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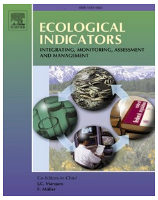

Original Articles

Biodiversity responses to land-use change in the equatorial Andes

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ABSTRACT

Land-use change is a primary driver of biodiversity loss. Tropical ecosystems face rapid conversion rates due to the encroachment of agricultural lands and supply needs for goods and services from an increasing population and changing market demands. Measuring the effect of land conversion on species diversity is challenging due to incomplete and uneven knowledge of different taxonomical groups. Here, we contrast different metrics for measuring biodiversity loss across three land-use typologies: secondary forest, agroforestry, and monoculture for five taxonomic groups: birds, frogs, fish, dung beetles, and macroinvertebrates in the Andean piedmont forests of the western equatorial Andes. Albeit our limited and uneven sample in space and time, we found that rarity, Non-Metric Multidimensional Scaling, and Multinomial Classification Model (i.e., classifications of habitat specialists and generalists) constitute a more sensitive set of indicators to assess land-use change impacts on tropical mountain biodiversity compared to classical metrics. Likewise, our results showed that land-use intensification influenced community assemblages in the five taxonomic groups. These non-classical biodiversity metrics can provide better insight into the effect of land conversion on these highly biodiverse ecosystems composed of many rare species.

1. Introduction

Rates of pre-human or background extinction levels were estimated at 0.1 extinction per million species per year (E/MSY). Current extinction rates are 1,000 times higher than pre-human rates, and future extinction rates are likely to be 10,000 times higher (Vos et al., 2015). Twenty to fifty per cent of all species are expected to be lost by the end of the 21st century. Most of these ongoing and projected extinctions are driven by habitat loss and degradation caused by land-use changes (Jaureguiberry et al., 2022; Le Provost et al., 2020; Marques et al., 2019; Newbold et al., 2015; Pendrill et al., 2022; Powers and Jetz, 2019; Stuart et al., 2004), particularly in tropical ecosystems (Lindenmayer and Fischer, 2013). Therefore, identifying what type of species are more sensitive to land-use change and measuring its impacts on species diversity becomes of utmost importance.

However, measuring changes in species diversity in tropical ecosystems is challenging, even when assessing shifts in the abundance and distribution of species in time and space (Moreno et al., 2017). Major challenges are 1) the uneven geographical distribution of long-term series of prolonged monitoring efforts; 2) few long-term data or not readily accessible; 3) natural fluctuations of species abundance and, therefore, detectability; 4) discrepancies in methodologies and different biodiversity metrics provided (Hudson et al., 2014; Pereira et al, 2012; Proença et al., 2017). Finding reliable metrics for conservation science is

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challenging since different methods are dispersed in the scientific literature (Moreno et al., 2017).

Recent efforts have been made to provide a set of metrics (for alpha-diversity: Hill numbers and rank-abundance graphs; functional and phylogenetic diversity; and account for nestedness in beta-diversity) that are sensitive to anthropogenic disturbance at various scales (Moreno et al., 2017). However, these same metrics can behave differently across unrelated taxonomical groups. For example, Dornelas et al. (2014), studying long-term data sets from a variety of taxa impacted by land use changes (e.g., birds, mammals, invertebrates, vascular plants), found that there was not a consistent negative trend across taxonomical groups and biomes regarding alpha diversity; nevertheless, they detected species substitutions in assemblages rather than systematic losses. Gossner et al. (2016) observed that increasing grassland intensification causes alpha diversity to increase, while other studies detected inconsistent richness patterns across land-use types among different soil invertebrate taxa (George et al., 2019). Thus, it is common to find inconsistent responses in the literature when assessing land-use effects on biodiversity. Further, conceptual debates remain about proper procedures for measuring diversity (Aloy, 2015; Jost, 2006; Legendre et al., 2015). Although we understand that rare species are prone to population size declines (Loh et al., 2005), it remains unclear which taxonomic groups and assemblages are less sensitive to habitat degradation.

In the Neotropics, studies show a variety of biodiversity responses to habitat degradation driven by land-use change. For example, in the western versant of the Ecuadorian Andes, Morabowen et al. (2019) found changes in aquatic macroinvertebrate assemblages in response to forest conversion to agroforestry or Palmetto (*Bactris gasipaes*) monoculture but not in the biodiversity metrics assessed. In other words, specific taxa disappeared from monocultures, but these changes were not reflected in the alpha diversity metric applied [i.e., Shannon diversity index; expressed as the number of equally abundant species but see Martínez et al. (2009)]. Further, fish abundance and community composition showed little relation with anthropogenic disturbance, including pastures and croplands encroachment (Miranda et al., 2022). A *meta*-analysis aimed at assessing dung beetles' responses to land-use changes (Nichols et al., 2007), using richness, abundance, and community similarity, found that secondary forest and agroforestry could harbour sensitive species that are lost in agriculture and cattle grazing lands (Nichols et al., 2007). However, in a subsequent study, Gardner et al. (2008) observed that dung beetles showed a marked decline in species numbers and biomass when comparing secondary and planted forests to mature forests, with major declines in species with a larger share of community biomass. Chapman et al. (2018) found considerable impacts of land-use change on the phylogenetic and functional diversity of tropical forest birds across a disturbance gradient, from old-growth tropical forests to oil palm plantations. They found a marked decline in phylogenetic diversity and an increase in phylogenetic distance (measured as the mean distance to the nearest taxon) from forest to oil palm, in line with declining species richness across the gradient. At the same time, recent models based on Chao1 and Chao2 estimators, which give importance to rare species to estimate the unobserved species in a sample (Chao 1984), detected substantial species loss (41 % of tree and animal species) from disturbed habitats in tropical forests (Alroy, 2017).

A recent study proposed that taxonomic and phylogenetic rarity is a relevant biodiversity metric to assess land-use change impacts on community assemblages. Its sensitivity was assessed in terrestrial invertebrates (Dopheide et al., 2020). Moreover, rare species can disproportionately contribute to ecosystem functioning (Dee et al., 2019; Leitão et al., 2016; Lyons et al., 2005). Rarity, in terms of distribution, occurrence, and density, has been identified as a very important measure for the conservation of Neotropical mammals (Arita et al., 1990), frogs (Mendoza and Arita, 2014; Toledo et al., 2014) and plants (Knapp, 2002). However, its use has been directly linked to the conservation status of individual species. Also, its sensitivity to environmental change, such as land use and habitat conversion, has not been deeply studied in Neotropical set-ups (Leitão et al., 2016). Also, recent models suggest that rare species constitute an important component of tropical ecosystems (Alroy, 2015). Although when assessing the relationships among communities with environmental and spatial gradients, rare species seem irrelevant for understanding the role of each predictor in community composition (Brasil et al., 2020). Furthermore, bioassessment studies reliant on bioindicators to establish reference levels for ecosystem health may yield flawed results if they omit rare taxa (Cao et al. 1998). Therefore, assessing rarity and its responses to environmental change bears significant implications for conservation science, particularly in landscapes characterized by a mosaic of forest fragments interwoven with low and high-intensity agriculture and cattle grazing, where traditional alpha diversity metrics may fail to capture significant trends.

