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RESEARCH ARTICLE

Sample coverage affects diversity measures of bird communities along a natural recovery gradient of abandoned agriculture in tropical lowland forests

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Abstract

1. Tropical old-growth forests continue to decline worldwide, resulting in a huge loss of biodiversity. The extent to which the expansion of second-growth forests can counteract biodiversity loss is context-dependent and controversial.
2. To test the recovery of bird communities along a gradient from active pastures and cacao plantations, through regenerating forest on land last used for agriculture between 1 and 38 years ago, to old-growth forest, we sampled simultaneous audio recordings from 66 plots, from which an expert identified all bird species detected at fixed time points throughout the day. The study area is characterized by typical small-scale agriculture with remnant trees in the Ecuadorian Chocó Forest. To quantify different aspects of biodiversity, we used incidence-based Hill numbers focusing on infrequent, frequent and highly frequent species in taxonomic, functional and phylogenetic diversity, considering sample coverage (an objective measure of sample completeness).
3. Bird community composition changed with the regrowth gradient represented on the first axis of the ordination. Differences in bird communities were also very robust to changes in sample coverage.
4. The sample coverage decreased significantly along the recovery gradient and affected the different measures of alpha diversity. Although the results controlled by sample coverage showed no change in taxonomic and phylogenetic diversity, the functional diversity of infrequent, frequent and highly frequent species decreased along the recovery gradient.

For affiliations refer to page 488.

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5. Cacao plantations exhibited particularly high diversity values, highlighting the potential of these patches to support woodland and shrubland species in agriculture. Furthermore, several forest species regularly used the agricultural areas, attracted by remnant trees characteristic of the small-scale agricultural landscape in our study region.
6. *Synthesis and applications*. Our results highlight the importance of standardizing biodiversity measures and incorporating beta diversity in biodiversity monitoring. We demonstrate that taxonomic, phylogenetic and functional bird diversity can be high in secondary forests within smallholder agricultural landscapes. This underscores the potential for natural forest recovery, particularly when recovery patches are embedded within a forest matrix that includes old-growth stands.

KEYWORDS
acoustic recorder, cacao plantations, functional diversity, Hill numbers, iNEXT3D, phylogenetic diversity, secondary growth

1 | INTRODUCTION

Tropical primary forests are important for biodiversity, but they are affected by disturbance and deforestation globally. Still, second-growth forests cover increasingly large areas (Rozendaal et al., 2019) and have the potential to counteract species loss (Chazdon et al., 2009). However, our understanding of the potential this secondary growth holds for forest conservation is incomplete. One concern is that secondary forests may not meet the habitat requirements of rare and specialized species (Chazdon et al., 2009).

Many nations have committed to restore deforested landscapes, but strategies and success vary greatly (Farrell et al., 2022; Holl, 2017). To promote second growth with high biodiversity values, it is crucial to assess how biodiversity changes with increasing forest recovery (Chazdon et al., 2009; Hua et al., 2022). This knowledge could support the long-term success of reforestation goals and concomitantly reduce the loss of biodiversity (Sutherland & Wordley, 2017).

Several scientific studies analyse changes and differences in bird communities in secondary forests compared to agricultural areas and old-growth forests. In general, bird communities in secondary forests become more similar to old-growth bird communities over time (Owen et al., 2020), with species composition recovering more slowly than species richness (Dunn, 2004; Rozendaal et al., 2019). However, changes in species richness and phylogenetic and functional diversity are less consistent. While some studies report similar or higher species richness in second growth compared to primary forest (Andrade & Rubio-Torgler, 1994; Blake & Loiselle, 2001; Borges, 2007), others report reduced species richness in second-growth (Barlow et al., 2007; Gibson et al., 2011). Functional diversity has been reported to be higher in forests than in pastures and oil palm plantations (Chapman et al., 2018; Edwards et al., 2013; Prescott et al., 2016) and to be similar in primary forest and second-growth forest (Sayer et al., 2017). Previous studies also show increasing phylogenetic diversity with ongoing succession with highest levels in old-growth (Chapman et al., 2018; Edwards et al., 2017; Letcher et al., 2012). Since taxonomic, phylogenetic and functional diversity may respond differently to habitat changes, it is important to study them simultaneously.

