Oecologia (2021) 195:719–736
https://doi.org/10.1007/s00442-020-04831-5

COMMUNITY ECOLOGY – ORIGINAL RESEARCH

Short- and long-term temporal changes in the assemblage structure of Amazonian dung beetles

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Received: 2 April 2020 / Accepted: 9 December 2020 / Published online: 10 February 2021

Abstract

Species diversity varies in space and time. Temporal changes in the structure and dynamics of communities can occur at different scales. We investigated the temporal changes of dung beetle assemblages in the Amazonian region along seasons, years, and successional stages. We evaluated if assemblage structure changes between temporal scales and whether such changes affect the functional structure of communities. To achieve these goals, we sampled dung beetles using linear transects of baited pitfall traps during the dry and rainy seasons at two natural reserves in the Amazon region, each representing different time scales: one covering successional variations (80, 30, 5, and 1 years of recovery from logging) and the other one encompassing three consecutive years at two successional stages (20 and 10 years from logging). We used Generalized Linear Models to analyze interannual and successional changes in diversity, described assemblage structure with a NMDS, and examined compositional variation by partitioning beta diversity into its nestedness and turnover components. Abundance and richness decrease from the rainy to the dry season and towards earlier successional stages but do not differ between years. Assemblage diversity changes differently in interannual and successional scales. During succession, dung beetle assemblages change drastically, following a nested structure due to the appearance of species and functional groups in later successional stages. In contrast, functional group composition does not show consistent changes between years, displaying a turnover structure. This pattern supports non-deterministic changes in dung beetle assemblage structure along forest succession.

Keywords Beta diversity · Functional groups · Interannual variations · Nestedness · Scarabaeinae · Species turnover

Introduction

Species diversity varies across both space and time (Rosenzweig 1995). The structure and dynamics of communities vary at multiple temporal scales, from daily and seasonal changes to variations throughout geological periods (Villéger et al. 2011; Fritz et al. 2013; Grøtan et al. 2014). Within short ecological time scales, local communities show regular and, to some extent, predictable seasonal variations, coupled with seemingly stochastic interannual changes (e.g., Grimbacher and Stork 2009; Labidi et al. 2012). Such

Communicated by Liliane Ruess.

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stochasticity is produced by phenological and populational processes (e.g., Tanner et al. 2009; Hodgson et al. 2010) that are in turn dependent on interannual changes in climate and temporal variations in resource availability (e.g., Voss et al. 2009; Encinas-Viso et al. 2012). Over longer time periods, the effects of large-scale processes, such as climate change, biological invasions, or land transformation, also promote different kinds of responses and changes to community dynamics (see Forister et al. 2010; Dijkstra et al. 2011).

Long-term changes in community composition have been traditionally studied under the umbrella of ecological succession. In general, successions can be described as the non-random changes in the structure and composition of an ecological community that take place over time after a disturbance event (e.g., Walker and Del Moral 2003). Currently, many successions take place after habitat perturbations are caused directly or indirectly by human activities (e.g., logging, agricultural intensification, or cattle expansion), and it is believed that they can have negative effects on biodiversity and the associated ecological functions and ecosystem services (Nichols et al. 2007; Horgan 2008; Barragan et al. 2011; Braga et al. 2013).

The classical view of ecological successions hypothesizes that communities in a new or post-disturbed habitat are formed by a few pioneering species that are subsequently replaced by competitively dominant ones (Connell and Slatyer 1977). This hypothesis, initially proposed by Clements (1916), has received considerable support. However, its view of temporal community dynamics as a directional deterministic process has also been traditionally questioned (Walker and Del Moral 2003). Since the first criticisms of Gleason (1927), detractors of this idea argue that community dynamics are not completely deterministic, giving more relevance to historical contingencies and large-scale processes, such as the individualistic responses of species to the environment (Hortal et al. 2012). Under this paradigm, communities assemble from the dispersal of species that are present and/or arrive in the landscape, with local interactions playing a comparatively less important role. Here, local assembly becomes a density-dependent phenomenon, where the first arrivals correspond to species that are frequent and/or abundant in the landscape, receiving comparatively less rare species. Following this idea, the core–satellite species hypothesis (Hanski 1982) states that the first colonizers would become the core species (i.e., species that make up the bulk of the individuals of the local community), whereas the satellite species (i.e., species that hold small local abundances) would be the ones arriving to the community at a later stage. Although both the pioneering species and the core–satellite species hypotheses predict similar trends of temporal increase in the richness and abundance of communities, their predictions are markedly different in terms of temporal beta diversity patterns. The pioneer hypothesis predicts a temporal turnover between pioneer and non-pioneer species (Connell and Slatyer 1977; Denslow 1980), while the core-satellite hypothesis expects that temporal changes in species composition should be driven by a non-random gain of species, generating greater richness, since satellite species would be sequentially added to the community (Menéndez 1994). Therefore, a preeminence of species replacement with time will be in accordance with the pioneering hypothesis, whereas a preeminence of nestedness will provide evidence for the core-satellite hypothesis. It follows that by studying temporal trends in beta diversity components (i.e., turnover and nestedness sensu Baselga 2010), it should be possible to elucidate the main process governing the (re)assembly of communities along short and long time periods.

The Amazon rainforest is the largest contiguous and most biodiverse tropical rainforest in the world, hosting a large proportion of known diversity (Peres et al. 2010). The spatial heterogeneity, seasonal regimes (e.g., pluviosity, river pulse, seasonal humidity and temperature), and anthropic disturbances that characterize the Amazonian region result in a complex mosaic of temporal and spatial changes in its communities (Andresen 2002; Noriega et al. 2007; Korasaki et al. 2013). During the past 50 years, the Amazon may have lost up to 29% of its forest cover due to an increase in deforestation for the creation of cattle ranches, agriculture, and logging (Peres et al. 2010; INPA 2017). These activities have led to the appearance of a mosaic of habitat fragments holding communities ongoing different successional stages, which provide an ideal scenario for understanding how communities reassemble after disturbance (Braga et al. 2013; Franca et al. 2016; Cajaiba et al. 2017).

Dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) are an excellent study system to explore temporal variations in biodiversity. They are sensitive to environmental changes and respond quickly to habitat destruction, fragmentation or isolation (Halffter and Arellano 2002; Barlow et al. 2007; Nichols et al. 2007). Indeed, dung beetle abundance and richness are affected by human disturbance, usually following a gradient of increasing negative effects when moving from natural forests to secondary forests, plantations, and pastures (e.g., Howden and Nealis 1975; Barragan et al. 2011; Braga et al. 2013). By burying and using dung as both food and nesting resource, dung beetles provide key ecological functions and services like nutrient cycling, soil fertilization and aeration, seed dispersal, and biological pest control (Andresen 2002; Bang et al. 2005; Nichols et al. 2008), which makes them important for economy and human welfare (Losey and Vaughan 2006). Therefore, they have been widely used as indicators for evaluating and monitoring spatial and temporal changes and the impact of disturbances on natural communities (e.g., Davis et al. 2001; McGeoch et al. 2002; Gardner et al. 2008; Otavo et al. 2013; Da Silva and Hernández 2018; Noriega et al. 2020).

In this study, we evaluate both interannual and successional trends in the diversity and composition of dung beetle assemblages in the Amazonian rainforest. To do this, we use data from two dung beetle surveys with different temporal extents: one including four successional stages with a temporal extent of 80 years (using a space-for-time substitution), and another including three consecutive years of sampling with two successional stages. We address the following specific questions: (1) Do diversity and assemblage structure change in short (interannual) and long (successional) temporal scales? (2) How different are beta diversity patterns between these two temporal scales? and (3) How do temporal changes affect the functional structure of dung beetle assemblages at these two scales?

Materials and methods

Study sites

Surveys were conducted in two nearby Natural Reserves of the Amazon basin, Palmari (Brazil) and Monilla (Colombia) (Fig. 1). The climate is humid with a mean rainfall of 2500 mm and a mean annual temperature of 25 °C. The area has a monomodal pluviometric regime with two seasons: rainy—November to May (≥ 300 mm/month average), and dry—June to October (≤ 100 mm/month average). The two Natural Reserves are contiguous to indigenous human settlements, so they are subject to significant anthropic pressures that vary with their distance from the villages. These human settlements affect the forest in different ways and intensities: from cutting small-medium areas for "slash and burn" shifting cultivation (see below), to extracting big trees for construction and wood, to the collection of fruits and seeds, and occasionally hunting for food.

