Original Articles

Understanding what bioindicators are actually indicating: Linking disturbance responses to ecological traits of dung beetles and ants

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ABSTRACT

Biological responses to a disturbance can vary among taxa, which challenges the use of bioindicators for representing biodiversity responses more broadly. Linking ecological traits to disturbance response helps clarify what different bioindicator groups are actually indicating, providing a mechanistic basis for predicting the responses of other taxa. Dung beetles and ants are ecologically contrasting but widely used bioindicator taxa. Here we link variation in dung beetle assemblages to body size and dung-feeding behavior, and variation in ant communities to habitat preferences, foraging behaviour and competitive dynamics, to clarify what dung-beetles and ants are indicating in terms of biodiversity responses to pastoral land management in a Brazilian savanna landscape. Dung beetles and ants were sampled at 24 pastoral sites that varied in grass cover, tree density, pasture age, cattle density, and frequency of parasiticide use. Community metrics (abundance, richness, composition, functional group composition) of both dung beetles and ants varied markedly with pastoral land management, but this variation was not correlated, or only weakly, between taxa. For dung beetles, abundance, biomass and richness were all best predicted by frequency of parasiticide use, whereas species composition was best predicted by cattle density. Tree density was the most important variable for explaining ant abundance (both total and of several functional groups) and was also significantly related to ant species composition. Dung beetles and ants provided different indications of the impacts of pastoral management on biodiversity. However, by linking responses to ecological traits we were able to clarify what they were actually indicating. Leaf-cutter ants showed a similar response to dung beetles; collectively they are indicating an impact of parasiticide use on dung-feeders. The abundance of small-sized roller beetles was negatively related to grass cover; along with ants they are indicating the importance of vegetation structure. Such a linking of disturbance responses to ecological traits allows for more-robust predictions of likely responses of other faunal groups. We believe that such an approach provides a substantially improved foundation for the use of bioindicators in land management.

1. Introduction

Biological responses to a disturbance can vary markedly among taxa (Barlow et al., 2007; Filgueiras et al., 2019), and this severely challenges the use of bioindicators (sensu McGeoch, 1998) for representing broader biodiversity responses (Lawton et al., 1998; Barlow et al., 2007). Given highly idiosyncratic responses, the extent to which any bioindication can be generalized is unclear. Moreover, bioindicator responses are often assessed using univariate metrics such as species richness, which often provides little insight into the ecological processes that drive biodiversity responses (Lawton et al., 1998).

An understanding of the relationship between ecological traits of

species and environmental factors can reveal important insights into community dynamics and can substantially increase the predictive power of ecology (Neilly et al., 2018; Wong et al., 2018). A trait-based approach is therefore increasingly being applied to assessments of biodiversity responses to disturbance (Wong et al., 2018). The variability of biodiversity responses to disturbance reflects differences in key ecological traits that mediate these responses. For example, terrestrial and arboreal reptiles have contrasting ecological drivers, which relate to ground-layer complexity in the former, and tree characteristics such as hollows in the latter (Bryant et al., 2012). As a consequence, terrestrial species are sensitive to the impact of livestock grazing, whereas arboreal species are not (Neilly et al., 2018). Similarly, among birds,

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ground-nesting or feeding species are most detrimentally affected by livestock (Bonnaud et al., 2009), whereas the abundance of birds can remain unaffected or even be promoted by pastoralism if trees are not cleared (Lusk and Koper, 2013). Terrestrial vs arboreal reptiles, and ground-active vs arboreal birds, thus provide very different indicators of biodiversity responses to grazing. However, linking of ecological traits to disturbance response provides a mechanistic basis for understanding what the bioindicator is actually indicating, and therefore what other taxa are likely to show similar responses to those of a bioindicator taxon.

Here we take the novel approach of linking the disturbance responses of two widely used bioindicator taxa, dung beetles (Coleoptera: Scarabaeinae) and ants (Hymenoptera: Formicidae), to their ecological traits in order to clarify what the bioindicators are actually indicating in terms of ecological responses to disturbance. Dung beetles are broadly distributed across the tropics (Hanski and Cambefort, 1991), where they play a key role in nutrient cycling through the removal and burial of vertebrate (mostly mammalian) dung (Nichols et al., 2008). The consumption and relocation of dung by Scarabaeinae beetles can also play other important ecological roles, such as soil excavation, secondary seed dispersal, and the control of dung-dwelling pests and intestinal parasites (Nichols et al., 2008). Ants are an ecologically dominant faunal group in most terrestrial ecosystems (Hölldobler and Wilson, 1990), contributing a substantial proportion to total terrestrial faunal biomass and playing fundamental roles in soil development, nutrient cycling, the regulation of insect populations, and plant growth and recruitment (Del Toro et al., 2015). Dung beetles and ants have very different environmental drivers and consequently show very different responses to disturbance (Filgueiras et al., 2019). They therefore can be expected to indicate very different things when used to assess the ecological impacts of disturbance, which they frequently are (Andersen and Majer, 2004; França et al., 2017).

Both dung beetles and ants are frequently classified into functional groups based on ecological traits that facilitate an understanding of their responses to disturbance (Andersen, 1995; Buse et al., 2015). This provides a basis for linking ecological traits to disturbance responses *within* both taxa, thus gaining a more-refined understanding of what they are actually indicating. Dung beetles are commonly classified into functional groups based on body size and their feeding and nesting behavior, traits that have important implications for ecosystem functioning (Hanski and Cambefort, 1991; Barragán et al., 2011). These groups can have markedly different environmental associations. For example, small-sized species tend to have higher thermal tolerances and lower humidity tolerances than large-sized species (Barragán et al., 2011). Similarly, roller species are typically more sensitive to changes in vegetation cover than are other feeding groups (Escobar, 2004). The different dung-beetle groups can, therefore, be expected to provide different indications of disturbance responses.