In ecology, the simplest and most common metric of biodiversity is species richness. The use of species richness, however, can be problematic because it is highly dependent on sample size and does not represent relative abundances or frequencies (Gotelli & Colwell, 2001). To analyse responses of rare, common and dominant species within a studied community, it is common practice to use Hill numbers, as they consider relative frequency distributions (Hill, 1973). Originally developed for abundance data the concept of Hill numbers has been extended to replicated incidence data (Colwell et al., 2012; Chao, Chiu, & Jost, 2014; Chao, Gotelli, et al., 2014), which is the typical data format when using acoustic recorders. Under the adapted model for incidence data, only species incidence (detection/non-detection) in any sampling unit is required; species abundances are not needed. As with abundance data, Hill numbers based on incidence data can be similarly formulated by replacing species relative abundances with species relative incidence frequencies. For $q=0$, the incidence-based Hill number reduces to species richness and thus is more sensitive to infrequent species; the measures with $q=1$ and $q=2$ can be interpreted as the effective number of frequent and highly frequent species in the community, respectively. It has been shown that replicated incidence data support statistical approaches to diversity estimation that are just as powerful as corresponding abundance-based approaches (Chao & Colwell, 2017; Colwell et al., 2012). When interpreting the results, it is important to bear in mind that the incidence-based frequencies derived from audio files represent the vocal presence of a species, rather than the actual number of individuals.

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Hill numbers have also been extended to quantify phylogenetic and functional diversity (Chao et al., 2021), which give us information beyond species richness and can represent ecosystem functioning and resilience (Bregman et al., 2016; Cadotte et al., 2012). In detail, taxonomic diversity quantifies the effective number of species, phylogenetic diversity quantifies the effective number of lineages and functional diversity quantifies the effective number of virtual functional groups (or functional 'species') based on a selection of traits.

Birds are a well-studied taxonomic group (Trimble & van Aarde, 2012) with comprehensive phylogenetic (Jetz et al., 2012) and trait (Tobias et al., 2022) information, which makes them a suitable indicator group for biodiversity studies. In general, data on birds are collected visually and acoustically often along a transect or within a fixed radius and timeframe (Hutto et al., 1986). In all methods used to collect bird data, the detection of species can vary greatly. First, field observations cover a small snapshot in time with varying times of day for each site, and species vary in their detectability (Morelli et al., 2022). Second, observer biases may complicate the interpretation of results, as they vary in their skills and assessments. In addition, any observer causes small disturbances by entering a study site and hence might miss more elusive species (Gutzwiller & Anderson, 1999).

One way to standardize the sampling of birds is to use autonomous acoustic recorders, a practical tool that allows recording of birds simultaneously at different study sites and covering huge timespans that can be standardized afterwards (Darras et al., 2019). Acoustic recordings are hence less prone to observer bias. However, differences in habitat structures can translate into variation in the detectability of species by their sound, as with traditional field surveys (Anderson et al., 2015).

Taking these limitations into account, samples of species assemblages are always incomplete, making sample standardization very important (Chao & Jost, 2012; Gotelli & Colwell, 2001). The term 'sample coverage', originally developed by Alan Turing in his cryptographic work during WWII for abundance data, is defined as the proportion of the total number of individuals in the entire assemblage that belong to the detected species in a sample (Chao et al., 2015). Chao et al. (2020) extended Turing's concept of sample coverage to its incidence version to quantify sample completeness of replicated incidence data. This extension is based on the distribution of incidence frequencies obtained from multiple sampling units such as audio files with records.

Still, most studies do not standardize for sample coverage to overcome differences in detectability (but see Alducin-Chávez et al., 2022). If differences in sample coverage do not occur randomly, failing to control for it can lead to directional biases.

To analyse how bird communities change with forest recovery, we studied bird vocalizations along a recovery gradient that ranges from cacao plantations or pastures to old-growth forests in a small-holder agricultural area in the Ecuadorian Chocó. As former cacao plantations already have a tree layer, we predicted a slight advance of former cacao plantations over pastures in the recovery gradient. To test the ecological value and resilience of the different habitat types, we analysed not only taxonomic, but also phylogenetic and functional diversity. We assume that ecosystem functioning and stability increase with functional and phylogenetic diversity. In addition, we analysed diversity values for infrequent, frequent and highly frequent species based on incidences. Our goal was to standardize bird sampling, data processing and analysis in a comprehensive way to exclude the above-mentioned biases. We analysed if sample coverage varied along the recovery gradient and how taxonomic, phylogenetic and functional diversity developed with ongoing recovery.