The first study area, used to characterize long-term successional changes, was located in the Palmari Natural Reserve (home of the Marubo indigenous community) in the municipality of Atalaia do Norte (4°17′1″ S–70°17′0″ W, 77 m a.s.l.), 22 km from the city of Benjamin Constant, in the Brazilian state of Amazonas (Fig. 1). Here we sampled four types of habitats, representing a long-term successional recovery from human-induced disturbances: primary forest, with ~80 years of recovery after logging; secondary forest, with ~30 years of recovery after logging; an old chagra, abandoned approximately 5 years before sampling; and a new chagra, abandoned the same year of the sampling. Here, "*chagras*" are forest areas that were completely cut and burn in a "slash and burn" shifting cultivation regime used for different types of crops like cassava, maize, rice, sugarcane, soybean, and plantain (see van Vliet et al. 2013).

The second study area, used to characterize both short-term yearly variations and short-term successional changes, was located in the Monilla Amena Natural Reserve (herein Monilla; home of Ticuna indigenous community), in the municipality of Leticia (4º06′46″ S–69°55′52″ W, 60 m a.s.l.), 9.5 km from the city of Leticia, in the Colombian state of Amazonas (Fig. 1). We assessed differences in short-term temporal variations (i.e., between sampling years, see below) by sampling this locality during three consecutive years. In addition, we evaluated whether these between-year differences are similar in different moments of long-term community evolution by doing these surveys in two different successional stages, secondary old forest and secondary new forest, with approximately 20 and 10 years of recovery after logging, respectively. This also allows us to evaluate whether the successional changes eventually identified in the Palmari dataset hold up in other similar communities, rather than responding to local idiosyncrasies.

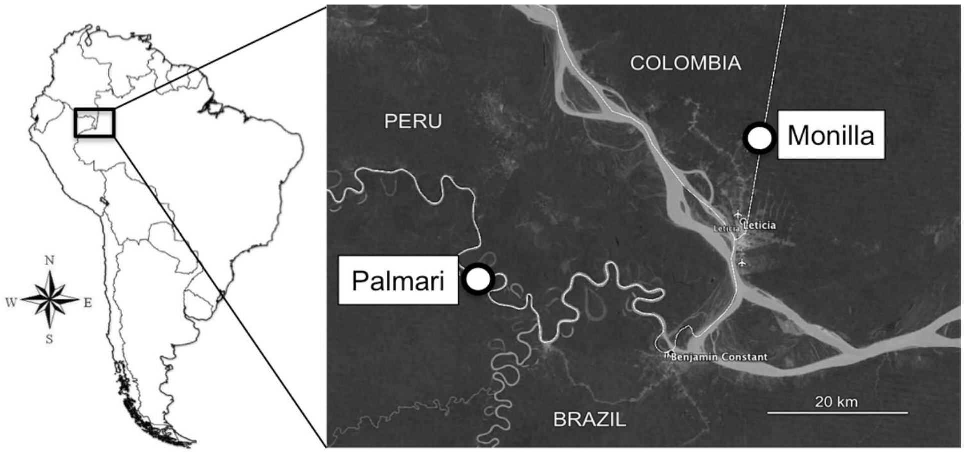


Fig. 1 Map of the study region. Location of the two sampling localities: Palmari (Brazil—Natural Reserve Palmari) and Monilla (Colombia—Natural Reserve Monilla Amena) in the Amazon region

Dung beetle sampling and processing

Dung beetle assemblages were sampled in Palmari in April (herein dry season) and September (herein rainy season) 2009. Surveys were conducted using one linear transect of ten pitfall traps in each type of habitat (primary forest, secondary forest, old chagra, and new chagra) with 50 m between traps (following Larsen and Forsyth 2005). The pitfall traps were baited with 30 g of a 1:3 mixture of human and pig dung (a combination that allows high quantities of bait with a high attraction level). In Monilla, dung beetle assemblages were sampled during three consecutive years (2002–2004), in the same months and seasons than in Palmari (April, dry season; and September, rainy season). In this case, because of the large extension of the forest, the sampling was conducted using ten linear transects of ten pitfall traps in each type of habitat (secondary old forest and secondary new forest) with 10 m between each trap and 20 m between transects (see Noriega et al. 2007). The pitfall traps were baited with 30 g of carrion or human dung. Due to the short distance between traps, and in order to make both datasets more comparable, the sampling unit was considered to be the trap in the case of Palmari and the entire transect in Monilla ($n = 10$ per habitat type and season).

The model of the pitfall trap (plastic containers with the bait hanging above the trap; see Noriega and Fagua 2009) and the time that the traps were active in the field (48 h) were the same in both localities. The dung beetle specimens collected were stored in 70% alcohol and identified to species level using several taxonomic keys (Edmonds 1994; Genier 1996; Cook 2002; Edmonds and Zídek 2004, 2010; Camero 2010; Vaz-de-Mello et al. 2011; Cupello and Vaz-de-Mello 2013) and expert support. After identifying and labelling all the specimens, the ones from Palmari were deposited at the Natural History Museum of Los Andes University, Bogotá (EANDES), and those from Monilla at the Natural History Museum of the Pontificia Javeriana University, Bogotá (MPUJ).

All individuals were assigned to functional groups based on the dung beetle functional classification proposed by Doube (1990), which combines their main food relocation strategies (i.e., guilds) with the size of the individuals. We inferred dung beetle guilds from the food relocation behavior known for each genus, assigning each species to one of the three distinct guilds: paracoprids (or tunnelers), which dig under the dung pile and make tunnels where they relocate a brood mass of dung; telecoprids (or rollers), which construct a brood ball in the dung pile, roll it apart from the main source, and bury it; and endocoprids (or dwellers), which nest and feed exclusively inside the dung pats or build their nests right beneath the resource in the dung–soil interface (Halffter and Matthews 1966; Halffter and Edmonds 1982; Cambefort and Hanski 1991). Average body size was measured from the captured individuals as the total length from the external border of the clypeus to the pygidium for each species, with recourse to the literature for species with low abundances. These measurements were performed using an electronic digital caliper (Powerfix—Z22855 , ± 0.01 mm). Each species was assigned to one of the three size categories (defined by the gaps in species' body size distribution; see Appendix S1): large (> 18 mm), medium (10–18 mm), and small (< 10 mm). We combined guilds and average body size to define nine functional groups (Appendix S1): large paracoprids, medium paracoprids, small paracoprids, large telecoprids, medium telecoprids, small telecoprids, large endocoprids, medium endocoprids, and small endocoprids.

Data analysis

We described dung beetle assemblages for each year, season, and type of forest through total abundance, richness, and the abundance of each species and functional group. We assessed inventory completeness as the percentage of the estimated total species richness that were observed in each locality (Lobo 2008) to ensure that the surveys attained a fair description of the studied assemblages. We estimated total species richness with four nonparametric estimators (ACE, ICE, Chao 1, and Jacknife 1) that are commonly used to characterize dung beetle communities for the ease of comparison with other studies. All estimators were calculated with EstimateS v 9.1.0 (Colwell 2016).

We explored whether dung beetle species richness and abundance vary through time using generalized linear models (GLMs) on each one of these diversity attributes at the sampling unit level, as a function of successional stages in the Palmari dataset, and as a function of sampling year and successional stage in the Monilla dataset. In both datasets we also included the season as a predictor variable. We conducted this analysis separately for the diversity attributes related with species diversity and functional group diversity. We assumed a Poisson error distribution to fit richness and abundance models, following a backward model selection based on Akaike Information Criterion corrected by sample size (Burnham and Anderson 2002; AICc).

We described temporal variations in assemblage composition with a non-metric multidimensional scaling ordination (NMDS) performed on matrices of sampling sites by species and by functional groups. To avoid an excessive influence of rare taxa, species with less than 5% occurrences were excluded from the NMDS analysis (see McCune and Grace 2002). Data were subjected to Wisconsin double standardization, where each value is first standardized by the column maximum (i.e., for each species or functional group), abundance is divided by its largest value in the surveys before being standardized by the row total (i.e., for each trap), and species or functional group abundance is divided by the total abundance of all species or functional groups in that sampling unit. We used the Bray–Curtis index to measure the dissimilarity in species or functional groups between the two datasets. We assessed the goodness of fit of the ordination through the percentage of variance represented (see McCune and Grace 2002 for details). To select the main factor affecting assemblage composition, we performed Spearman correlations between the NMDS axes resulting from previous analyses and the potential explanatory variables (Matos et al. 2015). We also analyzed the relationship between the NMDS ordination and the explanatory variables through vector fitting. Then, those variables presenting significant correlations were overlaid in the NMDS ordination (McCune and Grace 2002; Oksanen 2009).

