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# Diversity and distribution patterns of Ecuador's dung beetles (Coleoptera: Scarabaeinae)

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**Introduction:** Ecuador harbors an astounding number of ecosystems and species. However, anthropogenic land-use changes are the primary drivers of biodiversity loss in major taxonomic groups, especially insects. Among them, the Scarabaeinae subfamily containing dung beetles, is an excellent taxon for studying taxonomic and functional diversity, as they are relatively stable taxonomically and have a wide variety of ecological services. Their distribution is mainly influenced by biogeography and climate as their main ecological and environmental factors will allow us to quantify what aspects of diversity are being impacted under different circumstances and at different scales.

**Methods:** To understand the main of dung beetle distribution drivers, we analyzed a museum database from the National Institute of Biodiversity, Ecuador (INABIO) of over 5000 dung beetle specimens with 122 species collected throughout the country, we addressed the following questions: i) How does tribe distribution vary across climatic and elevational gradients? and ii) How does functional and taxonomic beta diversity vary across spatial scales? To address them, we focused on three main tribes: Canthonini, Coprini, and Phanaeini. We constructed GLM's and niche-based models to estimate Ecuador's distributions based on climate variables to explore potential predictor variables, using tree classification models, along with taxonomic and functional beta diversity across scales.

**Results:** The main variables influencing dung beetle distribution were elevation, and precipitation. The Phanaeini niche model is significantly better at predicting dung beetle presence throughout Ecuador than Canthonini and Coprini. We found high turnover in functional groups at larger scales, suggesting that dung beetles show high levels of habitat specialization, which associates to our findings where taxonomic beta diversity was higher in the Amazon basin compared to the coastal region. This may be due to the higher rate of dung production in Amazonia. Our findings also suggest that dung beetles are not found in areas above 2000m, mainly because dung beetles are well adapted to warmer and moist climatic regions. Precipitation and elevation are consistently essential variables for predicting Canthonini and Coprini presence, while temperature explains Phanaeini presence. Low levels of species turnover at the regional scale may be because the total species

richness in Ecuador is different, where divergence in taxonomic beta diversity between the two regions is an artifact of such differences in richness in Amazonia versus the coast, the distinction is also due to nonrandomly low taxonomic beta diversity levels in the coastal region.

**Conclusions:** Our results provide an essential framework for evaluating potential dung beetle habitat and diversity at different scales; therefore, by identifying dung beetles' diversity, combined with considerations of habitat fragmentation, human land-use alteration, and climate change, will be an important next step to inform better and prioritize dung beetle conservation efforts in other countries.

#### KEYWORDS

Amazonia, biodiversity, distribution modeling, ecological niche modeling, functional beta diversity, Neotropics, Scarabaeidae, species turnover

## Introduction

Ecuador is the smallest of the 17 megadiverse countries (Mittermeier et al., 1998) harboring an astounding number of ecosystems and species, with many endemic species occurring in small geographic ranges (Brooks et al., 2002, 2006; Bass et al., 2010). Unfortunately, the country has experienced profound changes to its natural habitats (Cuesta et al., 2017). In 2014, the country reported an estimated 1.83 million-hectare (14%) loss of forest area since 1990 (Sierra et al., 2021). The annual deforestation rate for 2008–2014 was – 0.37%, equivalent to an average annual loss of 47,000 hectares (Sierra et al., 2021). Due to these recent trends in habitat loss and extensive historical changes that occurred during the mid-20th century, only ~30% of the original natural vegetation remains in the coastal plains, 60% in the Andean region, and 88% in the Amazon lowlands. In this context, anthropogenic land-use changes are the primary drivers of global biodiversity loss in major taxonomic groups (Reid et al., 2005), and Ecuador is not the exception. Invertebrates are often particularly susceptible to landscape changes (Dunn, 2004; Samways, 2005), and because of the key roles they play in many ecosystem processes, their loss could produce cascading effects on the entire communities (Coleman and Hendrix, 2000). Despite this, our knowledge about the response of many insects to climate conditions and human activity is minimal (Nichols et al., 2008; Wagner, 2020). Understanding the response of insects to human activity and climate is necessary to support conservation policies and assess the functional consequences of human disturbance (Balmford and Bond, 2005; Halsch et al., 2021).

The order Coleoptera constitutes the richest group of species of any animal taxa, with more than 400,000 species described so far (McKenna et al., 2015; Zhang et al., 2018). Among this diverse order, dung beetles belong to the Scarabaeoidea superfamily, one of the largest superfamilies of beetles in the world, with approximately 150 families and 30,000 species (Carvajal et al., 2011). Scarabaeoidea is the most diverse group within the Coleoptera order in terms of its biology, ecology, and behavior

(Woodruff, 1973). Dung beetles are an excellent taxon for studying both taxonomic and functional diversity. They are widely distributed, diverse, and abundant in tropical and warm temperate ecosystems. Additionally, the ecological roles of dung beetles are known (Hanski and Cambefort, 1991) and the group has a relatively stable taxonomy (Philips et al., 2004). Adults and larvae are part of a specialized group that feeds mainly on the feces of herbivorous mammals, thus playing an integral role in recycling nutrients, improving plant growth, reducing pests, bioturbation, pollination, and secondary seed dispersal (Nichols et al., 2008). In addition, this taxon has been proposed as an excellent bioindicator group of environmental processes, being very sensitive to anthropic disturbance events (Halffter and Favila, 1993; McGeoch et al., 2002; Spector, 2006; Otavo et al., 2013; Noriega et al., 2021).

