richness, number of individuals, biomass and functional diversity increase with restored forest age? (3) Are restoration areas progressing towards the reference system and deviating from the degraded system based on these parameters?

2. Materials and methods

2.1. Study area

The study was conducted in the south of Bahia state, Brazil, covering the municipalities of Eunápolis, Porto Seguro, Belmonte and

Itagimirim. This region was originally dominated by tropical lowland rainforest and is in the Atlantic Forest domain (IBGE, 2012). Atlantic Forest is considered one of the five biodiversity hotspots, is internationally recognized for its high levels of biodiversity and endemism (Myers et al., 2000). Although the region south of Bahia still holds large remnants of Atlantic Forest (Ribeiro et al., 2009), most of the original forest was cleared during the 1960s and 1970s mainly for timber exploitation, pastures and plantations of exotic tree monocultures (Carvalho et al., 1994; Nascimento et al., 2009; Oliveira et al., 1997). In 1990, <7% of the original Atlantic Forest remained (Carvalho et al., 1994).

According to the Köppen classification (Kottek et al., 2006), the regional climate is Af (tropical rainforest climate), without a dry season and with rains well distributed throughout the year. Mean annual temperature is 22.6 °C and is fairly constant over the year, with a range of 18.9–27.9 °C. Average elevation of the region is 180 m, and mean annual precipitation is 1600 mm (Veracel, 2007).

2.2. Sampling sites

Since 1994, Veracel Cellulose SA company has been restoring Atlantic rainforest vegetation in areas of degraded pasture in the south of Bahia. This company has an enormous influence in the study region, owning ~210 000 hectares of land in 10 municipalities. Of this total, more than 105 000 ha is set aside for conservation and protection of native vegetation and 90 453 ha is planted with *Eucalyptus* sp. In 2004 the company started to restore a minimum of 400 ha per year, and at the end of 2011 it had replanted a total of 4300 hectares of Atlantic Forest (Veracel, 2011), offering an excellent opportunity to assess tropical rainforest restoration success.

The restoration techniques employed by Veracel consist of active planting of Atlantic rainforest tree species (1111 seedlings per hectare) mainly in valleys, riversides, steep slopes and other protected areas. Initially ants are controlled using formicide baits, and grasses and herbaceous weeds are controlled with herbicide if they occur in high densities (2 kg/ha). Manual mowing is implemented in areas with weeds \geq 1 m tall and subsoiling is used to reduce soil compaction. The restored area is also fertilized before seedlings are planted. Monitoring of planting success is frequent in the first 3 years of the restoration process and after this period, it is conducted every 5 years.

Dung beetle sampling was conducted in 15 forest restoration areas of varying ages (with size of restored area in parentheses): 0 years (2 months since planting – 64 ha), 1 year (400 ha), 2 years (64 ha), 3 years (15 ha), 4 years (191 ha), 5 years (7 ha), 8 years (106 ha), 9 years (5 ha), 11 years (36 ha), 12 years (3 ha), 13 years (54 ha), 14 years (14 ha), 15 years (3 ha), 17 years (9 ha) and 18 years (11 ha). The restoration areas included in the study were typically separated by \geq 500 m. We also sampled reference and degraded sites in order to quantify restoration success. We considered primary Atlantic Forest and old secondary forest (>40 years old) as the reference sites, representing the desired end point of restoration. Areas that have been converted by humans to pastures were considered degraded sites, representing the starting point of restoration. Collections were carried out in five areas of each of these systems (primary forest, old secondary forest and pasture). The sampled areas of primary and old secondary forest were located in the Veracel Station Private Reserve of Natural Heritage (RPPN Estação Veracel), one of the largest private reserves in the Atlantic Forest with an area of 6069 ha and a continuous mosaic of primary and secondary forest in advanced stages. Each of the reference and degraded sampled areas were \geq 1 km from each other.

One sampled restoration area (15 years) was located inside RPPN at a distance of 5 m from the preserved rainforests, but >1 km from the sampled primary and secondary forest sites. The

other studied restoration areas were situated between 20 km and 70 km from the RPPN Estação Veracel. We found a negative relationship between restoration age and distance to the RPPN ($r^2 = -0.42$, $p = 0.004$). However, we found no evidence for effects of distance to the reserve on the dung beetle assemblage (Table A.1 in Appendix A). Because the size of the restoration areas also varied widely (from 3 to 400 ha), we also tested effects of restoration area size on the dung beetle assemblage, and found no effects of this variable (Table A.1 in Appendix A). Therefore, we did not include distance to the RPPN or restoration area size in subsequent analyses.

2.3. Dung beetle sampling

Sampling was conducted during the rainy season, in May–June 2012. We used pitfall traps baited with ~25 g of human feces, carrion (bovine spleen) or rotten banana in order to attract the main feeding guilds of dung beetles. The traps consisted of a plastic container (19 cm diameter, 11 cm height), half-filled with a saline solution and detergent, a bait recipient (5 cm diameter, 5 cm height) suspended in the center of the trap and a plastic lid placed above ground to protect from rain and sun.

