



# Functional Responses of Bird Assemblages to Land-Use Change in the Colombian Llanos Region

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Land-use change in the Colombian Llanos due to agro-industrial expansion affects biodiversity. This change alters species occurrence probability, consequently impacting species' composition. For some species, the occurrence probability increases with land-use changes, while it stays unchanged or decreases for others. This interspecific variation in the response to land-use change may be mediated by functional traits, among other factors. We investigated response functional traits to land-use changes and their influence on the occurrence probability of bird species in the Colombian Orinoquia region. We compiled data for 13 morphological and life-history traits of 364 species recorded in forests, savannas, rice fields, palm oil crops, and livestock pastures in the piedmont and flooded savanna landscapes. We used a novel framework to identify response functional traits (i.e., traits with a significant effect on occurrence probability) through multiple statistical tests. We used random forest models to identify response functional traits to land-use change for pairwise comparisons of natural vs. agricultural land use types. For the functional traits, we estimated the influence of their states as trait attributes on species' responses to land-use changes. We identified functional groups based on hierarchical clustering analysis. Functional groups corresponded to different levels of response, that is, different changes in probability occurrence. Land-use changes altered the multidimensional space of bird traits (i.e., functional diversity), implying modifications in species' composition, functional redundancy, and functional group turnover. Functional traits were similar for random forest classifications of the same natural cover but differed among landscapes. In the piedmont forests, social behavior—migratory status—was a functional trait combination common to all classifications, while foraging behavior—nest location trait combination was common to all forests scenarios in flooded savannas landscape classifications. Migratory status was a functional trait for all savanna classifications. Functional groups described the impacts of land-use changes on bird assemblages. Identification and characterization of these groups using trait attributes can help predict species' responses to land-use changes and guide conservation efforts toward groups with decreased occurrence probability, including recommendations for agricultural practices that can reduce impacts on the Orinoquia biodiversity.

**Keywords:** functional diversity, functional traits, trait attributes, machine learning classification, Orinoquia

## INTRODUCTION

The loss and degradation of natural habitats due to land-use changes are among the main drivers of biodiversity loss (Foley et al., 2005; Millenium Ecosystem Assessment, 2005; Baan et al., 2013; Deinet et al., 2018). It is estimated that vertebrate populations decreased by at least 60% worldwide and 89% in the Neotropics between 1970 and 2014, where more than half was due to loss and degradation of natural habitats (Deinet et al., 2018). Agriculture is the primary driver of land-use changes (Lambin et al., 2001; Meyfroidt et al., 2013). Understanding its effects on biodiversity can help identify practices that lessen these impacts, predict and mitigate future biodiversity changes, and design monitoring approaches for conservation strategies, including sustainable agriculture (Wezel et al., 2014). The Sustainable Development Goals program promotes sustainable agriculture and reduces its effects on the degradation of natural habitats. Such sustainability could be supported by developing indicators that aid in understanding and predicting the impacts of anthropic pressures and the design and monitoring of conservation strategies (Burchart et al., 2010; Biodiversity Indicators Partnership, 2011).

Traditionally, land-use impacts on biodiversity are measured using taxonomic metrics (based on the species count), limiting the possibility of thoroughly understanding the effects of anthropic activities (Branquinho et al., 2019). However, the impact may occur at different levels of biodiversity (e.g., genetic, species, and ecosystem), as well as in the underlying mechanisms that sustain it, leaving taxonomic metrics telling only part of the story (Flynn et al., 2009; Mouillot et al., 2013; Pearson et al., 2014; Titeux et al., 2016). Taxonomic metrics do not take into account the multidimensional space that each species represents and assume them as units of ecological equivalence, for instance, regarding their effects on the ecosystem and their survival probabilities (Chave, 2004; De Souza et al., 2013; Luck et al., 2013; Córdova-Tapia and Zambrano, 2015). Accordingly, the taxonomic approach should be complemented with additional ecological metrics to better understand the impacts of land cover transformations on biodiversity, leading to better-informed strategies to prevent or mitigate them (Pereira et al., 2013).

Functional ecology studies assign values to each species based on functional traits and their different states as the range of functional attributes it occupies within the multidimensional space representing species assemblage (Luck et al., 2012). We refer to trait attributes as different values, levels, or states of a trait. Functional traits can be classified into effect or response traits (Luck et al., 2012). The former describes the effect patterns of a species assemblage on ecosystem processes (e.g., dispersal strategy), while response traits describe responses of a species assemblage to environmental disturbances or changes (Hooper et al., 2002; Lavorel and Garnier, 2002; Naeem and Wright, 2003). Therefore, the effect trait analysis allows describing the ecosystem functions, while the response trait analysis is useful in understanding the assemblage's responses to the impacts of environmental disturbances. The functional response refers to the influence of functional traits on the response of the

assemblage to environmental changes. Functional trait analyses are based on the collection of multiple individual traits and the assessment of their effects on ecosystems or responses to ecosystem disturbance, leading to the identification of the functional groups of species that represent particular effects or response patterns (Diaz and Cabido, 2001; Hooper et al., 2002; Luck et al., 2012). These add up to our understanding of how ecosystems function and their tolerance to disturbances. Global meta-analyses conducted to assess the impacts of anthropic interventions on bird assemblages show a decrease in functional diversity and describe the implications of these changes for the provision of ecosystem services (Flynn et al., 2009; Newbold et al., 2013; Bregman et al., 2014; Matuoka et al., 2020).