Ants are frequently classified into functional groups based on their responses to environmental stress and disturbance, and these groups also have markedly different environmental associations (Andersen, 1995, 1997). For example, Dominant Dolichoderinae and Hot-climate specialists strongly prefer open habitats, Cryptic species, Subordinate Camponotini and Specialist predators have specialized habitat and resource requirements, and Epigaeic generalists and Opportunists occur in a wide range of environments (Hoffmann and Andersen, 2003). These different functional groups likewise can be expected to provide very different indications of disturbance responses (Escobar, 2004; Andersen, 2018).

In this study we link environmental responses of dung beetles and ants to their ecological traits for clarifying what they are actually indicating in the context of pastoral land management in a Brazilian savanna. Grazing by livestock is a dominant land-use throughout the world (Reid et al., 2008), and can have a marked impact on the structure of faunal habitat (Eldridge et al., 2011). In addition, intensive pastoral management often involves the use of veterinary medical

products (VMPs; especially ivermectin) for parasite control (Lumaret et al., 1993), and these products are highly toxic if consumed by non-target insects (Floate et al., 2005; González-Tokman et al., 2017). Our study addresses two specific questions: (1) How do responses to pastoral land management vary between dung beetles and ants, and among functional groups within them?; and (2) What environmental and management variables best predict different responses? The results will allow disturbance responses to be linked to ecological traits, and thus enable a better-informed assessment of how other taxa are likely to respond.

2. Material and methods

2.1. Study area

The study was conducted on cattle farms located in the rural outskirts of Uberlândia (18° 56′ 38″ S 48° 18′ 39″ W; approximately 900 m above sea level), Minas Gerais, in the Brazilian cerrado (savanna; Araújo and Haridasan, 1997). The region is characterized by a tropical climate with a cooler dry season (May to September) and a warmer wet season (October to April). The mean annual temperature and precipitation are 22 °C and 1,600 mm respectively (Rosa et al., 1991). The Cerrado is considered a biodiversity hotspot (Myers et al., 2000), and has been extensively converted to agricultural use, including cattle ranching (Sano et al., 2010), which is the dominant land use in the region (INDI network data, 2017). Throughout the study region, native grasses have been largely replaced by exotic species (primarily *Urochloa* spp.) to increase carrying capacity (Pivello et al., 1999), but the taller trees and those of economic importance have generally been retained (Frizzo and Vasconcelos, 2013). More recently, there has been a progressive replacement of traditional extensive grazing in favour of intensive systems (MAPA, 2003), such that the region now has some of the largest cattle herds in Brazil. Intensification has involved an increase in the use of VMPs, mainly based on ivermectin, doramectin and abamectin, which are highly toxic to non-target invertebrates (González-Tokman et al., 2017).

Sampling was conducted within a 4-ha plot in each of 24 pastures representing variation in grass cover (43–100%), tree density (0–40.8/ ha), pasture age (3–100 yrs), cattle density (0.4–389 head/ha), and frequency of VMP use (2–18 times/yr) (Table S1). All pastures were dominated by exotic grasses (*Urochloa decumbens*), and they were separated from each other by at least 3 km. They were located on farms ranging in size from 14 to 950 ha, which represents the size range of farms in the region (IBGE, 2018).

2.2. Dung-beetle and ant sampling

Sampling occurred in the rainy season (months of December 2016 and January 2017), the optimal period of the year to sample both dung beetles and ants in the tropics (Milhomem et al., 2003; Rabello et al., 2015). The same pitfall traps were used to sample both dung beetles and ants. Eight traps were established in each pasture, with traps located at the corners of a 200 × 200 m square, and at the mid-points of the sides of the square. All traps were at least 100 m distant from the pasture edge. Traps were plastic containers (19 cm diam, 11 cm height) filled with 150 ml of a saline solution and detergent. Each trap had a wire hoop suspended over it to accommodate a small (4 cm diam, 4 cm height) plastic container for holding a dung bait. We used a 20 cm diameter plastic cover supported by three sticks to protect traps from rain. Traps were baited with cow dung and left in the field for a 48-hr period in each pasture.

Collected specimens were transported to the laboratory for processing and identification. Dung beetles were identified to genera using the key provided in Vaz-de-Mello et al. (2011) and specialist assistance from Dr. Fernando Vaz de Mello. Ant species were identified to genus using keys in Baccaro et al. (2015) and where possible to species by

Table 1
Spearman correlation values for abundances of dung-beetle and ant functional groups that occurred in more than half of the sites (below the diagonal) and Mantel test statistic (above) of functional groups that were diverse enough for analysis. Statistical significance * P < 0.05, ** P < 0.01, *** P < 0.001.