Compositional variations in assemblage structure were evaluated based on the nestedness and turnover components of beta diversity patterns using the indices proposed by Baselga (2010): β_{SIM} (Simpson dissimilarity—spatial turnover), β_{NES} (nestedness dissimilarity), and β_{SOR} (Sørensen dissimilarity—total Beta diversity). These dissimilarity measures are additive fractions, so $\beta_{SOR} = \beta_{SIM} + \beta_{NES}$. Specifically, we measured nestedness and turnover for each pair of sampling units belonging to different time periods. Then, we measured beta diversity between consecutive periods and for each season and successional stage (in the case of Monilla dataset) independently. Finally, we used a Wilcoxon matched-pairs test to explore if nestedness and turnover measures differ between different pairs of time periods.

All analyses were performed in R v. 3.1.1 environment (R Core Team 2016), through different packages: *lsmeans* package (Lenth 2016) for the least-squares means; the functions metaMDS and envfit of *vegan* package (Oksanen et al. 2013) for NMDS; and *betapart* package (Baselga and Orme 2012) in the case of beta diversity components.

Results

A total of 1,073 individuals were collected in Palmari, representing 34 species from 12 genera and six tribes (Table 1). The most abundant species in this site were *Dichotomius* cf. *boreus* (Olivier, 1789), *Dichotomius* cf. *fortestriatus* (Luederwaldt, 1923), and *Onthophagus haematopus* Harold, 1875, which altogether encompass about a third of total abundance. In Monilla surveys rendered 822 individuals from 35 species belonging to 13 genera and six tribes (Table 1). In this case, the most abundant species were *Sylvicanthon aequinoctialis* (Harold, 1868), *O. haematopus*, and *Canthon luteicollis* Erichson, 1847, together constituting more than 40% of all individuals. The percentages of total species covered by the surveys were between 85.2 and 100% for Palmari and 73.6–98.9% for Monilla, indicating that sampling effort was sufficient to cover most of the assemblage (Appendix S2).

Abundance and species richness

Regarding successional variations, both richness and abundance increased along successional stages. In Palmari, primary forest held the highest recorded species richness and abundance (33 species, 14 of them unique, and 699 individuals), followed by secondary forest (19 species, one of them unique, 249 individuals), old chagra (10 species, 99 individuals), and new chagra (7 species, 26 individuals); neither of the two chagras had unique species (Table 1). In Monilla, richness and abundance were also higher at the secondary old forest (31 species, 17 of them unique, and 671 individuals), compared with the secondary new forest (18 species, five of them unique, and 151 individuals) (Table 1).

When considering yearly variations, in general, abundance did not differ substantially between years within neither habitat (i.e., successional stage) nor season in the Monilla dataset; however, it varied in the rainy season of one of the years for both habitats, remaining nonetheless similar between years for both habitats during the dry season (Fig. 2b, Appendix S3). Richness did not vary significantly between years for each combination of habitat and season (Fig. 2d, Appendix S3).

Both seasons show similar patterns of variation in abundance and species richness in both datasets (Fig. 2). In general, abundance and species richness decreased from rainy to dry season, when dung beetle faunas seemingly tend to homogenize along successional stages. During the dry season all stages presented low abundances in Palmari, and the two chagras did not differ in neither abundance nor richness (Fig. 2a, c). These patterns were similar in Monilla, where the differences in abundance and richness between the old and the new forest were lower, though significant during the dry season (Figs. 2b, d, Appendix S4). Indeed, the interaction between season and successional stage was the best supported model for richness, and a model describing the joint effects of seasons and successional stages was in both datasets the best model for abundance (Appendix S3).

Assemblage composition

The main variations in species composition described by NMDS ordinations can be summarized by axes related to successional and seasonal gradients in both datasets (Fig. 3a, b). At Palmari, the two first axes (final stress = 0.17, total variability explained = 56%; Fig. 3a) identify a seasonal gradient between the rainy and the dry season, and a successional gradient from the new chagra to the primary forest (see Appendix S4). In Monilla, the obtained NMDS axes (final stress = 0.16, total variability explained = 52%;

Table 1 Species list and abundance in Palmari (Brazil—successional) and Monilla (Colombia—interannual) in each type of habitat sampled (*ChN* new abandoned "chagra", *ChA* old abandoned "chagra", *SF* secondary forest, *PF* primary forest) and year (2002–2004) in the Amazon region. *FG* corresponds to functional groups built based on relocation food behavior and body size (*P* paracoprids, *T* telecoprids, *E* endocoprids and *S* small: < 10 mm, *M* medium: 10–18 mm and *L* large: > 18 mm; Appendix S1); *AS* is the average individual length in mm; and *Code* is the species code (used in Fig. 5)

Tribe	Genus	Species	FG	AS	Code	Palmari				Monilla			
						ChN	ChA	SF	PF	2002	2003	2004	Total
Ateuchini	*Ateuchus*	*A. murrayi* (Harold, 1868)	PS	6.5	*Ate_mur*	0	0	0	0	2	3	1	6
		A. cf. *connexus* (Harold, 1868)	PS	7.3	*Ate_con*	0	0	0	7	0	0	0	7
		A. aff. *scatimoides* (Balthasar, 1939)	PS	5.2	*Ate_sca*	0	0	0	3	0	1	1	5
		A. sp. 1	PS	8.2	*Ate*_sp1	0	0	0	4	0	0	0	4
	Uroxys	*Uroxys* sp. 1	PS	3.2	*Uro*_sp1	0	0	0	11	0	0	0	11
		Uroxys sp. 2	PS	4.1	*Uro*_sp2	0	0	0	0	12	13	15	40
		Uroxys sp. 3	PS	7.0	*Uro*_sp3	0	0	0	5	0	0	0	5
		Uroxys sp. 4	PS	5.6	*Uro*_sp4	0	0	0	0	0	2	0	2
Coprini	*Canthidium*	*C. cupreum* (Blanchard, 1843)	PS	6.5	*Can_cup*	0	0	0	0	1	1	2	4
		C. funebre Balthasar, 1939	PS	7.2	*Can_fun*	0	0	0	0	8	9	5	22
		C. gerstaeckeri Harold, 1867	PS	8.1	*Can_ger*	0	0	0	0	5	2	4	11
		C. aff. *centrale* Boucomont, 1928	PS	9.8	*Can_cen*	0	0	0	0	9	6	9	24
	Dichotomius	*D. mamillatus* (Felsche, 1901)	PL	20.7	*Dic_mam*	5	29	29	18	11	9	8	109
		D. nisus (Olivier, 1789)	PM	16.8	*Dic_nis*	0	0	0	0	1	3	3	7
		D. cf. *boreus* (Olivier, 1789)	PL	26.2	*Dic_bor*	7	20	29	81	14	12	16	179
		D. cf. *fortestriatus* (Luederwaldt, 1923)	PM	12.9	*Dic_for*	7	10	23	73	0	0	0	113
		D. cf. *ohausi* (Luederwaldt, 1923)	PM	15.7	*Dic_oha*	0	0	0	9	0	0	0	9
		D. cf. *robustus* (Luederwaldt, 1935)	PM	14.9	*Dic_rob*	0	0	7	12	0	0	0	19
		D. aff. *podalirius* (Felsche, 1901)	PL	19.5	*Dic_pod*	0	8	21	37	0	0	0	66
		D. sp. 1	PM	16.4	*Dic*_sp1	0	0	0	9	0	0	0	9
	Ontherus	*O. pubens* Génier, 1996	PM	14.6	*Ont_pub*	0	0	6	12	0	0	0	18
Deltochilini	*Canthon*	*C. juvencus* (Harold, 1868)	TS	3.5	*Can_juv*	0	0	0	0	3	7	1	11
		C. luteicollis Erichson, 1847	TS	9.6	*Can_lut*	0	0	0	0	23	19	24	66
		C. smaragdulus (Fabricius, 1781)	TM	14.8	*Can_sma*	0	0	0	4	1	0	1	6
		C. triangularis (Drury, 1770)	TS	9.2	*Can_tri*	0	0	0	0	0	1	0	1
	Cryptocanthon	*C. peckorum* Howden, 1973	TS	3.4	*Cry_pec*	0	0	0	0	0	2	1	3
	Deltochilum	*D. amazonicum* Bates, 1887	TL	23.1	*Del_ama*	0	0	0	8	0	0	0	8
		D. carinatum (Westwood, 1837)	TM	16.5	*Del_car*	0	0	0	0	9	9	1	19
		D. orbignyi (Blanchard, 1846)	TL	21.3	*Del_orb*	0	0	0	0	7	5	1	13

Table 1 (continued)