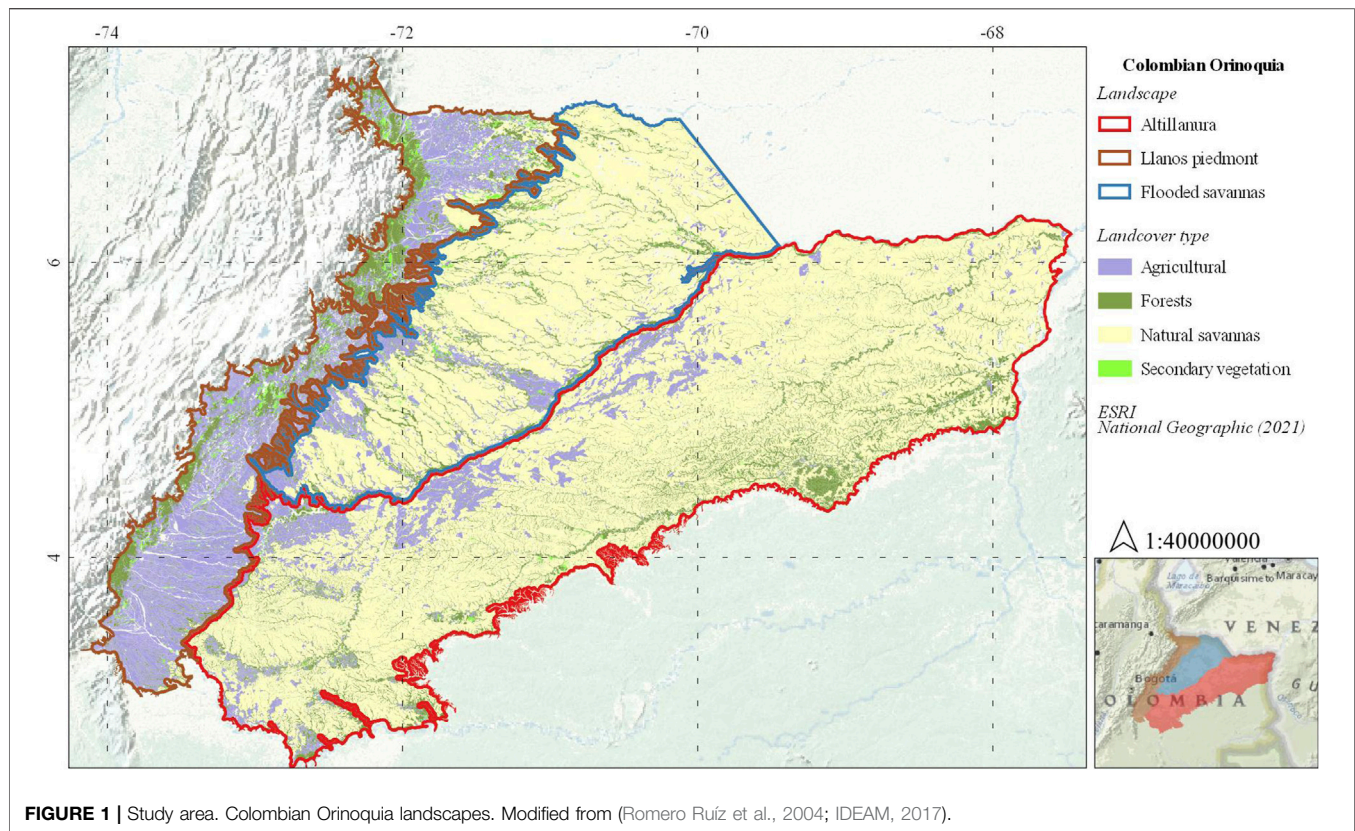
The Colombian Llanos or the Orinoquia region is a region of great environmental heterogeneity that supports a high biological diversity (Romero Ruíz et al., 2004; Lasso et al., 2010, 2011). In recent decades, socioeconomic development has accelerated the expansion of livestock farming, oil exploitation, and agribusiness related to oil palm crops, rice, and others, which have exposed the region to the socioecological transformation processes of uncertain environmental and socioeconomic impacts (Romero Ruíz et al., 2004, 2011; Andrade et al., 2009). Furthermore, current national policies promote the Orinoquia region as the focal area for agricultural expansion, with 56% of this region being part of the agricultural frontier and available for agricultural activities (UPRA, 2021). This generates an urgency for developing mechanisms to assess and account for the potential impacts that this transformation could impose on the biodiversity and for integrating this information into decisions that support the region's sustainable development.

We identified "response functional groups" to land-use changes from natural to agricultural land cover types to identify and understand patterns of changes in bird assemblages in response to land cover transformation. We determined the response of a set of functional traits (functional response traits) to changes of natural land cover (forests and savannas) to agriculture (livestock, rice, and oil palm crops) in the Llanos piedmont (LP) and flooded savanna (FS) landscapes of the Colombian Llanos. We identified the functional response patterns to land-use changes and the functional traits and attributes that modulate such responses. These functional groups and response patterns are helpful indicators to assess land-use change impacts and monitor biodiversity in response to agricultural activities.

## MATERIALS AND METHODS

### Study Area

The Colombian Llanos is a savanna-dominated region with high ecosystem diversity, it is bounded by the Orinoco River basin in the north of South America and extends for about seventeen million hectares and covering three general types of large-scale landscapes (i.e., LP, FS, and the Altillanura) (Romero Ruíz et al., 2004). Due to its extension, there are sites with a greater number of bird records, for instance, there are more complete datasets of



**FIGURE 1** | Study area. Colombian Orinoquia landscapes. Modified from (Romero Ruíz et al., 2004; IDEAM, 2017).

avifauna both in natural and agricultural covers for LP and FS than Altillanura. Therefore, our study focused on LP and FS landscapes (**Figure 1**), which include around 54 and 69% of all bird species present in the entire region, respectively (Acevedo-Charry et al., 2014). The Colombian Llanos has an annual average temperature ranging between 25 and 28°C, showing a binomial rain regime with a dry period between January and April, and a rainy season from March to December with higher precipitation in June (IDEAM, 2021).

The Llanos piedmont is an ecotone landscape between the mountain ranges of the Andes at 1,100 m elevation and the Orinoco plains at 400 m, characterized by erosional ridges, alluvial terraces, mountains, and piedmont forests (Romero Ruíz et al., 2004). However, anthropic intervention changed the natural landscape by turning over 80% of the area into a matrix dominated by livestock pastures, crops, and degraded natural ecosystems. Forests currently represent around 10% of the landscape distributed in small fragments and riparian vegetation (IDEAM, 2017).

The flooded savanna corresponds to a “flooded landscape” between 0 and 400 m elevation characterized by seasonally flooded savannas, riverine forests, wetlands, and swamps (**Figure 1**) (Romero Ruíz et al., 2004). Anthropic intervention in this landscape has transformed at least 20% of the area, making it fit mainly for livestock pastures, and crops, degrading natural ecosystems until reduce them as patches around rivers. In the FS landscape,

forests comprise around 10% of the territory, while seasonally flooded savannas represent around 60% (**Figure 1**) (IDEAM, 2017).

