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Functional trait filtering of aerial insectivorous forest bats in Amazonian cattle-dominated landscapes

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ABSTRACT

The conversion of forest to cattle pasture is a major driver of biodiversity loss, particularly in the tropics. Bats provide essential ecosystem services and are widely used as indicators of ecosystem integrity, yet how functional traits mediate their vulnerability to land-use change remains poorly understood. Here, we combined bioacoustic surveys with functional trait data to investigate the relationship between functional traits and sensitivity to land-use change in aerial insectivorous bats across forest and cattle-farmed sites in Mato Grosso State, Brazil. We sampled bats using passive acoustic recorders across 20 cattle farms, recording 66,301 bat passes representing 28 sonotypes. Regression models revealed no differences in taxonomic or functional diversity between forest and pasture sites. However, multivariate RLQ and fourth-corner analyses identified strong associations between bat activity, functional traits, and environmental variables. Wing morphology, echolocation call structure, and foraging strata emerged as key predictors of sensitivity to land-use change. Understory and canopy foragers with low relative wing loading and aspect ratio, and call characteristics associated with cluttered environments, were positively associated with forest cover. In contrast, above-canopy foragers with higher wing loading and aspect ratio were associated with open, fragmented pasture landscapes. These findings suggest that forest conversion does not necessarily reduce overall bat diversity, but instead filters species according to functional traits, disproportionately affecting clutter-adapted bats and the ecosystem services they provide. Beyond maintaining forest cover, conservation strategies in agricultural landscapes should prioritize reducing fragmentation to safeguard bat functional diversity and associated ecosystem services.

1. Introduction

As global population growth and per-capita food consumption increase, natural landscapes are increasingly being replaced by agricultural land uses, including extensive livestock-producing landscapes (Laurance et al., 2014). By 2021, agriculture constituted one-third of the

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world's land area (FAO, 2023). The Neotropics are on the forefront of agricultural expansion, with Brazil having experienced one of the highest rates of deforestation globally since 1970 (Zarin et al., 2016). Livestock farming, particularly of cattle, is one of the leading drivers of deforestation in the Amazon, accounting for ~60% of total forest loss (Lapola et al., 2023; Aleixandre-Benavent et al., 2018).

In human-modified landscapes, habitat loss and conversion are often accompanied by increasing fragmentation, resulting in smaller and more isolated patches of primary habitat embedded within matrices of altered land (Haddad et al., 2015). These processes are closely linked and jointly contribute to biodiversity loss by reducing habitat area, increasing isolation, and altering resource availability and ecological niches (Rocha et al., 2017; Moir et al., 2021; Palmeirim et al., 2021). At the same time, habitat conversion alters environmental conditions in ways that may still be suitable for some species, depending on their functional traits (Farneda et al., 2015). Consequently, species persistence is shaped not only by patch size and isolation, but also by the composition of the surrounding matrix and species' trait characteristics, which together determine how organisms respond to changing habitat conditions (Ewers and Didham, 2006; Newbold et al., 2014; Fletcher 2024).

Functional traits are defined as the 'phenotypic, observable, or operational characteristics that affect species performance' (Violle et al., 2014). Studying functional traits provides insights into species' ecological roles (Suárez-Castro et al., 2020), whereby species with certain traits are better suited to particular environmental conditions and resource structures, such as specific habitat types or roosting opportunities. Importantly, functional traits mediate whether species persist or decline in human-modified landscapes (Gonçalves et al., 2017). Species whose traits are poorly matched to altered environmental conditions are more likely to decline or be lost following land-use change (Wolf et al., 2021). In contrast, species with traits suited to open landscapes are often more resilient to land-use changes, reflecting the typically open nature of many modified landscapes. Forest-specialists, however, may decline or even become locally extinct from such landscapes (Farneda et al., 2018). A trait-based approach can therefore help to direct conservation efforts towards the most sensitive species (Wolf et al., 2021).

Bats comprise one-fifth of all mammal species and have a wide range of morphologies, echolocation characteristics, foraging styles, diets, and habitats (Frank et al., 2017). They perform vital ecosystem services such as pollination, insect control, and seed dispersal (Kunz et al., 2011; Chaves et al., 2026). Unfortunately, agricultural expansion and other drivers of biodiversity loss have severely impacted bat conservation, resulting in 15% of the ~1400 bat species worldwide being threatened with extinction according to the IUCN (Frick et al., 2020). Livestock production, in particular, influences bat activity and assemblage composition, generating complex, species-specific responses that are strongly mediated by landscape context (Gonçalves et al., 2017; Ancillotto et al., 2017, 2021; Szabadi et al., 2025; Wiesinger and Suarez-Rubio, 2026).

Aerial insectivorous bats (AIBs) constitute almost half of all 160 described bat species in Brazil (Garbino et al., 2022), and play a fundamental role in controlling insect pests (Russo et al., 2018). They vary greatly in their echolocation calls, vertical strata foraging preferences, wing shape, and body shape/size, all of which have been found to affect their sensitivity to land-use changes (Núñez et al., 2019; Colombo et al., 2023; Díaz-B et al., 2023). For instance, AIBs with echolocation calls adapted for open-space foraging (low, CF calls) are more likely to explore modified landscapes than those adapted for foraging in cluttered environments (high, FM, CF-FM calls) (Núñez et al., 2019). Some AIBs tend to forage above the canopy and are fast flyers that can travel considerable distances to locate patchy resources, while others are more associated with the understory (Yoh et al., 2022). Wing morphology directly correlates with flight speed, manoeuvrability, and agility (Marinello and Bernard, 2014), with AIBs with shorter, wider wings typically exhibiting high manoeuvrability and low flight speed, advantageous in cluttered environments, whereas those with longer, more narrow wings being less manoeuvrable, but able to fly faster allowing for greater travel distances in open spaces such across modified landscapes (Denzinger and Schnitzler, 2013; Marinello and Bernard, 2014). Both body mass and size are also linked to mobility and agility (Díaz-B et al., 2023) with larger bats being better suited to travel across fragmented landscapes (Farneda et al., 2015). In addition to functional traits, environmental variables such as the amount and fragmentation of remaining forest and the distance of water bodies have been found to be important in determining the composition of AIBs within a landscape (López-Baucells et al., 2022; Mancini et al., 2024; Díaz-B et al., 2023).