Two principal ecological factors influence present tribal, genera, and species distribution patterns of Scarabaeinae dung beetles worldwide (Davis and Scholtz, 2001): suitable climate and the number of dung types. At the species and generic level, there is a strong correlation between dung beetle taxon richness and the area of suitable climate in each of the world's biogeographical regions. However, at the tribal level, taxon richness and composition strongly correlate to both climatic area and the number of dung types. Dung type diversity also varies between biogeographical regions according to the evolutionary history of mammals (Davis et al., 2002). However, their relative influence differs according to the two main components of biodiversity: overall numerical richness and taxonomic identity. In the first instance, current distributional variance in taxon richness is often correlated strongly with current ecological or environmental factors (Francis and Currie, 1998; Davis and Scholtz, 2001; Moura et al., 2016). Scarabaeinae dung beetles also show strong spatial specializations stemming from their Gondwana land origin (Halffter and Matthews, 1966; Halffter, 1974; Silva and Hernández, 2014) centered on warmer, moister, climatic regions (Halffter, 1991; Davis et al., 2002; Birkett et al., 2018). At a regional scale, climate type exerts a significant influence on dung beetle diversity (Kirk and Ridsdill-Smith, 1986; Davis and Dewhurst, 1993; Davis,

1997; Duncan et al., 2009), which appears to be a general rule in the large-scale distribution of any taxonomic group (Currie et al., 1999; Clark et al., 2011). At a local scale, soil and vegetation types, influence dung beetle distribution (Nealis, 1977; Doube, 1983; Cambefort, 1991; Davis, 1996; Daniel et al., 2021); which, could strongly affect ecosystem functioning and disrupt all ecosystem services provided by this group of insects. Potential distribution and/or niche models for this group of species in Ecuador are scarce.

To quantify the effects of this habitat alteration and climate change, we need to understand which roles, functions, and ecological services exist on the landscape. Understanding where, when, and how species change in relation with the environment will allow us to quantify what aspects of diversity are being impacted under different circumstances and at different scales of land-use change (Barragán et al., 2011). These patterns allow for more effective management of natural areas to avoid biodiversity loss in critical regions (Hayes et al., 2009). In this context, beta diversity may be a handy metric for elucidating the processes underlying dung beetle community assembly at a regional scale. Beta diversity, which measures how species composition changes across space, can allow us to evaluate how community structure and assembly processes change as a function of the environment (McKnight et al., 2007; Buckley and Jetz, 2008; Lepori and Malmqvist, 2009). At local scales, high beta diversity measurements can reflect a decisive role of environmental filtering and species interactions in community organization (Fukami et al., 2005). At regional scales, high beta diversity can reflect a strong role in trait evolution, habitat specialization, and speciation (Graham and Fine, 2008). Taxonomic diversity, however, is often sensitive to stochastic effects such as genetic and ecological drift due to dispersal limitations (Baiser and Lockwood, 2011). And, furthermore, the presence of functionally redundant species limits the ability of taxonomic diversity to reflect environmental filtering (Swenson et al., 2011; Siefert et al., 2012). To tease apart these processes, one solution is to compare taxonomic and functional beta diversity. In comparison to taxonomic diversity, functional trait diversity is highly responsive to deterministic environmental processes but not to the stochasticity caused by ecological drift and dispersal limitation (Villéger et al., 2012; Myers et al., 2013). When functional beta diversity and taxonomic beta diversity respond similarly to spatial or temporal changes, communities are likely to assemble deterministically, while opposed responses suggest that stochastic effects may be causing mismatches in functional and taxonomic levels (Condit et al., 2002; Chase and Myers, 2011; Leibold and Chase, 2017). The dung beetle assemblages of Ecuador span a large and heterogeneous area, making it is critical to also consider regional habitat type, which can affect beta diversity (Swenson et al., 2011). By measuring the correlation between taxonomic and functional beta diversity, we hope to understand whether dung beetle assemblages in Ecuador are organized *via* habitat filtration and species interactions, which act at the functional level, or dispersal limitation and ecological drift, which operate at the species level.

To understand distribution and biodiversity patterns among Ecuador's dung beetles, we conducted two analyses utilizing a database of over 5,000 dung beetle specimens collected throughout the country, addressing the following questions: (i) How does tribe distribution vary across climatic and elevational gradients? And (ii) How does taxonomic and functional beta diversity vary across spatial scales? We first examined the distribution of three widespread tribes that play distinct roles in ecosystem functioning (Canthonini, Coprini, and Phanaeini) using distribution models to evaluate which environmental and topographic variables are significant drivers of tribe presence. We hypothesized that elevation and temperature would be the most important drivers of these tribes' distributions because of the dung beetle's small body size and dependence on mammal populations, which likely vary according to vegetation assemblages driven by elevation and moisture. Second, to assess the relative importance of stochastic versus ecologically driven community assemblage processes throughout Ecuador, we compared the relationship between alpha and beta diversity at the taxonomic level (taxonomic alpha/beta diversity) and functional group level (functional alpha/beta diversity) using 20 different spatial scales. Spatial scale was represented here as 20 spatial grids which all covered the same extent of Ecuador, but which differed in grain size, ranging from a 4-bit grid to a 256-bit grid. Based on their sensitivity to climate and specialization to dung type, we hypothesized that dung beetle community assemblage processes are likely driven by ecological factors such as niche specialization and biotic interactions both at the local and regional levels. We thus expected functional beta diversity and taxonomic beta diversity to respond similarly to spatial scale and alpha richness. Finally, to assess the importance of habitat type on stochastic versus ecologically driven community assembly processes, we compared the response of taxonomic and functional beta diversities to scale in the northern coastal region to the northern Amazonian region of Ecuador. We hypothesized that highly productive and more environmentally stable regions, such as the Amazon basin, would show high beta diversity at a much finer scales than heterogeneous regions such as the northern Coast.

## Materials and methods

Data were analyzed from the Coleoptera Collection of the National Institute of Biodiversity, Ecuador. This database includes adult dung beetle collections with records from the 1970s, with more than 5,000 entries, encompassing 122 species from three natural regions (Coast, Andes, and Amazonia), 19 provinces, and 11 vegetative formations. All the collections belong to more than 200 locations across Ecuador. All analyses focused on the three main tribes: Canthonini (42 species), Coprini (42 species), and Phanaeini (17 species), as they belong to groups with broad distributions and adapted to high percentage of canopy cover. Ecuador is divided into four unique geographical regions; the Coast, which has seven provinces ranging from 0 – 900 m and

limiting with the western Andes cordillera; the Sierra region (Andes) has 10 provinces all in high elevations ranging from 900 to 6,263 m, the Amazon has six provinces all located in the Amazon Basin from the Eastern Andes foothills at 800 m towards the evergreen forests at 200 m.

