ORIGINAL ARTICLE

Critical tipping points in dung beetle communities: Implications for conservation in the Atlantic Forest biome

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Abstract

1. Anthropogenic land-use changes represent a significant but poorly understood threat to global biodiversity, particularly among invertebrates. Dung beetles, a diverse and widely distributed group, play key roles in ecosystem functioning and are highly sensitive to environmental changes, making them valuable bioindicators for assessing human impacts. One approach to understanding these impacts involves identifying ecological thresholds, which indicate nonlinear shifts in biodiversity along land-use and land-cover gradients. Identifying ecological thresholds offers critical insights into how species and ecosystems respond to human-induced environmental changes. The Brazilian Atlantic Forest, a global biodiversity hotspot, is well suited for studies exploring ecological thresholds as it faces ongoing ecological transformations driven by deforestation, agricultural expansion and urbanization.

2. In this study, we aimed to (i) identify key environmental drivers of shifts in dung beetle communities, (ii) determine critical thresholds for compositional turnover in these communities and (iii) explore patterns across taxonomic, functional and phylogenetic dimensions within this taxon.

3. We found that even minor land-use changes trigger abrupt biodiversity shifts across all diversity dimensions, consistently benefiting generalist species while excluding sensitive specialists. The observed shifts occurred at lower levels of environmental change rates than previously recognized, with significant changes evident after just 25% of habitat loss.

4. Our results challenge existing conservation thresholds and provide an evidence-based framework to update environmental laws, guide protected area expansion and direct targeted restoration efforts. We recommend conducting more comprehensive studies to assess ecological thresholds across a broader range of taxa and geographic regions within the Atlantic Forest biome. Advancing conservation

strategies with improved threshold knowledge will be critical to maintain the forest's ecological resilience and functional integrity.

INTRODUCTION

Biodiversity change resulting from anthropogenic impacts represents one of the most striking aspects of global environmental transformation (Barlow et al., 2016; Malhi, 2017). However, it is far more complex than the mere loss of species and involves changes in different dimensions including taxonomic, functional and evolutionary, each with different impacts on ecosystem properties such as function and resilience (Anunciação et al., 2021; Maurenza et al., 2024; Staude et al., 2020). Local and regional scales typically reveal the first signs of biodiversity change, with shifts in assemblage composition often leading to the formation of novel communities (Hillebrand et al., 2018; Schittko et al., 2020). Such transformations, or turnover processes, constitute direct responses to environmental drivers frequently linked to human activities. While natural changes often develop gradually, human-induced impacts can trigger drastic habitat changes within a short period of time, leading to significant ecological responses even after minor disturbances (Folke et al., 2004; Groffman et al., 2006; Moreno-Mateos et al., 2020). Under such rapid and intense environmental pressures, ecosystems may cross ecological thresholds—critical points at which community composition and ecosystem properties undergo profound transformations (Groffman et al., 2006; Scheffer et al., 2001).

Ecological thresholds have recently gained prominence as pivotal benchmarks for delineating acceptable boundaries of human interventions within ecosystems (Sardanyés et al., 2024; Shennan-Farpón et al., 2021). While species composition shifts are typically observed when only 30%–50% of the original habitat remains (e.g., Banks-Leite et al., 2014; Pardini et al., 2010; Shennan-Farpón et al., 2021), recent studies in rainforest ecosystems indicated that such transitions can already be observed with a loss of less than 20% of the original habitat (Anunciação et al., 2021), suggesting that these systems are much more sensitive to habitat loss than previously assumed. Moreover, taxon-based threshold analyses are criticized for lacking complexity, often focusing on the use of one-dimensional taxonomic response metrics, limiting generalizations at the ecosystem or community level (Banks-Leite et al., 2014; Boesing et al., 2018; Magioli et al., 2015; Roque et al., 2018).

Previous studies showed that simple taxonomic diversity dimensions often fail to capture the true impact of land-use change (Anunciação et al., 2021; Boesing et al., 2018; Ernst et al., 2006), while multidimensional diversity analyses provide a more comprehensive understanding of ecosystem responses to land-use change and therefore support more effective conservation strategies (Cadotte & Tucker, 2018). Therefore, we propose a broader, multidimensional threshold approach that encompasses not only the taxonomic

dimension but also functional and phylogenetic dimensions, ensuring a more precise and comprehensive understanding of responses (Linquist et al., 2016).

We applied our approach to one of southern Brazil's most dynamically changing ecosystems, the exceptionally species-rich and highly threatened Brazilian Atlantic Forest, which has lost more than 75% of its original cover primarily due to urbanization, industrialization and agricultural expansion (Marques & Grelle, 2021; Vancine et al., 2024). While these factors have driven economic growth, they have also led to a historic loss and fragmentation of natural habitats, rendering this biome one of the top biodiversity hotspots (de Lima et al., 2020; Hrdina & Romportl, 2017). Our analysis focused on dung beetles, a group highly sensitive to environmental changes and particularly diverse in the Atlantic Forest (Nichols et al., 2007). Dung beetles serve as critical ecosystem engineers, influencing ecosystem functions through processes such as secondary seed dispersal, nutrient cycling and soil aeration. As such, they are valuable indicators of habitat change (Nichols et al., 2007, deCastro-Arrazola et al., 2023).

Our study followed a three-step approach: (i) identifying relevant environmental predictors of dung beetle community shifts, (ii) determining critical values (thresholds) corresponding to compositional turnover for these communities and (iii) identifying patterns among taxonomic, functional and phylogenetic dimensions within this taxon.

We hypothesize that forest conversion to pastures, and the associated increase in domestic herbivores (e.g., cattle), may enhance food availability for generalist dung beetles. In contrast, we expect that forest-dependent specialist species will decline due to habitat loss and reduced access to suitable microhabitats and resources (Arellano et al., 2023; Nichols et al., 2009). Concerning diversity dimensions, while we expect similar environmental predictors, the actual explanatory power may vary depending on the extent of trait redundancy (evolutionary convergent patterns) and response similarity between closely related species (phylogenetic signal) in our study system (Cadotte et al., 2017; Funk & Wolf, 2016). Our integrative assessment methodology enhances the understanding of the multifaceted impacts of habitat modification and transformation, offering support for effective biodiversity conservation and land-use management.