Although restricted to capture data, a previous meta-analysis on the effects of livestock ranching on Neotropical bat taxonomic and functional diversity found that high-dispersal AIBs (e.g., molossids) were benefited by cattle ranging-associated habitat change, whereas low-dispersal species (e.g., vespertilionids) were among the most impacted (Gonçalves et al., 2017). Here, we use bioacoustic data to compare the taxonomic and functional alpha (α) diversity of Amazonian AIBs between forest and pasture habitats, and evaluate the relationship between AIB distribution, functional traits, and environmental variables in the important beef-producing state of Mato Grosso, Brazil. Specifically, we address the following questions:

I. How does Simpson's D (taxonomic α-diversity), Rao's Q (functional α-diversity) and Functional Uniqueness – capturing complementary faces of community structure – vary between forest and pasture sites? Notwithstanding previous evidence of negligible assemblage-level differences in the frequency of occurrence of bat species in old-growth forest vs. areas influenced by livestock (Gonçalves et al., 2017), we anticipate that forest habitats, due to their greater habitat complexity, will have higher taxonomic and functional α-diversity than modified, pasture habitats (Farneda et al., 2018; Kinap et al., 2024).
II. Which functional traits relate to which environmental variables (trait-environment relationships) across cattle-dominated landscapes? Previous studies have consistently highlighted the importance of traits related to mobility in determining disturbance sensitivity in bats (Gonçalves et al., 2017; Núñez et al., 2019; Colombo et al., 2023; Díaz-B et al., 2023). We therefore hypothesise that wing morphology, a key trait influencing mobility, will strongly influence sensitivity to land-use chang, with highly mobile species being more able to explore the open environments associated with pasture.
III. Which trait-environment relationships are the strongest predictors of bat distribution? Prior research has emphasised the role of native vegetation cover in conserving vulnerable species within altered landscapes (Otálora-Ardila et al., 2024; García--Morales et al., 2016). Accordingly, we hypothesise that environmental variables related to forest cover will be the most important to maintain functional diversity across the study area.

2. Methods

2.1. Study area

Data collection was conducted from May to December 2023 in Mato Grosso, Brazil's third largest State (over 90 million ha). Data were collected in the north of Mato Grosso, in the Amazon biome (Fig. 1). The study area has a mean annual temperature of 26°C and mean rainfall of 111 mm a month (ranging from 248 mm in February to 0 mm in July). Mato Grosso is biologically diverse, comprising portions of the Amazon (480 000 km^2), the Cerrado (360 000 km^2), and the Pantanal biomes (60 000 km^2) (Spera et al., 2014). However, this state also holds the largest cattle herd in the country (Spera et al., 2014). Rapid expansion of agricultural areas in the early 2000s, most significantly for soy and cattle farming, resulted in Mato Grosso becoming a deforestation hotspot

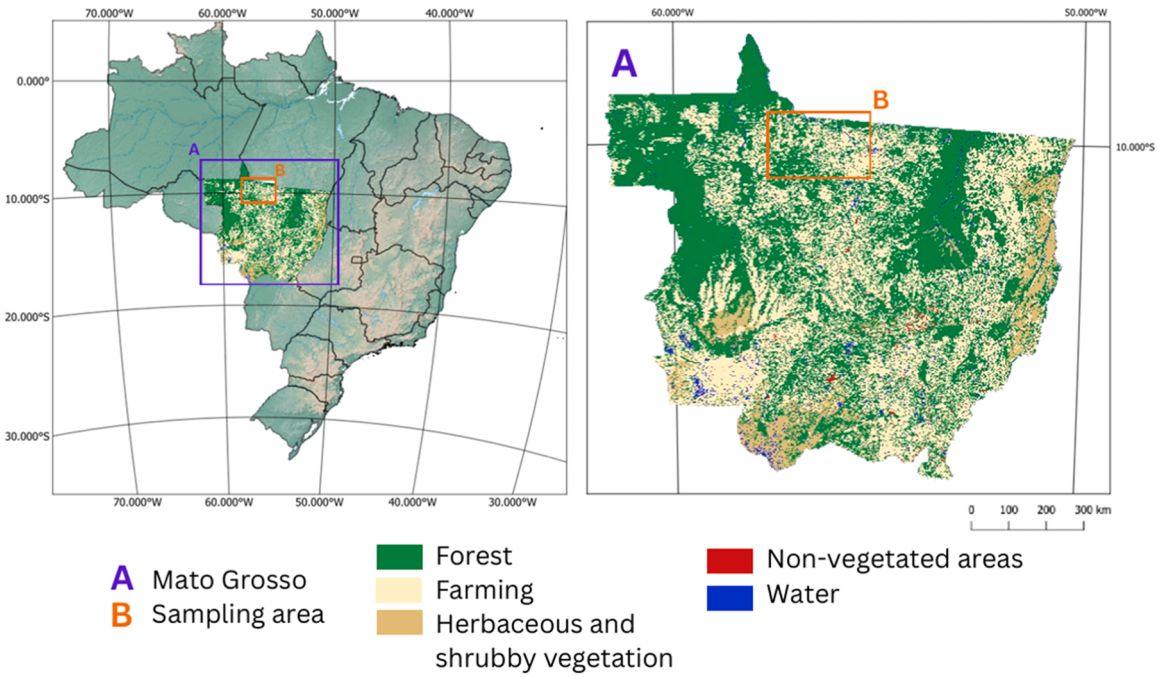

Fig. 1. Map of the study area, showing A) the state of Mato Grosso, where sampling was conducted, and B) a close up of the region in which the 20 cattle farms were sampled. Land cover was imported from MapBiomas Brazil for the year 2023 (MapBiomas, 2023). Exact farm locations are not shown to preserve participant anonymity in accordance with ethical approval requirements.

(Zalles et al., 2019). From 1985–2023, the proportion of Mato Grosso that was forested decreased from 79% to 53% (MapBiomass, 2023).