Over the past four decades, Ecuador's natural landscapes have witnessed rapid transformations, primarily driven by agricultural expansion (Mena et al., 2006; van Der Hoek, 2017; Wilson et al. 2019; Kleemann et al. 2022). The increment in human population density between 2000 and 2010, coupled with projections for further growth in Quito and across the country by 2050 (Buytaert & De Bièvre, 2012), as well as the emergence of new extractive activities such as mining (Kleemann et al., 2022; Roy et al., 2018), are anticipated to exacerbate the impacts on the country's rich biodiversity. Understanding the differential effects of various land-use typologies on different taxonomic groups at the local level is of paramount importance in informing precise conservation strategies. While biodiversity metrics are valuable tools for comprehending and comparing the consequences of habitat conversion to different land-use types, conventional metrics like species richness, Shannon, and Simpson diversity indexes do not always respond to these changes as anticipated. The extent to which these differences in responses can be attributed to study design, methodological approaches, datasets, modelling techniques, assessed taxonomic groups, and the choice of metrics employed remains an unresolved question.

In light of this, metrics that incorporate the complexity of tropical diversity are needed to accurately measure human activities' impact, facilitating informed policy-making and conservation efforts (Dopheide et al., 2020; Leitão et al., 2016). Our study aims to answer the following questions: Can other biodiversity metrics overcome the limitations that classic biodiversity metrics (e.g., Species richness, Shannon and Simpson Diversity indexes) have? Are these standard and widely used metrics suited to assess limited abundance data? Which of these metrics better reflects biodiversity responses to land-use change? As a result, this study can contribute to a better understanding of how biodiversity metrics respond to sensitivity to land-use changes across several taxonomical groups with a high degree of rarity.

2. Methods

Given its high species diversity and singularity, the western Andes of Ecuador are a priority for biodiversity conservation (Cuesta et al. 2017). At the same time, the lowland and mountain forests of North-western Ecuador are one of the three regions of the country where most of the deforestation has occurred (Sierra & Stallings, 1998; Lepers et al., 2005: MAE, 2018; Kleemann et al., 2022). One of the largest remaining forest tracts is embedded in the UNESCO Chocó Andino Biosphere Reserve – RBCA hereafter. From 1991 to 2017, forest loss within the RBCA was estimated at an annual gross loss rate of 0.66 % (Wiegant et al., 2020), constituting one of the major national deforestation fronts (Kleemann et al., 2022). By 2020, native forest covered nearly 68 % (i.e., 195,000 ha) of the area, 3 % (i.e., 10,000 ha) mountain grasslands located above the forest line (above 3,900 m a.s.l.) and 9 % mountain shrublands (i.e., 25,000 ha). The remaining 20 % (i.e., 57,000 ha) were agricultural lands. (Wiegant et al., 2020). Agriculture and cattle raising constitute the main livelihood in the RBCA. Where 16.4 % of the territory is dedicated to agriculture, 12.6 % to pastures, and 5.3 % to sugarcane plantations (MAATE, 2013; SIGTIERRAS, 2011) (see Figure S1). Within the RBCA landscape, this study was carried out in the Mashpi watershed which 67 % is covered by tropical montane forest, 24 % by agriculture and 9 % by pastures. Our sampling extended to the Huaycuyacu watershed to increase our sampling dataset in similar land-use typologies and environmental conditions. This watershed is dedicated to agriculture (8.5 %) and pastures (30.5 %) with the remaining 61 % of montane forest (Figure S1).

We used abundance data from five taxonomic groups obtained in the lower section of the RBCA, named Area of Conservation and Sustainable Use of Mashpi, Huaycuyacu and Sahuangal (ACUS-Mashpi): amphibians, dung beetles, birds, fish, and macroinvertebrates. Data were collected in 20 sites with three different land-use typologies: secondary forest (F), agroforestry (AF), and monoculture (M) (Fig. 1, Table 1). In this study, the land-use typologies are described as follows: 1) Forests that in our study area are defined as late successional forests that in the 1980s where affected by human activities of burning and timber extraction but structurally preserves the five strata but with low abundance of big trees, which are trees with a DBH (Diameter at Breast Height) higher than 40 cm (Llerena-Zambrano et al., 2021; Cuesta et al., 2023) 2) agroforestry is a land-use system where crops and trees are integrated in a mosaic-like arrangement. In our study area the sampled agroforestry systems are characterized by three well defined strata: (i) ground strata of herbaceous plants, (ii) a shrub/tree strata composed of cacao (*Theobroma cacao*), *Gliricidia sepium* and other medium size trees, and (iii) a three strata composed of useful trees such as *Iriartea deltoides*) (Nair 1985; Atangana et al., 2014) and 3) monoculture is a land-use where only one species of crop is planted in a homogenous arrangement without the presence of trees. In our study area cacao and palmetto plantations were sampled. These land-use typologies are the three major land-uses observed in the landscape of the Mashpi watershed and reflect well the forest transitions and land-use change in the area (Figure S1). Moreover, these typologies have been used consistently in several fieldwork campaigns in the area (i.e. Morabowen et al, 2019). The monitored agroforestry sites are cacao agroforestry systems combined with diverse timber and fruit trees of different heights, mimicking forests in structure. The monoculture sites include mainly palmetto and non-shaded cacao plantations. The five taxonomic groups were chosen due to their widespread use as bioindicators in the Neotropics and given their sensitivity to land use change (i.e.: Chao et al., 2014; Chapman et al., 2018; European Comission, 2000; Fulgence et al., 2022; Larsen & Forsyth, 2005; Miranda et al., 2022). Additionally, the availability of comprehensive data for all these groups within the same geographical area and across the existing major land-use typologies enhances ecological understanding. The fieldwork campaign and data collection