Tribe	Genus	Species	FG	AS	Code	Palmari				Monilla			
						ChN	ChA	SF	PF	2002	2003	2004	Total
		D. cf. *parile* Bates, 1887	TM	15.2	*Del_par*	0	0	5	9	2	1	5	22
		D. cf. *peruanum* Paulian, 1938	TM	12.1	*Del_per*	0	0	0	0	15	14	9	38
		D. aff. *pseudoparile* Paulian, 1938	TM	13.4	*Del_pse*	0	0	0	14	0	0	0	14
		D. sp. 1	TM	12.7	*Del*_sp1	0	0	0	6	0	0	0	6
		D. sp. 2	TM	11.9	*Del*_sp2	0	0	0	6	0	0	0	6
	Scybalocanthon	*S. pygidialis* (Schmidt, 1922)	TS	8.6	*Scy_pyg*	0	0	13	30	2	1	2	48
	Sylvicanthon	*S. aequinoctialis* (Harold, 1868)	TM	12.3	*Syl_aeq*	0	6	10	58	81	35	48	238
Oniticellini	*Eurysternus*	*E. caribaeus* Herbst, 1789	EM	15.4	*Eur_car*	0	0	6	19	0	0	0	25
		E. hamaticollis Balthasar, 1939	EM	16.9	*Eur_ham*	3	3	7	34	14	13	35	109
		E. hirtellus Dalman, 1824	ES	6.7	*Eur_hir*	0	0	2	16	5	4	3	30
		E. inflexus (Germar, 1824)	EM	12.8	*Eur_inf*	2	8	20	57	0	3	0	90
		E. velutinus Bates, 1887	EL	21.5	*Eur_vel*	1	3	7	20	3	4	7	45
Onthophagini	*Onthophagus*	*O. clypeatus* Blanchard, 1846	PS	8.0	*Ont_cly*	0	0	0	0	4	2	2	8
		O. haematopus Harold, 1875	PS	6.1	*Ont_hae*	0	9	32	60	37	37	39	214
		O. marginicollis Harold, 1880	PS	4.9	*Ont_mar*	0	0	0	0	2	1	2	5
		O. rubrescens Blanchard, 1843	PS	5.5	*Ont_rub*	0	0	0	0	12	16	12	40
		O. cf. *xanthomerus* Bates, 1887	PS	6.7	*Ont_xan*	0	0	4	13	0	0	0	17
Phanaeini	*Coprophanaeus*	*C. callegarii* Arnaud, 2002	PM	13.2	*Cop_cal*	0	0	10	16	0	0	0	26
		C. suredai Arnaud, 1996	PL	20.8	*Cop_sur*	0	0	0	8	0	0	0	8
		C. telamon (Erichson, 1847)	PL	23.2	*Cop_tel*	0	0	11	15	6	6	8	46
	Gromphas	*G. amazonica* Bates, 1870	PM	15.3	*Gro_ama*	1	0	0	0	0	0	0	1
	Oxysternon	*O. conspicillatum* (Weber, 1801)	PL	24.6	*Oxy_con*	0	3	7	21	2	3	1	37
		O. lautum (Macleay, 1819)	PL	21.8	*Oxy_lau*	0	0	0	4	0	0	0	4
	Phanaeus	*P. bispinus* Bates, 1868	PM	15.0	*Pha_bis*	0	0	0	0	5	3	1	9
		P. cambeforti Arnaud, 1982	PM	13.7	*Pha_cam*	0	0	0	0	1	3	3	7
		P. chalcomelas (Perty, 1830)	PM	14.3	*Pha_cha*	0	0	0	0	2	3	0	5
		Abundance				26	99	249	699	299	253	270	1895
		Richness				7	10	19	33	30	34	31	55

Fig. 3b) were not related with variations throughout sampling years, but rather with easily identifiable successional and seasonal gradients like the Palmari dataset—although in this case these changes are summarized by the combination of both NMDS axes (Appendix S4).

Nestedness and turnover (i.e., β_{NES} and β_{SIM}) markedly changed between long and short temporal scales, showing that compositional changes are fundamentally different for these two distinct time scales. Nestedness is influential in the long successional gradient of Palmari (Fig. 4a, c), driven by a steep reduction of richness along the habitat disturbance gradient mainly due to the loss of rare species (while 14 species are unique to the primary forest, only one is unique for the new chagra). On the contrary, in the shorter temporal scales of the interannual variations at Monilla, beta diversity is mainly driven by a true turnover of species (Fig. 4b, d). Nonetheless, compositional differences are attenuated in both datasets during the dry season, a period when there were almost no differences of beta diversity between years (see Appendix S5 for results regarding the dry season and total β_{SOR}).

Functional diversity and structure

Both study sites presented all nine functional groups, defined according to resource allocation behavior and body size, but their patterns of diversity along temporal changes differ between datasets (Table 1). In Palmari, more than half of the functional groups (small paracoprids and endocoprids, and all telecoprids) appear towards the latter stages of the succession, while the composition of functional groups is maintained between years in Monilla, corroborating that responses to succession are fundamentally different from interannual variations. In general, paracoprids were dominant in Palmari, although some functional groups appear with increasing successional maturity: large paracoprids are exclusive of the primary forest, small telecoprids and small endocoprids appear only on the secondary forest, and medium telecoprids and small paracoprids do so at the old chagra (Table 1). This contrasts with Monilla, which is dominated by small paracoprids and medium and small telecoprids, and only the former functional group appears in the older successional stage, while the only large endocoprid species (*Eurysternus velutinus* Bates, 1887) appears just in the secondary new forest (Table 1).

The abundance of all functional groups (except large telecoprids) increased significantly with habitat succession in Palmari in the rainy season, while small and large paracoprids and medium endocoprids were the only groups showing abundance differences between successional stages in Monilla (Fig. 5j, l, q). Also, there was an important decrease in abundance—accompanied with a functional homogenization of the successional stages—from the rainy to the dry season in most functional groups in both datasets, except for large telecoprids in Palmari and small telecoprids in Monilla (Fig. 5f, m, respectively). Such successional and seasonal variability contrasts with the interannual similarity in the abundance of functional groups found in the Monilla dataset, which holds up for all groups except for medium telecoprids and endocoprids in the secondary old forest during the rainy season (Fig. 5n, q). In fact, medium telecoprids were the only functional group showing a distinct response, with changes in abundance between years, successional stages, and seasons (Fig. 5n).

The NMDS ordinations describing variations in functional group composition for both datasets identified similar gradients of joint successional and seasonal change, from the young stages in dry season to old stages in the rainy season. In Palmari, the two axes selected (final stress = 0.17, total explained variability = 61%) show an increasing trend in all types of telecoprids and small endocoprids in both the rainy season and the older stages of the successional gradient (Fig. 3c, Appendix S4). In Monilla (two NMDS axes, final stress = 0.19, total explained variability = 52%), the first axis selected was not correlated with any of the explanatory variables studied, but the second was clearly related with both successional and seasonal variations, showing a gradient of functional change from new forest assemblages in the dry season to old forest assemblages in the rainy season (Appendix S4). Here, small and medium telecoprids and small endocoprids are related with secondary old forest, while large endocoprids and telecoprids and medium paracoprids are related with the rainy season (Fig. 3d).

Discussion

Our results show that changes in assemblage structure are fundamentally different between interannual and successional temporal scales, but they also show that there is some coherence between seasonal and successional variations. Amazon dung beetles present relatively similar trends towards higher abundance, richness, and functional diversity both in the older successional stages and during the rainy season. Another important result is the almost negligible effect of interannual variations for the overall diversity and structure of the assemblage, which is limited to significant species turnover between years. In contrast, composition and diversity change in a more estimated way throughout the succession, as variations between successional stages show a clear nested structure. Indeed, changes in functional group structure are also different between time scales, with drastic shifts throughout succession and seasonally (with some groups disappearing from assemblages), which contrast with the maintenance of functional structure at short temporal scales despite changes in the identity of some of the species.