MATERIALS AND METHODS

Study area

We conducted our research in the northeastern region of São Paulo state, located within the Atlantic Forest biome in southeastern Brazil

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(Figure 1). Despite the presence of several protected areas and relatively large forested regions, much of its natural habitat has historically been converted into agricultural fields, grasslands managed for livestock and commercial plantations (Barros et al., 2019).

Study design, data acquisition and preparation

Dung beetles were sampled across 30 sample units (SUs), representing a forest cover gradient from 13% to 98%, using a 300-m radius identified as the optimal response scale for dung beetle richness (Tavares, 2018). To ensure independence, the SUs were spaced at least 2 km apart (Table S1, Figure 1).

For each SU, we used high-resolution satellite imagery (1:7000 scale, DigitalGlobe satellites 2010–2011, ArcGIS 10.3 basemap imagery) and conducted field verification as needed to map land use, hydrography and road corridors. Land use and cover were classified into eight categories: forest, *Eucalyptus* monoculture, bare soil, urban areas, agriculture, pioneer vegetation, water bodies and wetlands (Table S2). We defined nonlinear environmental gradients by calculating the percentage of land cover for each category within the SUs.

To address collinearity among environmental predictors, we employed variance inflation factor (VIF) with a conservative threshold of 0.5 as the exclusion criterion. While thresholds of 5 or 10 are more commonly used to identify severe multicollinearity (Dormann et al., 2013; Zuur et al., 2010), we adopted a stricter cut-off to ensure maximal independence among predictors, given our limited sample size and the sensitivity of tree-based models to redundant variables.

This process reduced the original eight predictors to seven: forest, eucalyptus, urban areas, pioneer vegetation, water bodies, bare soil and agriculture. Although both wetlands and forest exceeded the VIF threshold, we retained forest due to its ecological importance for dung beetles and its relevance to our hypotheses.

In addition to the VIF analysis, we examined the Pearson correlation matrix for all predictors. While VIF inherently accounts for correlations among predictors, the correlation matrix allows the inspection of bivariate relationships, confirming minimal collinearity among the retained variables (Tables S3 and S4).

We sampled dung beetles using baited pitfall traps arranged in a linear transect at each SU from February 2016 to January 2017. We buried the pitfall traps, which were plastic containers (11 cm depth, 19 cm diameter), in the ground and shielded them from rain with a suspended plastic cover. Each trap contained a lethal solution of water, salt and detergent. At each SU, we deployed four traps, spaced 50 m apart, baited with a 50-g mixture of human and pig faeces for the first trap and 500 g of cattle dung for the others (Marsh et al., 2013). Each baited pitfall trap remained in the field for 48 h to document beetle activity across all diel periods (diurnal, crepuscular and nocturnal). Continuous exposure avoids bias toward any single activity phase and is supported by standardized dung beetle sampling protocols in both tropical and temperate regions (Lobo & Cuesta, 2021; Mora-Aguilar et al., 2023). All collected beetles were preserved in 70% ethanol. FZVM identified specimens to genus level using (Vaz-De-Mello et al., 2011) and to species level with references from previous literature (Vaz-de-Mello & Génier, 2009; Vaz-de-Mello, 2008) and newer revisions
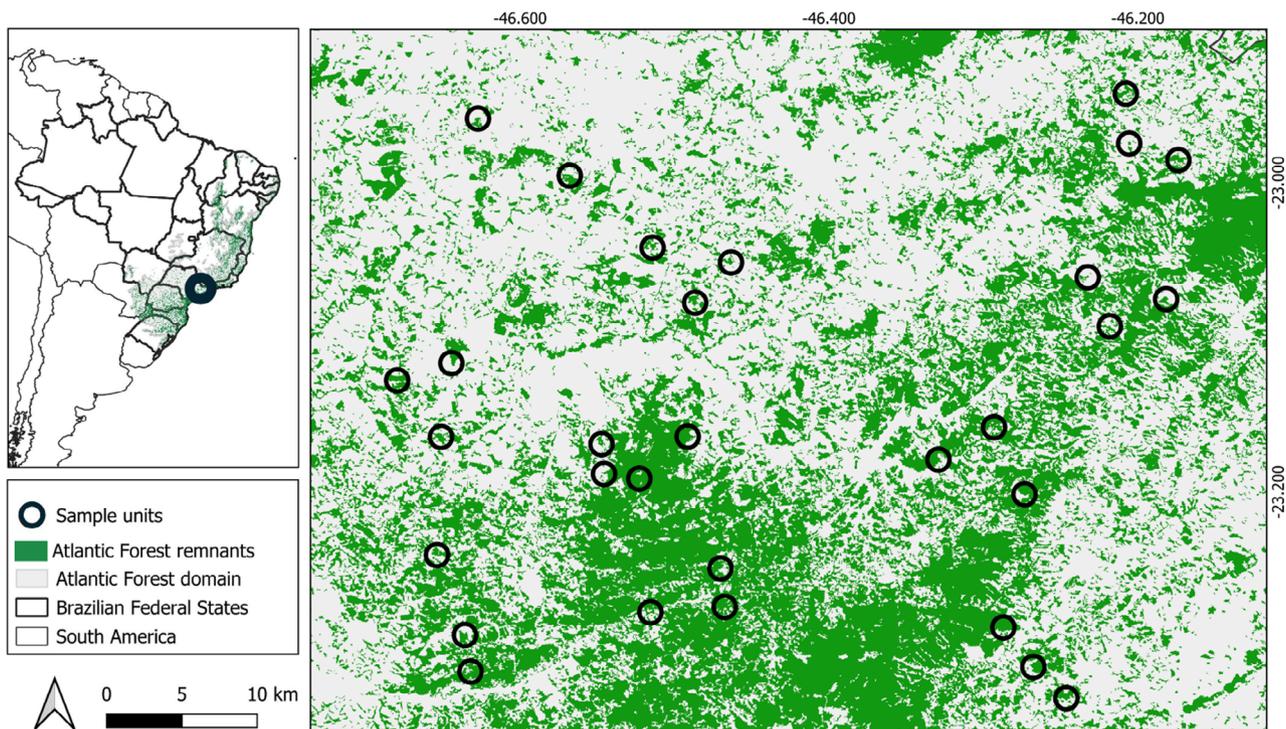
FIGURE 1 Study region in the southeastern Brazilian Atlantic Forest, showing the sample units for dung beetles. Green patches indicate native forest cover, while the background represents the non-forest matrix.