Functional Group	Small-sized rollers	Small-sized tunnelers	Large-sized tunnelers	Small-sized dwellers	Dominant Dolichoderinae	Epigaeic generalists	Higher Attini	Lower Attini	Opportunists	Specialist predators	Subordinate Camponotini
Small-sized rollers	–										
Small-sized tunellers	0.290	–	−0.096		−0.015	−0.008			0.088	0.104	0.157
Large-sized tunnelers	0.206	0.445*	–		−0.068	0.145			−0.002	−0.039	−0.106
Small-sized dwellers	0.382	0.482*	0.368	–							
Dominant Dolichoderinae	0.167	0.073	−0.102	−0.057	–	0.107			0.128	−0.084	0.071
Epigaeic generalists	0.001	−0.097	0.130	0.366	−0.026	–			0.095	−0.025	−0.008
Higher Attini	0.400	−0.393	−0.007	−0.271	0.019	−0.082	–				
Lower Attini	0.615***	−0.122	0.259	0.020	−0.038	0.492*	0.395*	–			
Opportunists	0.450*	−0.155	0.201	−0.028	−0.445*	−0.033	0.026	0.490*	–	0.074	0.462**
Specialist predators	0.081	−0.450*	−0.025	−0.379	0.375	0.218	0.230	0.466*	0.617	–	0.061
Subordinate Camponotini	0.487*	−0.268	0.130	−0.125	−0.048	0.115	0.707***	0.580**	0.407*	0.067	–

Table 2
Model averaged coefficients and relative importance (within parentheses) of environmental (grass cover and tree density) and management variables (pasture age, cattle density and frequency of application (number per year) of veterinary medical products – (VMP)) used to model the community attributes and functional groups of dung beetles and ants in the pastures of southeastern Brazil. Also shown are the variables included in the minimum adequate model (ΔAICc = 0), the relative weight (w_i) of the model and the amount of variance explained. Significant predictor variables are marked in bold.

Dung beetles	Minimum adequate model			Averaged coefficients (relative importance)				
	Model	w_i	PseudoR^2	Grass cover	Tree density	Pasture age	Cattle density	VMP
Richness	VMP	0.30	0.27	−0.076 (0.23)	0.021 (0.17)	0.034 (0.16)	−0.113 (0.28)	**− 0.210 (0.82)**
Abundance	VMP	0.30	0.24	−0.043 (0.16)	0.118 (0.19)	0.072 (0.18)	0.437 (0.39)	**− 0.579 (0.96)**
Biomass	TD + VMP	0.36	0.32	0.068 (0.18)	0.430 (0.69)	−0.077 (0.15)	−0.036 (0.22)	**− 0.627 (0.81)**
Small- sized roller	GC + VMP	0.27	0.31	**−0.771 (0.83)**	0. 492 (0.24)	0.208 (0.16)	0.649 (0.29)	**− 0.785 (0.83)**
Small-sized tunneler	TD	0.16	0.15	0.166 (0.18)	−0.427 (0.45)	−0.115 (0.17)	0.492 (0.32)	− 0.524 (0.55)
Large-small tunneler	TD + VMP	0.18	0.26	0.123 (0.19)	−0.286 (0.21)	0.172 (0.22)	−0.246 (0.27)	**− 0.438 (0.69)**
Small-sized dwellers	VMP	0.19	0.14	−0.055 (0.15)	−0.438 (0.28)	0.473 (0.23)	0. 830 (0.46)	**− 0. 901 (0.82)**
Ants								
Richness	TD + PA	0.16	0.31	−0.070 (0.51)	0.076 (0.55)	**0.116 (0.88)**	−0.003 (0.18)	0.003 (0.17)
Abundance	TD + VMP	0.29	0.39	−0.074 (0.23)	**0.284 (1.00)**	−0.062 (0.19)	−0.018 (0.19)	−0.165 (0.51)
Arboreal specialists	GC + PA	0.2	0.45	**−0.607 (0.87)**	−0.091 (0.16)	0.527 (0.53)	−0.224 (0.23)	0.325 (0.34)
Cryptic species	Null	0.23		0.559 (0.30)	0.032 (0.17)	− 0.123 (0.16)	0. 490 (0.24)	0.471 (0.23)
Dominant Dolichoderinae	Null	0.22		− 0.318 (0.34)	0.063 (0.18)	−0.215 (0.27)	− 0. 149 (0.23)	−0.001 (0.16)
Epigaeic generalists	TD + CD	0.13	0.28	0.277 (0.34)	0.367 (0.50)	0.317 (0.36)	0.401 (0.61)	−0.099 (0.21)
Hot-climate specialists	GC	0.32	0.39	**−0.484 (1.00)**	− 0.014 (0.17)	0.266 (0.38)	0. 042 (0.17)	0.078 (0.18)
Higher Attini	TD + VMP	0.25	0.36	−0.473 (0.39)	**0.841 (0.88)**	0. 252 (0.22)	− 0.397 (0.24)	**− 0. 842 (0.79)**
Lower Attini	PA	0.16	0.10	− 0.162 (0.22)	0.270 (0.31)	0.419 (0.51)	0.230 (0.24)	− 0. 212 (0.24)
Opportunists	TD + VMP	0.14	0.25	−0.119 (0.15)	0.659 (0.66)	0. 235 (0.16)	− 0. 312 (0.32)	−0.470 (0.52)
Specialist predators	TD + CD	0.20	0.41	0.008 (0.14)	**0.464 (0.79)**	**0.486 (0.56)**	−0.324 (0.50)	0.174 (0.21)
Subordinate Camponotini	TD	0.30	0.27	− 0.035 (0.16)	**0.568 (0.90)**	− 0. 131 (0.19)	−0.036 (0.17)	− 0. 321 (0.31)

comparison with named species in the Zoological Collection at the Federal University of Uberlândia (UFU). For species that could not be confidently named we assigned a morphospecies code. Vouchers of all ant and beetle species were deposited at UFÚs Zoological Collection.