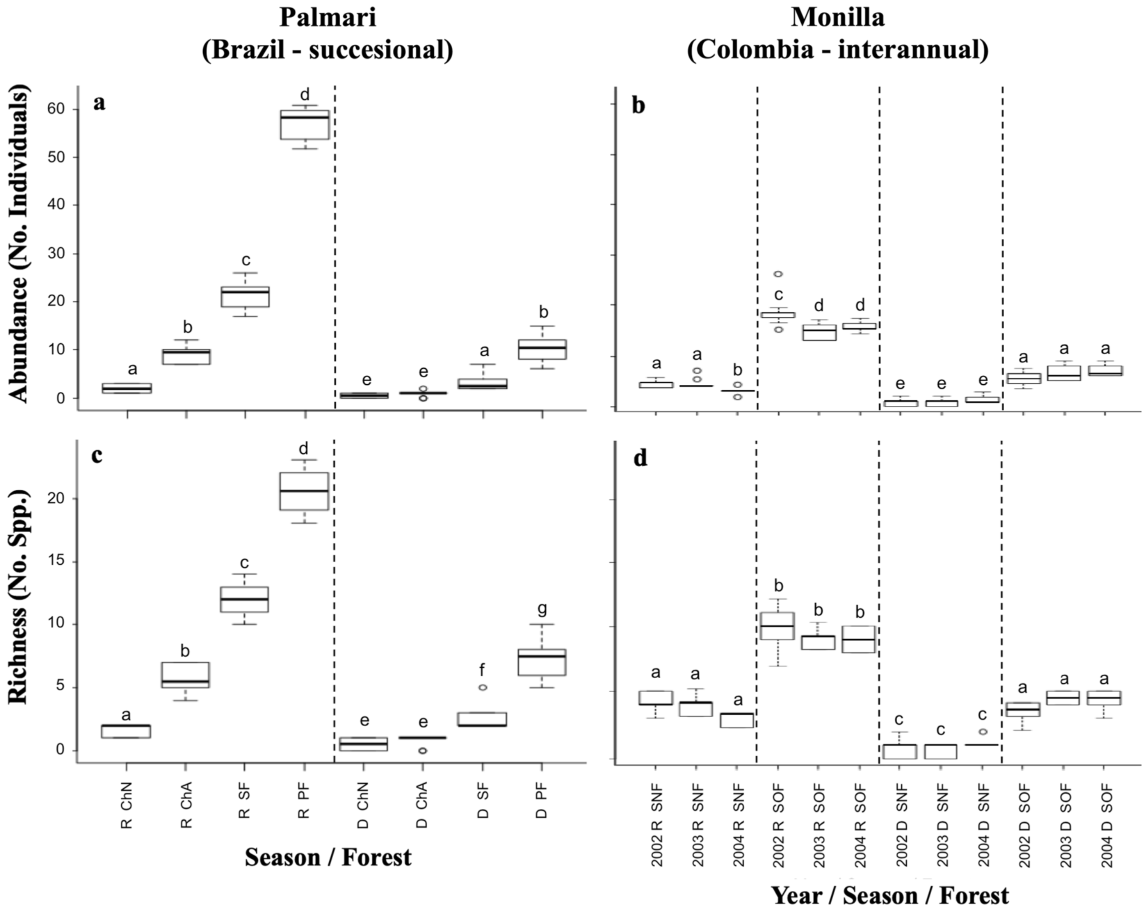


Fig. 2 Abundance (**a**, **b**) and richness (**c**, **d**) of the two sampling localities in the Amazon region: Palmari (Brazil—successional) and Monilla (Colombia—interannual) in each year (2002–2004), sampling season (R: Rainy and D: Dry) and type of habitat (ChN: new abandoned "chagra", ChA: old abandoned "chagra", SF: secondary forest, PF: primary forest, SNF: secondary new forest and SOF: secondary old forest). Different letters, above bars, indicate statistically significant differences (Wilcoxon's test; $p < 0.05$) among years/seasons/forests. Error bars represent average ± SE

Successional variations in assemblage diversity, composition and structure

The increase of perturbation in Amazon forests generates poor dung beetle assemblages in terms of both abundance and species richness (Barragan et al. 2011; Braga et al. 2013; Beiroz et al. 2017), a well-known trend that we also identify in both Palmari and Monilla. This decay in diversity could be related to the loss of vegetation cover, changes in soil texture, and the disappearance of vertebrate fauna that affects resource availability and drastically changes the microclimatic conditions for dung beetles (Andrade et al. 2011; Beiroz et al. 2017; Cajaiba et al. 2017; Ferreira et al. 2019). Many low-intensity anthropogenic disturbances (e.g., reduced-impact logging, moderate hunting, or logging roads) may also affect negatively dung beetle assemblage structure (Bicknell et al. 2014; Feer and Boissier 2015; Edwards et al. 2017) and alter ecological functions (Hosaka et al. 2014). This result is a clear nested pattern of compositional change over the long temporal scales of succession, contrasting with the turnover that defines the compositional variation at the short interannual time scales studied in the Monilla dataset (Fig. 6; see below).

This nested pattern along successional stages suggests an effect of a non-random species loss towards increasingly disturbed habitats. Indeed, some eurytopic species (i.e., species with wide habitat requirements, such as *Dichotomius mamillatus* (Felsche, 1901), *Dichotomius* cf. *boreus*, or *Sylvicanthon aequinoctialis*) seem to be able to pioneer the recovery of dung beetle assemblages after disturbance by persisting in the majority of successional stages. In contrast, some stenotopic species (i.e., species with a narrow habitat requirement, such as *Canthon luteicollis*, *Deltochilum* aff. *pseudoparile* Paulian, 1938, or *Onthophagus rubrescens* Blanchard, 1843) are probably more sensitive and restricted to the less disturbed habitats of the later successional stages. The ability to colonize habitats at different levels of disturbance may be the result of several local factors that constrain

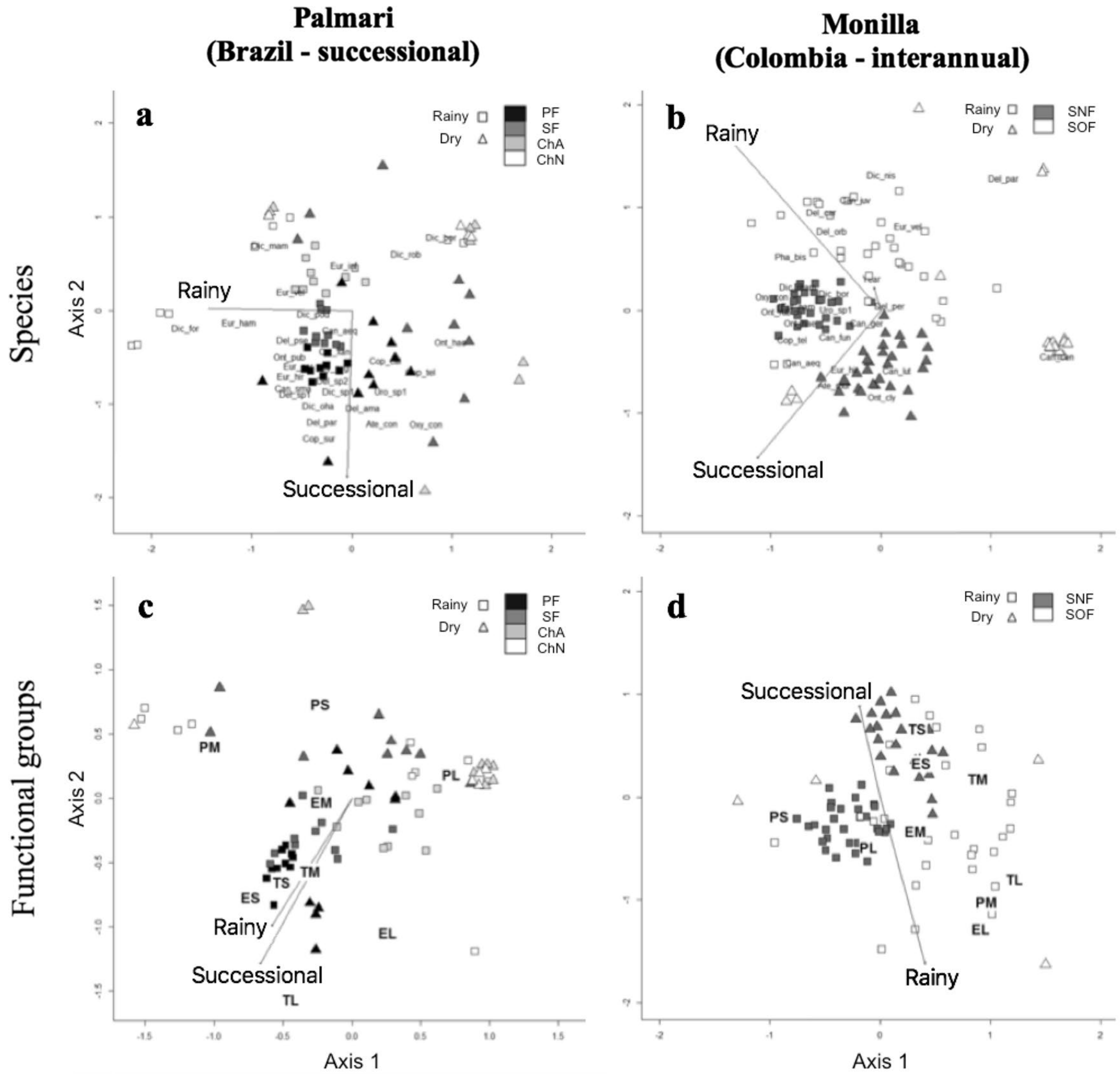


Fig. 3 Non-metric multidimensional scaling (NMDS) analyses of species (**a**, **b**) and functional groups (**c**, **d**) composition in Palmari (Brazil) and Monilla (Colombia) in the Amazon region. Season (rainy and dry) and type of habitat (ChN: new abandoned "chagra", ChA: old abandoned "chagra", SF: secondary forest, PF: primary forest, SNF: secondary new forest and SOF: secondary old forest). Vectors represent significant correlations between assemblage composition and significant explanatory variables: successional and rainy (rainy season of the year). Functional groups and species code correspond to those listed in Table 1 (P: paracoprids, T: telecoprids, E: endocoprids and small (S): < 10 mm, medium (M): 10–18 mm and large (L): > 18 mm)

assemblage structure, whose importance decreases along the succession. These include loss of vegetation cover, abundance, diversity of the available resources, and a significant change in microclimatic conditions related to open areas (i.e., loss of humidity, increase of temperature, changes in soil texture, etc. Beiroz et al. 2017).