The Coleoptera Collection was trimmed to include only one entry per species per location to account for sampling bias. We analyzed the data in two ways. First, to understand how different tribes are distributed across the landscape, we fitted distribution models using several climate variables and elevation data (Supplementary Table S1). Second, we analyzed how grain size affects  $\beta$ -diversity using taxonomic and functional approaches, where the largest grain size divides the region (Amazonia or Coast) into fourths, each plot about 22,000 km<sup>2</sup>, and the smallest grain size divides the region into 256 plots each equal to 344 km<sup>2</sup>. All data analysis was conducted in R (R Core Team, 2022).

## Distribution modeling of dung beetle tribes

We constructed a niche-based model to infer climatic processes driving the species spatial distribution. To characterize the niche climatic space, we used 9 bioclimatic variables (Supplementary Table S1) obtained from the WorldClim database (Fick and Hijmans, 2017), including global monthly climate data from 1970 to 2000 at approximately 1 km resolution. We selected climate variables related to temperature and precipitation. These raster data and elevational data were imported in the statistical software R (R Core Team, 2022) as a raster stack for spatial analysis and the models were generated using the “sf” (Pebesma, 2018), “dismo” (Hijmans et al., 2022) and “raster” (Hijmans, 2022) packages. Since elevation data were available as spatial polylines, the data were converted to a raster using nearest-neighbor interpolation with the same extent and resolution as the climate data for ease of analysis. Global climate data were cropped to Ecuador, then extracted to the location of each dung beetle specimen. Although vegetation data were also available, we did not use these data in distribution modeling because of the large number of different vegetation classes for the number of observations available, then we performed distribution models separately for each tribe.

Because our data were presence-only, we generated pseudo-absences by randomly sampling background locations across Ecuador to produce approximately equal sample sizes of presence/absence data, as recommended by Barbet-Massin et al. (2012). Climate and elevation data were again extracted to these background locations.

In order to select the most appropriate climate variables, we used a classification and regression tree model (CART) (Lewis, 2000, de Ona and de Ona, 2012) to identify potential predictor variables for determining tribe presence/absence. Classification trees partition the response recursively into

hierarchical subsets that are increasingly homogeneous in presences/absences (Urban et al., 2002). The model uses single predictor variables for partitioning at each branch of the tree. Classification trees were ‘pruned’ using a cost-complexity parameter that minimized the relative misclassification rate from 10-fold cross-validation to avoid overfitting. To evaluate each reduced classification tree, we fit a model on a training subset

TABLE 1 AIC and BIC data for model selection for each of the three tribe distribution models using binomial generalized linear regressions.

Model	AIC	BIC
Canthonini		
PA ~ Elev + MAT + MAP + PPT seasonality + PPT warmest quarter + PPT coldest quarter	462.00	489.91
PA ~ Elev + MAP + PPT seasonality + PPT coldest quarter	489.13	509.06
PA ~ Elev + MAP + PPT coldest quarter	494.27	510.21
PA ~ (Elev + MAP + PPT coldest quarter) <sup>2</sup>	460.11	484.03
PA ~ Elev + MAP + PPT coldest quarter + Elev:MAP + MAP:PPT coldest quarter	456.08	483.99
Coprini		
PA ~ Elev + PPT driest month + PPT seasonality + PPT warmest quarter + PPT coldest quarter	496.48	520.52
PA ~ Elev + PPT driest month + PPT seasonality + PPT warmest quarter	499.51	519.54
PA ~ Elev + PPT driest month + PPT seasonality	510.48	526.51
PA ~ (Elev + PPT driest month + PPT seasonality) <sup>2</sup>	447.97	476.01
PA ~ Elev + PPT driest month + PPT seasonality + Elev:PPT driest month + PPT driest month: PPT seasonality	446.42	470.46
Phanaeini		
PA ~ Elev + MAT + MAP + PPT wettest month + PPT driest month + PPT warmest quarter + PPT coldest quarter	232.85	248.44
PA ~ Elev + MAT	232.80	244.49
PA ~ Elev + MAT + Elev:MAT	189.25	204.84

Models with the lowest AIC and BIC were selected for further evaluation and final predictions.

TABLE 2 Coefficients and significance statistics of final tribe distribution models using logistic generalized linear regression.

<b>Canthonini</b>					
P ~ Elevation + Annual precipitation + Precipitation of coldest quarter + Elevation: Annual precipitation + Annual precipitation: Precipitation of coldest quarter					
	Odds estimate	Log odds estimate	Standard error	Z value	Pr (> z )
Intercept	2.133088	0.7575708	0.4221209	1.7946772	0.0727052
Elevation	0.997687	-0.0023156	0.0004102	-5.6446864	0.0000000
Annual precipitation.	0.998669	-0.0013321	0.0003237	-4.1147182	0.0000388
Precipitation of coldest quarter	1.009537	0.0094921	0.0014441	6.5728855	0.0000000
Elevation: Annual precipitation	1.000001	0.000001	0.0000002	4.4234679	0.0000097
Annual precipitation: Precipitation of coldest quarter	0.999998	-0.0000016	0.0000003	-4.5809495	0.0000046
<b>Coprini</b>					
P ~ Elevation + Precipitation of driest month + Precipitation seasonality + Elevation: precipitation of driest month + Precipitation of driest month: Precipitation seasonality					
	Odds estimate	log odds estimate	Standard error	Z value	Pr (> z )
Intercept	4.1780556	1.4298460	0.9994721	1.4306012	0.1525445
Elevation	0.9984615	-0.0015397	0.0003580	-4.3015037	0.0000170
Precipitation of driest month	0.9745912	-0.0257371	0.0040670	-6.3282093	0.0000000
Precipitation seasonality	0.9707436	-0.0296929	0.0087657	-3.3873942	0.0007056
Elevation; Precipitation of driest month	1.0000148	0.0000148	0.0000035	4.2638772	0.0000201
Precipitation of driest month: precipitation seasonality	1.0009903	0.0009898	0.0001930	5.1290686	0.0000003
<b>Phanaeini</b>					
P ~ Elevation + Mean annual temperature + Elevation: Mean annual temperature					
	Odds Estimate	Log Odds Estimate	Standard error	Z value	Pr (> z )
Intercept	0.0051192	-5.2747593	1.3899440	-3.7949439	0.0001477
Elevation	1.0017771	0.0017755	0.0005362	3.3110261	0.0009295
Mean annual temperature	1.4615541	0.3795003	0.0662990	5.7240707	0.0000000
Elevation; Mean annual temperature	0.9998195	-0.0001805	0.0000277	-6.5169304	0.0000000