In each of the reference, degraded and restoration areas, we placed four sample points spaced 100 m apart along a linear transect. Each sample point contained three pitfall traps separated by 3 m, one with each bait type (feces, carrion, fruit), for a total of 12 pitfall traps per study area. Traps were placed at a minimum distance of 50 m from the edge whenever possible and left in the field for 48 h prior to collection. All captures were processed in the laboratory, and dung beetles were identified to the species level by Dr. Fernando Z. Vaz-de-Mello. Vouchers were deposited in Laboratório de Ecologia e Conservação de Invertebrados, Universidade Federal de Lavras (Lavras, Minas Gerais, Brazil) and in Setor de Entomologia da Coleção Zoológica do Instituto de Biociências da Universidade Federal de Mato Grosso (Cuiabá, Mato Grosso, Brazil).

2.4. Dung beetle traits

Species were characterized in terms of five ecological attributes: habitat specificity (forest specialists = only found in primary or old secondary forest; open environment specialists = only found in pasture; forest generalists = found in *Eucalyptus* plantations, primary and old secondary forests, i.e. species that occur in natural and human-altered forested environments; or habitat generalists = found in multiple habitats, i.e. species that occur in natural and human-altered forested and open environments), food relocation habit (rollers, tunnellers or dwellers), diet (coprophages, necrophages, carophages or generalists), diel activity (nocturnal or diurnal) and biomass (Table B.1 in Appendix B). Protocols for trait assignments are described in Appendix B. When necessary, we also obtained additional information on dung beetle traits from the literature and specialists.

2.5. Data analysis

2.5.1. Species composition and categories of habitat specificity

To determine whether species composition of dung beetle assemblage is progressing towards or deviating from the degraded and reference sites we performed a principal coordinates analysis (PCO) and a permutational multivariate analysis of variance (PERMANOVA), using the software Primer v.6 with PERMANOVA+ (Anderson et al., 2006; Clarke and Gorley, 2009). PCO was used to map the similarity between sites and PERMANOVA to test for significant differences in species composition between groups formed by PCO. These analyses were based on Bray–Curtis similarity, using standardized and square root transformed abundance

data. To carry out this comparison the restoration areas were categorized as early-stage (0–4 years), mid-stage (5–12 years) and late-stage restoration (13–18 years) (this categorization follows criteria defined by Brazilian law, see Conama, 1994).

Bray–Curtis similarity of the restoration areas to primary forest, secondary forest and pasture was used as a response variable to verify if there was a relationship with restoration age. We performed a regression analysis using generalized linear models (GLMs) with Gaussian errors in the R software (R Development Core Team, 2012).

We used GLMs to test for a relationship between restoration age and the proportion of species and individuals classified as forest specialists, forest generalists, open environment specialists and habitat generalists. We used binomial errors for the proportion of species richness of open environment specialists and binomial errors corrected for overdispersion (quasi-binomial) for the other variables.

2.5.2. Species richness, number of individuals and biomass

We tested for effects of restoration age on total species richness, rarefied species richness, number of individuals and biomass using GLMs. We used Poisson errors for species richness and Poisson errors corrected for overdispersion (quasi-Poisson) for the other variables. Because numbers of individuals varied among sites, we also rarefied species richness to six individuals, which was the minimum number of dung beetles sampled in an area. This analysis was implemented using the vegan package and rarefy function (Oksanen et al., 2013) in the R software (R Development Core Team, 2012).

To test for differences among habitat types (early, mid, late-stage restoration, primary forest, secondary forest and pasture), we used GLM with Poisson errors for species richness and quasi-Poisson for rarefied richness, abundance and biomass. Subsequently, we performed a contrast analysis to verify which categories were distinct in relation to the response variables.

2.5.3. Functional diversity

To calculate functional diversity we used dung beetle traits that have particular importance in ecosystem functioning, specifically: food relocation habit, diet, diel activity and biomass (e.g. Barragán et al., 2011). We calculated three indices of functional diversity for each study area: functional richness (FRic), functional evenness (FEve) and functional dispersion (FDis). FRic represents the amount of functional space occupied by the species present in a community and is measured as a convex hull volume. FEve corresponds to the distribution of species abundance in the functional space (Villéger et al., 2008). FDis is the mean distance of individual species to the centroid of all species in the multidimensional trait space (Laliberté and Legendre, 2010). Functional diversity calculations were implemented with the dbFD function in the FD package for R (Laliberté and Shipley, 2012).

We evaluated the influence of restoration age and habitat categories on FRic, FEve and FDis using GLMs with Gaussian errors. All GLMs were performed in the R software package (R Development Core Team, 2012), followed by residual analysis to check for the error distribution and adequacy of the model.