(Arias-Buriticá & Vaz-de-Mello, 2012; Cupello & Vaz-de-Mello, 2014, 2018; González-Alvarado & Vaz-De-Mello, 2014, 2021; Rossini & Vaz-de-Mello, 2015; Silva et al., 2015; Nunes & Vaz-De-Mello, 2016, Nunes et al., 2020; Maldaner et al., 2017; Valois et al., 2017; Pacheco & Vaz-De-Mello, 2020; Rossini et al., 2018; González-Alvarado et al., 2019; Vaz-de-Mello & Silva, 2017; Arias-Buriticá et al., 2023, 2024; Cupello et al., 2023; Costa-Silva et al., 2024), by comparing specimens with reference collections from CEMT (Coleção Entomológica de Mato Grosso Eurides Furtado, Universidade Federal de Mato Grosso, Cuiabá, Brazil) and type-specimen images. Most specimens are deposited at CEMT. To determine the biomass for each species, we weighed 15 individuals of each species using a precision balance (0.001 g) and calculated the mean weight per species.

We compiled the trait matrix for functional analyses of dung beetle communities based on a combination of data from literature, the assignment by experts to predefined categories and directly measured traits of collected specimens. We assessed seven traits: body size, body mass, diet, time of activity, relocation behaviour and measurement-based traits (wing aspect ratio and wing load). For wing aspect ratio and wing load, we measured the left wing of 10 specimens per species, when possible. We measured a total of 355 specimens representing 51 species (Anunciação et al., 2025a, 2025b). We dissected the wings, prepared microscope slides for photography and measurements and mounted cards below voucher specimens. Using a Leica model m205C stereo microscope with an image capture system, we measured wing length, wing width and wing area. We calculated wing aspect ratio as $(4 \times \text{wing length}^2)$/total wing area and wing loading as the ratio of body mass to total wing area. We selected these traits for their effectiveness in predicting the responses of species to anthropogenic environmental changes (deCastro-Arrazola et al., 2023; Nichols et al., 2007). After performing collinearity analyses with a generalized variance inflation factor (GVIF) threshold of 0.5, we retained only six traits (excluding relocation behaviour) (Tables S5 and S6).

The dung beetles' dataset covered three diversity dimensions: (1) taxonomic composition (species), (2) functional composition (functional groups = FGs) and (3) phylogenetic composition (phylogenetic groups = PGs). We defined FGs using the species-by-functional trait matrix (Table S6). For the FG analyses, we calculated distance matrices and a Ward. D dendrogram based on Gower distance (Podani & Schmera, 2006), with a cut-off value of <1.5, resulting in eight FGs (Figure S1, Table S8). FG occurrence within a sampling unit (SU) was defined by the presence of at least one species assigned to that group. For PG analyses, we used species lists and the topology of a previously published phylogenetic backbone (Tarasov & Dimitrov, 2016), grouping species at the generic level into 18 PGs. PG occurrence within an SU was similarly defined by the presence of at least one species belonging to the group (Table S9).

Data analysis

We used the GradientForest (GF) analysis model (sensu Ellis et al., 2012) to assess environmental thresholds affecting taxonomic,

functional and phylogenetic turnover. Based on random forest methods, GF analysis effectively detects compositional patterns and ecological thresholds that are often overlooked by logistic regression and generalized linear models. The method involves constructing regression or classification trees on bootstrap samples of biological data through recursive partitioning, making it particularly effective for different species data across different sampling schemes, surveys, regions or scales. Interpretation of sensitivity is based on the known biology or ecological traits of the responsive taxa. GF analysis objectively derives thresholds from the distribution of split points across thousands of decision trees. For each predictor, splits are selected to maximize changes in community composition between resulting partitions, and these split points are aggregated into cumulative importance curves. Peaks in these curves mark points along the gradient where the turnover is greatest. Although GF analysis does not provide p-values for these thresholds, their significance is inferred from the relative magnitude of the cumulative importance compared to other parts of the gradient. GF analysis does not indicate the direction of effects (i.e., whether a predictor benefits or harms a species or group), but rather pinpoints where compositional change is most rapid and identifies the taxa most strongly associated with these changes.

Compositional turnover was quantified using a dimensionless R^2, with GF's flexibility minimizing distortion effects. The model grew 10,000 decision trees without predictor transformation; data compacting was disabled, and the number of bins was unspecified. A maximum of five splits per tree was imposed to avoid inflated importance measures, and a correlation threshold of 0.5 excluded highly correlated predictors. The density plots were used to illustrate compositional changes along environmental gradients, while the cumulative plots helped identify the species, FGs and PGs most associated with turnover events.

The resulting models included the taxonomic response for species composition, the functional response for FG composition and the phylogenetic response for PG composition. We conducted all analyses in R version 4.3.2 (R Development Core Team, 2023), assessed collinearity using the vifstep function from the "usdm" package (Naimi et al., 2014) and vif from the "car" package (Fox and Weisberg 2019) and generated distance matrices and dendrograms using the "FD" and "vegan" packages (Laliberté et al., 2014; Oksanen et al., 2015). We performed threshold analyses using the "gradientForest" package (Ellis et al., 2012).

RESULTS

We collected a total of 371 dung beetle individuals, representing 74 species (Table S7). None of these species is currently classified as threatened.