(70% of the data), then predicted tribe presence/absence on the holdout dataset. Variables identified through each pruned classification tree were then used to model tribe distribution using generalized linear models using the package “rpart” (Therneau et al., 2015) in R (R Core Team, 2022). The final models specify the logit ( $\ln(P/(1-P))$ ) of presence probability,  $P$ , as a linear combination of the specified predictor variables and interactions between predictors.

We selected elevation, mean annual temperature, annual precipitation, precipitation of the wettest and driest months, precipitation seasonality, and precipitation of the warmest and coldest quarters for inclusion in our models based on a threshold Pearson's correlation of 0.7 (Sedgwick, 2012). Classification tree models predicting tribe presence/absence allowed us to reduce the number of potential predictor variables for further consideration in logistic regression.

## Generalized linear models

We began our analysis by exploring potential predictor variables for explaining the distribution of dung beetle tribes across Ecuador. We first plotted univariate histograms of the possible predictor variables (Supplementary Figure S1), the response variable, and tribe presence to understand the underlying distribution of each variable. We then explored a correlation and

bivariate scatterplot matrix of all variables to understand the full scope of correlations between the potential predictors. After considering redundancy in several variables and visualizing possible important predictor variables graphically and through the CART model, we decided to explore elevation and all bioclimatic variables, as potential predictor variables in generalized linear models. Because the response variable, tribe presence/absence, is discrete binary count data bounded at zero, we specified a full generalized linear model (GLM) with a binomial distribution and logit-link function for each tribe. We then identified several reduced models predicting tribe presence/absence with predictor variables and determined the statistical significance with an ANOVA – chi-squared test in the entire model. The final models for each tribe were selected by comparing Akaike Information Criteria (AIC) and Bayesian Information Criteria (BIC) (Table 1), as well as their evaluation performance. Using the last models for each tribe (Table 2), we predicted the probability of occurrence across Ecuador based on the climate and elevation raster inputs.

## Model diagnostics and validation

To assess whether a binomial GLM with a logit link function was appropriate for characterizing the distribution of different dung beetle tribes, we produced diagnostic plots for the model

and performed ANOVA, chi-square analyses to compare its ability to explain variance in the data with the full binomial model. We assessed linearity by plotting the residuals versus the model's fitted values and examining the normal quantile-quantile (Q-Q) plots. The residual versus fitted values plot was used to detect non-linearity, unequal error variances, and outliers. We used Cook's distance and plotted hat values in an index plot to determine if any outliers were exerting undue influence on the model. We examined response, Pearson, and deviance residual plots for each final model to assess for normality. To determine the accuracy of our distribution models, we used a threshold-dependent metric. We took an initial random sample of 70% training data to fit the top distribution models. We then predicted dung beetle tribe presence/absence using the validation set on the training model. We performed this holdout model selection and validation five times to examine consistency in the top model's covariates, parameter estimates, and accuracy, afterwards, we specified the threshold for each validation set around the

prevalence of a tribe in the data and converted our predicted probabilities to presence/absence predictions, and produced a contingency table to gauge overall accuracy, false positives, and negatives. We also assessed the error rate in classification using the same threshold. The class agreement command produced the overall accuracy metric and the kappa coefficient, which measures the agreement between predicted and observed data beyond chance agreement between classes. Furthermore, we used receiver operating curves (ROC) based on the overall accuracy to calculate an area-under-curve statistic (AUC) given our specified threshold.

### Taxonomic and functional alpha and beta diversity across scales

For our taxonomic approach, within the three tribes, we used the collection data of 100 species spread among 682 observation points throughout Ecuador. Afterwards, we identified 14 functional groups