3. Results

We sampled 52 species in a total of 10 154 dung beetles across the habitat types, with 29 species and 4 467 individuals from primary forest, 31 species and 3941 individuals from old secondary forest, 20 species and 280 individuals from late-stage restoration, 17 species and 744 individuals from mid-stage restoration, 10

species and 171 individuals from early-stage restoration and 13 species and 551 individuals from pasture (Appendix C, Table C.1).

3.1. Species composition and categories of habitat specificity

According to PCO, species composition in the restoration areas are clearly progressing towards the reference sites (primary and old secondary forest) and deviating from the degraded site (pasture) with increasing restoration age (Fig. 1). Late-stage restoration areas are closer to primary and secondary forest compared with early and mid-stage restoration. The relationship of Bray–Curtis similarity with restoration age confirmed these patterns: similarity of the restoration areas to primary and secondary forest was positively influenced by restoration age (primary forest: $F = 14.33$, $p = 0.002$ – Fig. 2a; secondary forest: $F = 13.69$, $p = 0.002$ – Fig. 2b). In contrast, similarity to pasture was negatively influenced by restoration age ($F = 14.11$, $p = 0.002$ – Fig. 2c). However, PERMANOVA (Table D.1 in Appendix D) revealed that with the exception of primary forest and old secondary forest ($t = 1.04$; $p = 0.41$), all the categories in PCO were significantly different from each other based on species composition (pseudo- $F = 7.45$; $p = 0.0001$).

Percentage of species that were forest specialists increased with restoration age ($F = 7.56$, $p = 0.016$ – Fig. 3a), but this pattern was not found for the percentage of individuals ($F = 2.00$, $p = 0.1805$ – Fig. 3b). There was no relationship between the percentage of species that were forest generalists and restoration age ($F = 2.19$, $p = 0.16$ – Fig. 3c), however the percentage of forest generalist individuals increased with restoration age ($F = 13.16$, $p = 0.003$ – Fig. 3d). The percentage of species that were open environment specialists ($\chi^2 = 10.83$; $p = 0.01$ – Fig. 3e) and percentage of individuals ($F = 7.15$, $p = 0.01$ – Fig. 3f) both declined with restoration age. The same pattern was found for habitat generalists (species richness (%): $F = 9.13$, $p = 0.009$ – Fig. 3g; number of individuals (%): $F = 13.21$, $p = 0.003$ – Fig. 3h).

3.2. Species richness, number of individuals and biomass

Species richness ($\chi^2 = 10.98$; $p = 0.17$ – Fig. 4a), rarefied species richness ($F = 1.40$; $p = 0.26$ – Fig. 4b) and number of individuals ($F = 0.81$; $p = 0.38$ – Fig. 4c) did not have a significant relation with restoration age. Biomass was the only variable influenced by restoration age, increasing in older restoration areas ($F = 8.3108$, $p = 0.01282$ – Fig. 4d).

Mean species richness ($\chi^2 = 38.05$; $p < 0.001$ – Fig. 4e) differed among habitat types, while rarefied species richness was similar

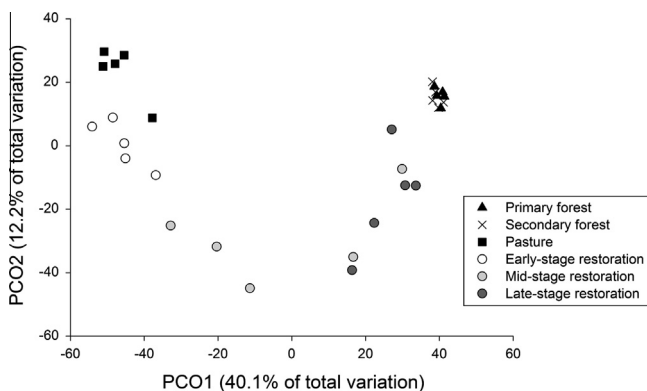


Fig. 1. Principal coordinates analysis (PCO) of dung beetle species composition based on Bray–Curtis similarity to compare forest restoration areas with the reference (primary forest and secondary forest) and degraded (pasture) sites. Early-stage restoration is represented by areas that have 0–4 years, mid-stage restoration: 5–12 years and late-stage restoration: 13–18 years.