2.3. Response variables and functional group classification

For both dung beetles and ants we analysed variation in abundance, species richness and functional-group composition among pastures. We also used body mass as a response variable for dung beetles. To obtain an estimate of the total biomass of dung beetles we first weighed up to 30 individuals of each species (and where possible, a similar proportion of males and females), drying all specimens in a constant-temperature oven at 40 °C for 4 days before weighing them on a precision scale (0.0001 g). The average mass of each species was then multiplied by its abundance in each pasture.

Based on the distribution of body masses (as a measure of size; Barragán et al., 2011; Carvalho et al., 2018 (Fig. S2)), we classified the species as small (< 100 mg) or large (> 100 mg). We also classified

dung beetle species based on feeding/nesting behavior as: rollers (species that make a dung ball and roll it away for burial), tunnelers (species that store dung in tunnels dug immediately below the dung source) or dwellers (species living within or immediately below the dung, without moving it) (Hanski and Cambefort, 1991) (Table S3). Such classification was based on leg morphology (roller species have curved and elongated posterior tibias, tunnelers have well-developed anterior tibias, and dwellers have developed medium legs (Halffter and Edmonds, 1982)), behavioural observations of some species *(Canthon lituratus, Dichotomius bos, Onthophagus hircus, Trichillum heydeni and Trichillum externepunctatum),* published information (Halffter and Edmonds, 1982; Hanski and Cambefort, 1991; Koller et al., 2007; Almeida and Louzada, 2009; Filgueiras et al., 2011), or with the assistance of a dung-beetle specialist (Dr. Fernando Vaz-de-Mello). We chose to classify species based on body size and feeding/nesting behavior because these traits are especially sensitive to habitat disturbance (Escobar, 2004; Imura et al., 2014). Food preference was not considered because the vast majority (> 90%) of dung beetles in our pastures are coprophagous (F. Vaz-de-Mello, unpublished data). We
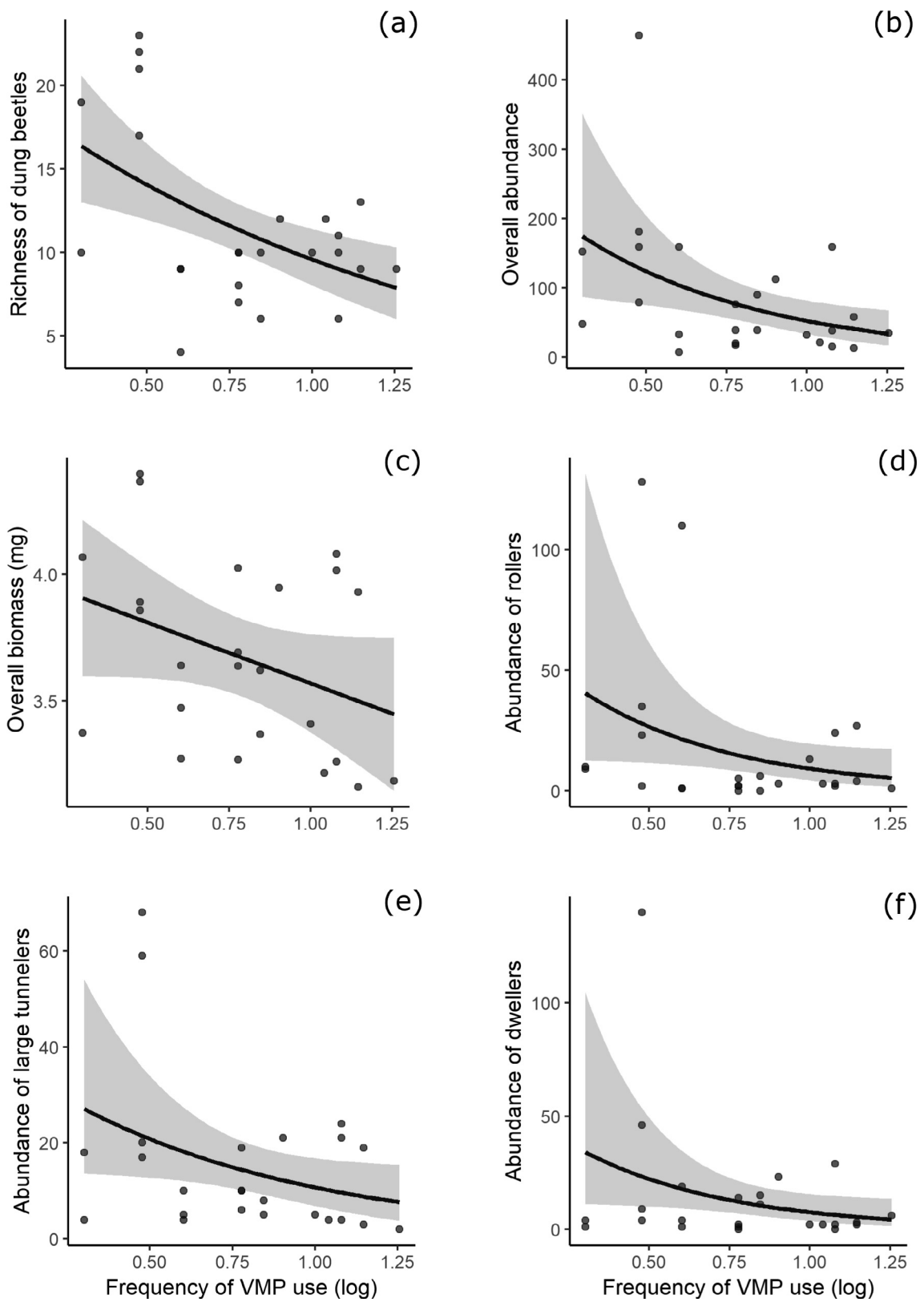
Fig. 1. Effect of the frequency of application (number per year) of Veterinary Medical Products (VMP) on various attributes of the community of dung beetles: (a) species richness, (b) overall abundance, (c) biomass, (d) abundance of small-sized rollers, (e) large-sized tunelers, and (f) small-sized dwellers. The shaded area shows the 95% confidence interval of the best-fit generalized linear model. Analyses were performed using log-transformed VMP frequency data to improve model fit.