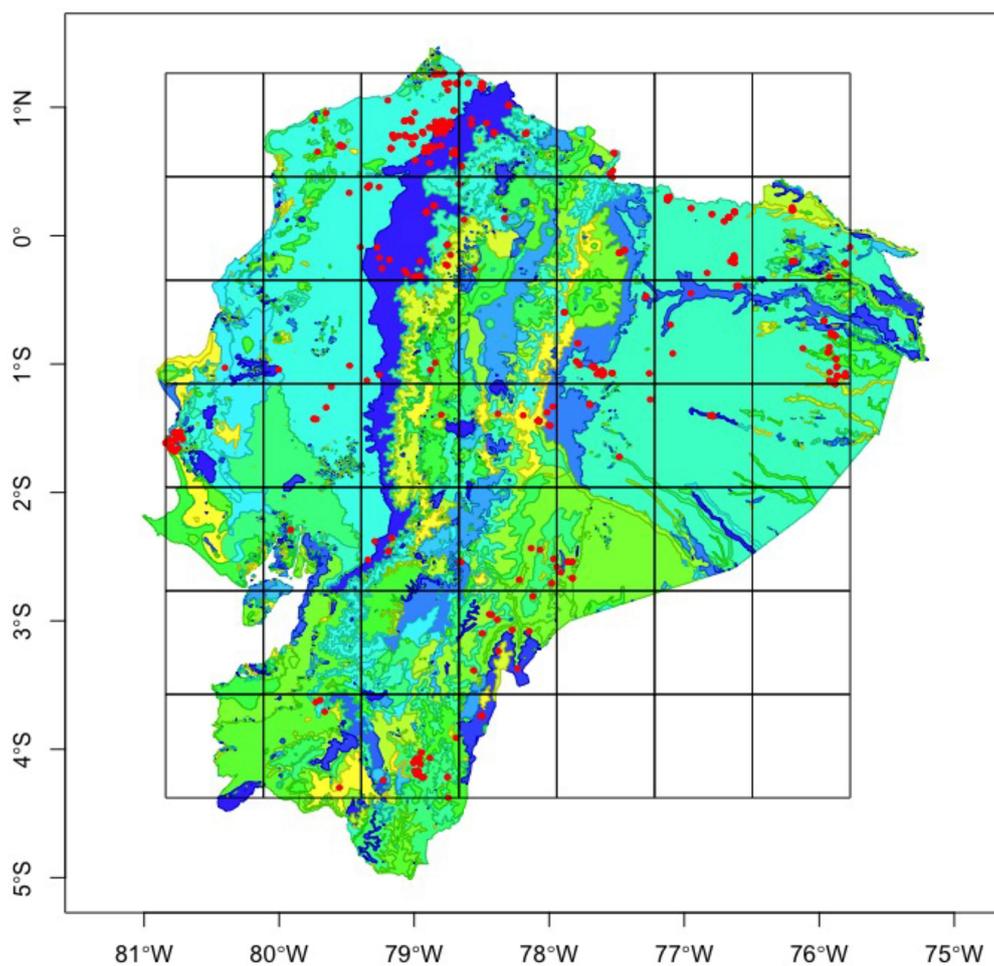


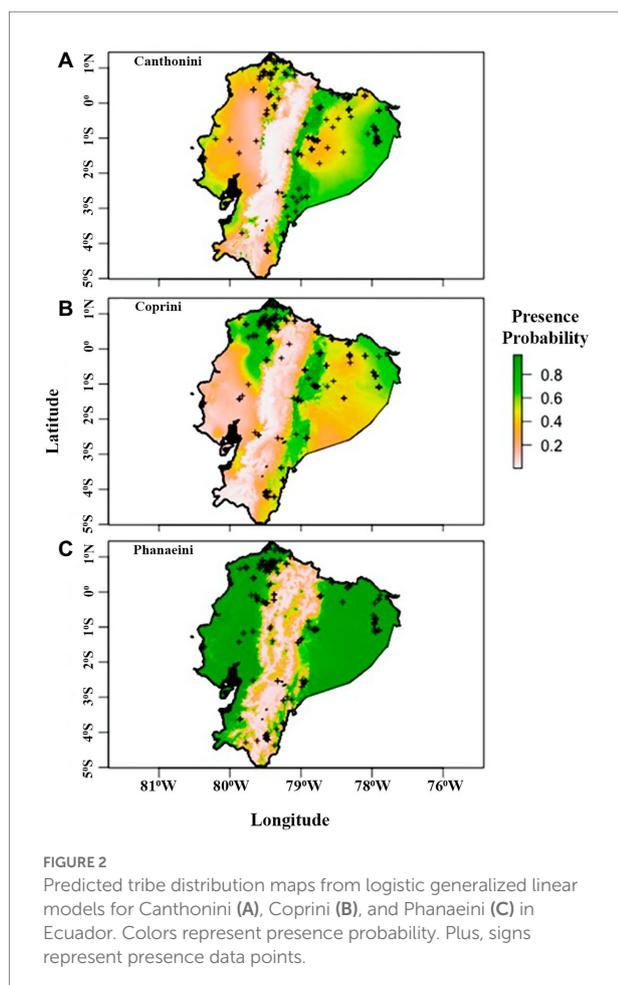
FIGURE 1

Dung beetle occurrence records (red) throughout Ecuador, fitted with a 64-bit grid to calculate taxonomic and functional beta diversity. Base map colors represent vegetation regimes.

**TABLE 3** Predictor variables selected in the final distribution model for each tribe.

Tribe	Predictors	Error rate	AUC	Threshold
Canthonini	Elevation	31.02%	0.73	0.40
	Annual precipitation			
	Precipitation of coldest quarter			
Coprini	Elevation	30.88%	0.76	0.40
	Precipitation of driest month			
	Precipitation seasonality			
Phanaeini	Elevation	9.28%	0.97	0.31
	Mean annual temperature			

Average error rate, AUC, and maximum accuracy threshold from five trials of model validation on a holdout data set are also shown.



(Supplementary Table S2) conceptualized as non-phylogenetic, aggregated units of species sharing an important ecological characteristic and playing an equivalent role in the community