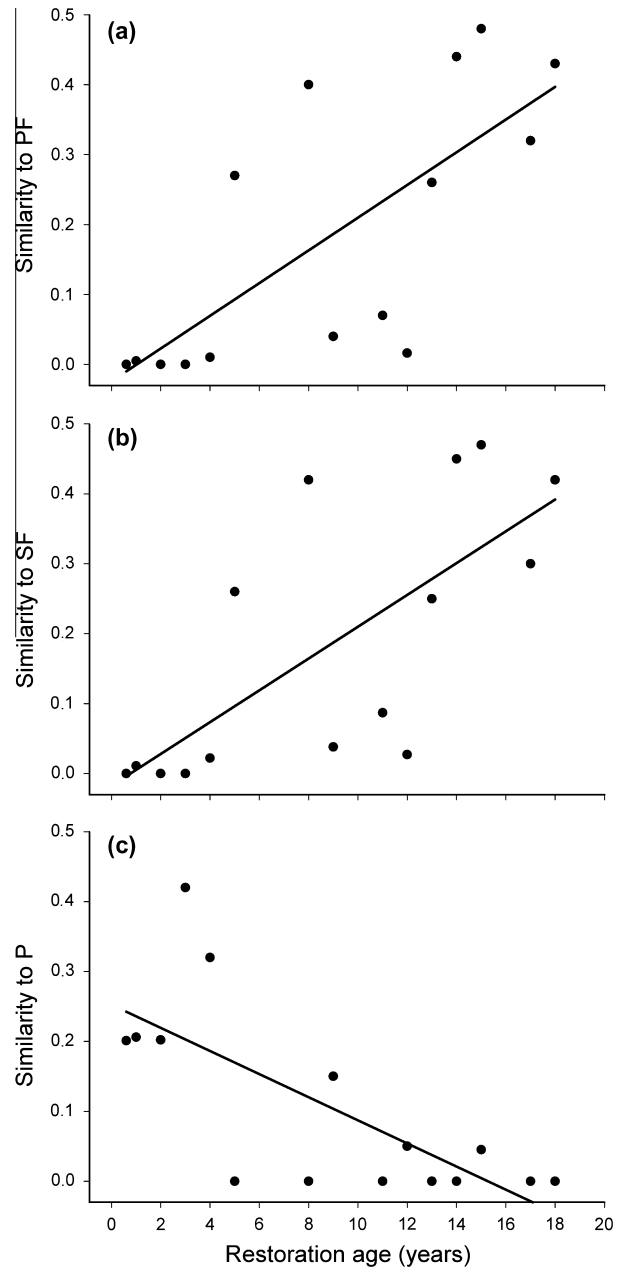


Fig. 2. Relationship between restoration age and dung beetle assemblage similarity (Bray–Curtis index) to primary forest (a), secondary forest (b) and pasture (c). PF = primary forest; SF = secondary forest; P = pasture.

($F = 0.48$; $p = 0.8162$ – Fig. 4f). Species richness was highest in primary and secondary forest and lowest in early-stage restoration areas, while pasture, mid-stage and late-stage restoration had intermediate levels of species richness and were not significantly different from each other. Species accumulation curves for each habitat type are shown in Appendix C, Fig. C.1. Number of individuals ($F = 25.77$; $p < 0.001$ – Fig. 4g) and biomass ($F = 45.71$; $p < 0.001$ – Fig. 4h) also differed among habitat types. Primary forest and secondary forest were similar to each other and had the highest number of individuals compared with the other systems. There were no significant differences in mean number of individuals found in pasture, early-stage, mid-stage and late-stage restoration. Biomass showed the same pattern found for species richness (Fig. 4h).