## Data Collection

We compiled species occurrence data from bird surveys taken between 2000 and 2018 in the FS and LP landscapes. We generated an occurrence database from survey data and referred publications that included bird records at the species level with associated data on the date, locality, coordinates, and land cover types (Gilroy et al., 2015; López-Ricaurte et al., 2017; GBIF.org, 2018; Diaz Lopez et al., 2020; Rodríguez Posada et al., 2020). We classified records in the FS landscape as natural (forest or savanna) or agricultural (livestock pastures, rice fields, or oil palm crops). In the LP region, records of the natural land cover corresponded only to forests, while agricultural land uses include the same classes used in the FS landscape. We verified species occurrences based on the most updated bird species checklist for this region (Acevedo-Charry et al., 2014) and followed the taxonomical classification proposed by Remsen et al. (2021).

## Trait Data

We performed a systematic literature review on studies concerning functional diversity in birds. We examined with particular emphasis on studies covering the Colombian Llanos region and global studies that analyzed functional traits in the anthropic cover, compared functional diversity between natural and anthropic covers, or analyzed functional response traits to

anthropic disturbances. We chose 13 potential response traits to environmental changes, following the selection framework for vertebrate response traits as proposed by Luck et al. (2012), including morphological and life-history traits that could influence birds' responses to land-use changes based on a literature review (see **Supplementary Material S1**). The life-history traits considered were social behavior, diet, migratory status, foraging stratum, foraging behavior, and nest location, which were compiled from the scientific literature (Hilty and Brown, 1986; Ridgely et al., 1989; Restall et al., 2007; Ridgely and Tudor, 2009; Birds of the World, 2021). Morphological traits included bill depth, bill width, wing length, tail length, culmen length, tarsus length, and weight. These were measured on specimens collected in the Orinoquia region and preserved in Colombia's biological collections at the Instituto de Ciencias Naturales de the Universidad Nacional de Colombia, Instituto Alexander von Humboldt, and Museo de Historia Natural of the Pontificia Universidad Javeriana (Stiles et al., 2017; Córdoba Córdoba et al., 2018; Laverde Rodríguez et al., 2018). We measured six adult specimens of every species, three females and three males, depending on availability. If not enough individuals were available, we would complete the information with measures reported in the literature. We averaged morphometric species values for each species. Morphometric measures were taken only by the first author to minimize interobserver bias. However, for 5% of the species, we obtained morphometric data from field reports, which may have added bias due to differences in measurements between preserved and live individuals or between observers. The databases of life-history and morphometric traits collected are available in the EDI data repository (Rincon-Parra, 2021).

## Data Analysis

We generated pairwise classification models between each natural and agricultural land cover type for each landscape. These predictive models  $mg(X, Y)$  were fitted using a random forest analysis (RF). The RF algorithm is a statistical machine learning classifier that uses an  $X$  training dataset for  $k$  independent variables to estimate classification patterns of a categorical dependent variable  $Y$  through  $n$  decision trees. Each decision tree is divided hierarchically into  $j$  dichotomous decision nodes according to the information provided by every independent variable  $h_k$  for classifying  $Y$ , followed by the selection of the best-fit branching classification output  $I(\cdot)$ .  $n$  decision trees are combined into a fitted consensus predictive decision tree according to the equation (Breiman, 2001; Cutler et al., 2007):

$$mg(X, Y) = \frac{\sum_{k=1}^k I(h_k(X) = Y)}{k} \max_{j \neq y} \left[ \frac{\sum_{k=1}^k I(h_k(X) = j)}{k} \right] \quad (1)$$

The model  $mg(X, Y)$  is tested through cross-validation on an  $X$  test dataset including the same independent variables. The model's predictive power is assessed by estimating the predictive error and complementary success rates (Breiman, 2001; Liaw and Wiener, 2002). Importance values given by the Mean Decrease Accuracy metric represent the importance of each variable for  $Y$

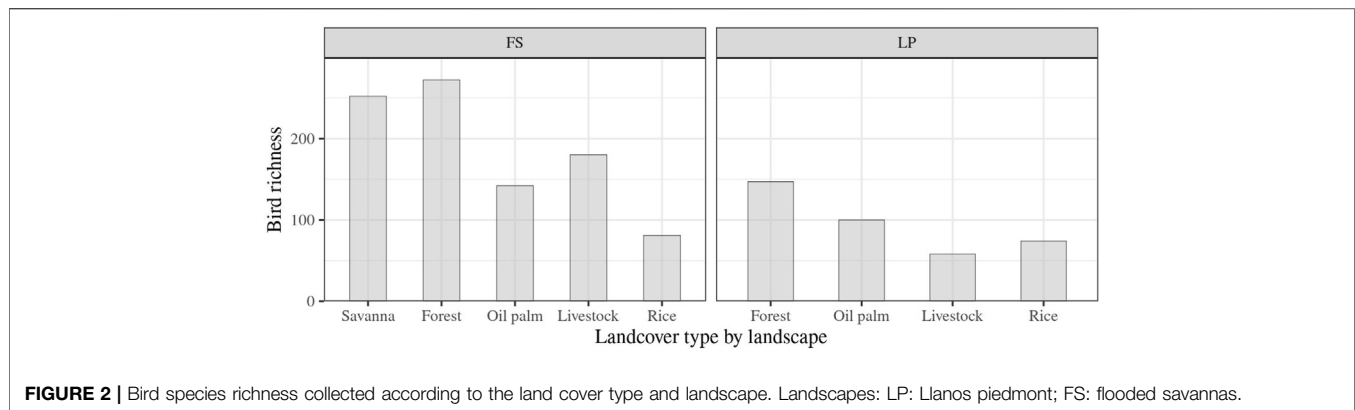
classification, with their statistical significance obtained through comparison with null distribution models for each variable (Breiman, 2001; Liaw and Wiener, 2002; Eric and Archer, 2020). Through partial dependence analysis ( $f_{h_{k_i}}(Y)$ ), we estimate the importance value of each variable attribute  $h_{k_i}$  as the marginal effect of  $h_{k_i}$  if all other variable attributes were kept constant for  $Y$  classification (Friedman, 2001; Cutler et al., 2007; Hastie et al., 2009). Given the number of  $Y$  classes  $C$ , the partial dependence equation is:

$$f_{h_{k_i}}(Y) = \log \left[ p_{h_{k_i}}(X) \right] - \frac{1}{C} \sum_{h_{k_i}=1}^C \log p_{h_{k_i}}(Y) \quad (2)$$