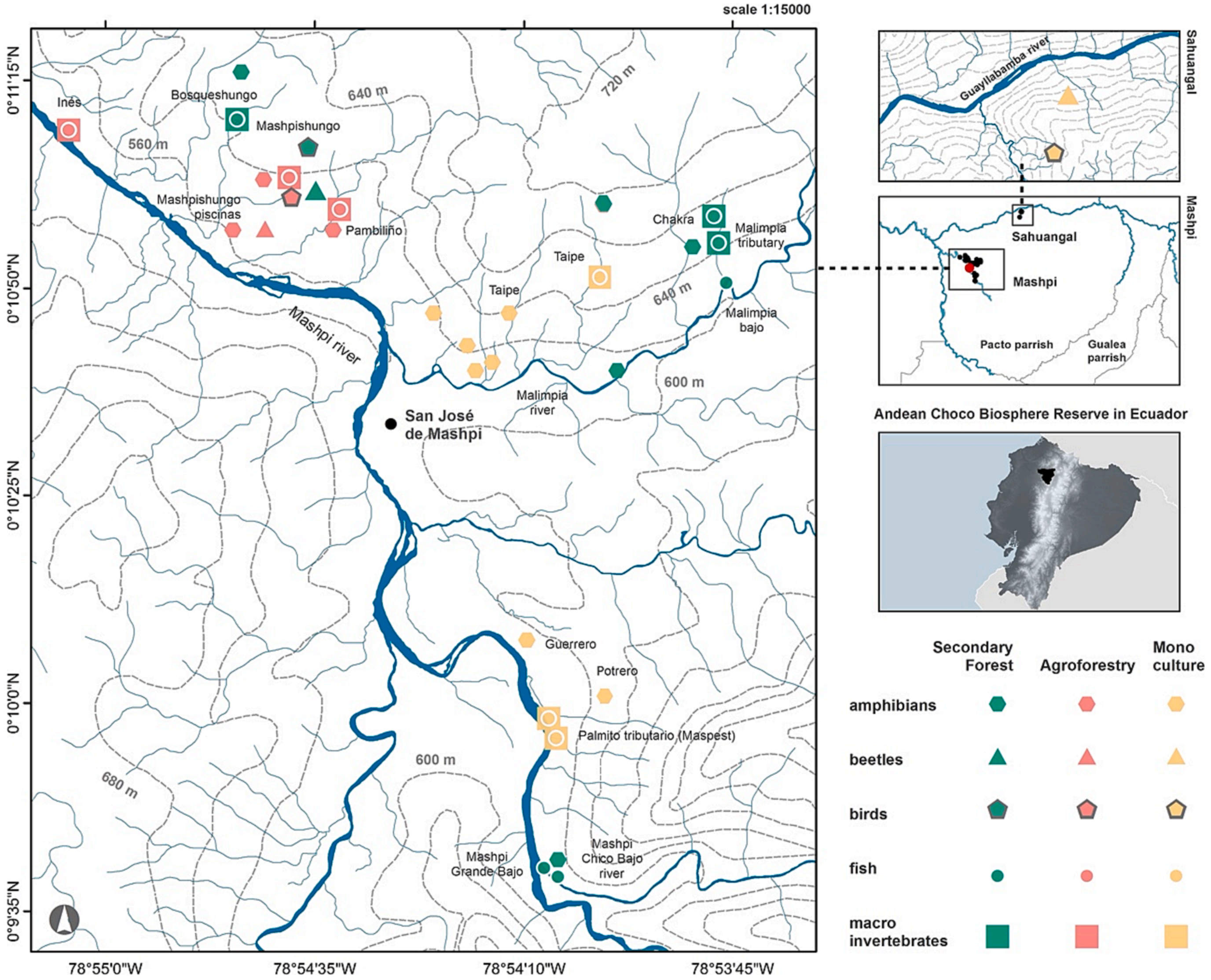

Fig. 1. Study site. Distribution of monitored sites of five taxonomic groups in the Area of Conservation and Sustainable Use of Mashpi, Guaycuyacu and Sahuangal, within the Chocó Andino Biosphere Reserve-RBCA. Colours depict land-use typologies and geometric forms, the corresponding taxonomic group.

Table 1

Monitored sites and sampling scale of species abundance of five taxonomic groups in the Area of Conservation and Sustainable Use of Mashpi, Guaycuyacu and Sahuangal, at the Andean Chocó Biosphere Reserve.

Group	Land use	n sites	n replicates	Sites
Amphibians	forest	4	4 land, 5 river	Chakra, Mashpishungo, Malimpia River, Mashpi Chico River
	agroforest	3	5 land, 4 river, 1 flooded	Mashpishungo, Mashpishungo piscinas, Pambiliño
	monoculture	3	4 land, 3 river	Guerrero, Potrero, Taipe
Beetles	forest	1	3 dry, 3 rainy	Mashpishungo
	agroforest	1	3 dry, 3 rainy	Mashpishungo
	monoculture	1	3 dry, 3 rainy	Sahuangal
Birds	forest	1	3 transects	Mashpishungo
	agroforest	1	3 transects	Mashpishungo
	monoculture	1	3 transects	Santa Rosa
Fish	forest	6	na	Boshungo, Chakra, Malimpia Bajo, Mashpi Chico Bajo, Mashpi Grande, Tributario Malimpia
	agroforest	3	na	Mashpishungo, Inés, Pambiliño
	monoculture	3	na	Taipe, Palmito tributario (=Maspest 1), Palmito (=Maspest 2)
Macroinvertebrates	forest	3	3	Boshungo, Chakra, Tributario Malimpia
	agroforest	3	3	Mashpishungo, Inés, Pambiliño
	monoculture	3	3	Maspest 1, Maspest 2, Taipe

methods for each taxonomic group are described below.

2.1. Taxonomical groups assessed and collecting methods

2.1.1. Amphibians

We established three to five transects, 300 m each, along land and streams, within each land-use typology (Table 1). Our sampling strategy aimed to cover as much habitat heterogeneity as possible; thus, we favoured surveys at different transects rather than sampling the same transect multiple times. Two or three people searched amphibians through visual encounter surveys [VES; Heyer et al., (1994)], usually for 2 to 3 h per night (19:00–22:00; Appendix 1.). Amphibians were identified in situ using up-to-date guides (Arteaga et al., 2013; Ortega-Andrade et al., 2010). In cases when identifications were uncertain, amphibians were photographed, and their identifications were assessed by specialists.

2.1.2. Dung beetles

Collections were made during the dry (September 2016) and rainy seasons (April 2017) (Table 1). Permanent plots established in secondary forest remnants (van Manen et al., 2020; Pinto et al., in press) acted as controls, which are located at similar elevations as the agroforestry systems. For each land-use typology, the collections were implemented within three 60 × 60 m replicate quadrats containing nine dung beetle pitfall traps each (27 traps per treatment). Traps were placed in a gridded pattern separated by 25 m. Coprotraps (Larsen and Forsyth, 2005) were baited with 25 g of fresh human faeces (Halffter and Favila, 1993; Lobo et al., 1998; Morón and Terrón, 1984; Newton and Peck, 1975). Beetles were collected daily and placed in Whirl-pak® bags (946 mL) filled with 96 % ethanol. Then the samples were cleaned in the laboratory and identified to species level with reference to specialized taxonomic keys (Edmonds and Zídek, 2010; Génier, 2009, 1996; Jessop, 1985; Medina Uribe, 2011; Sarmiento-Garcés and Amat-García, 2009) and curated specimens housed in the entomological collection of the National Institute of Biodiversity – Ecuador (INABIO) (Villamarin-Cortez et al., in press).