Table 3

Distance-based linear modelling (DistLM) of dung beetle and ant species composition with environmental (grass cover and tree density) and management variables (pasture age, cattle density and frequency of application (number per year) of veterinary medical products (VMP)). Statistical significance * P < 0.05.

Variable	AICc	SS (trace)	Pseudo-F	P	Prop	res.df
Marginal tests – Dung beetles						
Grass cover	–	1053.1	0.681	0.705	0.030	22
Tree density	–	1148.1	0.745	0.685	0.033	22
Pasture age	–	1169	1.100	0.387	0.047	22
Cattle density	–	2904.3	1.998	0.040*	0.088	22
VMP	–	2374.3	1.598	0.127	0.067	22
Sequential tests – Best solution						
Cattle density	176.8	–	–	–	0.088	–
Marginal tests – Ants						
Grass cover	–	2551.3	1.947	0.010*	0.081	22
Tree density	–	2179.4	1.793	0.010*	0.075	22
Pasture age	–	1644.9	1.327	0.171	0.056	22
Cattle density	–	965.15	0.759	0.759	0.033	22
VMP	–	1423.1	1.139	0.340	0.049	22
Sequential tests – Best solution						
Grass cover + Tree density	172.14	–	–	–	0.157	–

also did not consider diel activity because it is not directly relevant to responses to land use (see Slade et al., 2011). However, we note that diurnal activity is often associated with smaller body size (Slade et al., 2007), while nocturnal species are often larger (Chown and Klok, 2011), and we already have incorporated body size into our classification.

Ant species were classified into functional groups based on their responses to environmental stress and disturbance. Such functional group classification was originally proposed by Andersen (1995), and then adapted for the Neotropics by Leal et al. (2012): (1) Arboreal specialists, comprising tree-nesting species of *Cephalotes* and *Pseudomyrmex;* (2) Cryptic species, comprising specialist cryptobiotic taxa that nest and forage exclusively in soil and litter; (3) Dominant Dolichoderinae, comprising mass-recruiting, behaviourally dominant species of *Dorymyrmex* and *Forelius*; (4) Epigaeic generalists, comprising a range of generalized, ground-nesting taxa; (5) Hot-climate specialists, comprising a single species, the specialist granivore *Pogonomyrmex naegelii*; (6) Higher Attini, comprising species of the leaf-cutting genera *Atta* and *Acromyrmex,* which are functionally herbivorous; (7) Lower Attini, which grow their fungus on dead organic material and are functionally detritivorous; (8) Opportunists, comprising species of the disturbance-tolerant genera *Ectatomma, Brachymyrmex* and *Nylanderia*; (9) Specialist predators, comprising species that feed primarily on live prey (Ponerinae, Dorylinae and *Gnamptogenys*); (10) Subordinate Camponotini, comprising species of *Camponotus*, whose submissive behaviour allows them to co-exist with behaviourally dominant species (Table S4).

Voucher specimes of all dung beetle and ant species have been deposited in the Zoological Collection at the Federal University of Uberlândia.

2.4. Predictor variables

A range of predictor variables relating to vegetation structure and cattle management (collectively referred to as pastoral land management variables) were quantified. Grass cover and tree density were used as measures of vegetation structure. Grass cover was visually estimated within a 1 × 1 m quadrat centred on each pitfall trap, and tree density was calculated by counting the number of trees (height > 1 m) in each 4-ha plot. Three variables associated with cattle management were quantified based on interviews with farmers: time since the pasture had been established (pasture age), cattle density, and frequency of application (number per year) of veterinary medical products – VMP. Cattle

density reported by farmers (cows per unit of area) represented the average value over the three years prior to our interview.

2.5. Data analysis

All analyses were performed on plot-level data (n = 24). We used Spearman rank correlation (due to the absence of normality and homoscedasticity) to test for associations between dung beetles and ants in terms of overall abundance and species richness. We also conducted Spearman rank correlation analysis for the abundances of each pair of functional groups that occurred at more than half of the sites. This excluded three ant functional groups, Arboreal specialists, Cryptic species and Hot-climate specialists. To compare compositional responses of dung beetles and ants, we first constructed Bray-Curtis similarity matrices, based on abundance data. We then conducted Mantel tests to assess the correlation between the matrices within and between taxa in the "vegan" package in R (Oksanen et al., 2016; R Core Team, 2018). We repeated this for each pair of functional groups that occurred in at least 23 sites: Small and large tunneler dung beetles, and Dominant Dolichoderinae, Generalist epigaeic, Opportunist, Specialist predador and Subordinate Camponotini ants.