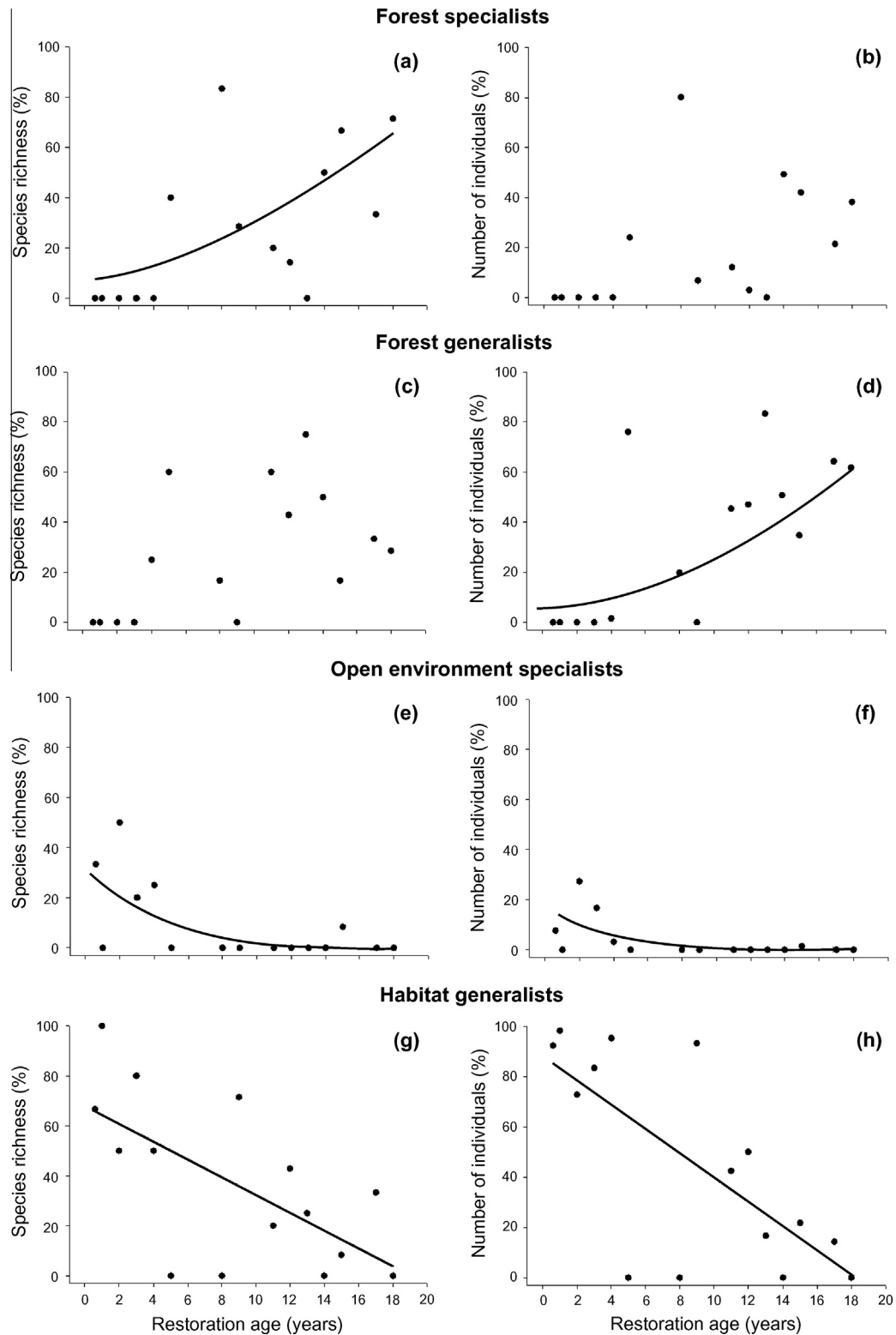


Fig. 3. Relationship between restoration age and the percentage of species (a) and individuals (b) classified as forest specialist, the percentage of species (c) and individuals (d) classified as forest generalists, the percentage of species (e) and individuals (f) classified as open environment specialists, and the percentage of species (g) and individuals (h) classified as habitat generalists.

3.3. Functional diversity

Restoration age did not influence FRic ($F = 0.0982$; $p = 0.759$ – Fig. 5a), FEve ($F = 0.475$; $p = 0.5028$ – Fig. 5b) or FDis ($F = 0.9125$; $p = 0.3569$ – Fig. 5c). However, there was significant variation in mean FRic ($F = 16.476$; $p < 0.001$ – Fig. 5d) among habitat types.

Lowest mean FRic was found in the restoration areas, and was similar among early-stage, mid-stage and late-stage restoration. This index was higher in the pasture compared with restored forest, but secondary and primary forest recorded the highest values. FEve ($F = 1.5455$; $p = 0.2001$ – Fig. 5e) and FDis ($F = 2.143$; $p = 0.07964$ – Fig. 5f) were not statistically different among the habitat types.