2 | MATERIALS AND METHODS

2.1 | Study area

We used 66 study plots within the REASSEMBLY research unit (www.reassembly.de). The study area, design and sampling procedure are described in detail in Appendix S3 and in Müller et al. (2023). We conducted research with the permission of the Ministry of Environment of Ecuador through Contrato Marco MAE-DNB-CM-2021-0187. We did not require ethical approval for fieldwork and data sampling. The study area of Canandé (Esmeraldas Province of northwestern Ecuador) is characterized by rather small agricultural fields and settlements within a matrix of selectively logged, secondary and old-growth forests, a typical landscape type in the tropics (Feng et al., 2022; Scales & Marsden, 2008). The plots covered a chronosequence of forest recovery, including (i) active pastures and cacao plantations; (ii) pastures and plantations previously used, which were secondary forests that regrew for 1 to 38 years at the time of the study and (iii) old-growth forests, with no indication of recent use by humans (Figure 1). A map of the study plots is shown in Appendix S3 (Figure S3.1).

2.2 | Bird recordings

We deployed a bioacoustic recorder (BAR-LT, Frontier Labs, Meanjin, Australia) with a downward facing omnidirectional microphone at a height of ~1.70 m above ground level in each plot in 2021 and 2022. The recorders were placed in the middle of each habitat type. We analysed fourteen 2-min audio files of each study plot. Methods are explained in detail in Appendix S3 (*Bird recordings*).

2.3 | Traits and phylogeny

We used morphological and ecological bird traits from the AVONET database (Tobias et al., 2022). A detailed description of the selected traits can be found in Appendix S3. A table with all traits and species can be found in Appendix S2. Information on the phylogenetic tree can be found in Appendix S3 (*Phylogenetic tree*).

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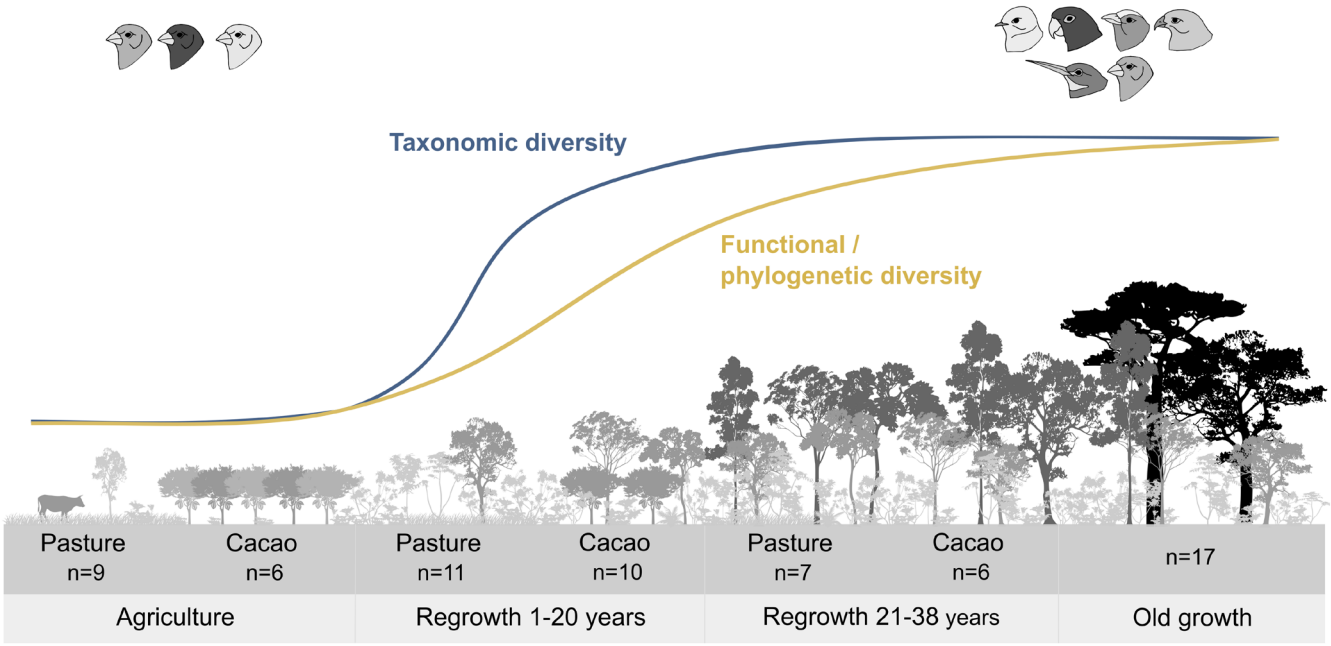


FIGURE 1 Recovery gradient with managed pasture and cacao, forest recovery and old-growth in the Ecuadorian Chocó and hypothesized response curves for taxonomic, phylogenetic and taxonomic diversity. Diversity curves are without dimensions and only represent the course of the diversity measures over the gradient. In general, we expect phylogenetic and functional alpha diversity to be lower than taxonomic alpha diversity due to a repetition of functional traits and phylogenetic groups within a community.