The anthropic pressure represented along the succession gradient also affected the functional structure of the assemblages. Functional group richness is known to decrease in disturbed areas as a result of changes in land use (Barragan et al. 2011; Beiroz et al. 2018). In our study, some functional groups are absent or rare in the most perturbed successional stages, especially those that include larger species. The loss of large dung beetles is a common trend that occurs in several ecosystems and regions due to the increase in anthropic perturbations (e.g., Lobo 2001; Tonelli et al. 2018). These changes result in the existence of gradients in the composition of functional groups found in our NDMS analyses. Interestingly, while the different functional groups of telecoprids and endocoprids show a successional (and seasonal, see below) replacement, paracoprids show no evident correlation with the succession. Under Hanski's (1982) core-satellite hypothesis (see below), this could be attributed to many species with this nesting behavior being "core" elements of the community that are present since the beginning of assembly after the disturbance occurs.

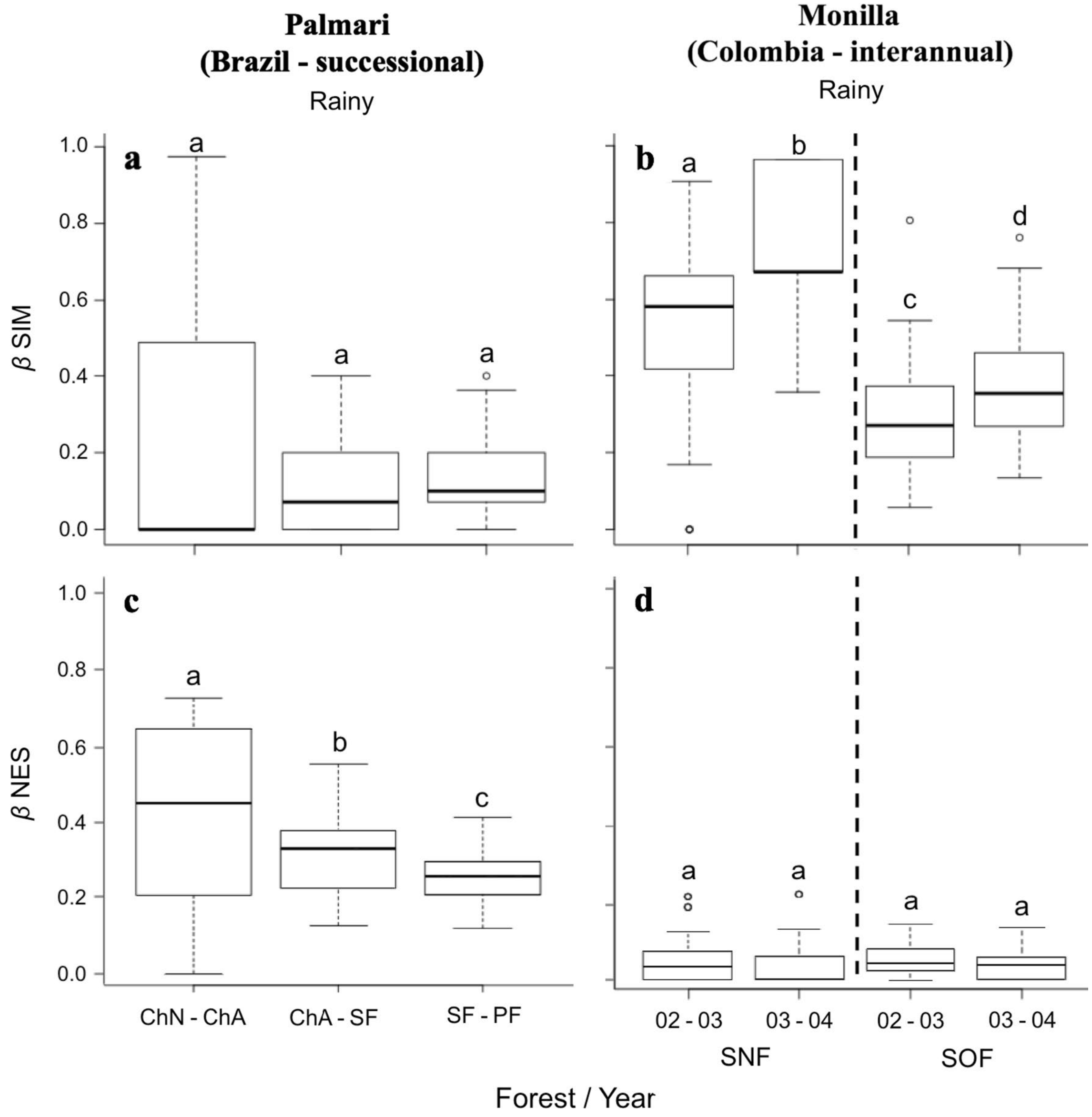
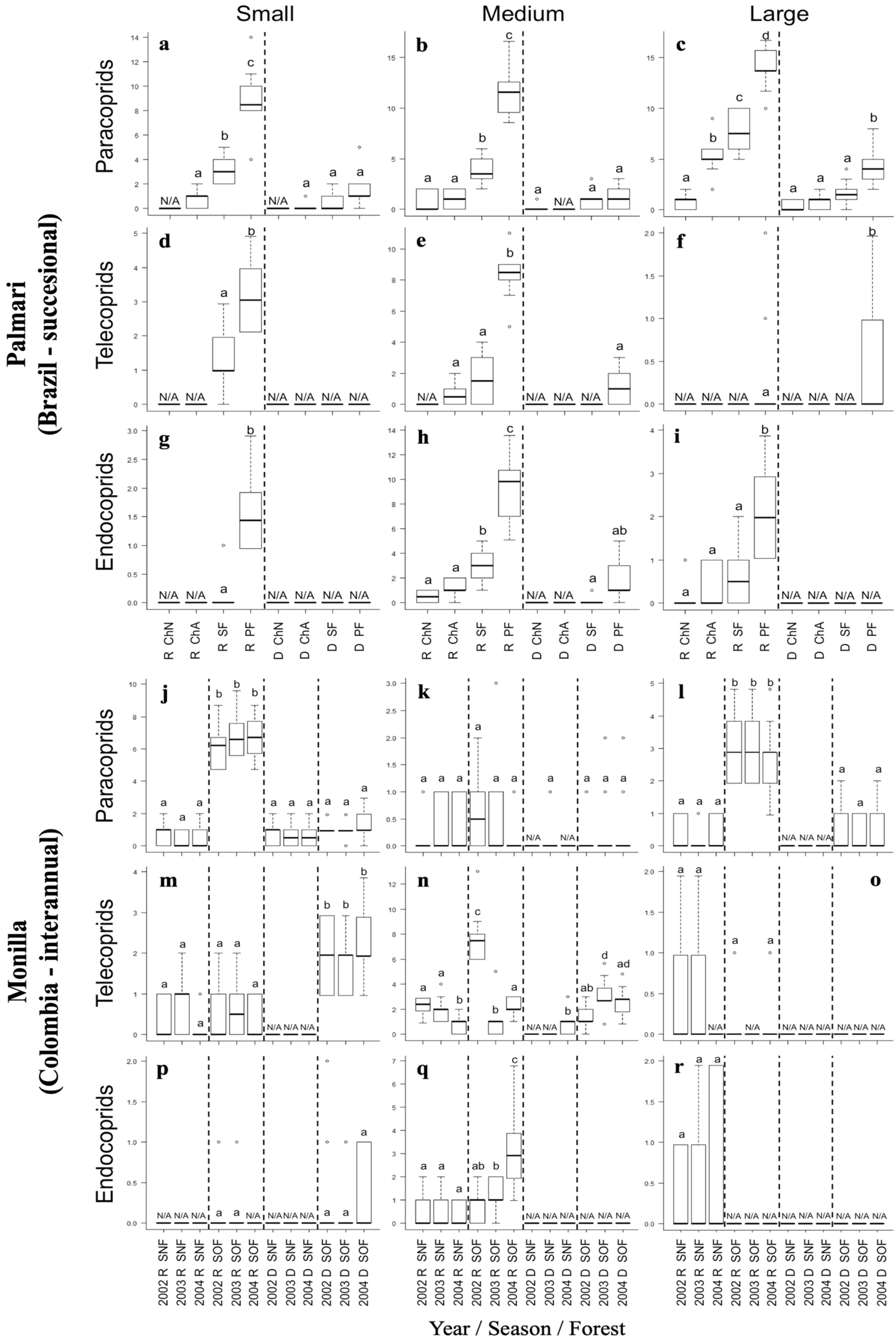