2.1.3. Birds

To perform bird counts we used the Latin American Landbird Monitoring Protocol (Ruiz-Gutierrez et al., 2020). At each study site, we established three 100 m transects with double 25 m bands at each side (Table 1). These were sampled for three days, both in the morning and afternoon. Additionally, a night count was performed at each site. We registered all birds seen or heard, recording complementary data on feeding strata and behaviour for categorization in trophic gilds following Remsen and Robinson (1990). Bird counts were performed both in the wet (September to December 2016) and dry season (May to August 2017), totalling 12 rounds for morning and afternoon, an overall of 36 rounds in each site.

2.1.4. Fish

Fish sampling was carried out in 12 wadable stream stretches (<1 m of depth) using a backpack electrofishing gear (Hans Grassl model IG200/2D, 300–600 V, 0.2–2 A), during July 2015 (dry season) (Table 1). We estimated fish abundance following a single-run depletion methodology based on catch per unit effort (Meador et al., 2003). Collected fish were anesthetized and subsequently counted, photographed, and released after the survey, except for some representative specimens kept for laboratory identification. Those voucher specimens were deposited in the fish collection of the Museo de Zoología de la Universidad Tecnológica Indoamérica (MZUTI), Quito, Ecuador, preserved in alcohol (75 %), and identified following Barriga, 2012 and Jiménez-Prado et al., 2015.

2.1.5. Macroinvertebrates

Macroinvertebrates were sampled bi-monthly from December 2014 to May 2015 to include different hydrological conditions (Morabowen et al., 2019). We sampled nine first-order streams, three in each land-use typology (Table 1). At each sampling event we collected three transversal kick samples, separated by 25 m from downstream to upstream. Samples were preserved in 96 % ETOH in ziplock plastic bags and transported to the laboratory. We identified samples to the lowest taxonomical level possible, following Domínguez and Fernández (2009). Voucher specimens were deposited in the invertebrate collection of MZUTI. Details of the sampling can be found in Morabowen et al. (2019).

2.2. Statistical analysis

Our analysis focuses on comparing species diversity between the three land-use typologies for the five taxonomic groups. For this, we performed a Non-Metric Multidimensional Scaling (NMDS) analysis to observe the (dis)similarities in the species compositions among the land-use typologies; rank abundance curves; and a mantel test statistical analysis on the correlation between geographical and ecological distances of the sampled sites (Dray et al., 2012). NMDS has been used in multiple biological and ecological studies. Methodologically its performance is good without data pre-processing (Taguchi and Oono, 2005) and constitutes a powerful tool that enables the visualization of multivariate data sets in a reduced number of dimensions. NMDS uses a matrix of (dis)similarities of species compositions (of our five taxonomic groups) based on the Bray-Curtis dissimilarity metric between sites to ordinate these multivariate data on few axes, enabling the recognition and interpretation of patterns and differences among groups (in our case, land uses). The ordination fit is measured as "stress", which when is less than 0.2, shows a dataset visualization with the minimum number of dimensions without inducing high levels of distortion (Dexter et al., 2018). Moreover, we use rank abundance curves to have an overview of the dominance and rarity of species in our sample and illustrate how the communities in the three land-use typologies differ in number and abundance of species (Avolio et al., 2019).

To characterize the total biodiversity of different treatments, we used three integrated extrapolation analyses based on three Hill numbers (considered as "classic biodiversity metrics"): species richness (Rch), the exponential of Shannon entropy (Shannon Diversity) (Sh) and the inverse Simpson (Simpson Diversity) concentration (S) (Chao et al., 2014), complemented with Rarity (Rr). As these metrics are highly dependent on sampling efforts, we implemented Chao rarefaction and extrapolation models to measures of taxon diversity where relative abundance is incorporated. As a result, these metrics are expressed in comparable units of the effective number of species (Chao et al., 2014). Dopheide et al. (2020) described that rarity (Rr) could explain the highest proportion of land-use-related variance in biodiversity by measuring the proportion of a species unique to a site. Additionally, according to the results of Levene's test for homogeneity of variances (Appendix 2.), we implemented a Kruskall-Wallis non-parametric test to detect significant differences between land-use typologies on the four referred biodiversity metrics (Rch, Sh, S, Rr). Finally, we complement our analysis by measuring specialists and generalists using a Multinomial Classification Model (MCM) based on estimated species' relative abundance (Chazdon et al., 2011). This approach compares two distinct habitats by classifying species into three groups: habitat specialists, generalists, and rare species, which are not specialists or generalists. In our analysis, we implemented a pair-wise comparison between the three land-use typologies. The pair-wise comparison was carried out in the following way: MCM between forest-agroforest, MCM forest-monoculture, and MCM agroforest-monoculture, for each taxonomic group. MCM was especially designed to overcome differences in sampling intensities and bias o insufficient sampling of rare species, which is common in biodiversity surveys in the tropics (Chao, 2005; Coddington et al., 2009; Colwell and Coddington, 1994; Longino and Colwell, 1997; Thompson et al., 2016).

We performed all the statistical analyses in R using the Vegan package (Oksanen et al., 2020) with the corresponding functions: metaMDS() for the NMDS, vegdist() for the ecological distance matrix as input for the Mantel test (Vegan mantel function), and clamtest() for the Multinomial Species Classification Model. We calculated the geographical distance matrix with QGIS (QGIS Development Team, 2009). The iNEXT package (Hsieh et al., 2022) was used for the estimation of species Richness, Shannon, and Simpson diversity. Figures were plotted with plot() and ggplot() R functions. All scripts are included in the supplementary material (Appendix 3.).

3. Results

3.1. Community composition

Overall, we found major differences in community assemblages across land-use typologies for all taxa. The NMDS formed three groups for each taxonomical group (Fig. 2). Birds (stress = 0,0046) and dung beetles (stress = 0,0293) showed very differentiated communities across the three land-use typologies. For amphibians (stress = 0,0921) and macroinvertebrates (stress = 0,1204), forest composition differed from monoculture and agroforestry, while these last two had some composition similarities. For fish (stress = 0,0438), we found an overlap in the composition of forest and monoculture, whereas agroforestry differed from the other two.

Rank abundance curves (Fig. 3) showed that, for all taxa, monocultures had more dominant species and lower richness than the other land-use typologies, with greater differences for beetles, birds and fish. Secondary forests and agroforestry systems had similar rank abundance curves, with slight differences in dominance for birds, fish and macroinvertebrates. Likewise, we found greater differences for amphibians and beetles in the dominance of the most abundant species. For dung beetles, birds and fish, it is also noticeable that monoculture had fewer species than the other two land-use typologies. Secondary forests showed more evenness across taxa, except for dung beetles, where evenness was higher in agroforestry systems.

The Mantel test only revealed significant results for amphibians (Table 2). This shows that, for most groups, geographic proximity does not play a role in explaining community composition across land-use typologies. On the other hand, for amphibians, this might explain the similarity between monoculture and secondary forest assemblages (NMDS results). Overall, despite the proximity of some sampled sites with different land-use typologies, the community composition differs for four taxonomic groups, evidencing that land-use plays an important role in community composition, overriding the effect of geographic proximity, even at small spatial scales.