We built generalized linear models (GLMs) using the R package "MASS" (Venables and Ripley, 2002) to evaluate the effect of the pastoral land management variables on the abundance and richness of dung beetles and ants, the biomass of dung beetles, and the abundance of each dung-beetle and ant functional group. To improve the linearity of our models we log$_{10}$-transformed the variables tree density, pasture age, cattle density and frequency of VMP use, and logit-transformed percentage of grass cover prior to the analyses. For analyses of species richness we used the Poisson distribution (Hilbe, 2007), whereas the negative binomial distribution was used for analyses involving abundance and biomass. We used the logarithimic link function in all cases, except for non-count data (namely, beetle biomass) and for data on abundance of Generalist and Opportunist ants as in these cases the identity link function provided a better model fitting. The residuals of all models were analysed to verify the adequacy of the models (Crawley, 2013).

We assessed collinearity among our predictor variables using the Variance Inflation Factor (VIF). Predictors holding VIF values > 10 are considered multicolinear and should be removed from the model (Kutner et al., 2004). As none of our predictors achieved VIF > 2.37 (Table S2), all were maintained in our analyses. We selected our models based on the Akaike criterion corrected for small sample size (AICc). Most of the best models had a low support value (as indicated by the Akaike weight; w_i), and so we implemented a model averaging procedure (Burnham and Anderson, 2002). For each response variable, we used standardized coefficients of the weighted model to compare the effect size across predictor variables (Burnham and Anderson, 2002). We established the individual contribution of each variable by the sum of the values of w_i of all the models that included the variable. Multi-model selection and model averaging were conduted in R (R Core Team, 2018), using the "MuMIN" package (Barton, 2016).

We tested the importance of pastoral land management variables as predictors of variation in species composition (as shown by our Bray-Curtis matrices), by building Distance-based Linear Models (DistLM) (Legendre and Anderson, 1999). DistLM uses a "best method" AIC-model selection procedure (Burnham and Anderson, 2004) considering the value of the selection criterion for all possible combinations of predictor variables. Marginal tests, evaluating the relationship between species composition and each predictor variable individually, were also carried out and the results compared with the "best solution" models derived from the conditional tests above. All P-values were generated by permutation (n = 999). Analyses using DistLM were conducted in PRIMER V.7 with PERMANOVA (Clarke and Gorley, 2015).
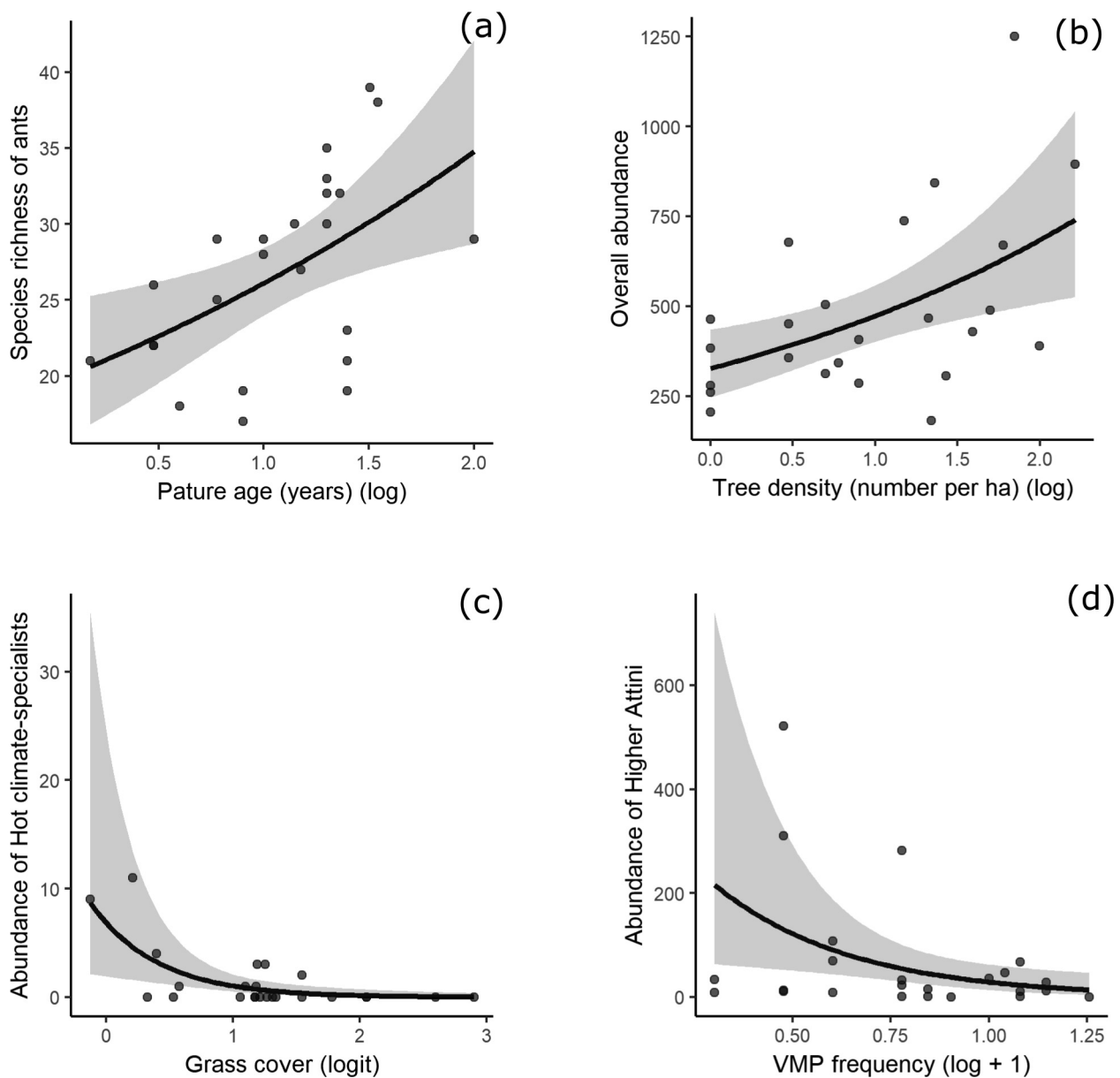
Fig. 2. Effect of the environmental and pasture management variables on some attributes of the ant community: (a) species richness, (b) overall abundance, (c) Abundance of Hot-climate specialists (d) Abundance of Higher Attini. The shaded area shows the 95% confidence interval of the best-fit generalized linear model. Data on pasture age, tree density and VMP frequency of use were log-transformed, whereas data on grass cover was logit transformed to improve model fit.