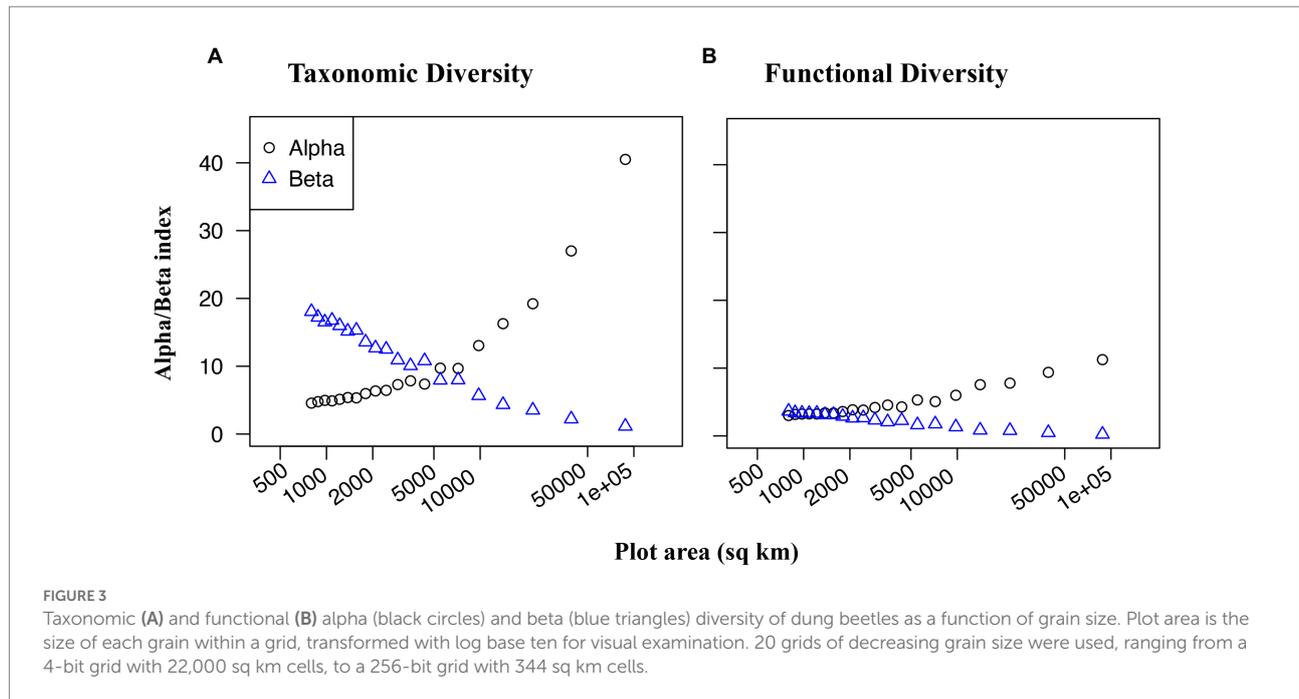
(Orfanidis et al., 2011), based on their feeding strategy (coprophagous, necrophagous, generalist), nesting behavior (paracoprid – tunnellers and telecoprid – ball-rollers), and size (big, medium, and small). Using the sf package (Pebesma, 2018), we created 20 different spatial grids, dividing the area of the total spatial extent by ( $x^2$ ), where  $x$  equals two through 21 (Figure 1). The largest grid divided the total area of Ecuador into fourths, each 22,000 km<sup>2</sup>, while the smallest grid had 256 cells of area 343.9 km<sup>2</sup>. Alpha diversity was calculated as the number of species (taxonomic richness) and the number of functional groups (functional richness) present on each cell; while Beta diversity was calculated for each cell as the total number of species or functional groups present within the entire grid, divided by the species/functional group richness within a given cell, minus one ( $\beta = \text{gamma}/\text{richness} - 1$ ), following Whittaker (1960) approximation.

To compare the coastal and Amazonian regions, we subsetted the data from these two regions and repeated the above methodology for each using 15 different spatial grids with cell sizes from 5,264 km<sup>2</sup> down to 82.3 km<sup>2</sup>. We then compared the coefficients from each linear model. To evaluate whether differences in beta diversity between the two regions was an artifact of differences in species richness between the two regions, we used a null model to compare the observed beta diversity to the expected beta diversity, given richness (Crist et al., 2003; Myers et al., 2013). The null model randomly sampled individuals from the regional species pool to fill each cell within the grid, while keeping the number of individuals sampled per cell equal to that observed and the number of records per species in the regional pool equal to that observed. We then compared the observed beta diversity values to the mean of 1000 iterations of the null model outputs and calculated  $p$ -values for each grid as the ratio of iterations with values less than the observed beta diversity value.

## Results

### Distribution modeling of dung beetle tribes

The probability of presence for each tribe is a function of the predictors specified in Tables 2 and 3, being elevation the most significant predictor variable in all three models. Canthonini presence varied as a function of elevation, annual precipitation, and precipitation of the coldest quarter and based on the tree model, all the precipitation variables worked as important predictor variables, with a 21% error rate predicting on a holdout dataset; its probability decreased as elevation increased, with a much more pronounced negative trend as annual rainfall increased, indicating the importance of the timing of precipitation for this tribe (Figure S5). Coprini presence increased slightly as elevation increased, precipitation of the driest month, and precipitation seasonality, and its classification tree suggested precipitation and seasonality as potentially important variables, with a 24% error rate predicting on a holdout dataset (Figure S6). Finally, Phanaeini presence varied as a function of elevation and



mean annual temperature. The probability of Phanaeini presence increased with mean annual temperature but decreased as elevation increased with the classification tree suggesting elevation, mean annual temperature, and precipitation of the wettest month as potentially important variables, with a 5% error rate predicting on a holdout dataset (Figure S7).

The distribution model for the Phanaeini tribe performed significantly better than the final distribution models for Canthonini and Coprini (Table 3). The average error rate from five trials of validating the last models on a holdout dataset was 31.02% for Canthonini, 30.88% for Coprini, and 9.28% for Phanaeini. These error rates are based on average threshold values for each tribe of 0.40 for Canthonini, 0.40 for Coprini, and 0.31 for Phanaeini. The threshold values used were optimized to maximize accuracy in each trial while minimizing false positives and negatives. To evaluate each model with a threshold-independent metric, we used the area under the receiver operating curve (AUC), representing the tradeoff between true positives and false positives. The average AUC for five holdout validation trials were 0.73, 0.76, and 0.97, respectively. Therefore, the Phanaeini distribution model is significantly better at predicting dung beetle presence throughout Ecuador compared to the final Canthonini and Coprini models (Figure 2).