2.2. Bat sampling

Bats were surveyed using bioacoustics across 20 cattle farms. At each farm, six sampling sites were surveyed for one night: three sites located in the pasture, and three in the forest. This amounted to a total of 120 sampling sites, although due to equipment malfunctioning, only 112 were included in the analysis (56 forest and 56 pasture). Each sampling site was surveyed using one Song Meter bat mini detector (Wildlife Acoustics, Inc, USA), set to record during the night, defined as 30 min post and prior to sunset and sunrise (respectively), using a sample rate of 384 kHz. Detectors were attached to a tree trunk at a heigh of between 1.5 and 2 m. The average distance between detectors exceeded 1 km in both habitats (mean ± SE: 1056 ± 178 m in forest, range 187–3321 m; and 1040 ± 165 m in pasture, range 106–4608 m). Bats surveys were carried out throughout the lunar cycle. Although moonlight intensity can influence bat activity (e.g., Appel et al., 2021) as forest and pasture sites in each farm were sampled simultaneously, we anticipate that the potential influence of moon phase is likely to have affected both habitat types equally and thus should have negligible impacts on our results. To reduce data volumes, the detectors were set to trigger detection of ultrasonic sounds at frequencies > 15 kHz, suitable for AIBs which locate prey using ultrasonic echolocation.

2.2.1. Bioacoustic analysis

Bioacoustic data was manually analysed using Kaleidoscope Software v5.6.8 (Wildlife Acoustics, Inc, USA), following the bat ultrasound key in López-Baucells et al. (2018) to identify the bat calls in each sound file. Only the first four hours of the night (18:00–22:00) were analysed, as AIB activity has been found to decrease substantially after 22:00 (Estrada-Villegas et al., 2010; López-Baucells et al., 2021). Echolocation call characteristics of call shape, frequency of maximum energy (FME), start frequency (SF), and end frequency (EF) were used for identifications.

Species were identified at the sonotype level i.e., groups of species with indistinguishable echolocation calls, whenever identification was not possible at the species level (López-Baucells et al., 2021). Henceforth, the term 'sonotypes' is used to refer to both single species and sonotypes (see Table 1 for the 'sonotypes' used in this study). In addition to the given sonotypes in López-Baucells et al. (2018), we grouped *Saccopteryx leptura* and *Saccopteryx bilineata* into a single 'Sac bil/lep' sonotype, as it was not possible to differentiate between the two species' calls. Following Colombo et al. (2023), we also separated *Pteronotus parnelli* into two sonotypes based on their FME, as a new species was found in the region (Pavan et al., 2018): *Pteronotus* 55 kHz (*P. rubiginosus*) and *Pteronotus* 60 kHz (*P. alitonus*). Bat activity was measured using the unit of a 'bat pass', defined as any call sequence of 5-seconds containing a minimum of two distinguishable pulses of one sonotype (López-Baucells et al., 2021). Only passes with an intensity that exceeded 15 dB from background noise were identified.

2.3. Functional traits of bats

For each sonotype detected, we considered seven functional traits as potential predictors of vulnerability to habitat loss and modification: Frequency of maximum energy, call structure, body size, body mass, vertical stratification, relative wing loading, and aspect ratio (Table 2).

Frequency of maximum energy is defined as the most intense frequency of the search-phase call. Call structure is the shape of the echolocation call, divided into four categories: constant frequency (CF), frequency-modulated (FM), constant frequency frequency modulated (CF-FM), quasi-constant frequency (qCF). Forearm length (FA; measured as the average distance (mm) between an adult's elbow and wrist) is used as a surrogate of body size and was obtained from López-Baucells et al. (2018). Body mass (average adult body weight (g) excluding pregnant females) was obtained Núñez et al. (2019) and Colombo et al. (2023). Vertical stratification was defined as either under-canopy (VertS 1), canopy (VertS 2), or above-canopy (VertS 3) as this is the typical classification for AIBs (Núñez et al., 2019). Wing morphology was measured using two variables: wing loading and aspect ratio: wing loading (WL) represents the force exerted on the wings during flight, and aspect ratio (AR) represents the velocity that a bat must reach to sustain

Table 1
The 19 sonotypes retained in the analysis, identified from bioacoustic data across the 20 sampled farms in Mato Grosso, Brazil.

Sonotype name	Species included Family Genus Species	Total sites	Total n. passes
Sac bil/lep (S)	Emballonuridae *Saccopteryx* *S. leptura* *S. bilineata*	110	5995 (9.04%)
Emballonuridae I (E1)	Emballonuridae *Saccopteryx* *S. gymnura* *S. canescens*	12	49 (0.07%)
Emballonuridae II (E2)	Emballonuridae *Centronycteris* *C. centralis* *C. maximiliani*	46	642 (0.97%)
Cor bre (CB)	Emballonuridae *Cormura* *C. brevirostris*	68	546 (0.82%)
Per kap (PK)	Emballonuridae *Peropteryx* *P. kappleri*	75	5408 (8.16%)
Per mac (PM)	Emballonuridae *Peropteryx* *P. macrotis*	59	1513 (2.28%)
Per tri (PT)	Emballonuridae *Peropteryx* *P. trinitatis*	44	2200 (3.32%)
Rhy nas (RN)	*Rhynchonycteris* *R. naso*	9	29 (0.04%)
Eptesicus I (EP)	Vespertilionidae *Eptesicus* *E. brasiliensis* *E. chiriquinus* *E. furinalis*	94	5065 (7.64%)
Myo rip (MR)	Vespertilionidae *Myotis* *M. riparius*	43	1023 (1.54%)
Myo nig (MN)	Vespertilionidae *Myotis* *M. nigricans*	71	855 (1.29%)
Pter parn 55 (P5)	Mormoopidae *Pteronotus* *P. rubiginosus*	43	601 (0.91%)
Pte gym (PG)	Mormoopidae *Pteronotus* *P. gymnonotus*	30	114 (0.17%)
Pte per (PP)	*Pteronotus* *P. personatus*	25	130 (0.20%)
Noc alb (NA)	Noctilionidae *Noctilio* *N. albiventris*	20	124 (0.19%)
Molossus I (M1)	Molossidae *Molossus* *M. molossus*	96	5278 (7.96%)
Molossus II (M2)	Molossidae *Molossus* *M. sinaloae* *M. currentium* *M. rufus*	109	12025 (18.14%)
Molossidae D (MD)	Molossidae *Neoplatymops* *N. mattogrossensis* *Nyctinomops* *N. macrotis* *Eumops* *E. auripendulus* *E. glaucinus* *E. dabbenei* *E. hansae* *E. maurus* *Nyctinomops* *N. laticaudatus*	107	22818 (34.42%)
Promops sp. (P)	*Tadarida* *T. brasiliensis* Molossidae *Promops* *P. nasutus* *P. centralis*	69	503 (0.76%)

Table 2
Summary of functional traits used in the analysis of aerial-insectivorous bat vulnerability to habitat loss and fragmentation in Mato Grosso, Brazil.