Overall model performance

The taxonomic model accurately predicted 67 of 74 dung beetle species, showcasing strong predictive power of the chosen environmental
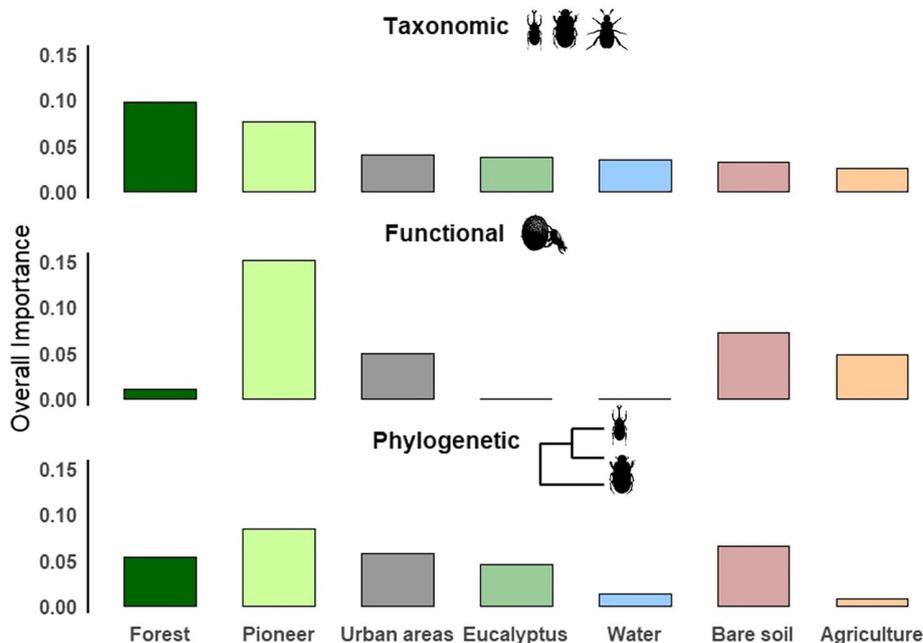
FIGURE 2   Overall conditional importance of environmental variables for the taxonomic, functional and phylogenetic components of dung beetles from the Atlantic Forest. "Pioneer" refers to pioneer vegetation, and "Water" to water bodies.

predictors (Table S7). Similarly, the functional model successfully identified six of eight dung beetle FGs (Table S8), while the phylogenetic model predicted 14 of 18 groups (Table S9).

Across all models, moderate mean R^2 values were observed, with the explanatory power of the three main predictors remaining consistent (Figure 2, Table S10). Pioneer vegetation, bare soil and urban areas were consistently the top environmental predictors for functional and phylogenetic models, with forest replacing bare soil in the taxonomic model (Figure 2).

Taxonomic, functional and phylogenetic response patterns

In the taxonomic model, forest emerged as the most influential predictor (Table 1, Figures 2 and 3). The dung beetle community underwent a noticeable shift when around 75% of the forest remained in the sampling units. Then, the community reached a second threshold at around 45%. The initial shift was primarily driven by *Phanaeus dejeani*, *Chalcocopris hesperus*, *Eurysternus francinae* and *Dichotomius fissus*. The subsequent and more pronounced threshold was influenced by *Dichotomius fimbriatus*, *E. francinae* and *C. hesperus*. These species are large-bodied, have a coprophagous diet and are mainly tunnelers. Except for *D. fimbriatus*, which can be found in open environments and pastures, all other species are forest specialists (Table 1, Figures 2 and 3).

The second most influential environmental predictor was pioneer vegetation. Here, community shifts were already observed at low levels of around 5%. Key species triggering this shift were the small-bodied and primarily tunnelling *Uroxys* sp.7, *Canthidium* aff. *cavifrons*

TABLE 1   Summary of the three main environmental predictors and their threshold values for taxonomic, functional and phylogenetic dimensions of dung beetles in the Brazilian Atlantic Forest.

| Dimension	Environmental predictor	1st threshold (%)	2nd threshold (%)
Taxonomic	Forest cover	75	45
	Pioneer vegetation	15	3
	Urban areas	8	1
Functional	Pioneer vegetation	50	1
	Bare soil	20	1
	Urban areas	4	2
Phylogenetic	Pioneer vegetation	50	1
	Bare soil	20	1
	Urban areas	8	2

Note: The two most important threshold values (approximate) are presented for each dimension of diversity. The predictors are colour-coded, as shown in Figure 1, to visually illustrate patterns among dimensions.

and *Canthidium* aff. *korschefskyi*. All these species are either true forest specialists or show strong associations with forested areas (Table 1, Figures 2 and 3).