2.4 | Statistics

All statistical analyses were conducted with R 4.3.1 (R Core Team, 2023). In our incidence-based model, each 2-min audio file is regarded as a 'sampling unit'; species is 'detected' by the activity and vocal presence. For each study site, we calculated the observed taxonomic, phylogenetic and functional diversity for all Hill numbers $q = 0, 1, 2$ (representing infrequent, frequent and highly frequent species or, respectively, species richness, Shannon diversity, Simpson diversity) with the iNEXT3D function from the iNEXT.3D package (Chao et al., 2021). In addition, we calculated estimated diversity for a standardized sample coverage of 90%. More details can be found in Appendix S3 (*iNEXT3D*).

To analyse changes in diversity along the recovery gradient, we fitted linear models for all observed and estimated diversity values (taxonomic, phylogenetic, functional and Hill numbers) with the different habitat types as ordered factors. We ordered the habitat types along the recovery gradient as pictured in Figure 1 based on our assumption that cacao and former cacao plantations are always slightly closer to old-growth sites than pastures and former pastures with respect to the structure of their bird communities.

To analyse differences in gamma-diversity, we calculated species accumulation curves with iNEXT3D for the four categories (agricultural sites, early recovery stage, late recovery stage and old-growth sites) based on number of species detections. We performed additional analyses to exclude potential effects of the surrounding habitats on our results which can be found in Appendix S3 (*Additional analyses of potential effects of surrounding habitats*).

We calculated community distances for observed and coverage-standardized dissimilarities, an approach just recently developed (Chao et al., 2023), again with focus on infrequent, frequent and highly frequent species based on Jaccard, Horn and Morisita-Horn index using an adapted function based on the inext.beta3D function for incidence data. The coverage-based distance matrices were standardized for a coverage of 90%. Distance matrices were then used to calculate an NMDS using the metaMDS function from the vegan package (Dixon, 2003) to visualize shifts in species communities along the second-growth gradient.

3 | RESULTS

Our final data set comprised 4462 detections for 224 bird species. The community consisted of 41 families from 13 orders, with Passeriformes dominating in terms of species number (Figure 2). Of the observed species, 185 were associated with forest (e.g. tree-dominated habitats with a closed canopy) and 39 with more open habitats (e.g. shrubland, agriculture, tree-dominated habitats with scattered trees and forest edges) according to the AVONET database (Tobias et al., 2022).

Ordinations of the bird communities along the Hill numbers showed that the first axis represents the ecological gradient from agricultural sites over recovery sites to old-growth sites with cacao and former cacao sites ahead of pasture and former pasture sites in early regeneration (1–20 years after abandonment). In later regeneration (21–38 years), the pattern changed and varied between estimated and observed species. In general, results were very similar