3.2. Biodiversity metrics

Overall, the biodiversity metrics (Sh, S, Rch, and Rr) estimated higher mean values between forest and agroforestry sites than biodiversity mean values between monoculture sites (Fig. 4, Appendix 5–7). However, those differences were not significant for all the groups and metrics. Significant differences were only present in dung beetles for most metrics (S: p = 0.027, Sh: p = 0.027, Rr: p = 0.034) (Appendix 4.) and rarity for birds (p = 0.027). For dung beetles, we found significant differences only between agroforest-monoculture (S: p = 0.021, Sh: p = 0.021) and forest-monoculture (Rch: p = 0.021, Rr: p = 0.033) but not between agroforestry and secondary forests. For birds, rarity was significantly different in forests compared to monoculture (Rr: p = 0.021) (Appendix 4.). However, when analysing the dispersion of bird biodiversity metrics across land-use typologies, it is evident that all of them were sensitive to land-use change (Fig. 4, Appendix 5–7). Also, rarity in monoculture showed a significant decline in fish assemblages compared with the other metrics. Rarity dispersion (Fig. 4, Appendix 5–7) was different in the three land-use typologies for dung beetles and birds, declining monotonically from forests to monoculture. Although the patterns observed between richness and rarity do not differ much among taxonomic groups and land-use typologies, the statistical test of differences showed significant differences in rarity for beetles and birds, especially when forest and monoculture were compared (Appendix 4).

Rarity described the same trend in four out of five taxonomic groups, declining in the number of rare species between the three land-use typologies, suggesting that rarity is a more suitable indicator for measuring biodiversity responses to land-use change. On the contrary, the other set of metrics showed lower differences between forest and agroforestry.

Our analysis of specialists and generalists using a Multinomial Classification Model (Table 3) revealed that the amphibian and fish assemblages consisted of mainly generalist species, with no significant affinity to any land-use typology. On the contrary, dung beetles and birds had more forest specialists than the other taxonomical groups (Table 3). Dung beetles had higher agroforest specialists, while birds had higher monoculture specialists (Table 3). Fish had a higher number of forest specialists than agroforestry systems specialist (F = 0.095, AF = 0.048) but, contrary to our expectations, those forest specialist were absent when compared to monoculture (F = 0, M = 0.059). For macroinvertebrates, forest specialists were slightly higher (F = 0.049) than monoculture (M = 0.041) but lower than agroforestry (F = 0.024, AF = 0.072). As expected, agroforest specialists were higher than monoculture (AF = 0.076, M = 0.025). Is important to notice that all taxa had a considerable number of species that were too rare to classify with confidence, either as generalists or specialists (Table 3). These results agree with and complement our results on rarity as a sensible measure of land conversion. Nevertheless, it is important to notice that all taxa had

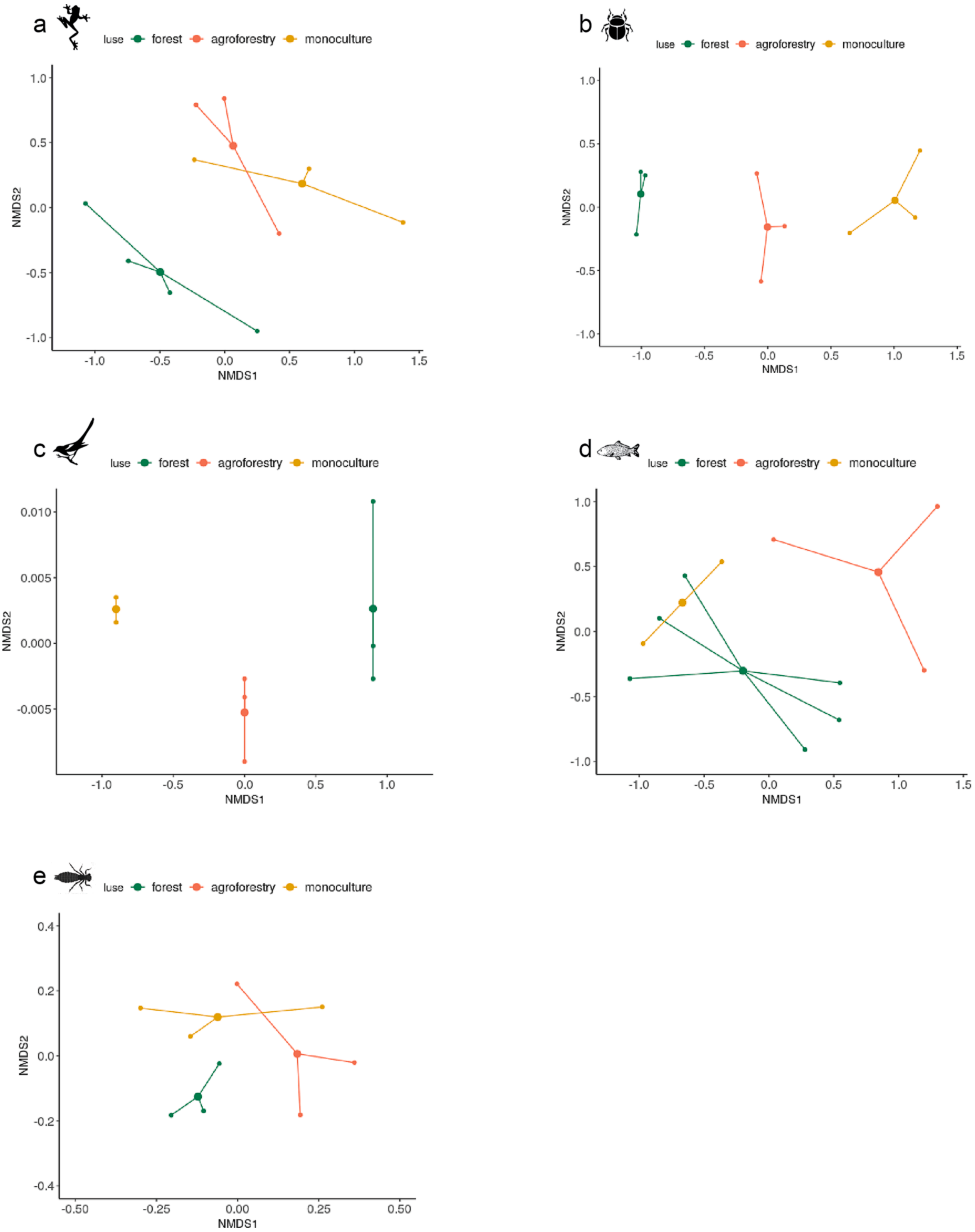

Fig. 2. NonMetric Multidimentional Scaling for (a) amphibians, (b) dung beetles, (c) birds, (d) fish and (e) aquatic macroinvertebrates in three land-use typologies (secondary forest, agroforestry and monoculture) in the Area of Conservation and Sustainable Use of Mashpi, Guaycuyacu and Sahuangal, Ecuador. Dissimilarity between sites and land-uses represented by a spider diagram, where small dots represent the sampled sites and the big dot the centroid of each land-use typology. Stress: amphibians = 0.0921, beetles = 0.0293, birds = 0.0046, fish = 0.0438, macroinvertebrates = 0.1204.