3. Results

3.1. The dung-beetle and ant faunas

We collected a total of 2,047 individuals (range of 7–464 per pasture) of 40 species (4–23) of dung beetles. *Dichotomius* was the most diverse genus with seven species, and the most common species were *D. bos* and *Trichillum externepunctatum,* which both occurred in 20 pastures. Small-sized tunnelers was the most abundant (44.5% individuals) and richest (40% species) functional group. All the roller and dweller species we collected were of small size (Table S3).

A total of 11,583 ants (range 312–738 per pasture) from 98 species (17–39) and 39 genera was recorded (Table S4). *Pheidole* was the most diverse genus, with 16 species, followed by *Camponotus*, *Solenopsis* and *Trachymyrmex* with 8 species each. *Pheidole subarmata* occurred in all pastures, and *P. oxyops* and *P. radoszkowskii* were each found in 23 of the 24 pastures. The richest functional groups were Epigaeic generalists (30 species), Lower Attini (16), Specialist predators (13) and Dominant

Dolichoderinae (10).

3.2. Cross-taxon congruence

There was no correlation between dung beetles and ants for either total abundance ($r_s = 0.063$, $p = 0.768$) or species richness ($r_s = 0.318$, $p = 0.129$) per site. Most (74.5%) of the 55 functional-group pairs analysed were not significantly correlated. The significant correlations ranged from weakly negative (Dominant Dolichoderinae and Opportunists: $r_s = -0.445$, $p < 0.05$) to strongly positive (Subordinate Camponotini and Higher Attini: $r_s = 0.707$, $p < 0.001$; Lower Attini and small-sized rollers: $r_s = 0.615$, $p < 0.001$; Table 1).

Similarity matrices for dung beetles and ants were not correlated (Mantel test: $r = 0.045$; $p = 0.281$), indicating that site variation in species composition was markedly different for the two taxa. Correlations among functional groups were either weak or not significant (Table 1), indicating that patterns of species composition were markedly different among functional groups within each taxon.

3.3. Reponse to pastoral land management variables

VMP use was by far the most important factor explaining variation in the abundance and diversity of dung beetles. VPM use was negatively related to overall beetle abundance, biomass and species richness, and to the abundances of large-sized tunnelers, small-sized rollers, and small-sized dwellers (Table 2; Fig. 1). The only other significant variable in any of the dung-beetle GLMs was grass cover, which was negatively related to the abundance of small-sized rollers. In contrast to univariate responses, VMP use was not a significant factor explaining variation in species composition of dung beetles, where cattle density was the only significant predictor variable (Table 3).

The most important variable for explaining ant abundance was tree density, which was significant in the GLMs for total abundance and for the abundances of Higher Attini, Specialist predators and Subordinate Camponotini (the relationship was positive in all cases; Table 2). VMP use was a significant variable only for Higher Attini. The only other significant variables in ant GLMs were pasture age, which was positively related to ant species richness, and grass cover, which was negatively related to the abundance of Arboreal and Hot-climate specialists (Table 2; Fig. 2). Grass cover and tree density were the only significant variables explaining variation in ant species composition (Table 3).

4. Discussion

The highly idiosyncratic responses of different taxa to disturbance pose a major challenge to the use of bioindicators for representing biodiversity more generally. An ecological trait approach can help provide a mechanistic understanding of disturbance responses of bioindicator taxa, and thereby clarify what they are actually indicating. We have taken the novel approach of linking environmental responses of dung beetles and ants to their ecological traits in order to clarify what they are indicating in the context of pastoral land management in a Brazilian savanna.

We first asked how responses to pastoral land management vary between dung beetles and ants, and among functional groups within them. We found that the abundance, richness and composition of both dung beetles and ants varied markedly among pastures with different management histories, as has been previously demonstrated (e.g. dung beetles: Imura et al., 2014; Tonelli et al., 2017; ants: Arcoverde et al., 2017; both groups: Verdú et al., 2011). However, dung beetles and ants showed no congruent spatial patterns of abundance and diversity, such that dung beetles and ants provided very different indications of the impacts of pastoral land management on biodiversity.