Fig. 4 Beta diversity components [βsim (**a**, **b**) and βnes (**c**, **d**)] of Palmari (Brazil—successional) and Monilla (Colombia—interannual) during the rainy season, between types of habitat (ChN: new abandoned "chagra", ChA: old abandoned "chagra", SF: secondary forest, PF: primary forest, SNF: secondary new forest and SOF: secondary old forest), and sampling years (2002–2004) in the Amazon region. Different letters, above bars, indicate statistically significant differences (Wilcoxon's test; $p < 0.05$) among years/seasons/forests

Different responses of dung beetle functional groups to ecological pressures are commonly found in the studies addressing the (generally negative) effects of habitat disturbance on dung beetle diversity in the Neotropics (Andresen 2005; Horgan 2008; Barragan et al. 2011; Braga et al. 2013; Nichols et al. 2013; Da Silva and Hernández 2015; Beiroz et al. 2017). Indeed, Audino et al. (2014) established that more than 18 years of recovery are needed to restore the functional diversity of dung beetle assemblages in tropical rain forests. Here, it is essential to include the identity of species and functional groups to understand restoration processes (Tonelli et al. 2020). Following our results and taking into consideration the successional process in Palmari, it is evident that, although some species from mature forest communities may endure disturbance, full recovery of species richness, abundance, and functional group diversity may take more than 30 years. Nonetheless, it is important to note that the analyses of succession based on space-for-time substitution may underestimate the negative consequences of human impact on local species diversity (Franca et al. 2016).


Small
Medium
Large
Palmari (Brazil - succesional)
Monilla (Colombia - interannual)
Paracoprids
Telecoprids
Endocoprids
a
b
c
d
e
f
g
h
i
j
k
l
m
n
o
p
q
r
N/A
R ChN
R ChA
R SF
R PF
D ChN
D ChA
D SF
D PF
2002 R SNF
2003 R SNF
2004 R SNF
2002 R SOF
2003 R SOF
2004 R SOF
2002 D SNF
2003 D SNF
2004 D SNF
2002 D SOF
2003 D SOF
2004 D SOF
Year / Season / Forest

◂**Fig. 5** Abundance of each functional group (grouped by relocation food behavior—Paracoprids, Telecoprids and Endocoprids, and body size—small < 10 mm, medium 10–18 mm, and large > 18 mm) for Palmari (Brazil—successional) and Monilla (Colombia—interannual) in each year (2002,–2004), season (R: Rainy and D: Dry) and type of habitat (ChN: new abandoned "chagra", ChA: old abandoned "chagra", SF: secondary forest, PF: primary forest, SNF: secondary new forest, and SOF: secondary old forest) in the Amazon region. N/A: no species collected for that functional groups. Different letters, above bars, indicate statistically significant differences (Wilcoxon's test; $p < 0.05$) among years/seasons/forests

Interannual turnover

In general, our results indicate that the diversity, composition, and structure of dung beetle assemblages change significantly more between successional stages and seasons than between years. Indeed, beta diversity between years in Palmari is mainly due to the turnover component of compositional variation. This pattern of apparently random species replacement can be related with the existence of climatic or biotic factors (such as unpredictable start of rains, strong variations in dry season rainfall, or a big reduction in food resources) that might affect the phenological cycles or generate local population declines and/or peaks. Besides the intrinsic environmental stochasticity of small time periods, these factors can include: species of longer phenological cycles (i.e., supra-annual cycles; cycles that took more than a year for the larvae to become an adult), explosive population outbursts (i.e., species that appear in high numbers during a brief window of time associated with complex life history cycles), or the presence of rare species that are active during very narrow windows of time (Wolda 1988; Ribeiro and Freitas 2011; Kishimoto-Yamada and Itioka 2015). Other groups like butterflies have life cycles longer than a year (Grøtan et al. 2014), evidencing the importance of sampling during longer time periods.

The differences between interannual and successional changes in Amazonian dung beetle communities have been seldom studied. The only study also addressing both temporal scales that we are aware of also reports large interannual oscillations during five years at an Amazonian primary forest (Beiroz et al. 2017), contrasting with the relatively constant turnover between years we found in Monilla. However, in this same study, dry season fauna in poorer years were comparable between primary forest and disturbed areas (Beiroz et al. 2017), showing a pattern of biotic homogenization of early and late successional stages with seasonality that coincides with the coherent successional-seasonal gradient we found. Indeed, despite the relatively short time period of our study in Monilla, the turnover between these three years could also be related to a small forest recovery that translates into an increase in the number of species between 2002 and 2004 (from 30 to 34 species, 5 new species appear and one disappears), similar to Beiroz et al. (2017) findings for their study area. Actually, the number and composition of functional groups in the Monilla dataset do not vary between years, which is congruent with the remarkable interannual stability in the relative abundance of functional groups found by these authors (Beiroz et al. 2017). Indeed, other studies exploring functional diversity trends after long temporal periods (i.e., 34 or 35 years; see Escobar et al. 2008 and Cuesta and Lobo 2019) did not find significant shifts in the composition of functional groups, reporting only changes in the proportion of individuals of each group, possibly connected with the effect of human activities.

Similarities between seasonal and successional gradients

Strikingly, the importance of the community enrichment along the successional process is relatively similar to that of the seasonal gradient towards more abundant and diverse assemblages in the rainy season. This common trend is particularly consistent for functional structure and is likely related with the biotic homogenization promoted by the low productivity characteristic of both disturbed habitats (see above) and the dry season (see Hernández and Vaz-de-Mello 2009). Dung beetle assemblages are characterized by a strong seasonality (e.g., Hernández and Vaz-de-Mello 2009; Andrade et al. 2011; Lopes et al. 2011; Labidi et al. 2012; Viega et al. 2014), where the species active during the dry season represent an impoverished sample (i.e., a subsample) of those found during the rainy season (Agoglitta et al. 2012). In tropical rain forests, fruit and green leaf production peaks during the hot-humid season, increasing the amount of resources available for mammals and consequently the amount of excrements available for dung beetles (Estrada et al. 1993). In contrast, during the dry season, dung production is lower and its distribution is less spatially aggregated, with fewer dung pads being available and becoming drier faster due to climatic conditions (Andresen 2005). However, some studies have found little seasonal variation in dung beetle abundance, richness, and assemblage structure in the humid forests of the Amazon region (Gardner et al. 2008; Korasaki et al. 2013). Following the results of Beiroz et al. (2017), such small seasonal variations may be an effect of the stochastic interannual variations in climate, where climatically milder years allow the maintenance of richer faunas throughout the whole year (see also Ferreira et al. 2019).