The extent of urban areas displayed comparable patterns. A marked community shift occurred very early along the gradient, at approximately 1% urban cover. This shift was primarily driven by *Ateuchus carbonarius*, *Paracanthon rosinae*, *Dichotomius* aff. *punctulatipennis*, *Deltochilum furcatum* and *Canthon* aff. *luctuosus*. All species, except *Canthon* aff. *luctuosus*, are nocturnal. *A. carbonarius* is associated with pastures or open habitats, *P. rosinae* and *D. furcatum* are
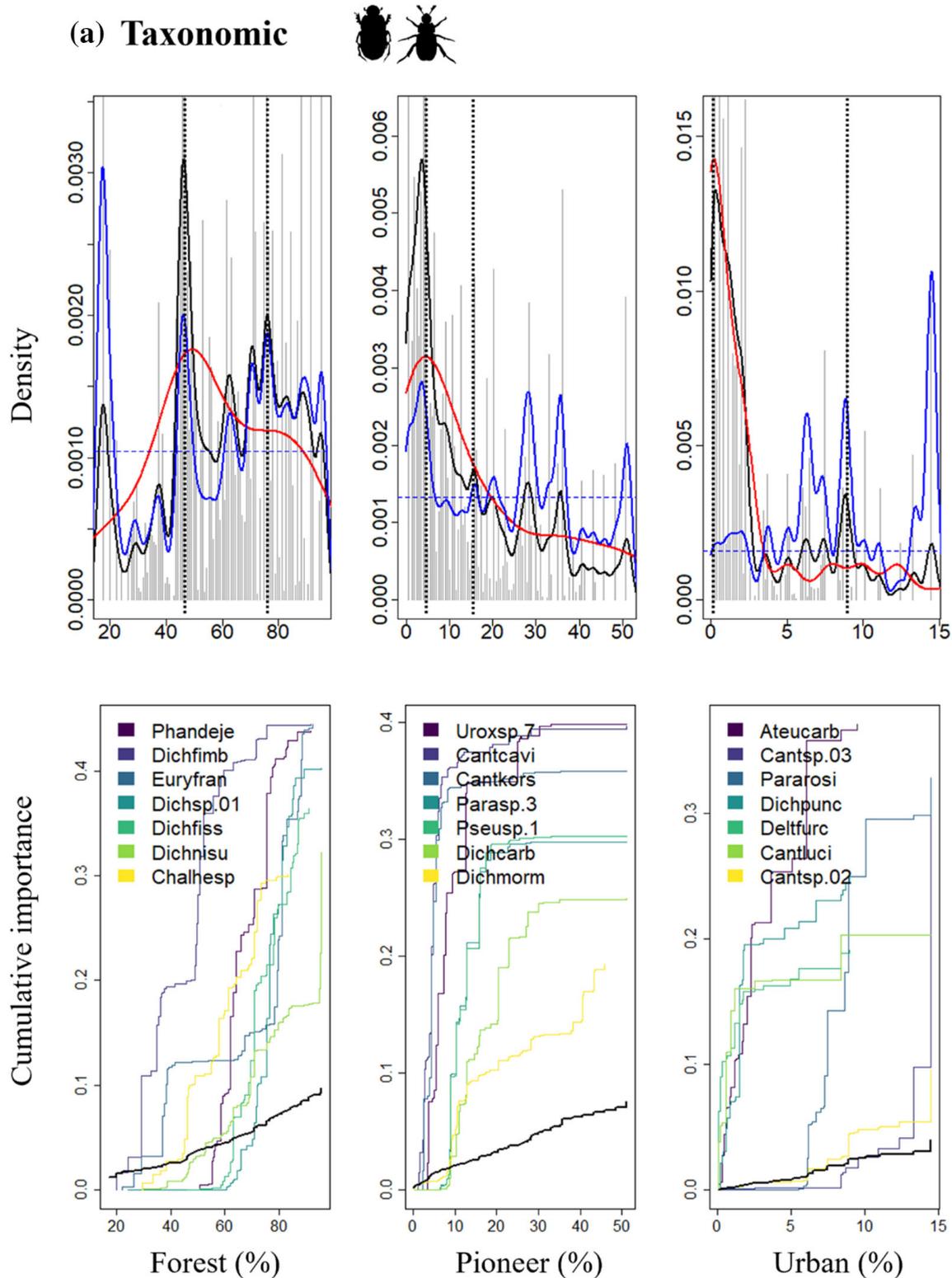
(a) Taxonomic

FIGURE 3 Splits, density and cumulative importance of the three most relevant predictors of compositional change in dung beetles for the taxonomic (a), functional (b) and phylogenetic (c) dimensions. The top panel displays binned raw importance density (grey histogram), density of splits (black line), observed predictor values (red line) and the ratio of splits standardized by the observed density (blue line). The horizontal dashed blue line indicates where this ratio equals 1. Ratios greater than 1 indicate locations of relatively greater change. Dotted vertical lines indicate major thresholds. The bottom panel shows cumulative distributions of the standardized splits' importance for the response groups scaled by R^2, with each curve representing a species. Only the most relevant species, functional groups and phylogenetic groups are included. The black line represents the cumulative importance curve showing the overall pattern of compositional change (R^2) for the combined species or phylogenetic response groups. Taxon names are provided as codes in Table S8, where the associated functional and phylogenetic groups are also specified.
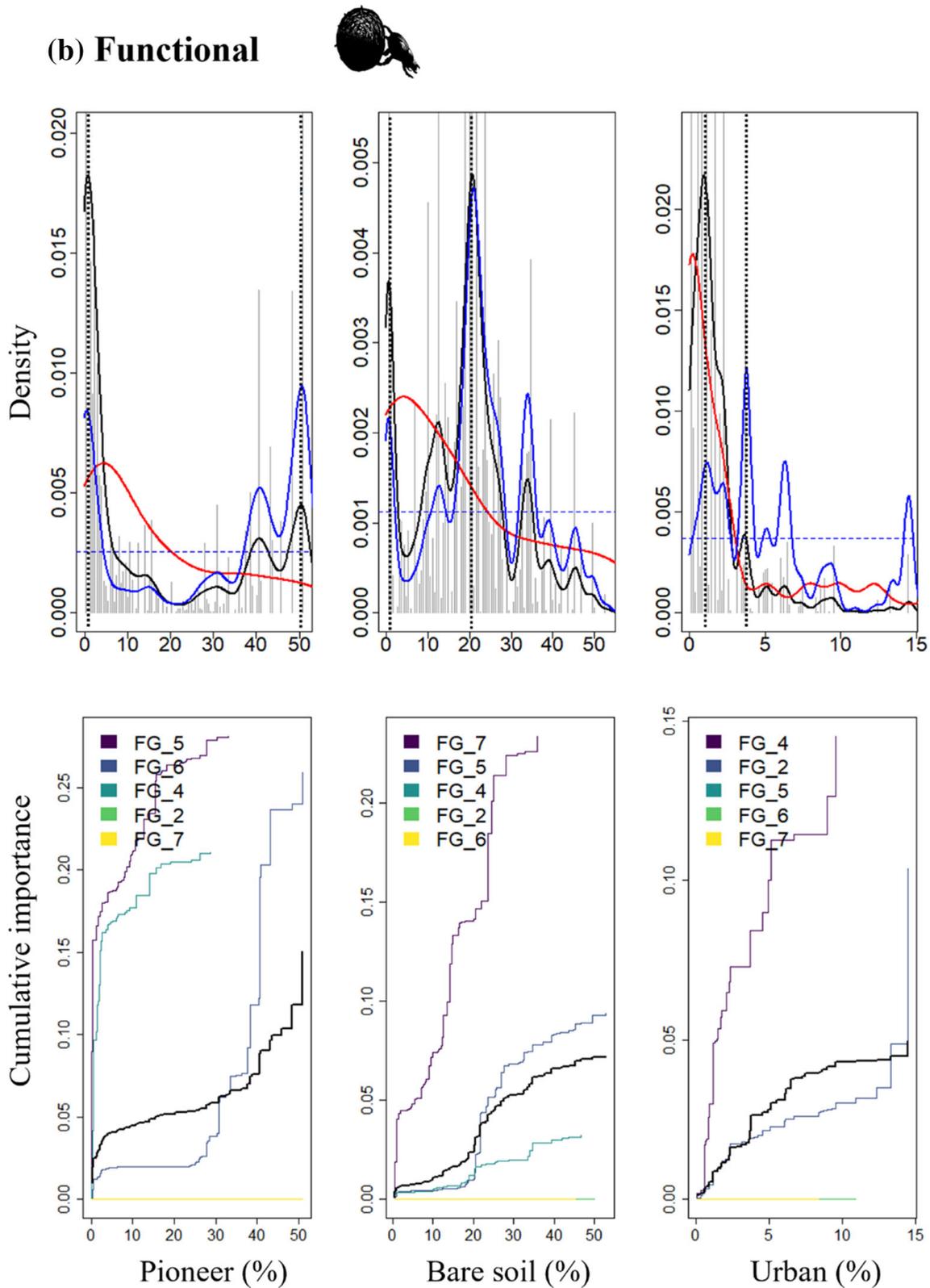
(b) Functional