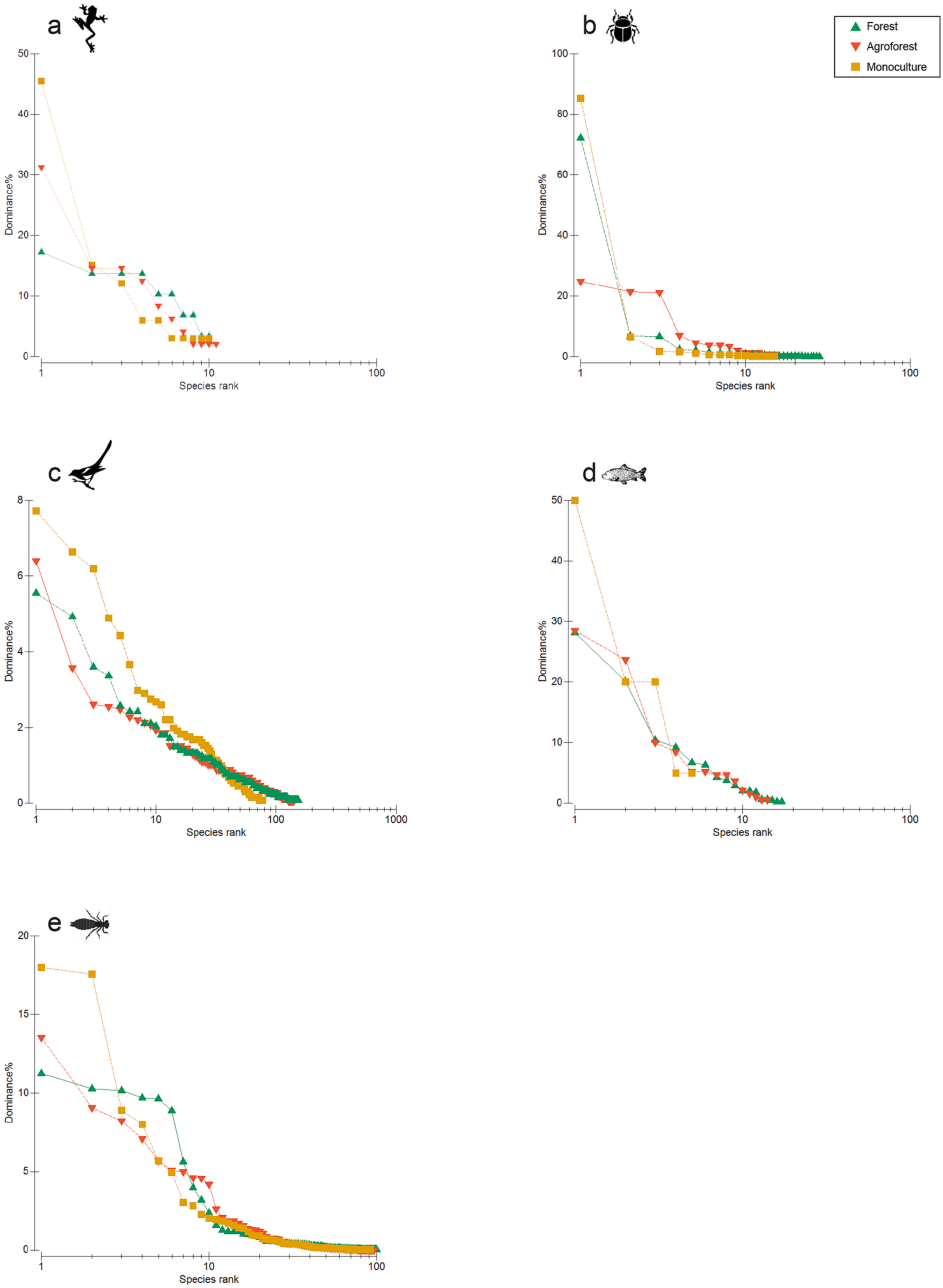

Fig. 3. Rank-Abundance curves for amphibians (a), dung beetles (b), birds (c), fish (d) and aquatic macroinvertebrates (e) in tree land-uses (secondary forest, agroforestry, and monoculture) in the Area of Conservation and Sustainable Use of Mashpi, Guaycuyacu and Sahuangal, Ecuador.

Table 2
Mantel Test for all biodiversity groups included. This analysis correlates the geographic distance between sites with the ecological distance between sites.

Group	Mantel	Significance
Amphibians	0.3449	**0.033**
Beetles	−0.5	0.833
Birds	0.5	0.5
Fish	0.02025	0.435
Macroinvertebrates	−0.0866	0.658

many species that were too rare to classify confidently, either as generalists or specialists (Table 3).

Finally, the two land-use typologies that share a higher proportion of generalist species were forest-monoculture for amphibians and fish, agroforest-monoculture for beetles, and forest-agroforest for birds and macroinvertebrates. Nonetheless, generalist species through the pairwise comparison of land-use typologies for macroinvertebrates were very similar across typologies (F-AF = 0.32, AF-M = 0.303, F-M = 0.317).

4. Discussion

We found some differences in community assemblages across land-use typologies for all taxa, especially for birds (stress = 0.0046) and beetles (stress = 0,0293). Our NMDs analysis showed that centroids of community composition for each land-use typology differed. Birds and dung beetles were ordered in three distinct assemblages (Fig. 2 b, c). For amphibians and macroinvertebrates, forest assemblages were different from agroforestry and monoculture; these last two typologies had some overlap (Fig. 2 a and e). Fish assemblages had a similar composition between monoculture and forest, while agroforestry had a distinct assemblage (Fig. 2d). In rank-abundance curves, monoculture clearly showed less evenness in community assemblages for all groups. Few species (1 to 3 taxa) were dominant, and the rest had low abundances (Fig. 3). These analyses linked community composition differences with land-use typologies in all groups, showing their value in assessing land-use effects on biodiversity. Our results agree with recent analyses at the global scale that have demonstrated that community composition and species population are metrics that are highly sensitive indicators to land-use change for terrestrial and freshwater ecosystems (Jaureguiberry et al., 2022).