A matter of core and satellite species and functional groups

Our results point to the importance of core rather than pioneering species along the successional gradients. The pioneering hypothesis predicts a strong temporal turnover

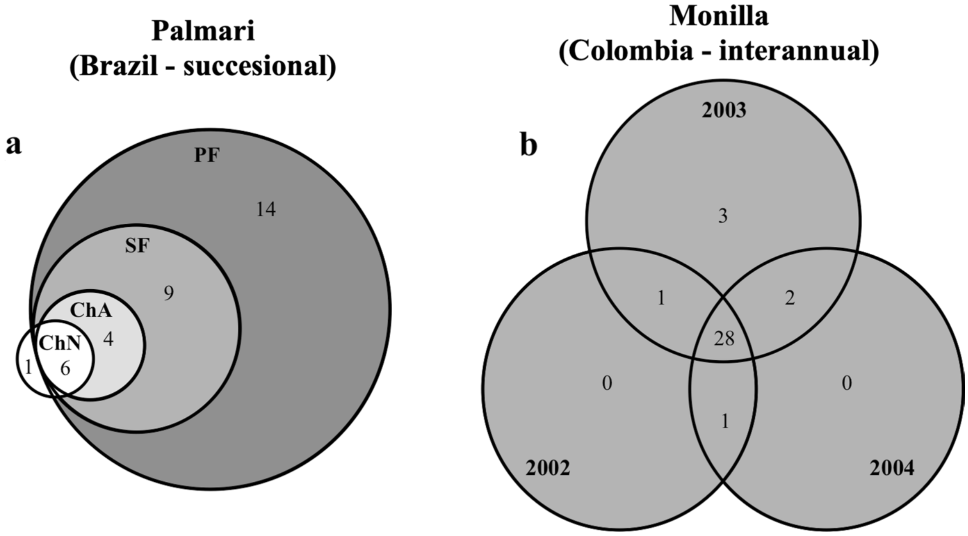


Fig. 6 Beta diversity components. **a** nestedness pattern in successional habitats (Palmari–Brazil, ChN: new abandoned "chagra", ChA: old abandoned "chagra", SF: secondary forest, PF: primary forest); and **b** turnover pattern in interannual comparisons (Monilla–Colombia) of dung beetle assemblage structure in the Amazon region. Numbers indicate the species found in each combination of either successional stages or years

between early successional stages and later stages, following a sequence of species over time (i.e., a deterministic process from few pioneer species to competitively dominant non-pioneering species: "Pioneer hypothesis"; Connell and Slatyer 1977). In contrast, dung beetle assemblages from Palmari indicate a negligible turnover and strong nestedness along the successional gradient, with early stages acting as species-poor sub-samples of the later and richer stages (Fig. 6). This nested structure is consistent with the core-satellite species hypothesis proposed by Hanski (1982) and found in the few studies that analyzed this hypothesis in dung beetle assemblages (e.g., Menéndez 1994). This hypothesis states that communities are primarily formed by an initial assembly of core species, which are widely distributed, locally frequent and/or abundant, and better adapted to environmental changes; satellite species, which present a patchy distribution and are locally rare and less adapted to environmental changes, are sequentially added to the assemblage (Hanski 1982). This consistency with a core-satellite pattern suggests that changes in dung beetle assemblage composition in the Amazon are not only a consequence of deterministic successional processes but also of context-dependent historical contingencies and neutral assembly of the species that are more abundant in the landscape.

Although patterns of successional change are seemingly not deterministic, they may have consequences for the functional structure of the assemblages. The species that could be playing the role of "core species" are medium-large paracoprids (such as *D. mamillatus*, *D.* cf. *boreus*, or *D.* cf. *fortestriatus* in the Palmari dataset) and medium-large endocoprids (e.g., *Eurysternus* spp.), whereas those seemingly acting as "satellite species" are small-large telecoprids (e.g., *Canthon smaragdulus* (Fabricius, 1781), *Deltochilum amazonicum* Bates, 1887, or *D.* aff. *pseudoparile*) and small paracoprids (e.g., *Ateuchus* and *Uroxys* spp.). Large paracoprids show the highest performance in terms of dung removal in the ecosystem (Slade et al. 2007), so their presence from the beginning would guarantee the maintenance of an important part of ecosystem functionality. In contrast, large telecoprids, which are more important for seed dispersal (Andresen 2002; Vulinec 2002), may be more vulnerable to habitat transformations (Lobo 2001; Nichols et al. 2013), appearing only in the later successional stages and well-preserved patches. This is congruent with our results which show a perceptible sequence in the dominance of different functional groups along successional stages, shifting first from paracoprids to endocoprids, and then towards large telecoprids. These sequences may relate to either species' specific ecological and physiological requirements or some type of guild facilitation in terms of assemblage structuring, which may affect ecosystem functionality. However, these hypotheses need to be tested in the field with a mesocosm experimental design. Regardless of the existence of a succession or not, a complete set of all functional groups is required in order to maximize ecosystem functioning (Slade et al. 2007; Braga et al. 2013; Milotic et al. 2018).

Caveats

Although Palmari and Monilla are located nearby (approx. 30 km, see Fig. 1), they show small differences in species composition. However, we believe that despite such differences, these two localities provide accurate representations of the variability in central Amazonian dung beetle assemblages at different temporal scales. Note that Korasaki et al. (2013) collected more species than us in a compositionally similar locality near Palmari, possibly due to the lower number of traps (80 vs. ~ 450), sampling points (4 vs. ~ 14–18), and habitats (4 vs. 6) sampled in our study. In any case, the differences between Palmari and Monilla study sites could be related to eventual variations in the soil and forest composition, because they belong to different geomorphological plates (Pebas formation at Palmari and Nauta formation at Monilla) with different evolutionary histories (Higgins et al. 2011). Differences could also be related with some distinctive methodological aspects between the two datasets, such as sampling years and types of bait. We believe that the effects of these differences are small, so the dissimilarities in the assemblages captured in this study correspond to the different temporal factors that we studied, allowing the comparison in terms of the magnitude of compositional change in the two datasets. Note that the differences between sampling designs in the two study sites are due to the specific questions addressed in each site (either successional or interannual changes). Despite these differences, the clear contrast between successional and interannual scales found in this study give us confidence about the reliability of our results.

Conclusions

In summary, dung beetle richness, abundance, and composition of functional groups differ between short- and long temporal scales. In long-term successional scales, dung beetle assemblage structure changes significantly through time, following a nested structure and causing many species and some of the functional groups to disappear in highly disturbed areas. Seasonal changes may follow the same structure, at least to some extent. On the contrary, in short interannual temporal stages richness and functional group composition remain stable, as the turnover between years only affects the identity of some species. Indeed, our results show that dung beetle assemblages in the Amazon region are highly dynamic in time but with contrasting structural beta diversity patterns depending on the processes involved in temporal changes. This evidence stresses the importance of promoting long-term studies (especially long-term trapping) that include temporal beta diversity analysis in order to elucidate insect community dynamics. The inclusion of temporal dynamics in sampling protocols and monitoring studies could favor the confidence and completeness of biodiversity inventories, positively affecting conservation planning strategies (Hewitt et al. 2016). Moreover, it is necessary to study the recovery process of ecological functions in restoration chronosequences, incorporating functional trait data to fully understand the re-establishment and resilience capacity of Amazon rain forests. This enhanced knowledge on the functional dynamics of this hyperdiverse biome will eventually aid specific management and long-term conservation strategies.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-020-04831-5.

Acknowledgements We thank the Faculty of Environmental Engineering of El Bosque University, the Palmari Natural Reserve, and its general manager Axel H. Antoine-Feill for helping with the logistics of field and laboratory work. To Jessica Veloza, Laura Alarcon, Eduardo Castaño, Laura Cifuentes, Felipe Cortes, Edgar Manosalva, Laura Martínez, Mery Tello, Lorena Velandia, and Andrés Vergara for their help during the field work in Palmari. To João Dos Santos, José Neris Da Silva Filho Bare, Franciney Pereira Tapudima “Maneu”, Carlos Acevedo Tapayuri “Maguila”, Francisco Hipolito Avila “Polo”, Ilke Coelho Ribeiro, and Kennedy López for their support and assistance in the Palmari Natural Reserve. To Giovanny Fagua and all the students of the Arthropods course of the Pontificia Javeriana University for their collaboration during the field and laboratory work in Monilla. To Juan Pablo Botero and Marcelo Viola for their valuable help in the cleaning, separation, and initial identification of the samples from Monilla. To Willson Teran and Pilar Marquez for the use of the analytical balance. To Fernando Vaz-de-Mello, David Edmonds, and Edgar Camero for their help in the species confirmation. And finally, to Lucía Maltez from English Syntax for her thorough English revision. This project was partly financed by the Faculty of Environmental Engineering of El Bosque University. JAN was supported by COLCIENCIAS-PDBC PhD scholarship No. 568 of 2012 (Colombia), and AMCS was supported by a ‘Juan de la Cierva’ Fellowship (IJCI-2014-19502) funded by the current Spanish Ministerio de Ciencia, Innovación y Universidades, and by the Portuguese Fundação para a Ciência e a Tecnología (contract CEEIND/03425/2017).

Author contribution statement JAN originally formulated the idea, designed, and performed the samplings; JAN, AMCS, and JH designed research; JAN, AMCS, and JH designed the analyses, with JC and SC; JAN, JC, and SC analyzed the data; all authors interpreted results; JAN, AMCS, and JH wrote the paper; all authors approved the final version of the manuscript.

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