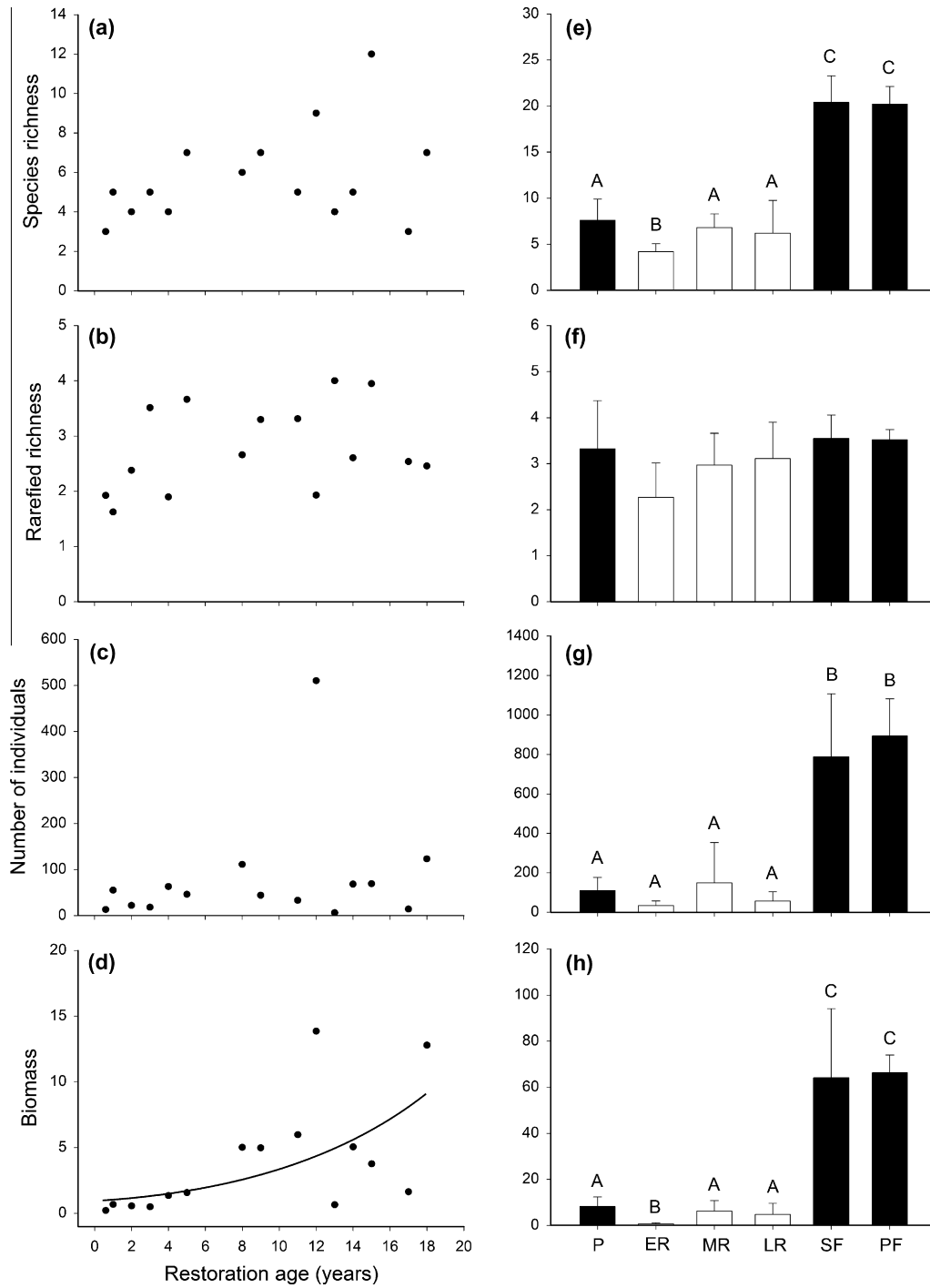


Fig. 4. (a–d) Relationship between restoration age and species richness, species richness rarefied to 6 individuals, abundance and biomass. (e–h). Mean \pm SD species richness, rarefied richness, abundance and biomass recorded in the different habitat types (P = pasture; ER = early-stage restoration; MR = mid-stage restoration; LR = late-stage restoration; SF = secondary forest; PF = primary forest). Unlike letters indicate significant differences ($P < 0.05$). Black bars represent the reference and degraded sites and white bars the forest restoration areas.

4. Discussion

This is the first study, to our knowledge, to evaluate the efficacy of tropical forest restoration combining measures of species diversity, composition and functional diversity. Our results underscore the importance of utilizing more than one metric to characterize assemblages found in restored areas in order to better evaluate restoration success. The increasing similarity of dung beetle species composition to primary and old secondary forest with increasing time since restoration suggests that these areas are successfully

progressing towards the reference systems. However, analyses of species diversity and functional diversity reveal that dung beetle assemblages are severely impoverished in the restored sites, and even after 18 years remain the same or worse in relation to the starting point of restoration (e.g. pasture).

4.1. Species composition and categories of habitat specificity

We demonstrated a clear trajectory of the restored areas, according to similarity in dung beetle species composition, from