Classic biodiversity metrics (i.e., Richness, Simpson and Shannon indexes) only showed significant differences for dung beetles in the pairwise comparison of some land-use typologies (Appendix 4). A common weakness of these classic biodiversity metrics is that they are highly sensible to sampling effort and relative abundance, and its estimation is strongly influenced by rarest species (Roswell et al., 2021). The distribution of those rare species is observed in the rank abundance curves, which also reflect differences in the dominant and rare species between land-use typologies. We found significant differences in Rarity and for birds and beetles between secondary forests and monocultures and when all the land-use typologies were compared (Appendix 4). Rarity was consistently lower for monoculture assemblages across groups, except amphibians. The biodiversity of amphibians was likely influenced by the proximity between monitored sites (Table 2, Mantel test), and by the conspicuousness of generalist species in this group (e.g., *Pristimantis achatinus, Hypsiboas pellucens;* see MCM, Table 3). These results can also explain the lack of difference in amphibians' assemblages and biodiversity metrics among land-use typologies. Although the sensitivity of amphibians to land use change is well documented (Catenazzi, 2015; Fulgence et al., 2022), it is also possible that current frog communities have reduced species richness and abundance because of the chytrid pandemic (Berger et al., 1998; Scheele et al., 2019). Such impoverishment of species has been recorded at localities where the chytrid fungus has produced local extinctions and drastic population declines (Catenazzi et al., 2014; Lips et al., 2006). It is also possible that an increased sampling effort is necessary to assess habitat-specific communities. Also, measures related to functional traits of the anuran community could be a better-suited approach to detect changes across land-use typologies. However, complete life history traits are available for a limited number of amphibian species, compared to European species (Trochet et al., 2014). Habitat suitability models and metanalysis have shown that biological traits, especially those related to larval development, are sensitive to land-use changes (Agudelo-Hz et al., 2019; Nowakowski et al., 2017). Likewise, functional redundancy is very sensitive to land-use history, especially for amphibians and dung beetles (Díaz-García et al., 2022). Thus, at local scales, classic alpha biodiversity metrics (Richness, Shannon, Simpson indexes) might not be the best indicators to assess land-use impacts in complex landscapes at local scales.

Contrary to our expectations, fish assemblages were more similar among forest and monoculture than agroforestry. However, the forest assemblages showed two clearly distinct and distant groups: three river sites with high alpha diversity on one hand, and three sites on tributaries with low alpha diversity values on the other. The sites on forest tributaries are the ones that overlap with monoculture sites, more influenced by low habitat diversity than by land use. Hydro-morphological features highly influence fish communities in the tropical Andes more than agricultural uses (Miranda et al., 2022), which can explain the overlap between forest-monoculture fish communities. Macroinvertebrates, unlike our expectations, showed weak differences across land use typologies. Much of the material collected is larvae, virtually impossible to identify at the species level with classic taxonomical tools and without the knowledge of the life history and species identities. The taxonomical resolution level of differentiation of the specimens collected could partially explain this unexpected result. Differences in taxonomical resolution can strongly influence statistical analyses aimed at assessing differences in the relationship of the macroinvertebrate community with human-driven hydrological alterations. Some authors showed weak relations at the family level, compared to the species level (Monk et al., 2012), and others found consistency worldwide in the responses at the order and family taxonomic resolution levels in scoring systems to assess human impacts on rivers (Chang et al., 2014).

Fish and macroinvertebrates are highly used as bioindicators to assess the ecological integrity of lotic ecosystems, including the European Water Framework Directive for assessing the ecological status of these ecosystems (European Commission, 2000). Both taxa are also recognized in the Ecuadorian norm as sensitive indicators to assess the impacts of mining in rivers (MAE, 2018). In this norm, all the taxa included in this study are mentioned, but besides species conservation status (i.e., IUCN red list) and endemicity, which only exists for some groups, does not state, or recommend how to assess them. Richness and Shannon biodiversity index are usually reported. However, as seen in the literature (p.e: Connell, 1978; Rubin et al., 2017) and in our results, classic biodiversity metrics can lead to wrong or partial conclusions. Thus, using adapted scoring systems for both fish and macroinvertebrates groups, that consider natural hydro-morphological features, and their related human impacts are more suitable than classic biodiversity metrics (Chang et al., 2014; Villamarín et al., 2013).

Our data had important limitations of replicates in space and time that can limit our conclusions about using different metrics as reliable tools to measure the impact of land-use change on biodiversity. Nevertheless, significant changes were observed across most of the analyses and metrics for dung beetles and in composition and rarity for birds. These two groups also have been considered robust indicators of ecosystem health (p.e: Alroy, 2015; Chapman et al., 2018; Karp et al., 2012; Nichols et al., 2007) and showed significant responses to land-use intensification. Rarity was consistently lower in monoculture for all taxa, except for amphibians, which shows that this metric can be a sensitive indicator to assess the impacts of land-use change, as seen in other highly biodiverse systems (Dopheide et al., 2020; Maciel and