We classified both dung beetles and ants into functional groups in order to provide a clearer perspective on their disturbance responses. Responses varied markedly among functional groups within both taxa, as illustrated by generally weak or no correlations in abundance or species composition. This further highlights the lack of generality of biodiversity responses, and the need for a mechanistic understanding to allow for an interpretation of the responses.

We sought such a mechanistic understanding by examining which environmental variables best predicted dung-beetle and ant responses. We found that significant environmental predictors varied markedly between dung beetles and ants, and often among their component functional groups, consistent with their contrasting responses to pastoral land management. The major driver of variation in dung beetle communities was VMP use, with overall abundance, biomass and species richness, and the abundances of most functional groups, all negatively related to the frequency of VMP use. VMP residue within dung retains insecticidal activity (Schmidt, 1983) and can negatively affect larval and adult survival, along with the reproductive, sensorial and locomotor activity of dung beetles (Lumaret et al., 1993; Verdú et al., 2015). Among ants, VMP use was related only to leaf-cutter ants (Higher Attini). In our study area, leaf-cutter ants were frequently seen

removing large amounts of bovine dung, presumably for fungus-culturing. We are not aware of any study that has directly analyzed the effect of VMPs on the fungus cultivated by leaf-cutter ants, but long-term exposure to ivermectin is known to decrease the formation and germination of spores in some types of fungi (Kollmann et al., 2003). High concentrations of VMPs have been shown to affect the reproduction and survival of leaf-cutter ant queens (Antunes et al., 2000). The parallel responses of dung beetles and leaf-cutter ants suggest that VMP use would be a major driver of the diversity of insects and other invertebrates more generally that feed on cattle dung.

Species composition of dung beetles was not related to VMP use, suggesting that most species were similarly affected. The major predictor of species composition was cattle density, which also had a near-significant relationship with total abundance of dung beetles. Variation in cattle density is likely to have both direct and indirect effects on dung beetles. More cattle means more dung and thus more food resources for beetles, and previous studies show that dung availability can affect both the abundance (Tonelli et al., 2017) and species composition of dung beetles (Lobo et al., 2006). The abundances of *Dichotomius glaucus, Oxysternon palaemon* and *Sulcophaneus menelas* (large-sized tunnelers) were all negatively related to cattle density, whereas that of *Onthophagus appendiculatus* (small-sized tunneler) was positively related. All these species are coprophagous (Almeida and Louzada, 2009; Vaz-de-Mello, personal observation), and so their different responses to cattle density do not appear to be related to diet. Rather, we suggest that such responses are due to soil compaction, given that soil compaction can also increase with cattle density (Negro et al. 2011; R. Carvalho unpublished data). Soil compaction is an important factor influencing the composition of dung beetles, having a particularly detrimental effect on large-sized tunnelers (Jankielsohn et al. 2001; Negro et al. 2011). Large tunnelers are known to be more sensitive to cattle disturbance through soil compaction than other functional groups (Jankielsohn et al. 2001; Negro et al. 2011).

In contrast to dung beetles, vegetation structure (tree density and grass cover) was the main driver of variation in ant communities in our pastoral system. Total ant abundance was positively related to tree density, which reflects the importance of trees in providing ant nesting sites (Frizzo and Vasconcelos, 2013) and food resources (Arnan et al., 2007), and in ameliorating the microclimate (Perfecto and Vandermeer, 1996). Tree density was also a predictor of the abundance of the ant functional groups Higher Attini, Subordinate Camponotini and Specialist predators, which is consistent with their ecological traits. Trees provide Higher Attini with their favoured leaf resources (Leal et al., 2012), and many species of Subordinate Camponotini nest and forage in trees for honeydew or extra-floral nectar (Camarota et al., 2015). The response of Specialist predators suggests that trees provide important prey resources for ants.

Another vegetation attribute, grass cover, was negatively related to the abundance of Arboreal specialists and Hot-climate specialists. The latter strongly prefer open environments (Andersen, 1995), and often benefit from moderate disturbance (Andersen, 2018). The abundance of small-sized roller dung beetles was also negatively related to grass cover, as also found by Louzada et al. (2010). This is presumably because high grass cover impedes the rolling of dung balls. The responses of Hot-climate specialist ants and small-sized roller dung beetles are likely to reflect those of other arthropod groups that favour open environments. Both grass cover and tree density were significant predictors of variation in ant species composition, which is consistent with the known sensitivity of ant communities to variation in vegetation structure, and particularly the effects of habitat openness on microclimate and locomotory activity (Andersen, 1995, 2018).

In conclusion, we have found that two commonly used bioindicator groups show contrasting responses to pastoral land management in a Brazilian savanna, and therefore provide very different indications of the impact of pastoral land management on biodiversity. However, by linking responses to ecological traits we have been able to clarify what

the bioindicators are actually indicating. Dung beetles and leaf-cutter ants are indicating an impact of VMPs on dung-feeding invertebrates (Floate et al., 2005) and other invertebrates relying on food derived from dung (Puniamoorthy et al., 2014). Ant communities are indicating the importance of vegetation structure, and particularly the role of trees in providing nesting and food resources for fauna (Frizzo and Vasconcelos, 2013; Neilly et al., 2018). Ants and small-sized roller beetles are indicating the effects of ground-layer openness on microclimate and locomotory activity. We believe that such a linking of disturbance responses to ecological traits provides a substantially improved foundation for the use of individual taxa as bioindicators in land management.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.105764.

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