For every pairwise classification model, we considered all the compiled species traits as the independent variables  $h_k$  and their presence in natural or agricultural land covers as  $Y$ , based on the species occurrence data. We identified traits or trait combinations that indicated a response to land-use changes for each pairwise classification, based on a four-step process, including the RF model fitting with 5,000 ( $n$ ) trees, 5,000 permutations, and subsamplings without replacement to avoid problems related to unbalanced data (Sun et al., 2009; Tillé and Matei, 2016). First, we calibrated the RF model for each classification using a stepwise backward and forward recursive elimination of traits and selected the trait combinations with a classification success rate of at least 0.5 (Genuer et al., 2010; Hapfelmeier and Ulm, 2013; Speiser et al., 2019). Second, we selected models that included only significant traits after comparison with null models ( $p$ -value < 0.1) (Eric and Archer, 2020). These traits can all be considered functional response traits. However, since collinearity may affect the model fitting, we filtered out traits based on the multicollinearity assessment of partial dependence results across models (Pearson coefficient > 0.7). Finally, we fit the model with the combination of the selected traits, which corresponded to response functional traits to land-use changes that influenced the species occurrence probability in each land cover type (Breiman, 2001; Liaw and Wiener, 2002; Eric and Archer, 2020).

RF models with high success rates represent a high probability of species with a particular trait pattern occurring differentially in the classified land cover types. In contrast, RF models with low success rates suggest the lack of significant differences in trait patterns among compared land cover types. High success rates also indicate a high probability of change in the species occurrence as a response to land-use changes as determined by their traits.

We estimated the importance of attributes' combinations of response functional traits through partial dependence analysis (Breiman, 2001; Liaw and Wiener, 2002; Eric and Archer, 2020). We standardized partial dependence values on a scale between  $-1$  and  $1$ , in which an attribute's combination closer to  $1$  indicated an increased probability of species with those attributes occurring in the agricultural land cover. In contrast, values closer to  $-1$  indicated an increased probability of species with those attributes occurring in the natural cover. Thus, in a land-use change scenario (e.g., forests to livestock pastures, and savannas to oil palm crops), species with attribute combinations with



**FIGURE 2** | Bird species richness collected according to the land cover type and landscape. Landscapes: LP: Llanos piedmont; FS: flooded savannas.

values closer to  $-1$  would experience a decrease in their occurrence probability, while those with attribute combinations with values closer to 1 would result in increased occurrence probability. On the other hand, species with attribute combinations with partial dependence values around zero do not show a particular response pattern to land-use changes.

We applied a hierarchical cluster analysis to the species characterized by the partial dependence values of attributes combinations to identify functional response groups. The number of functional groups was defined by multiscale bootstrap resampling (Hennig, 2020). Functional groups corresponded to cluster-wise, highly stable groups (i.e., stability values higher than 0.75) (Hennig, 2007; Hennig, 2020).