FIGURE 3 (Continued)

forest-specialist species, while *C.* aff. *luctuosus* is regularly associated with forested areas (Table 1, Figures 2 and 3).

Overall, the functional model showed response patterns consistent with the taxonomic model for the three shared predictors, except for forest, which in this model was replaced by bare soil. Pioneer vegetation triggered a significant shift at the beginning of the gradient, involving groups consisting of medium-sized tunnelers or rollers (FG_5) and small coprophagous species with nocturnal behaviour

(c) Phylogenetic
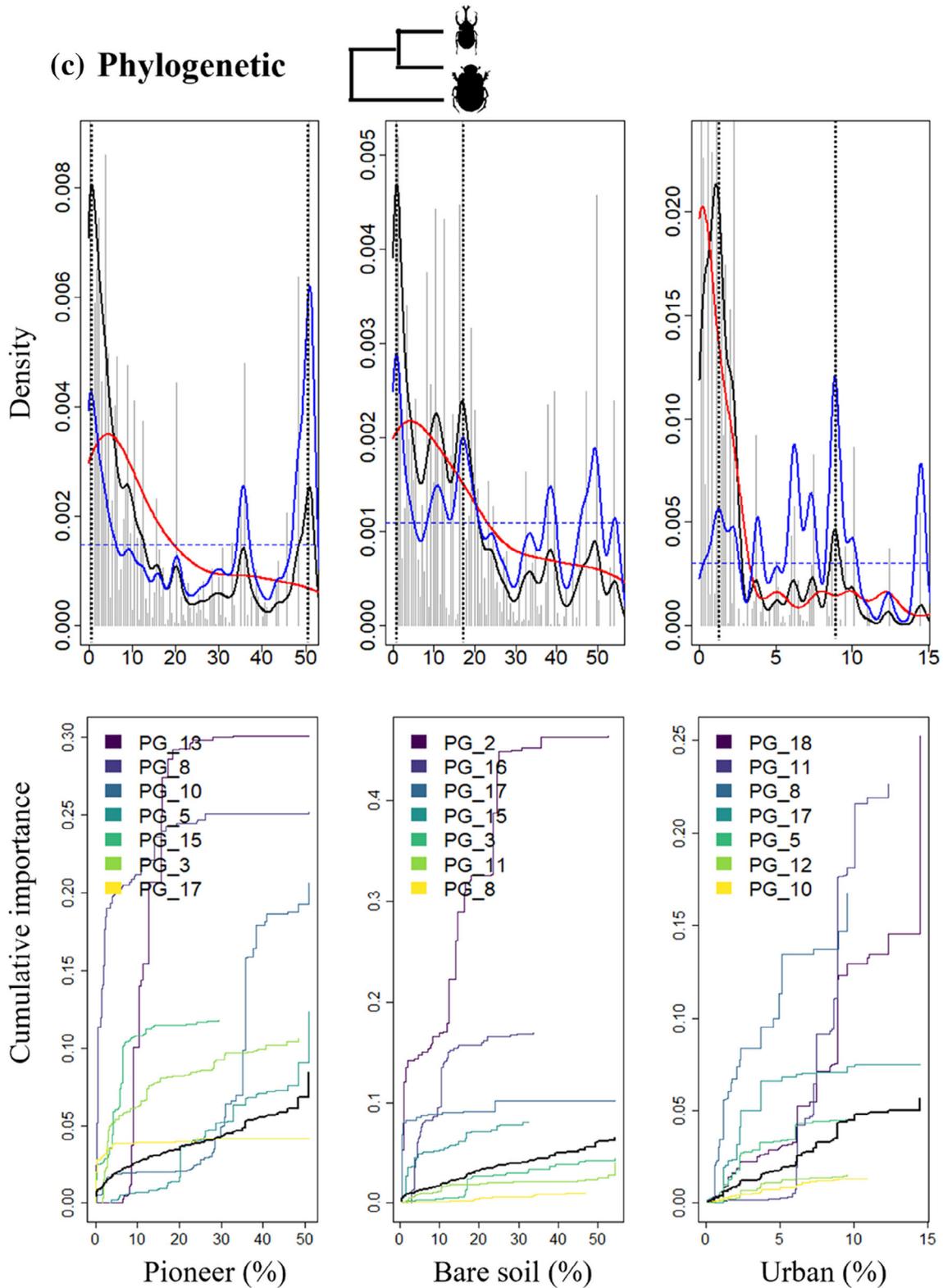
FIGURE 3 (Continued)

(FG_6). Similarly, urban areas displayed an early community shift at approximately 2% and 4% urban cover, primarily driven by small- to medium-sized coprophagous dwellers capable of being active during both day and night (FG_4). A turnover in community composition was observed at the onset of the bare soil gradient and again at threshold levels of around 20%. The FGs primarily responsible for this shift included small to medium tunnelers that are either diurnal or nocturnal (FG_7, along with FG_4 and FG_5, Table 1, Figures 2 and 3).