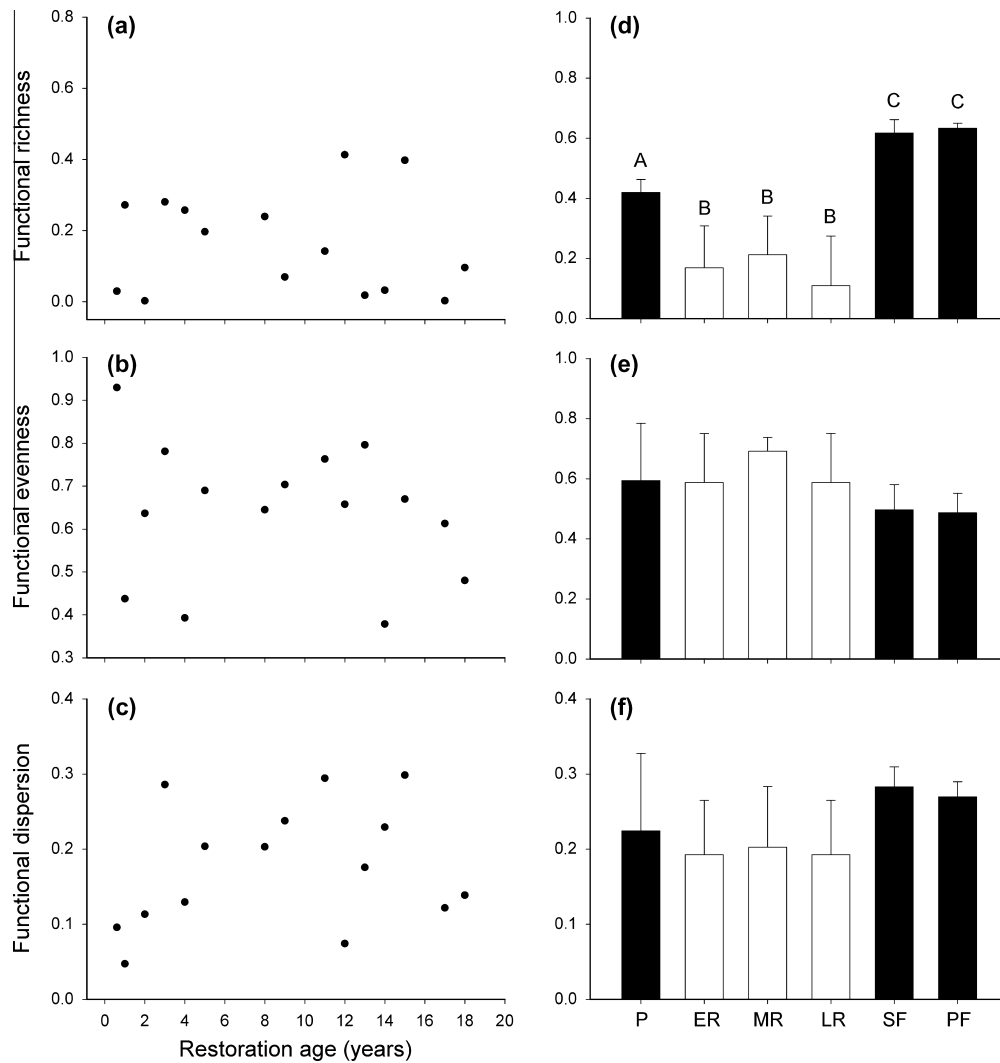


Fig. 5. (a–c) Relationship between restoration age and functional richness, functional evenness and functional dispersion. (d–e) Mean \pm SD functional richness, functional evenness and functional dispersion recorded in the different habitat types (P = pasture; ER = early-stage restoration; MR = mid-stage restoration; LR = late-stage restoration; SF = secondary forest; PF = primary forest). Unlike letters indicate significant differences ($P < 0.05$). Black bars represent the reference and degraded sites and white bars the forest restoration areas.

pasture to the preserve forests. The gradient of forest restoration ages in our study represents a transition from open environment to close-canopy forest habitats. Thus, increasing similarity to reference forests with restoration age can be attributed to a transition from open environment specialists to forest specialist species over the course of succession in these restored areas, consistent with patterns found when tropical forests have been allowed to regenerate naturally (Dent and Wright, 2009). This is supported by our results showing an increase in the proportion of species classified as forest specialists with restoration age and a decrease in the proportion of species classified as open environment specialists. Dung beetles are extremely sensitive to changes in vegetation structure, with species often showing patterns of fidelity to specific environmental properties (e.g. canopy cover, understorey vegetation, soil type and moisture) (Gardner et al., 2007; Halffter and Arellano, 2002; Horgan, 2007; Nichols et al., 2007; Noriega et al., 2007; Sowig, 1995). A higher degree of canopy cover can serve as a filter preventing the entry of open area species and increasing richness of forest-restricted species (Halffter and Arellano, 2002). Our results suggest that increasing similarity of the restored areas to the reference systems was also due to the decline of habitat generalists with restoration age.

While the proportion of species classified as forest specialists increased with restoration age, the proportion of individuals in this group did not. Rather, we found an increase in the proportion of individuals classified as forest generalists with forest age. Forest generalists are those species that depend on a certain degree of forest cover, however are matrix tolerant species and can establish in degraded forested systems. These results suggest that, in contrast to forest generalists, forest specialists are arriving in lower numbers and/or not surviving and reproducing well in the restored forests. Arrival of species into the restored forest areas will be highly influenced by the surrounding matrix, which can be extremely important in the local recovery of tropical forests (Chazdon, 2003). Although the restored areas in our study were typically located near forest fragments, our study region is dominated by human-managed habitats such as pastures and *Eucalyptus* plantations. Forest generalists may be poor competitors, but possess much better dispersal abilities compared to forest-restricted species and are also less sensitive to habitat change (Krauss et al., 2003; Larsen et al., 2008; Warren et al., 2001). Therefore, they can take advantage and dominate newly available environments that have some degree of canopy cover. In contrast, forest specialists avoid the landscape matrix and often stay confined to

the forest habitat (Feer and Hingrat, 2005; Klein, 1989; Larsen et al., 2008). The lower abundance of forest specialists in restored forests in our study system may therefore result from their reluctance or inability to cross non-forested areas and degraded forested systems (e.g. *Eucalyptus* plantations) in order to reach the restored forest areas.

4.2. Species richness, abundance and biomass

Contrary to expectations, we found that species richness, number of individuals and biomass in the restored areas were similar to or lower than in pastures and substantially lower than in forest reference sites. Our results are markedly different from a recent meta-analysis by Rey Benayas et al. (2009), which concluded that restoration efforts tend to increase species richness, diversity, abundance and biomass relative to degraded systems. Our results also contrast with another meta-analysis by Nichols et al. (2007), which found that land-use systems with a high degree of forest cover (such as secondary forests) can harbor dung beetle assemblages similar, in terms of species richness and abundance, to those found in intact tropical forest.