Functional trait	Label	Source
Frequency of maximum energy	FME	Núñez et al., (2019); Colombo et al., (2023)
Call structure	Call_CF Call_CF. FM Call_FM Call_QCF	López-Baucells et al., (2018); Arias-Aguilar et al., (2018)
Body size: Forearm length	FA	López-Baucells et al., (2018)
Body mass (weight)	Weight	Núñez et al., (2019); Colombo et al., (2023)
Relative wing loading	rWL	Núñez et al., (2019); Extrapolation following Colombo et al., (2023)
Aspect ratio	AR	Núñez et al., (2019); Extrapolation following Colombo et al., (2023)
Vertical stratification	VertS	Núñez et al., (2019)

flight (Norberg & Rayner, 1987). Studies typically use measures of relative wing loading (rWL) to ensure values are independent of size for similarly shaped bats (Marinello and Bernard, 2014).

Due to missing wing morphology data for *Noctilio albiventris*, *Saccopteryx canescens,* and *Peropteryx trinitatis,* we estimated rWL and AR using the equation of linear regressions of rWL and AR based on body mass values taken from Colombo et al. (2023) [rWL = 642.732*Weight + 2.187, adjusted R^2 = 0.7558; AR = 123.4593*Weight + 6.0485, adjusted R^2 = 0.6503] (Figure A1). When species were grouped into sonotypes, average trait values across species were calculated for Frequency of Maximum Energy, weight, forearm length, relative wing loading, and aspect ratio (Table A1). We note that even for species that exhibit alternating peak frequencies during search flight (e.g. many Molossidae and Emballonuridae) FME values represent averages. While this approach does not capture full within-species variability in call structure, it allows for consistent comparison across sonotypes and allows comparability with previous studies (e.g., Núñez et al., 2019 and Colombo et al., 2023). See Núñez et al. (2019) for additional information about the rationale behind the selection of the functional traits included in this study.

2.4. Environmental variables

For each sampling site, six environmental variables, reflecting both local and landscape scales, were measured using QGIS software v3.40 and Google Earth Pro (Figure A2). Local-scale variables were (1) land-cover type (forest or pasture) and (2) shortest distance to a source of water (i.e. pond, lake, river) (m). Landscape-scale variables were (3) forest cover (ha), (4) pasture cover (ha), (5) patch density (patches/ha), and (6) edge density (m/ha). Land-cover type was either classified as forest or pasture depending on the land cover type at the point where each of the recorders were deployed. Forest and pasture cover were measured with land-use data from MapBiomas Brasil, using QGIS to extract pixels of respective habitat types around each sampling site. All agricultural land, which includes livestock and crop farming, was grouped under ‘pasture’ cover, as cattle pastures constituted an average

of 95% of the agricultural land-use at each site. Patch and edge density are measures of landscape configuration related to fragmentation (see Appendix A). Shortest distance to water was calculated using Google Earth Pro as the shortest distance between each site and the nearest source of water. Landscape metrics were quantified within a circular buffer of 1500 m radius of the recording station. Buffer distance was selected based on the spatial scale at which AIBs have been found to respond to land-use changes, whilst aiming to reduce overlap between sites (Chambers et al., 2016).

2.5. Data analysis

All statistical analyses were conducted using RStudio v4.4.3 (R Core Team, 2024). Although 28 sonotypes were identified across the study, only 19 were retained for analysis (Table 1). Phyllostomidae were excluded as they are not suitably sampled with bioacouctics (Yoh et al., 2020; Carvalho et al., 2023). Similarly, *Noctilio leptura* was removed as it is mostly associated with water courses. There were no trait data for *Diclidurus* spp. or Vespertilionidae I and II sonotypes, whilst *Molossops neglectus* and Thyropteridae were excluded as they were only recorded once.

To increase comparability between variables, all functional traits and environmental variables were centred and standardised to have a mean of zero and standard distribution of one ('scale' function; base R package, R Core Team 2019).

2.5.1. Community-level analysis

We first compared taxonomic diversity, measured with Simpson's taxonomic index (D); functional diversity, measured with Rao's quadratic functional index (Q); and community-level functional uniqueness (U) between sampling sites located within forests and within pastures. Simpson's D assumes all species are 'equally and maximally dissimilar' (Ricotta et al., 2016). It ranges from zero to one, with lower values indicating higher diversity. To align with the other diversity indices, the R package *adiv* calculates Simpson's Diversity Index as $D = 1 - \Sigma n_i(n_i-1)/N(N-1)$, so that higher values indicate higher diversity. Rao's Q is a similar index to Simpson's D, except it considers differences in traits between pairs of species, as well as relative abundance (Rocchini et al., 2024). Higher values of Q indicate that more functionally unique or rare species are present, suggesting a more diverse community (Ricotta et al., 2016). Community functional uniqueness (U) captures the level of functional uniqueness of species in a community, given the species present and their abundances. It is measured as the ratio between Simpson's D and Rao's Q (U = Q/D), with higher values indicating a more functionally diverse community. Q, and U were calculated based on Gower's distance ('uniqueness' function, *adiv* package, Pavoine, 2020).

To examine how each of these three metrics of the insectivorous bat assemblages vary between forest and pasture sites, we ran beta regression models (generalised linear models with a beta distribution) for each metric, suitable for response variables which range between 0 and 1 (as these diversity indices do). We used the *betareg* package, with a logit link function to ensure response variables remained between 0 and 1, and land-cover type as a fixed effect. To account for the hierarchical structure in which data were collected, where multiple sites are nested within farms, we also ran generalised linear mixed models with a beta distribution (mixed-effect beta regression models), where we added the 'farm identity' as a random effect. This was done using the *glmmTMB* package. We compared marginal and conditional R^2 values (Nakagawa and Schielzeth, 2013) using the performance package (Lüdecke et al., 2021) and used Akaike's Information Criterion (AIC) to determine whether adding 'farm identity' as a random effect improved the fit of the model. Residual plots and tests of overdispersion were used to check for violations in model assumptions (R package *DHARMa*).