Important environmental predictors in the phylogenetic model for dung beetles reflected those shown to be important in the functional model, with shifts in the community that occurred at the beginning of the gradient (Table 1, Figures 2 and 3). Phylogenetic groups that mostly reacted to changes in the pioneer vegetation included the genera *Eurysternus* (small to medium species, active during both night and day), *Sulcophanaeus* (large diurnal coprophagous tunnelers) and *Trichillum* (small nocturnal dwellers). Unlike the functional model, the main threshold for the predictor bare soil was observed at the beginning of the gradient, with *Canthidium* (small to medium tunnelers), *Trichillum* and *Sulcophanaeus* driving these changes. All these genera can be found in both open environments and forested areas. Changes in the extent of urban areas resulted in turnover that was mainly driven by *Eurysternus*, *Trichillum*, *Coprophanaeus* (large crepuscular necrophagous tunnelers) and *Uroxys* (small nocturnal coprophagous species) (Table 1, Figures 2 and 3).

DISCUSSION

Our multidimensional study demonstrated that dung beetle communities underwent significant compositional shifts across taxonomic, functional and phylogenetic dimensions in response to relatively low levels of environmental disturbance. Key environmental predictors, such as forest cover, pioneer vegetation, bare soil and urban areas, consistently drove these turnover events, with notable thresholds identified at approximately 75% and 45% of forest cover. These results were consistent with recent findings showing that even minimal levels of forest degradation can trigger immediate ecological responses in tropical communities (Ewers et al., 2024). In our system, these shifts were characterized by the loss of large-bodied, forest-specialist species and the rise of smaller, more generalist or disturbance-tolerant species. Functional and phylogenetic patterns closely mirrored taxonomic changes, highlighting the tight linkage between species traits, evolutionary history and responses to habitat modification.

Given the complexity of the biological community studied and the critical functional roles of the organisms involved, it is very likely that these changes will ultimately affect the recovery potential of the ecosystem, in this case the Atlantic Forest biome, and thus its ecological resilience (sensu Holling, 1996). Our results also aligned with emerging evidence that large forest ecosystems, such as the Amazon, may reach ecological tipping points earlier than previously thought, as ecosystem feedbacks shift and overall resilience declines (Boulton et al., 2022, Wang et al., 2024, Flores et al., 2024). However, these studies usually focus on indicators like tree cover, carbon sequestration and photosynthetic rates, often overlooking changes at the organismal level, where novel biological communities with new functional and evolutionary traits can emerge.

In our system, factors related to deforestation, agricultural conversion and urban expansion were the main drivers of significant turnover processes, indicating community tipping points across all dimensions of diversity. Such patterns are expected, as the aforementioned factors are widely recognized as major contributors to the ongoing global biodiversity crisis (IPBES, 2019; Newbold et al., 2015). What should be alarming, however, is that these anthropogenic impacts may not only cause direct species extinctions but also induce changes in organismal traits that could ultimately alter how entire ecosystems respond to increasing pressures (Mouillot et al., 2013). Perhaps even more importantly, it is not only the current diversity and functioning of ecosystems that may be altered by new species and trait combinations. The formation of new combinations of phylogenetic lineages that make up local communities may also alter future evolutionary response potential (Cadotte et al., 2012; Tucker et al., 2016).

The broad-scale patterns of community restructuring, functional turnover and phylogenetic reshuffling in our study became particularly evident in landscapes where even small proportions of anthropogenic land use can drive significant ecological shifts. Dung beetle communities in disturbed landscapes were increasingly dominated by small, diurnal tunnelers like *Ateuchus carbonarius*. Such generalist species are better adapted to warmer, disturbed environments, whereas larger, nocturnal forest specialists, which depend on cooler, stable habitats, are excluded (Nichols et al., 2013; Salomão et al., 2019). Our documented shift in community composition aligns with past studies indicating that diurnal species are less sensitive than nocturnal species to forest conversion (Nichols et al., 2013). Thereby, daily activity emerged as a crucial trait, as climatic conditions influence the temporal and spatial distribution of dung beetle species (deCastro-Arrazola et al., 2023). The importance of daily activity relates closely to thermoregulation capacity and body temperature management (deCastro-Arrazola et al., 2023; Gallego et al., 2018; Giménez-Gómez et al., 2018). Land-use modification can alter micro-climatic conditions by changing characteristics such as canopy height, temperature and precipitation retention, which have been found to affect dung beetle species composition and abundance (Kenyon et al., 2016; Nichols et al., 2013). Moreover, nesting strategy also plays a role, with tunnellers exhibiting a stronger association with soil characteristics and displaying less dependence on environmental conditions compared to rollers, for example (Iannuzzi et al., 2016).

Our finding that even minimal levels of land-use alteration harmed biodiversity was supported by identified thresholds along the gradient of habitat loss. Shifts occurred as early as 75% of forest cover remained, excluding larger-bodied species with coprophagous diets, predominantly tunnelers like *Phanaeus dejeani* and *Chalcocopris hesperus*. This pattern is consistent with other research indicating that habitat alteration can lead to the exclusion of larger species (Braga et al., 2013; Nichols et al., 2007). Such findings challenge previous assumptions that community turnover is only evident with 60–70% habitat loss and align with early evidence that birds can experience community shifts at as little as 20% habitat loss, leading to decline and regional extinction of strict forest species (Anunciação et al., 2021, Shennan-Farpón et al., 2021, Pardini et al., 2010, Banks-Leite et al., 2014).