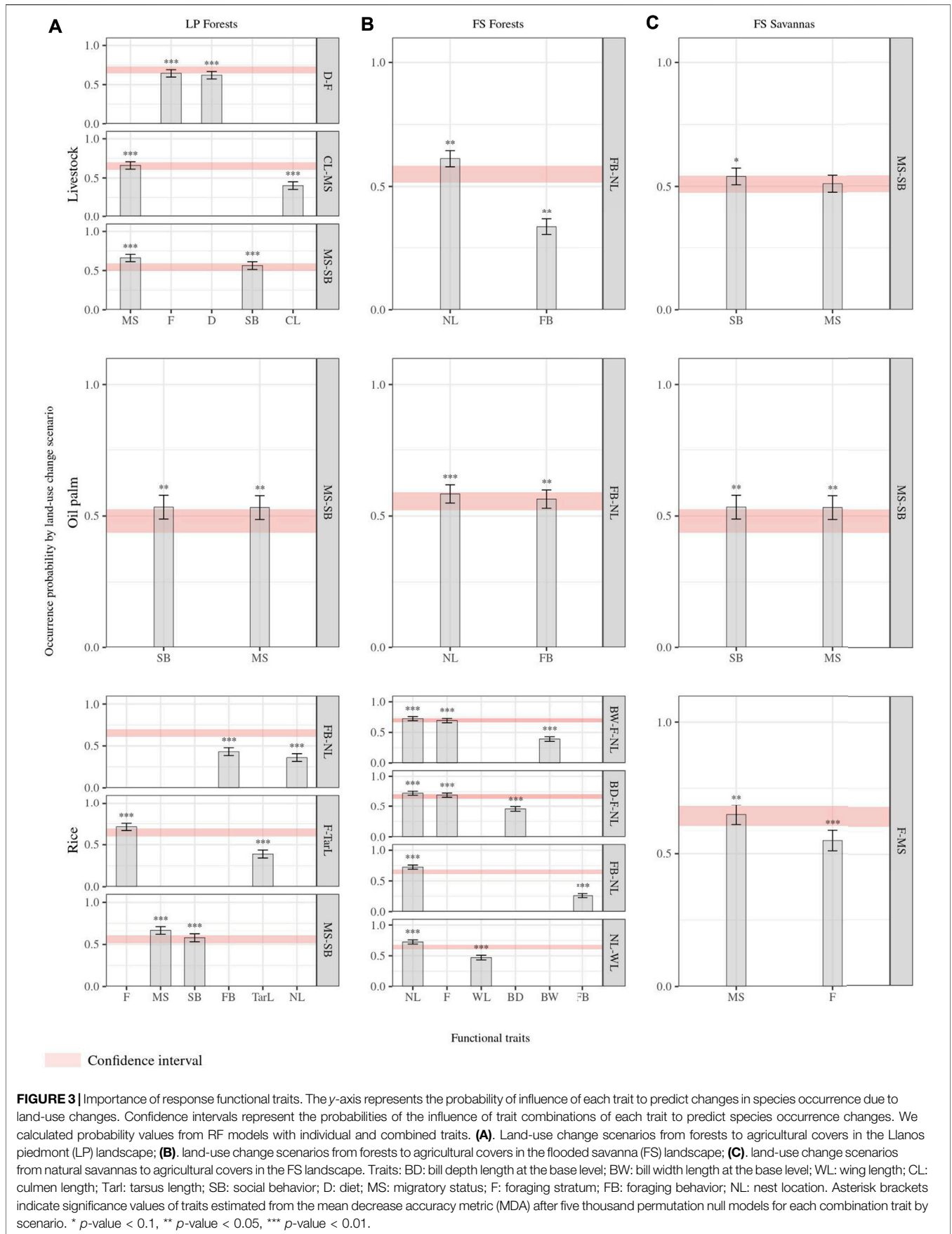
## RESULTS

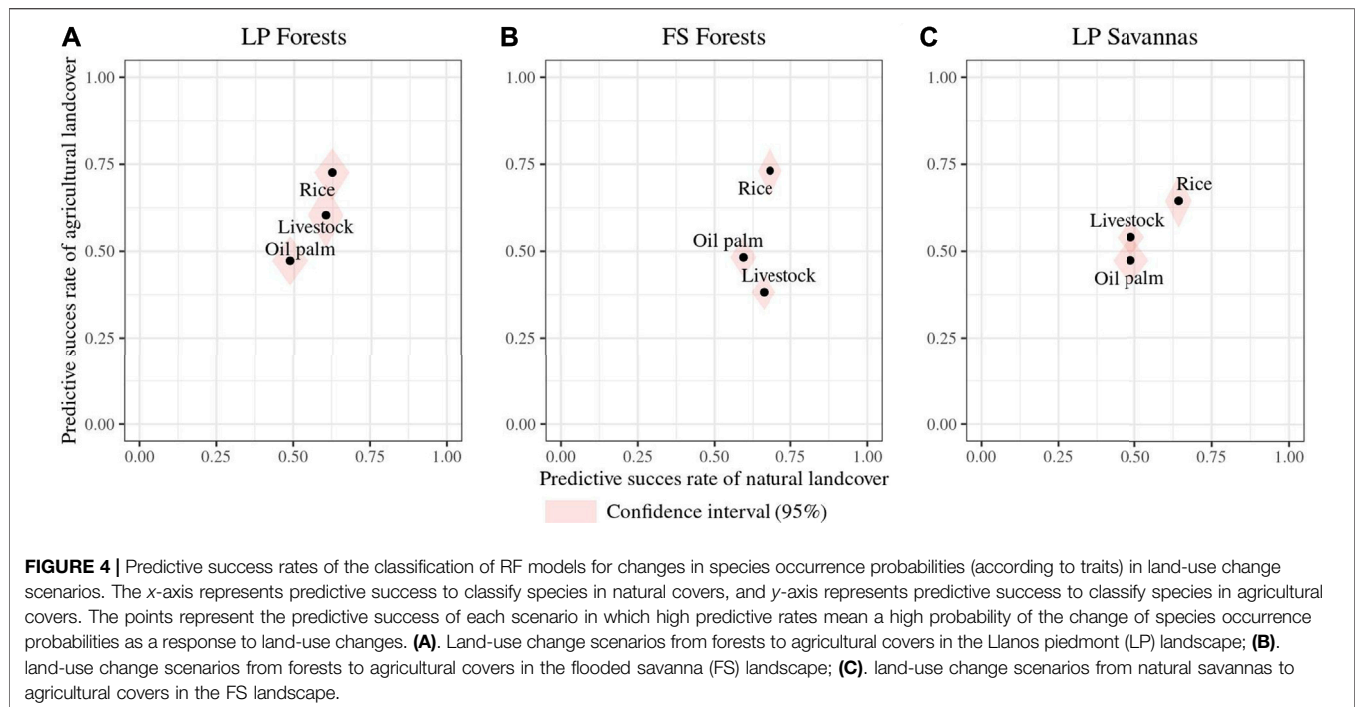
We collected 11,444 records representing 364 species, 193 in LP and 357 in FS. The two landscapes shared 186 species, while 171 were exclusively reported in FS, and only seven were recorded in LP. In the two landscapes, natural land covers showed greater species richness than agricultural ones, accounting for 21% of the total bird species recorded in LP, and for 38 and 36% of the total bird species in forests and savannas of FS, respectively (Figure 2).

Of the 13 traits measured and estimated for all species, 11 corresponded to response functional traits alone or in trait combinations for at least one classification. Tail length and weight were the only traits that did not show a functional response to land-use changes. Overall, functional response traits were similar for RF pairwise classifications of the same natural cover but differed among landscapes (Figure 3). For a given natural land cover, all possible classifications' included at least one response trait or a trait combination common to all for a given natural land cover. In LP forests, social behavior–migratory status was identified as a response trait combination in all classifications. For LP forests' livestock classification, foraging the stratum diet and migratory status–culmen length correspond to additional trait combinations showing a functional response, while foraging behavior–nest location and foraging stratum–tarsus length were added to social behavior–migratory status in the forests' rice classification (Figure 3). Foraging

behavior–nest location (FB-NL) was common to all RF forest models and is the only trait combination in classifications with livestock and oil palm crops. In the FS landscape forests' rice model, supplementary trait combinations corresponded to bill width–foraging stratum–nest location, bill depth–foraging stratum–nest location, and nest location–wing length (Figure 3). Despite nest location and foraging stratum being shared across trait combinations in this latter classification, we found no correlation between them. In savannas of the FS landscape, the migratory status was in pairwise classifications, combined with social behavior in the livestock and oil palm classification and with the foraging stratum in the rice comparison (Figure 3). Higher numbers of identified functional response traits corresponded to higher success rates in RF models (Figures 3, 4). These rates were the highest ( $>0.7$ ) for forests' rice scenarios in both landscapes (i.e., there is, on average, a 70% chance of species differing between land cover classes, given their response traits), followed by the FS savannas' rice classification (0.65) (Figure 4). All RF classifications, including oil palm, resulted in similar success rates in both landscapes, that is, there is, on average, a 50% probability of species differing between the natural land cover and oil palm, given their response traits. The forests' livestock classification showed a slightly higher success rate in LP (0.6) than in FS (0.55). The success rate of the FS savannas' livestock (0.51) suggested a close to random chance of correctly classifying species into savanna or livestock based on their attributes of response traits (Figure 4). However, these rates represent the classification probabilities for all species in the assemblages, overlooking the differences in the functional group's responses.