2.5.2. Trait-level analysis

To test our hypotheses relating sonotype activity, functional traits, and environmental variables, we used RLQ and fourth-corner analyses. These two complementary approaches, introduced by Dray et al. (2014), are widely used to infer trait-environment relationships. RLQ provides ordination scores to summarise the relationship between three matrices: sonotype functional traits (Q); environmental variables at each sampling site (R); and sonotype activity levels per site (L). The L matrix was analysed using Correspondence Analysis (CA). R and Q matrices contain both continuous and categorical variables so were analysed using Hill-Smith Principal Component Analysis (PCA) which allows the inclusion of qualitative and quantitative variables. In this framework, the sampling site (recording station) constitutes the unit of observation, linking environmental conditions and sonotype activity, while functional traits are defined at the sonotype level. To link traits (Q) and environmental variables (R) to bat activity (L), the ordinations of Q and R were weighted using sonotype and site scores (respectively) derived from the CA.

To statistically test the trait-environment relationships, we combined RLQ and fourth-corner approaches following Dray et al. (2014). Three permutation models were used in this RLQ-fourth corner analysis. Model 2 tests the null hypothesis that sonotype distribution with fixed traits is not influenced by environmental conditions, i.e. there is no relationship between sonotype activity and environmental conditions. Model 4 tests the null hypothesis that sonotype distribution with fixed environmental conditions is not influenced by functional traits. Model 6 tests the combination of the two models' outputs, against the null hypothesis that at least R or Q is not linked to L (with the alternative hypothesis that both environmental variables and traits influence sonotype distribution; Dray et al., 2014). Significance was based on 49,999 permutations, and the false discovery rate method was used to adjust p-values for multiple comparisons (FDR; Dray et al., 2014). All analyses were carried out using *ade4* package (Dray and Dufour, 2007).

3. Results

A total of 64,918 (of 66,301) bat passes were retained in the analysis, with 19 sonotypes identified across five families: Emballonuridae (8 sonotypes), Vespertilionidae (3 sonotypes), Mormoopidae (3 sonotypes), Noctilidae (1 sonotype), and Molossidae (4 sonotypes) (Table 1). All sonotypes were recorded in both forest and pasture sites, apart from *Rhynchonycteris naso*, which was only recorded in pasture. The most frequently recorded sonotypes were Molossidae D (n = 22818 bat passes), Molossus II (n = 12025 bat passes), and Sac bil/lep (n = 5995 bat passes), present in 107, 109, and 110 of the 115 sites, respectively. Yet, the most commonly detected sonotypes varied between the land cover type, with Molossus II and Molossidae D the most detected in the pastures (both n = 58 sites), and Sac bil/lep (n = 56 sites) the most recorded in the forests. Of all bat passes, ca. 81% were recorded in pasture.

3.1. Community-level analysis

The mean values of taxonomic diversity (measured by Simpson's D), functional diversity (Rao's Q) and functional uniqueness (Functional Uniqueness U) were not significantly different in forest compared to pasture in the beta regression models (0.695 vs 0.685; 0.244 vs 0.227; 0.344 vs 0.327 respectively) (Fig. 2). The best fitting models were those that included 'farm' as a random effect, suggesting that some of the variation in diversity was attributable to differences between farms. Nonetheless, even when accounting for this variation, the effect of habitat type (pasture compared to forest) still appeared small and remained insignificant across all diversity indices (Rao Q = −0.054, p = 0.468; Simpson's D = −0.053, p = 0.54; Functional Uniqueness = −0.053, p = 0.376; Table S2).