Lower thresholds associated with anthropogenic land uses (e.g., pioneer vegetation and urban areas), as well as along the forest cover gradient in the taxonomic dimension, highlight the rapid loss of species with similar ecological roles or evolutionary histories,

emphasizing the sensitivity of the system to disturbance. Such a trend among functionally and phylogenetically similar species suggests that anthropogenic impacts lead to the dominance of species adapted to habitat modification and the exclusion of sensitive specialists (Nowakowski et al., 2018). In contrast, the functional and phylogenetic dimensions appeared more resilient, which may be related to trait redundancy and evolutionary buffering. However, they also exhibited sharp declines, which likely occurred when key ecological thresholds were crossed. The loss of functional and phylogenetic diversity may signal the disruption of key ecosystem functions, such as dung removal and soil excavation by dung beetles, which are vital for nutrient cycling and soil health (García-Llamas et al., 2019). The erosion of these functions reduces ecosystem resilience, increasing vulnerability to further degradation and collapse (Boulton et al., 2022; Flores et al., 2024; Wang et al., 2024).

A multidimensional approach is essential to understanding such threshold dynamics (Anunciação et al., 2021; Anunciação et al., 2023; Boesing et al., 2018; Rurangwa et al., 2021). While taxonomic diversity captures immediate species turnover, functional and phylogenetic dimensions reveal deeper impacts on ecosystem functionality and evolutionary legacies (Flynn et al., 2011). The similarity between functional and phylogenetic responses found here highlights the connection of traits and evolutionary relationships in shaping ecosystem processes (Flynn et al., 2011). Integrating these dimensions allows for early detection of biodiversity shifts, providing informed conservation measures to mitigate land-use impacts (Cadotte & Tucker, 2018).

While our findings underscore the value of integrating taxonomic, functional and phylogenetic dimensions to anticipate biodiversity shifts and inform conservation strategies, it is equally important to acknowledge the limitations of this study. We focused on how abiotic environmental variables influence dung beetle communities. Although our continuous 48-h sampling protocol captures activity across diel periods and is widely used in dung beetle research, it does not allow for disentangling diurnal and nocturnal dynamics, patterns that can strongly shape community composition (Asha et al., 2021; Lobo & Cuesta, 2021; Mora-Aguilar et al., 2023), particularly when habitat–time interactions are important (Asha et al., 2022). Future research should consider temporally stratified sampling to uncover additional taxonomic, functional and phylogenetic patterns.

Moreover, mammal assemblages, as the primary source of dung, are widely recognized as strong biotic determinants of dung beetle richness and abundance. Indeed, mammal community composition can explain a significant portion of variation in dung beetle communities (Bogoni et al., 2016). In our case, matched mammal data were not available across our sampling units and were thus not included. We encourage future studies to integrate mammal presence data to better capture interactions between dung beetles and both biotic and abiotic drivers.

Conservation and management implications

The Brazilian Atlantic Forest is undergoing significant changes, leading to the emergence of novel communities and profoundly impacting ecosystem function (Anunciação et al., 2021). Although we did not directly assess ecosystem resilience, it is likely that anthropogenic activities are rapidly deteriorating the Atlantic Forest (Anunciação et al., 2021). This mirrors the situation in the Amazon, which is probably nearing a critical tipping point (Boulton et al., 2022; Flores et al., 2024; Wang et al., 2024). Together, these patterns indicate an increased risk of widespread ecological degradation in two of the world's most important tropical forests, driven by anthropogenic pressures masked as economic development (Anunciação et al., 2021; Boulton et al., 2022; Flores et al., 2024; Wang et al., 2024).

Our findings revealed that established habitat thresholds may underestimate the ecological responses occurring in human-altered landscapes, underscoring the dynamic nature of these responses (Banks-Leite et al., 2014; Pardini et al., 2010; Shennan-Farpón et al., 2021). Notably, significant shifts in dung beetle communities were evident when habitat cover dropped below 75%. Current legal requirements, such as the Brazilian Forest Code, which stipulates that only 20% of forest cover in the Atlantic Forest must be set aside (Law n. 12651, 2012), are inadequate. Policies must be revised to reflect the higher thresholds required to sustain biodiversity and ecosystem services effectively.

With only 23% of the original Atlantic Forest remaining, large-scale restoration efforts are crucial (Vancine et al., 2024), underscoring the importance of the Atlantic Forest Restoration Pact, which aims to restore 15 million hectares by 2050 (Atlantic Forest Restoration Pact; https://pactomataatlantica.org.br). Efforts must focus on strategic reforestation, connecting small fragments and enhancing the ecological integrity of degraded areas, supplemented by targeted natural regeneration strategies (Crouzeilles et al., 2019, 2020).

Community engagement is also essential for successful restoration. Financial incentives, expansion of payment programmes for ecosystem services and initiatives promoting local participation can drive meaningful forest recovery (Ruggiero et al., 2019). Additionally, with less than 5% of the Atlantic Forest currently protected (Hrdina & Romportl, 2017), expanding the protected area network is a critical priority. This includes both public protected areas and incentives for private landowners to establish reserves in deforestation hotspots through Reserves of Natural Heritage (Reservas Particulares do Patrimônio Natural, RPPNs). Multidimensional biodiversity assessments like ours can inform the designation of these areas to effectively capture biodiversity hotspots and critical habitats while supporting ecosystem resilience (Cadotte & Tucker, 2018).

Besides that, continuous monitoring and adaptive management are imperative. Ecological thresholds identified in this study should be integrated into management frameworks to enhance the resilience of forest ecosystems against ongoing human pressures.

Importantly, this research demonstrates the application of a multidimensional approach to ecological thresholds in an invertebrate group crucial to ecosystem functioning, offering new insights into biodiversity responses to habitat loss (Shennan-Farpón et al., 2021). Addressing taxonomic and geographic gaps, such as including vertebrates and plants in future research and covering additional regions of the Atlantic Forest, will refine understanding of community tipping points and strengthen conservation strategies across the biome.

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CRITICAL TIPPING POINTS IN DUNG BEETLE COMMUNITIES

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. Supporting Information.

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