We found similar numbers of functional groups (10–13) for all pairwise classifications (i.e., land-use change scenarios), except for forests' rice and savannas' rice scenarios in the FS landscape, for which the number of functional groups reached 20 and 17, respectively (Figure 5, Supplementary Material S2). Most scenarios produced homogeneous functional groups with low variability in their partial dependence values. Scenarios resulting in groups with more variable partial dependence values corresponded to classification models with morphometric traits as functional response traits (Figure 5). For example, LP forests' livestock response traits included culmen length, LP forest's rice included tarsus length,





and FS forest rice included bill width, bill depth, and wing length.

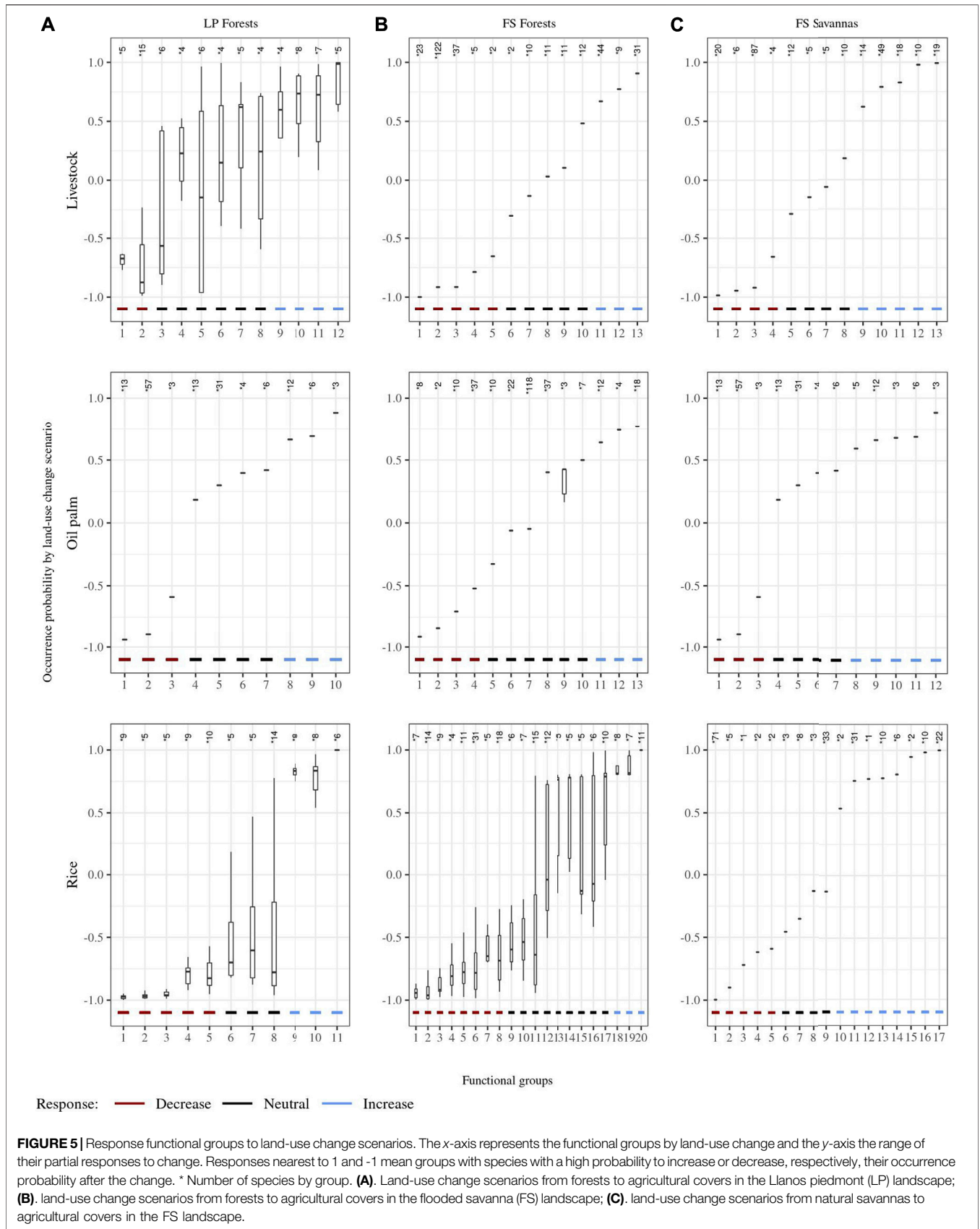
In all cases, land-use changes resulted in groups' turnover, with the occurrence probability decreasing for a proportion of groups (i.e., partial dependence value closer to  $-1$ ) and increasing (i.e., partial dependence value closer to  $1$ ) or staying unchanged for others (i.e., partial dependence values around zero) (**Figure 5**). In terms of functional groups, LP forests' rice scenario resulted in the largest proportion of groups (0.45), suffering a reduction in occurrence probability. In contrast, a change of LP forests to livestock reduced the occurrence probability in 17% of functional groups and 27% of species, representing the smallest proportion of groups with reduced occurrence probability across all land-use change scenarios. Savannas' rice scenario in FS savannas' rice scenario resulted in the largest proportion of functional groups (0.47) with increased occurrence probability, while only 15% groups in the FS forests' rice scenario, the smallest proportion among all scenarios, experienced an increment (**Figure 5**).

On average, the proportion of functional groups with decreased occurrence probability (0.32) was similar to that of groups with increased occurrence probability (0.31). Land-use change scenarios involving forest transformation resulted in similar or slightly larger proportions of groups with decreased occurrence probability than increased probability. However, FS savannas changes showed a higher proportion of groups with increased occurrence probability (0.42) than decreased probability (0.28).

The number of species differed among functional groups, influencing the response pattern for functional groups across land-use change scenarios (**Figure 5**). The largest proportion of species (0.59) with decreased occurrence probability corresponded to the FS forests' livestock scenario, followed by

the FS forests' rice scenario (0.51), and the LP forests' oil palm scenario (0.49). The highest proportion of species with increased occurrence probability appeared in the FS savannas' livestock scenario (0.42), followed by FS savannas' rice scenario (0.40). The average proportion of species across all scenarios with decreased occurrence probability was higher (0.42) than that of species with increased occurrence probability (0.25). In contrast with the results by functional groups, in the FS savannas scenarios, the proportion of species with decreased occurrence probability (0.43) was larger than that with increased probability (0.34) (**Figure 5**). On average, the occurrence probability for around a third of the functional groups (0.37) and species (0.33) remained unchanged across land-use change scenarios.