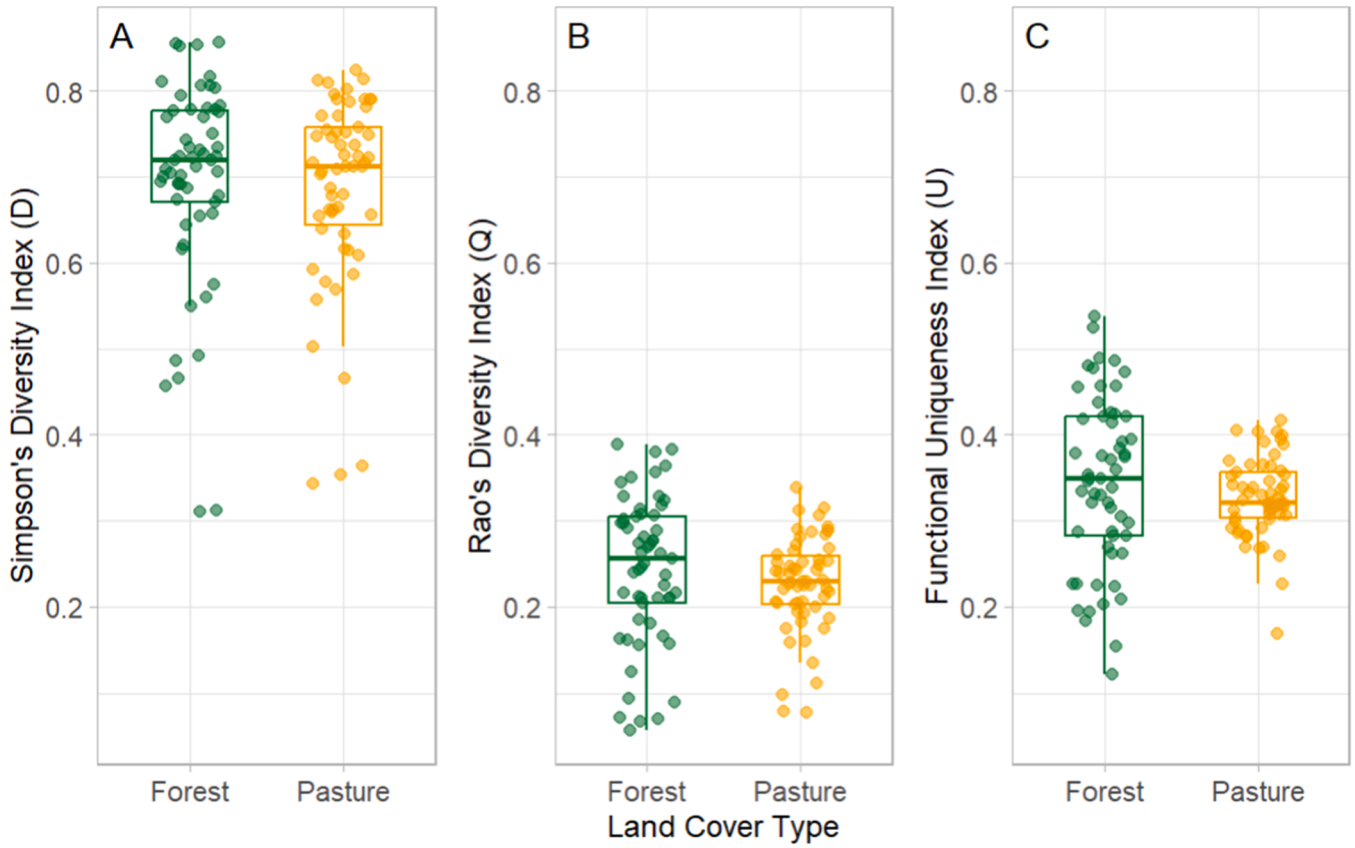

Fig. 2. Taxonomic diversity (Simpson's index D), functional diversity (Rao's index Q), and community-level functional uniqueness (U) of insectivorous bat assemblages in 56 forest and 56 pasture sites surveyed across 20 cattle farms in the Mato Grosso State, Southern Brazilian Amazon.

3.2. Trait-level analysis

The first axis of the RLQ ordination, which considers tables R, L and Q, explained 97.39% of the total variance between traits and environmental variables. The combination of the first and second axis explained 99.55%. According to the graphical representation of the RLQ, there was a slight grouping of sites according to proportion of pasture or forest cover in the site's buffer along the first axis of RLQ ordination (Figure A3). Pasture cover was also associated with patch density, and forest cover with distance to water. Sonotypes clustered according to family and certain traits, particularly call structure and foraging stratum (Figure A3). Sonotypes with CF-FM (*P. gymnonotus*, *R. naso*) and FM (*M. riparius, M. nigricans*) calls which forage in and among the canopy (VertS 1 & 2) were associated with forest area. In contrast, above-canopy foragers (VertS 3) clustered in ordination space with pasture area (*P. centralis*, Molossus II) (Figure A3).

The eigenvalues of the first axis of the RLQ analysis showed call structure as the most important trait variable, and habitat area as the most important environmental variable, explaining sonotype distribution (Fig. 3). Sonotypes with high-frequency CF-FM and FM echolocation calls that forage beneath and amongst the canopy were associated with greater forest cover and distances to water. In contrast, sonotypes with high relative wing loading and aspect ratio that forage above the canopy were associated with increased pasture area and patch density, corresponding to a more heavily fragmented landscape.

The fourth-corner analysis indicated that the distribution of AIBs was significantly associated with both environmental variables (model 2, $p < 0.001$) and functional traits (model 4, $p < 0.05$). Furthermore, model 6 which combines models 2 and 4 by measuring the link between sonotype activity, traits, and environmental variables was also significant ($p < 0.05$). The combination of the RLQ and fourth-corner analysis revealed that the first RLQ axis for functional traits (AxcQ1) was significantly associated with larger areas of forest and distances to water, and with smaller areas of pasture and values of patch density ($p < 0.05$) (Fig. 4). However, none of the traits were significantly related to the environmental axis after controlling for multiple comparisons (FDR) (Fig. 4).

4. Discussion

Biodiversity is declining at an alarming rate in major part due to degradation of tropical forests for the expansion of agriculture (Laurance et al., 2014). Yet, our understanding of how particular land-use types affect many species-rich taxonomic groups is limited, even for vertebrates. While previous studies have examined how cattle farming affects Neotropical bat assemblages (Gonçalves et al., 2017) this study is among the first to investigate the trait-based responses of Amazonian AIBs by explicitly linking functional traits to environmental variables. We uncovered several significant trait-environment associations, though no differences in α-diversity between forest and pasture sites.

4.1. Taxonomic and functional α-diversity in forest and pasture

Deforestation typically impacts bat functional diversity (García-Morales et al., 2016), but – in line with findings from Gonçalves et al., (2017) – we found little support for differences in taxonomic diversity, functional diversity, or functional uniqueness between forest and pasture sites. As all sites were sampled within a heavily fragmented landscape, both 'forest' and 'pasture' sites likely have similarly reduced α-diversity. Furthermore, many sites were close together, with 'forest' sites sometimes close to large patches of pasture and vice versa. Given