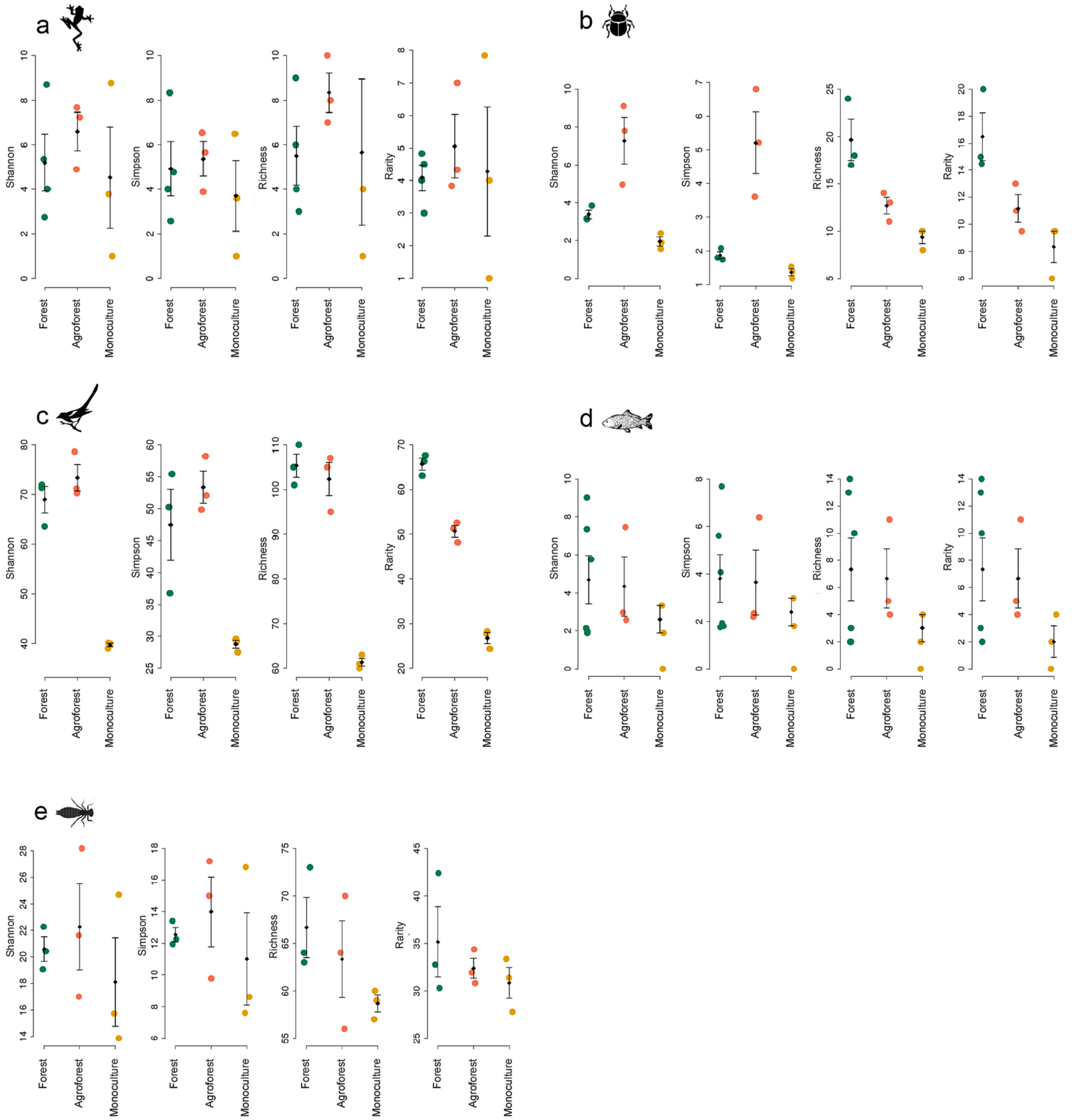

Fig. 4. Biodiversity Metrics (Shannon Index, H1; Simpson Index, H2; Richness and Rarity) for amphibians (a), dung beetles (b), birds (c), fish (d) and aquatic macroinvertebrates (e) in three land-use typologies (secondary forest, agroforestry and monoculture) in the Area of Conservation and Sustainable Use of Mashpi, Guaycuyacu and Sahuangal, Ecuador. Sampled sites (3 per land-use, except for fish and forest with 6 sites) are depicted in colours by land-use typologies (green: secondary forest, pink: agroforestry, yellow: monoculture), and the mean value is displayed with standard error whiskers. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Martins, 2021). Also, further research can be implemented to explore the differences in the strata and design of agroforestry systems, which can partly influence the differences and similarities between forest and agroforestry systems in species assemblages and biodiversity metrics.

5. Conclusions

A substantial number of studies developed in the Neotropics have shown that non-classical taxonomical and functional metrics are more sensitive predictors of the state of biodiversity under different land-use typologies (Arita et al., 1990; Leitão et al., 2016; Swan and Brown, 2014; Toledo et al., 2014). Here, we showed that even with our limited and

Table 3
Multinomial Classification Model based on relative abundance of taxa, across land-uses. Specialization threshold = 0.66, Alpha Level 0.005. na = the indicator does not apply for the pair of land-use typologies that are compared.

Group	Land use compared	Species proportion				Too rare	Estimated sample coverage			Minimum abundance for classification		
		Generalist	Specialist forest	Specialist agroforest	Specialist monoculture		Forest	Agroforest	Monoculture	Forest	Agroforest	Monoculture
Amphibians	Forest – agroforest	0.60	0.00	0.00	na	0.40	0.93	0.92	na	1.00	15.00	na
	Agroforest – monoculture	0.15	na	0.00	0.00	0.85	na	0.92	0.85	na	13.00	10.00
	Forest – monoculture	**0.77**	0.00	na	0.00	0.23	0.93	na	0.85	1.00	na	11.00
Mean		**0.51**	0.00	0.00	0.00	**0.49**						
Beetles	Forest – agroforest	0.09	0.03	0.11	na	0.77	1.00	0.98	na	59.00	8.00	na
	Agroforest – monoculture	**0.13**	na	0.13	0.04	0.71	na	0.98	0.99	na	9.00	20.00
	Forest – monoculture	0.03	0.14	na	0.06	0.77	1.00	na	0.99	31.00	na	8.00
Mean		0.08	**0.09**	**0.12**	0.05	**0.75**						
Birds	Forest – agroforest	**0.24**	0.04	0.05	na	0.67	0.98	0.99	na	12.00	14.00	na
	Agroforest – monoculture	0.18	na	0.10	0.12	0.60	na	0.99	1.00	na	14.00	12.00
	Forest – monoculture	0.04	0.14	na	0.16	0.66	0.98	na	1.00	13.00	na	13.00
Mean		0.15	**0.09**	0.08	**0.14**	**0.64**						
Fish	Forest – agroforest	0.29	0.10	0.05	na	0.57	1.00	0.99	na	22.00	9.00	na
	Agroforest – monoculture	0.67	na	0.00	0.06	0.25	na	0.99	0.90	na	1.00	6.00
	Forest – monoculture	**0.82**	0.00	na	0.06	0.12	1.00	na	0.90	1.00	na	6.00
Mean		**0.59**	0.05	0.02	0.06	**0.31**						
Macroinvertebrates	Forest – agroforest	**0.32**	0.02	0.07	na	0.58	0.99	0.99	na	13.00	13.00	na
	Agroforest – monoculture	**0.30**	na	0.08	0.03	0.60	na	0.99	0.99	na	12.00	13.00
	Forest – monoculture	**0.32**	0.05	na	0.04	0.59	0.99	na	0.99	13.00	na	13.00
Mean		0.31	0.04	0.07	0.03	**0.59**						

uneven samples in space and time, our metrics, rank abundance curves, NMDS and MCM, constitute a more sensitive set of indicators to assess land-use change impacts on different taxonomical groups. Despite the small spatial scale of our sampling campaigns, and the proximity between farms with different land-use typologies, or different land-use typologies within the same farm, our results showed that land-use intensification can have an important influence on community assemblages for four taxonomic groups (birds, dung beetles, macroinvertebrates and fish). These non-classical indicators can be easily applied without necessarily increasing the cost of field campaigns. Rarity was the only metric that showed significant differences for two taxa: dung beetles and birds. Therefore, their use is appealing and complements the information provided at community level analysis. The diversification of the analysis will provide better insights into the effect of land-use change at local scales in these highly biodiverse ecosystems. However, we acknowledge that achieving more robust insights necessitates the incorporation of long-term data collection methodologies as part of long-term research programs. These considerations are vital for gaining a deeper comprehension of the intricate effects of land-use change in complex tropical landscapes at local scales.

CRediT authorship contribution statement

Blanca Ríos-Touma: Conceptualization, Project administration, Methodology, Formal analysis, Writing – original draft, Writing – review & editing. **Paulina Rosero:** Data curation, Methodology, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Andrés Morabowen:** Investigation, Writing – review & editing. **Juan M. Guayasamin:** Investigation, Writing – review & editing. **Chelsea Carson:** Investigation, Writing – review & editing. **Santiago Villamarín-Cortez:** Investigation, Writing – review & editing. **Alejandro Solano-Ugalde:** Investigation, Writing – review & editing. **Ibon Tobes:** Investigation, Writing – review & editing. **Francisco Cuesta:** Conceptualization, Data curation, Methodology, Formal analysis, Writing – original draft, Writing – review & editing.

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.

Data availability

We share all data on the supplementary material

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2023.111100.

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