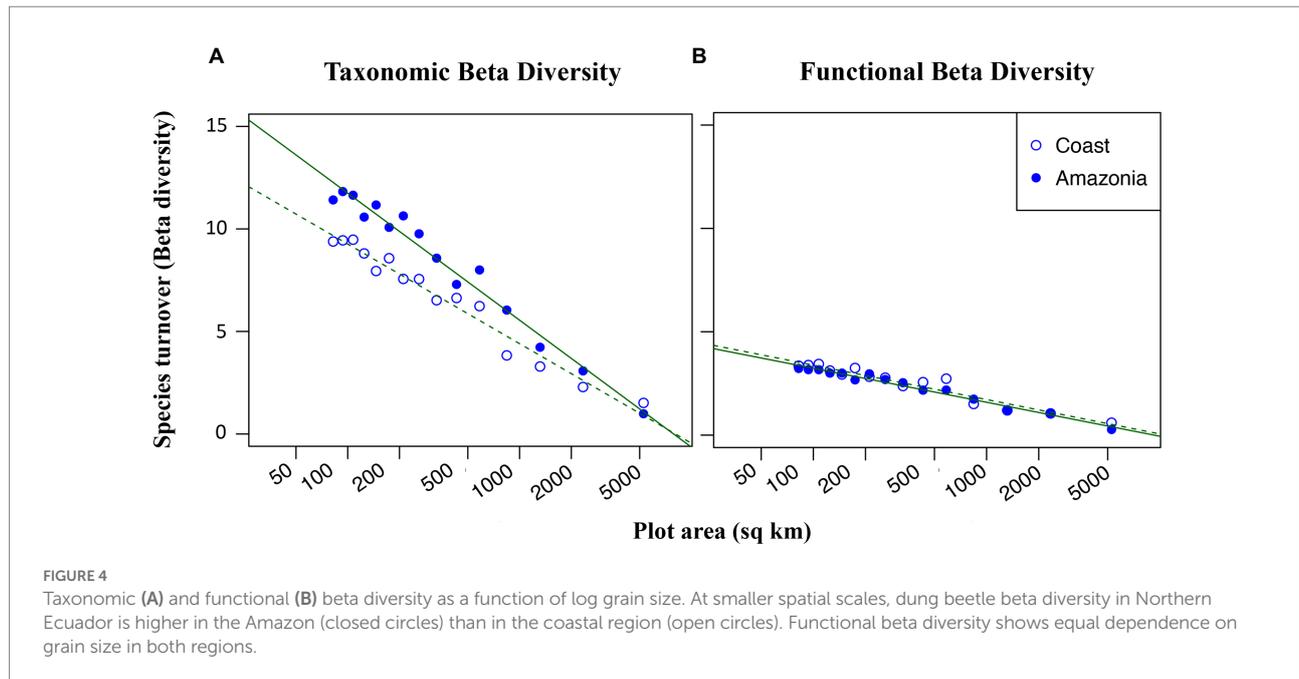
## Alpha and beta diversity analyses – Comparing functional and taxonomic diversity

Over the scope of Ecuador, taxonomic beta diversity (species turnover) had an inverse relationship to taxonomic alpha diversity

(species richness) (Figure 3A), such that at smaller spatial scales, the rate of species turnover among plots was much higher than the mean species richness of any individual plot. Functional beta diversity (functional turnover) also increased as plot size decreased (Figure 3B), however, unlike with taxonomic turnover, functional turnover was only marginally greater than functional richness at small spatial scales. In other words, even at small spatial scales, there was low variation of functional groups among plots.

## Beta diversity analyses – Comparing the coast and Amazonia regions

In this dataset, 72 species of dung beetle from 287 observations were recorded in Amazonia, and 38 species from 291 observations were recorded in the coastal region. Out of the 14 identified functional groups, all 14 were represented in Amazonia and 12 were represented in the coastal region. Taxonomic beta diversity was higher in Amazonia compared to the coast (Figure 4A) while functional beta diversity did not differ between the two regions (Figure 4B). Taxonomic beta diversity levels in Amazonia were in line with what null model analysis predicted based on the region's species richness: the higher levels of taxonomic turnover in Amazonia compared to the coast can be largely attributed to higher species richness in Amazonia (Figure S8A). However, taxonomic beta diversity levels from the coastal region were significantly lower than expected based on the null model in 9 out of the 15 grids and marginally lower in 11 out of 15 grids (Figure S8B). Thus, while some of the divergence in



taxonomic beta diversity between the two regions is an artifact of differences in species richness in Amazonia versus the coast, the distinction is also due to nonrandomly low taxonomic beta diversity levels in the coastal region. Functional beta diversity did not significantly differ from the null expectation in either region.

## Discussion

### Distribution modeling of dung beetle tribes

Precipitation and elevation were consistently significant for predicting presence of Canthonini and Coprini, while the temperature was more important for predicting presence of Phanaeini in Ecuador. These climatic distribution patterns of dung beetle taxa reflect historical and current ecological influences, where tribes are correlated to a combination of tropical climate types (Davis et al., 2002). Despite broad limitations to dung beetle diversity associated with annual temperatures below 15°C, and annual rainfall below 250 mm (Halffter, 1991; Espinoza, 2018), taxa distribution models reveal taxa-specific climatic niches, with some taxa exhibiting narrower climatic preferences and consequently more distribution-limited than others. The probability of Canthonini presence decreased with increasing elevation, with a much more pronounced negative trend as annual rainfall increased. Despite these trends, the probability of Canthonini presence increased as the precipitation of the coldest quarter increased, indicating the importance of the timing of precipitation for this tribe. In contrast to Coprini presence

increased slightly as elevation augmented, with a stronger positive trend as precipitation of the driest month increased. Furthermore, Coprini presence also increased as precipitation seasonality increased. Phanaeini had a much higher probability of occurrence across much of Ecuador, exhibiting a more generalized climatic niche. The probability of Phanaeini presence increased with mean annual temperature and decreased as elevation increased.