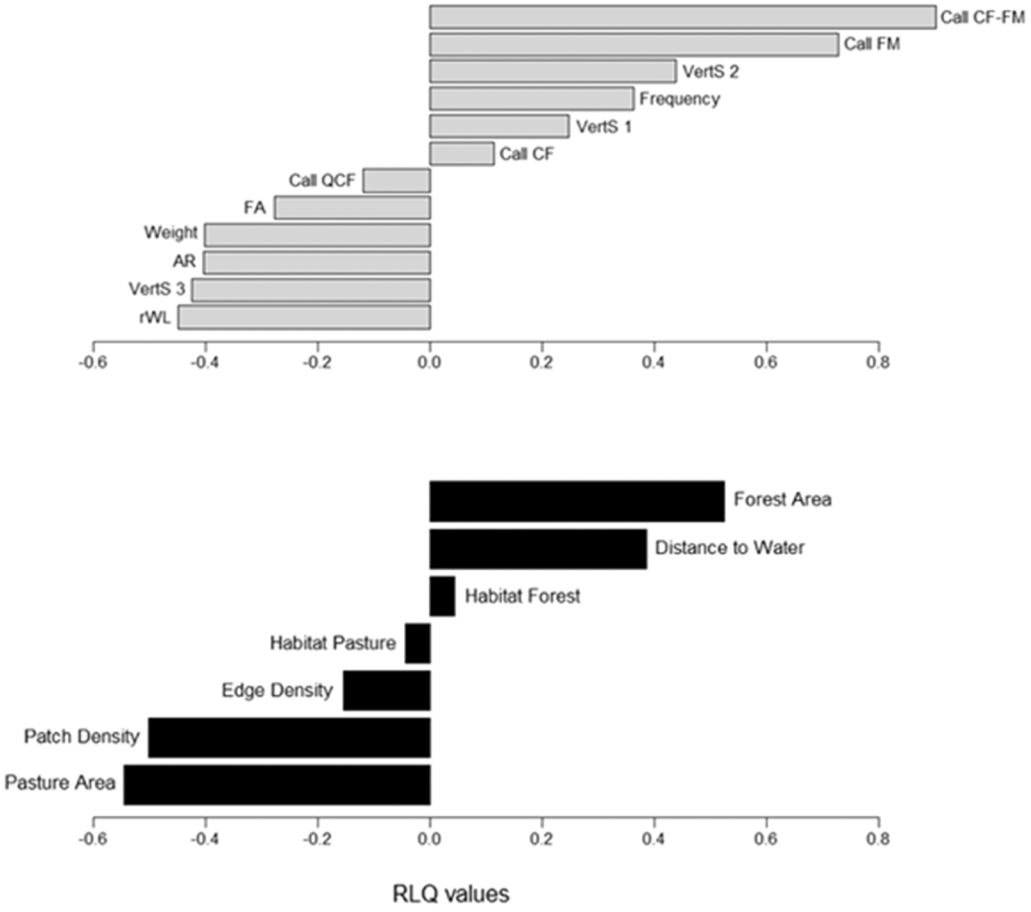

Fig. 3. RLQ eigenvalues showing the relationship between aerial insectivorous bat sonotype traits (grey bars) and environmental variables (black bars) along axis 1 across 20 cattle farms in the Mato Grosso State, Southern Brazilian Amazon.

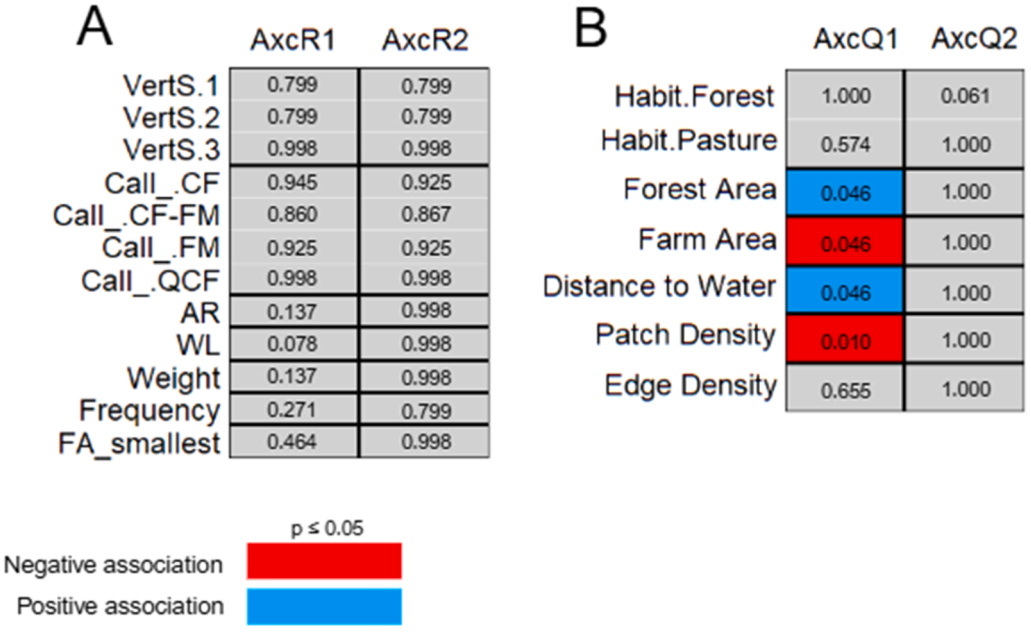

Fig. 4. Fourth-corner analysis showing the relationships between aerial insectivorous bat functional traits and environmental variables across 20 cattle farms in Mato Grosso State, Southern Brazilian Amazon. Tests were conducted between (A) the first two RLQ axes for environmental variables (AxR1/AxR2) and functional traits and (B) the first two RLQ axes for functional traits (AxQ1/AxQ2) and environmental variables. Blue = positive association, Red = negative association; after controlling for multiple comparisons (FDR). Variables are separated by black lines, and different levels of the same categorical variable are separated by grey lines. See Table 2 for trait abbreviations.

that bats can forage across several kilometres per night (Aharon et al., 2017), the lack of significant differences may be a result of this spatial overlap between sites and habitats.

Whilst measures of taxonomic diversity in both habitats were relatively high, functional diversity was noticeably lower. This discrepancy highlights the importance of using suitable diversity metrics, as important patterns of biodiversity loss may otherwise go undetected (Gonçalves et al., 2017; Farneda et al., 2018; Guillerme et al., 2025). These patterns suggest that habitat degradation may have reduced AIB functional diversity, with only certain traits able to persist in the modified landscape, though the absence of baseline data from before habitat modification limits the inference that can be drawn from this finding.

4.2. Functional trait variables

Consistent with other studies on Neotropical bats, we identified several functional traits influencing sonotype distribution across the study region, most importantly wing shape, call characteristics, and vertical foraging niche (Núñez et al., 2019; Colombo et al., 2023; Farneda et al., 2015). Two measures of wing morphology: relative wing loading and aspect ratio, are highly important predictors of bat mobility and habitat preference (Norberg & Rayner, 1987; Marinello and Bernard, 2014). High values indicate narrow, aerodynamic wings suited for fast and energy-efficient flight across open spaces (Altringham, 2011). In contrast, low values indicate short and wide wings, conferring high manoeuvrability in cluttered environments (Marinello and Bernard, 2014), but reduced ability to travel long distances (Estrada-Villegas et al., 2010; Bader et al., 2015). As hypothesised, we found that sonotypes with high relative wing loading and aspect ratio were associated with open, pastural landscapes, whereas those with low values were associated with forest. This supports that bats with wings adapted for cluttered habitats are less able to exploit and persist in the more open habitats associated with livestock (Gonçalves et al., 2017).

Echolocation call characteristics tend to reflect the habitat in which AIB sonotypes forage and are valuable predictors of vulnerability to habitat change (Luo et al., 2019; López-Bosch et al., 2022; Colombo et al., 2023). Frequency-modulated (FM) calls, which steeply sweep down the frequencies, are well-suited for cluttered habitats, providing detailed information on target prey and the surrounding environment (Altringham, 2011). In contrast, narrowband constant-frequency (CF) calls have high signal energy and low attenuation for long-range prey detection in open spaces (Luo et al., 2019). Constant-frequency frequency-modulated (CF-FM) calls are a special adaptation to foraging in cluttered spaces where many others may be echolocating (Denzinger and Schnitzler, 2013; Altringham, 2011), avoiding signal jamming through the complementary CF and FM components (Ding et al., 2024). In this study, we found strong RLQ associations between CF-FM and FM sonotypes and forest cover. This suggests sonotypes with calls adapted for cluttered, forested environments are more vulnerable to habitat loss and conversion to pastural landscapes than those with open-space (CF) or flexible (qCF) calls.