In all LP forest scenarios, functional groups with reduced occurrence probability included the traits and attribute combinations: (1) resident migratory status and solitary social behavior or (2) resident migratory status and opportunistic gregarious social behavior. Accordingly, functional groups with increased occurrence probability corresponded to 1) local migratory and social behavior in flocks or 2) continental migratory and social behavior in flocks. In LP forests' livestock scenarios, functional groups with increased occurrence probability were also characterized by a long culmen, piscivore or insectivore diet, and foraging in water and ground. At the same time, groups with decreased occurrence probability corresponded to such as a short culmen, insectivore diet, and foraging in the understory. The LP forests' rice scenario exhibited increased occurrence probability in groups that forage in water and have long tarsus, while groups with short tarsus and foraging in all forest levels characterized groups with decreased occurrence probability. Similarly, this probability decreased for groups characterized by gatherer foraging behavior and nesting in





cavities and branches but increased for groups with hunter foraging behavior (**Figure 3, Supplementary Material S3**). In FS forest scenarios with livestock and oil palm, functional groups with gatherer foraging behavior, nest location in branches, and cavities had reduced occurrence probability. However, functional groups with gatherer foraging behavior and foraging on the ground resulted in increased probability. In addition to these traits, groups with short wings, foraging in all forest levels, narrow bill, and hunter foraging behavior had reduced occurrence probability in FS forests' rice scenarios. This probability increased for groups with long wings, a long bill or narrow bill, and foraging in water (**Figure 3, Supplementary Material S3**).

In all savannas scenarios of the FS landscape, functional groups characterized by a resident migratory status showed lower occurrence probability, while groups with a local migratory status had increased probability. Moreover, both livestock and palm scenarios reduced probability for groups with solitary social behavior and increased probability for those with opportunistic social behavior or in flocks. In FS savannas rice scenarios, occurrence probability decreased for groups with foraging in the understory and increased for groups with foraging in water (**Figure 3, Supplementary Material S3**).

## DISCUSSION

Our results described probabilistic response patterns of bird assemblages to land-use changes and indicate that these responses are nonrandom but rather deterministic trait-mediated. This is the first study studying functional response traits of birds in the Orinoquia region to estimate functional groups' responses to land-use change scenarios and identifying the traits and attributes that determine them. It should be noted that, since morphological traits obtained from collection specimens could not be linked to specific land cover types, we assumed no intraspecific variation in these traits across different land cover types. For future studies, we recommend that morphometric variables are measured directly in the field, considering the land cover type on which individuals are sampled.

Shared response traits or trait combinations identified for all pairwise classifications of the same natural land cover type, indicate the presence of common functional response patterns of species assemblages to environmental disturbances. Changing forests to agricultural lands in LP influenced species occurrence probabilities based on their migratory status and social behavior, independently of the agricultural land cover type. Resident and solitary or opportunistic gregarious species would tend to disappear when replacing forests with agriculture, which could be associated with higher forest specialization in resident species and increased detectability of solitary species in more open vegetation, resulting in increased predation risk and reduced food availability (Hutto, 1989; Newton, 1998; Thiollay and Jullien, 1998; Sridhar et al., 2009; Barbe et al., 2018). This also explains why local or continental migratory species that flock are favored by transformation to agriculture (Smith et al., 2001;

Goldstein et al., 2003; Barbe et al., 2018). Similarly, forest conversion to agriculture in the FS landscape affected species occurrence based on foraging behavior and nest location, while migratory status influenced species responses in all savanna classifications. Additional trait combinations mediated the distinct responses exhibited in individual land-use change scenarios.

Classification models differed in their success rates, with models including rice showing higher rates than others. High rates indicate that selected response traits can effectively explain the differences in species occurrence probabilities between natural and agricultural land cover types. However, the success rates for models involving oil palm crops and cattle were close to 0.5, suggesting a poor classification performance of the RF model. Potential explanations for this poor performance include missing functional traits that could be important for the classifications considered in this study and model limitations by focusing solely on traits while ignoring other factors influencing species occurrence probabilities (Newbold et al., 2013). However, identifying functional groups and their responses suggests a potential bias in success rate estimation when all species are assumed equal. When functional group responses are highly variable, their increasing and decreasing response patterns cancel each other out, which does not allow the RF model to classify assemblages between land cover types differentially. This highlights the idea that posterior functional group evaluation can provide a better picture of the impact of environmental pressures on species assemblages.

Different studies have shown that the functional diversity of bird communities varies depending on particular environmental conditions such as environmental gradients and the transformation of the landscape (Clavero and Brotons, 2010; Bregman et al., 2014; Jarzyna et al., 2020). Our results show that changes in land use determine the occurrence of species with particular traits because anthropic disturbances produce changes in the functional spectrum of traits (Mayfield et al., 2010; Aiba et al., 2016). The scale of analysis of this research encompasses the response functional patterns to land-use changes of natural covers by anthropic ones as a process related to the transformation of the landscape. However, functional diversity analysis at finer scales could consider environmental gradients or of anthropic transformation to obtain more detailed results. For example, from a taxonomic perspective, the Colombian Llanos present the greatest changes in bird species toward areas with a greater altitudinal and latitudinal gradient (Acevedo-Charry, 2017; Trujillo and Henao-Cárdenas, 2018), for which it would be interesting to analyze patterns of functional diversity in future studies.

The identity of natural systems is determined by the functional traits that make them up, and their resilience is based on maintaining their functional space (Allen et al., 2005; Gladstone-Gallagher et al., 2019; Roberts et al., 2019). Differential responses between functional groups result in a turnover of functional groups and species, modifying the functional space of traits between land cover types, thus resulting in changes in the species number, composition, functional diversity, and functional redundancy (i.e., frequency

of representation of the same attribute traits) (**Figure 5**). The direction of these changes would depend on the proportion of functional groups showing a particular response (increase, decrease, or neutral) in occurrence probability and the number of species represented in these groups. When a larger proportion of functional groups containing a larger proportion of species increased their occurrence probability, an increase in functional diversity and species number increase as expected. However, none of the scenarios considered in this study showed this pattern. In the FS savannas rice scenario, a larger proportion of functional groups increased their occurrence probability, but the proportion of species represented in these groups (0.4) was similar to those in groups experiencing a decrease in occurrence probability (0.38), suggesting an increase in functional diversity and a species turnover. When a larger proportion of functional groups increases their occurrence probability, but the proportion of species represented in these groups is the smallest (e.g., FS savannas oil palm), the functional diversity might increase but with low functional redundancy and a reduction in species numbers.