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Our results suggest that dung beetles were not frequently found in areas above 2000 m, consistent with Halffter (1991) and Espinoza (2018), who emphasizes that dung beetles are well adapted to climatic regions which are warmer and moister than those found at high elevations (Figure 2). Specifically, dung beetles in Ecuador are unlikely to be found in the High Andes, where climatic conditions get colder and have low atmospheric pressure, where only few a species like *Dichotomius cotopaxi*, can tolerate elevations above 2,500 m (Villamarin-Cortez, 2010, 2013; Carvajal et al., 2011).

All tribes analyzed are well distributed throughout the Neotropics and are expected to be found in areas where environmental conditions are favorable to their survival, especially the Coast and Amazonia, consistent with our distribution predictions. These regions have an appropriate environment for dung beetles to accomplish their life cycle. For example, the Coast has the most fertile and productive land, along with a tropical climate and a mean temperature of

25°C (77°F). Amazonia, in contrast, has less productive soil but is comprised mainly of rainforest, with a mean temperature of 23–25°C. Despite known temperature limitations, tribes were most strongly correlated to both rainfall (Walter and Lieth, 1964; Noriega et al., 2015) and elevation (Espinoza, 2018), which may reflect past Cenozoic dispersal patterns into northern regions when their climates were warmer (Laporte and Zihlman, 1983; Parrish, 1987; Carvajal et al., 2011), these different climate conditions have helped dung beetles to evolve and survive since the megafauna extinction and Pleistocene climate oscillations (Maldaner et al., 2021). Nevertheless, these regions and ecosystems have changed drastically, due to the expansion of the agricultural border, such activities reflect deep modifications in dung beetle assemblage composition, mainly because they are a very sensitive group to even low-intensity habitat modification (Bicknell et al., 2014). While our results suggest differences in climatic niche breadth for the three taxa, it is important to recognize the limitations of the distribution models presented here, specifically, the lack of true absence data and the importance of species interactions and finer scale resource limitations in moderating habitat use and distributions. However, this broad scale understanding of taxa distribution and climatic preferences aids our understanding of potential climate change impacts and helps identify critical habitat for dung beetle diversity from Ecuador.

## Beta diversity patterns

Taxonomic beta diversity (species turnover) was more sensitive to spatial scale than functional beta diversity (functional group turnover) in assemblages of dung beetles throughout Ecuador (Figure 3). When plot size was decreased, species turnover increased at a greater rate compared to functional group turnover. In other words, plots were more likely to contain distinct species of beetle, but not necessarily distinct functional groups. This pattern signifies that a few key functional groups are present in most habitats, but that these functional roles are often filled by unique species. The presence of many functionally redundant species suggests that dispersal limitation may structure dung beetle communities in Ecuador. When species are dispersal limited, communities often become spatially heterogeneous through ecological or evolutionary drift (Baur, 2014), which creates high taxonomic beta diversity. However, it is also possible that the functional groups that we have delineated, which are based on size, feeding strategy, and nesting behavior, do not capture critical traits that distinguish a species' ability to survive in a particular habitat or community. Additionally, while this analysis considered an array of spatial scales, all were above 80 km<sup>2</sup>. Taxonomic and functional beta diversities may perform differently at smaller scales, where dispersal is likely to be less limiting.

According to our findings, taxonomic and functional beta diversity was higher in the Amazon basin compared to the coastal region. This may be due to the higher rate of dung production in Amazonia, which is known to influence dung beetles' abundance and diversity (Campos and Hernández, 2013, da Silva and Hernandez, 2014, Silva and Hernández, 2015, Silva and Hernández, 2016). The physical structure of the forest floor, which is influenced by leaf litter, can affect the nesting activities of certain dung beetles' guilds such as rollers (Nichols et al., 2008). Roller dung beetles roll food resources several meters away from their source until they find an adequate place to bury them. This behavior helps them escape high competition on ephemeral resources such as dung and carrion. In contrast, we see lower levels of species heterogeneity in the Coast. We expected the drier climate in this region to reduce the diversity of dung beetle nesting behaviors found in Amazonia. However, surprisingly, the two regions contained a similar number of functional groups (12 in the coast and 14 in Amazonia) and, furthermore, functional beta diversity responded to spatial scale equally in both regions (Figure 4B). This suggests that ecological drift and dispersal limitation, affect taxonomic diversity more than functional diversity, may play large roles in maintaining high species richness in the Amazonian region. While deterministic factors such as niche partitioning certainly must also be at play, the similarity of functional beta diversity between the coast and Amazonia suggests that stochastic processes are more responsible for the maintenance of species diversity in the Amazon.

In the context of threats due to land use, our results demonstrate the necessity of conserving landscapes across a wide variety of environmental gradients to respond to beetle diversity. Dung beetle communities can be sensitive to habitat change and it is common to see the reduction in diversity and compositional changes in degraded habitats (Nichols et al., 2007; Solar et al., 2016). Our results suggest that habitat changes primarily drive these responses to the microclimate and vegetation composition and structure. The high levels of taxonomic beta diversity at small spatial scales suggests that the Amazon maintains a high species richness by having higher species turnover, especially because vegetation is well preserved, maintaining good soil conditions, augmenting successful breeding and manure burial (Maldonado et al., 2019), which are essential for dung beetle survival.

Our results provide an essential framework for evaluating potential dung beetle habitat and diversity at different scales. Overall, our results are consistent with the knowledge of dung beetle biological and ecological requirements, and provides a country-wide analysis of Canthonini, Coprini, and Phanaeini dung beetle tribes distribution and diversity. Therefore, by identifying dung beetles' diversity, combined with considerations of habitat fragmentation, human land-use alteration, and climate change, will be an important next step to inform better and prioritize dung beetle conservation efforts in other countries.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

## Author contributions

SV-C: study concept and design. SV-C, LH, SC, and JM: analysis, interpretation of data, and statistical analysis. SV-C, LH, SC, JM, and JN: drafting of the manuscript. All authors contributed to the article and approved the submitted version.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2022.1008477/full#supplementary-material>

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