In line with previous studies, call frequency was strongly associated with habitat use, with high-frequency calls linked to forest environments and low-frequency calls to open habitats (Threlfall et al., 2011; Hanspach et al., 2012; Wordley et al., 2017). High-frequency calls have short wavelengths, enabling bats to detect small insect prey in cluttered environments (Altringham, 2011), but attenuate more quickly compared to lower-frequency calls, which are typically used by open-space foragers (Jung et al., 2007; Denzinger and Schnitzler, 2013). In our study, the lowest frequency calls were predominantly produced by Molossidae, which were strongly associated with pasture cover and qCF calls, suggesting that these call characteristics facilitate foraging in open, cattle-dominated landscapes. Conversely, sonotypes with high-frequency calls, such as the Vespertilionids and Mormoopids, appear less able to exploit these open environments.

The RLQ analysis also revealed that above-canopy sonotypes, which forage across open-spaces (Marques et al., 2016; Yoh et al., 2022), were associated with fragmented pastureland. Canopy and understory sonotypes, adapted to cluttered environments, were associated with forest, and are therefore more vulnerable to forest loss and fragmentation (Núñez et al., 2019; Díaz-B et al., 2023).

4.3. Environmental variables

The proportion of native vegetation in a landscape is an important predictor of bat activity (Mendes et al., 2017; Mancini et al., 2024; Rocha et al., 2024) and functional diversity (García-Morales et al., 2016; Jakobsson et al., 2020). Areas with less forest hold fewer appropriate roosting sites and reduced prey availability (Estrada-Villegas et al., 2010; Rodríguez-San Pedro and Simonetti, 2015). In line with our hypothesis, environments with less forest favoured bats with high mobility that can travel large distances to roosting sites, and those with low-frequency qCF calls suited to open-space foraging (e.g., the Molossidae). In contrast, more forested sites were associated with sonotypes with high manoeuvrability, and high-frequency FM calls suited for clutter-space foraging (e.g., the Vespertilionidae), making these more vulnerable to land use change.

Habitat conversion alters the structure and functioning of biodiversity by replacing complex forest habitats with more open environments (Haddad et al., 2015; Castro-Fernandes et al., 2025), and similarly to Gonçalves et al. (2017) we identified clutter-space foragers, particularly from the Vespertilionidae family, as less able to persist under these conditions. Their low relative wing loading and aspect ratio wings increase the energetic costs of movement in open environments, likely reducing their ability to persist in habitats where resources are more widely distributed (Estrada-Villegas et al., 2010).

AIBs frequently forage over water due to the increased densities of insects (López-González et al., 2015; Torrent et al., 2018). Díaz-B et al. (2023) reported that highly mobile, open-space foragers were associated with greater distances to water, reflecting their ability to travel longer distances and reduced reliance on nearby water sources. In contrast, our results indicated that sonotypes with lower mobility were associated with greater distances to water. This apparent discrepancy may reflect methodological limitations in how water sources were mapped. Water bodies were identified using Google-Earth pro, which may fail to detect streams or water sources beneath closed forest canopies, potentially biasing distance estimates. Under Brazil's Forest Code, riparian zones must be retained as forest, making the presence of undetected water sources within forested areas likely. Future studies should map water sources on the ground or use alternative mapping software for greater accuracy.

4.4. Potential impacts and recommendations

Changes to bat assemblage composition have important ecological consequences. As vulnerable sonotypes decline, so too will the ecosystem services they provide (Kemp et al., 2019; Rodríguez-San Pedro et al., 2020; Brasileiro et al., 2022). The loss of insectivorous bats will likely alter baseline insect populations, potentially leading to increases in pest species that were previously suppressed. For example, *Myotis nigricans* (Vespertilionidae) is a key predator of insect pests in rice crops, and *Eptesicus furinalis* (Vespertilionidae) and *Pteronotus gymnonotus* (Mormoopidae) have been reported to forage in crops such as coffee, banana, and pineapple (Azofeifa et al., 2019). As these sonotypes were all identified as vulnerable to land-use change in this study, the ecosystem services they provide may also be at risk in increasingly deforested and fragmented landscapes. Maintaining a functionally diverse bat community is of critical importance to preserve insect suppression, widely recognised as one of the most valuable ecosystem services bats provide to humans (Moir et al., 2021; Russo et al., 2018).

Given the findings from this study, we recommend that land managers not only maintain as much forest cover as possible, but also enhance connectivity among remaining forest patches. Promoting corridors and areas of secondary succession between fragments could facilitate movement and habitat use, enabling more clutter-adapted species, such as those from the Vespertilionidae and Mormoopidae families, to establish and forage within these agricultural landscapes, thereby supporting functional diversity.

5. Conclusion

Based on our findings, conservation efforts should prioritise sonotypes identified as most vulnerable, particularly clutter-space foragers within the families Vespertilionidae and Mormoopidae. Beyond maintaining forest cover, land-management strategies should aim to minimise habitat fragmentation across livestock-producing landscapes. Incentive schemes that encourage neighbouring farms to retain contiguous forest patches, rather than isolated forest reserves, could help safeguard vulnerable bat assemblages and preserve functional diversity and associated ecosystem services.

CRediT authorship contribution statement

Germana Vizzotto Osowski: Methodology, Investigation. **Márcia I G Zanella:** Methodology, Investigation. **Ricardo Rocha:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Alana Zammit:** Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Formal analysis, Conceptualization. **Rosenwyn Petherick-Davies:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ana Filipa Palmeirim:** Writing – review & editing, Visualization, Supervision, Methodology, Investigation, Conceptualization. **Harriet Bartlett:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Claudia Almeida Scariot:** Methodology, Investigation. **Adroaldo J Zanella:** Methodology, Investigation. **Luana Alves:** Methodology, Investigation. **André Luiz Gama Nogueira:** Methodology, Investigation. **Lais Silva Mariscal Baba:** Methodology, Investigation.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2026.123957.

Data availability

Data will be made available on request.

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