Consequently, a larger proportion of functional groups with decreased occurrence probability than with increased probability suggests a decline in functional diversity. This occurred in all FS forest scenarios and LP forests' rice scenarios. In these scenarios, the proportion of species in the groups with decreased occurrence probability was also larger, indicating a reduction in species numbers. This decline in species richness was greater for the FS forests' livestock scenario, followed by the FS forests' rice scenario, where these groups accounted for more than 50% of the species. In contrast, in the FS forests' oil palm scenario, a smaller percentage of species (20%) are represented in the functional groups with decreased occurrence probability, while 68% are included in the groups with neutral responses, suggesting smaller changes in species composition.

Land-use change scenarios that caused stronger responses on the functional group occurrence probability implied significant changes in the vegetation structure, mainly resulting in a simplification of the habitat complexity (Batisteli et al., 2018). This can be related to the habitat hypothesis, in which higher habitat heterogeneity, as indicated by its structural complexity, provides higher diversity of niches and thus sustains a higher diversity (Hurlbert, 2004; Tews et al., 2004). In turn, this may be reflected in the functional niche of organisms and groups so that higher spatial heterogeneity can lead to higher functional richness (Wiescher et al., 2012; Nooten et al., 2019). Increased diversity due to habitat complexity is not generalizable from taxonomic metrics (Tews et al., 2004; Cousin and Phillips, 2008), but complex habitats provide a high diversity of conditions from a functional perspective, increasing the diversity of functional groups. It should be noted that habitat structural complexity is just one heterogeneity dimension; thus, analyzing other landscape configuration metrics and environmental variability would lead to a better understanding of the species assemblages' responses (Stein et al., 2014; Tuanmu and Jetz, 2015).

The identification of the functional trait combination nest location–foraging behavior in all FS forest scenarios illustrates the importance of assessing combined traits. Neither nest location

nor foraging behavior was significant as individual traits in any forest scenario. Species that obtain resources through active search in different substrates (gatherer foraging behavior) were common in different land-use scenarios as part of functional groups that differed in their responses to land-use changes, based on the nest location attribute (Martin and Possingham, 2005; Hua et al., 2016; Sitters et al., 2016). Groups that forage by gathering and nest in tree cavities would suffer a decrease in occurrence probability because they usually forage vertically in the forests. The loss of vertical structures by deforestation would reduce habitat availability for foraging and nesting. In contrast, groups that forage by gathering and nest on the ground showed higher occurrence probabilities in agricultural areas as they would find an increased availability of open areas for nesting with sparse vegetation on which they scratch in search of food.

The methodological framework we used relied on probabilistic models to describe the impact of land-use changes on bird assemblages and the functional groups, traits, and attributes that explain the species response pattern. RF models estimate the response probabilities of bird assemblages and the occurrence probabilities of groups of species with particular traits that mediate the response to land-use changes. This method allows one to overcome one of the most significant challenges in studying functional diversity, that is, developing statistical procedures to assess and identify functional traits (Ricotta and Moretti, 2010; Luck et al., 2012; Villéger et al., 2017). Unlike previous studies on functional response diversity (Mouillot et al., 2013), our analyses estimated response functional groups, not just as species clusters with similar traits, but rather as groups of species with similar responses influenced by their traits. Thus, functional response groups should be defined based on their responses rather than on their traits (Hooper et al., 2002; Lavorel and Garnier, 2002; Naeem and Wright, 2003).

Our results coincide with previous studies assessing the impacts of agricultural transformation on birds in this region and showing a decrease in bird species richness in agricultural land cover types compared to natural ones (Edwards et al., 2015; Gilroy et al., 2015; Tamaris-Turizo et al., 2017). Few studies explored the impacts of land-use changes on functional diversity in the Orinoquia region. Prescott et al. (2016) concluded that functional diversity is greater in forests than in oil palm crops and livestock pastures in the FS landscape, while López-Ricaurte et al. (2017) found a decrease in taxonomic richness and functional diversity in livestock pastures and oil palm crops for bird assemblages of savannas.

Potential applications of our results include using species that represent response functional groups (e.g., in LP little wrens are vulnerable while medium size water birds of prey benefit from changing forest to livestock) as indicators to monitor impacts of land-use change on the Llanos biodiversity (**Supplementary Appendix S4**). In addition, changes in the composition of response functional traits associated with agricultural land cover could reflect changes in functional processes of ecosystems that may impact the provision of ecosystem services. We have explored how the different bird communities within and between land-cover respond to change. However, there is room to inquire about how these

remaining functional communities' impact or affect the land-cover themselves. We suggest assessing effect functional traits to understand these effects on ecosystem processes and services. Our results indicate that agricultural practices can be improved to reduce impacts on species with particular response trait attributes that are mostly affected by land-use change (**Supplementary Material S4**).

The analysis of response functional groups can be used as a predictive tool on the impact and/or monitoring of land-use changes on biodiversity, so that strategies to avoid or mitigate them can be designed and implemented. Furthermore, the functional response traits and species representing functional groups can be used as indicators of the assemblage responses to change as improved agricultural practices or conservation actions in agricultural areas. Patterns of functional traits expose conditions that can be targeted in the design of management strategies to minimize the impacts of agricultural expansion, while the identification of response functional groups support the identification of indicator species for monitoring the impact of such strategies on biodiversity in the Colombian Llanos.

## DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Materials**; further inquiries can be directed to the corresponding author

## ETHICS STATEMENT

Ethical review and approval was not required for the animal study because this research was carried out using secondary information and biological collections.

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## AUTHOR CONTRIBUTIONS

SA proposed the main idea of this study. VR-P reviewed the literature, proposed the methodological framework, collected the data, and performed the computations and analysis. SA and ME-G supervised the findings of this research. All the authors contributed to the discussion on the results and the preparation of the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fenvs.2021.689745/full#supplementary-material>

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