In contrast to total species richness, rarefied species richness was similar in all land-use systems, indicating that differences in number of individuals is driving observed differences in species richness (see Gotelli and Colwell, 2001). Both number of individuals and total biomass were substantially higher in the primary and secondary forest areas compared to restored forests. This suggests that the carrying capacity of restoration areas is still limited. In particular, availability of food resources may be restricting population sizes and limiting dung beetle species richness in the restored areas. Dung beetles depend on other groups of organisms, mainly vertebrates (especially mammals) and trees, for adult and larval food resources (Halffter and Matthews, 1966; Hanski and Camberfort, 1991). Therefore, the recovery of dung beetle assemblages in the restored areas also depends on the recovery of these groups. Culot et al. (2013) and Nichols et al. (2009) demonstrated the strong association between dung beetles and mammals, reporting a co-declining relationship between mammals and dung beetles. In our study, recovery time of the restoration areas (18 years) may not have been sufficient to successfully recuperate intact assemblages of dung beetles and the organisms on which they depend. Although all restored areas had significantly lower dung beetle biomass than primary and secondary forests, there was a significant positive relationship between biomass and restored forest age, suggesting that forests may eventually recover sufficient resources to support a diverse dung beetle assemblage. Continued monitoring of dung beetle populations, along with studies quantifying vertebrate densities and fruit availability in restored vs. reference systems are needed to confirm this hypothesis.

4.3. Functional diversity

FRic in the restoration sites was significantly lower than both the degraded and reference systems, suggesting that these areas may have low stability through time and be deficient in ecosystem processes provided by dung beetles (Cadotte et al., 2011; Díaz and Cabido, 2001; Montoya et al., 2012). A greater variety of functional traits translates into a higher amount of resources being used, representing stronger effects of diversity on ecosystem functioning (Díaz and Cabido, 2001). Also, greater functional trait richness can help to safeguard ecosystems against abiotic variation, since species with different traits may respond differently to environmental constraints, ensuring the long-term maintenance of ecosystem processes in a changing environment (Díaz and Cabido, 2001). When studying changes in ground-foraging ant assemblages along a successional gradient of secondary Atlantic Forest, Bihn

et al. (2010) found that the recovery of species richness and diversity was accompanied by a proportional increase in functional richness. In our study, functional richness is significantly correlated with species richness ($r^2 = 0.42$, $p = 0.004$), and therefore is unlikely to rebound unless species richness increases in these forests.

Most studies have found a reduction in functional evenness and dispersion with higher disturbance intensity (see Mouillot et al., 2013). One explanation for this pattern is that highly disturbed areas only support species with traits that allow them to tolerate the environmental conditions created by disturbance. This generates clustering and irregular distribution of abundances of co-occurring species in functional space, decreasing values of functional evenness and dispersion (Gerisch et al., 2012; Mouillot et al., 2013). However, we found no differences among study sites in FEve or FDis of dung beetle assemblages. Barragán et al. (2011) similarly found that FEve and FDis remained the same among pastures, forest fragments and continuous rainforest and between small and large forest fragments. This lack of difference between the systems can be an indication that only the identity of traits (functional richness) is being influenced by the environment and not the structure of the functional assemblage (i.e. abundance distribution and dispersion of traits in functional space). Similar values of FEve to the reference sites can suggest that niche space occupied in the restoration areas is being evenly exploited by the species and is not underutilized (Mason et al., 2005). According to Fonseca and Ganade (2001), assemblages with higher functional evenness can present more functional redundancy, because species are regularly distributed among functional groups. Similar values of FDis to the reference sites may indicate a higher dispersion of the functional traits in the restored areas, corresponding to a gain in response diversity (variability of responses to disturbances among species that contribute similarly to ecosystem function) (Elmqvist et al., 2009; Laliberté et al., 2010). Both high functional redundancy and high response diversity can increase the resilience of communities in the face of environmental change (Laliberté et al., 2010), including human and natural disturbances, and represent an interesting result from a conservation perspective.

5. Conclusions

Tropical forest restoration of degraded pastures can represent an important strategy to conserve biological diversity, but the knowledge we have about this strategy is still limited. Our study demonstrates that restored areas have the capacity to host forest-restricted species, but additional recovery time is likely needed to allow for the complete recovery of all biodiversity aspects. However, restored areas did not show any progress through time in relation to the starting point of the restoration, and after 18 years still harbor extremely depauperate dung beetle assemblages in terms of species and functional richness. Thus, it is unclear when the dung beetle assemblage will fully recover in restored forests, if ever. Since dung beetles are considered good indicators of environmental quality and overall biodiversity, our results suggest that further action may be needed to restore faunal diversity in this region. Our results also demonstrate how measures of composition, species diversity and functional diversity can complement each other and contribute to a better understanding of the efficacy of restoration practices.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2013.11.023>.

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