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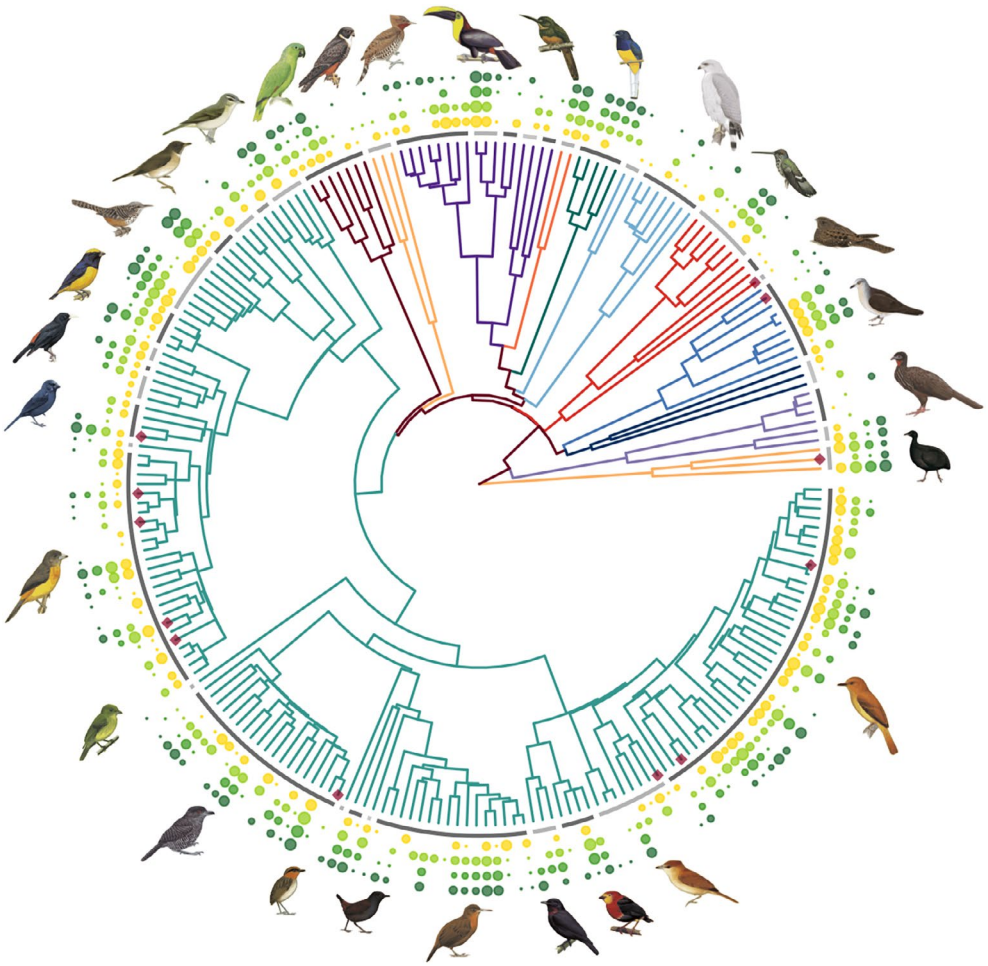


FIGURE 2 Phylogenetic tree of the studied bird community along a recovery gradient with managed pasture and cacao, forest recovery and old-growth in the Ecuadorian Chocó from 2021 to 2022. Tree branches are coloured according to the taxonomic orders. Families are symbolized by light and dark grey bars. Dot size symbolizes frequencies of each species in different habitat types. From inside yellow: Agricultural areas, light green: Forest recovery 1–20 years, green: Forest recovery 21–38 years, dark green: Old-growth older than 50 years. Red squares at the tree tips mark species with a range size smaller than 60,000 km^2, which are considered to be endemic and more prone to extinction risk. Bird icons are created based on Birds of the World, The Cornell Lab of Ornithology.

for all orders of q as well as observed and estimated species number (Figure 3).

Our results showed that sample coverage declined significantly along the recovery gradient (Figure 4). In other words, a given sampling intensity resulted in more complete recordings of the bird community at agricultural sites and in recovering forests compared to old-growth. After controlling for differences in sample coverage, there were no significant effects of recovery on taxonomic diversity ($p=0.24$ ($q=0$); $p=0.25$ ($q=1$); $p=0.51$ ($q=2$)) or phylogenetic diversity ($p=0.20$ ($q=0$); $p=0.27$ ($q=1$); $p=0.37$ ($q=2$)) (Figure 5). In contrast, functional diversity for all orders of q significantly decreased along the gradient ($p<0.001$ ($q=0$, 1, 2)) (Figure 5). Results with and without standardization for sample coverage differed in effect strength, but not in the direction of the effect (Figure 5). *p*-values and estimates are included in Figure 4. Further model results are in Appendix S1.

Species accumulation curves showed similar trends for gamma diversity and alpha diversity (Figure S1.1).

4 | DISCUSSION

Our results showed frequency-dependent and coverage-dependent changes in bird communities in second-growth forest succession. Our study revealed that bird community composition varied in a non-random fashion along the ecological gradient. The bird communities in agricultural sites displayed the greatest divergence from those in old-growth forests, whereas the bird communities in regrowth sites exhibited a progressive convergence towards those in old-growth forests. This was also shown in a previous study of vocalizing vertebrate communities on a subset of the study sites (Müller et al., 2023) and for bird communities in tropical forests in Costa Rica (Owen et al., 2020). This effect was very robust for observed and estimated species diversity as well as infrequent, frequent and highly frequent species (Figure 3). It also followed our expectations that the bird communities in early recovery on former cacao plantations are closer to the old-growth forest communities than those in the early recovery on

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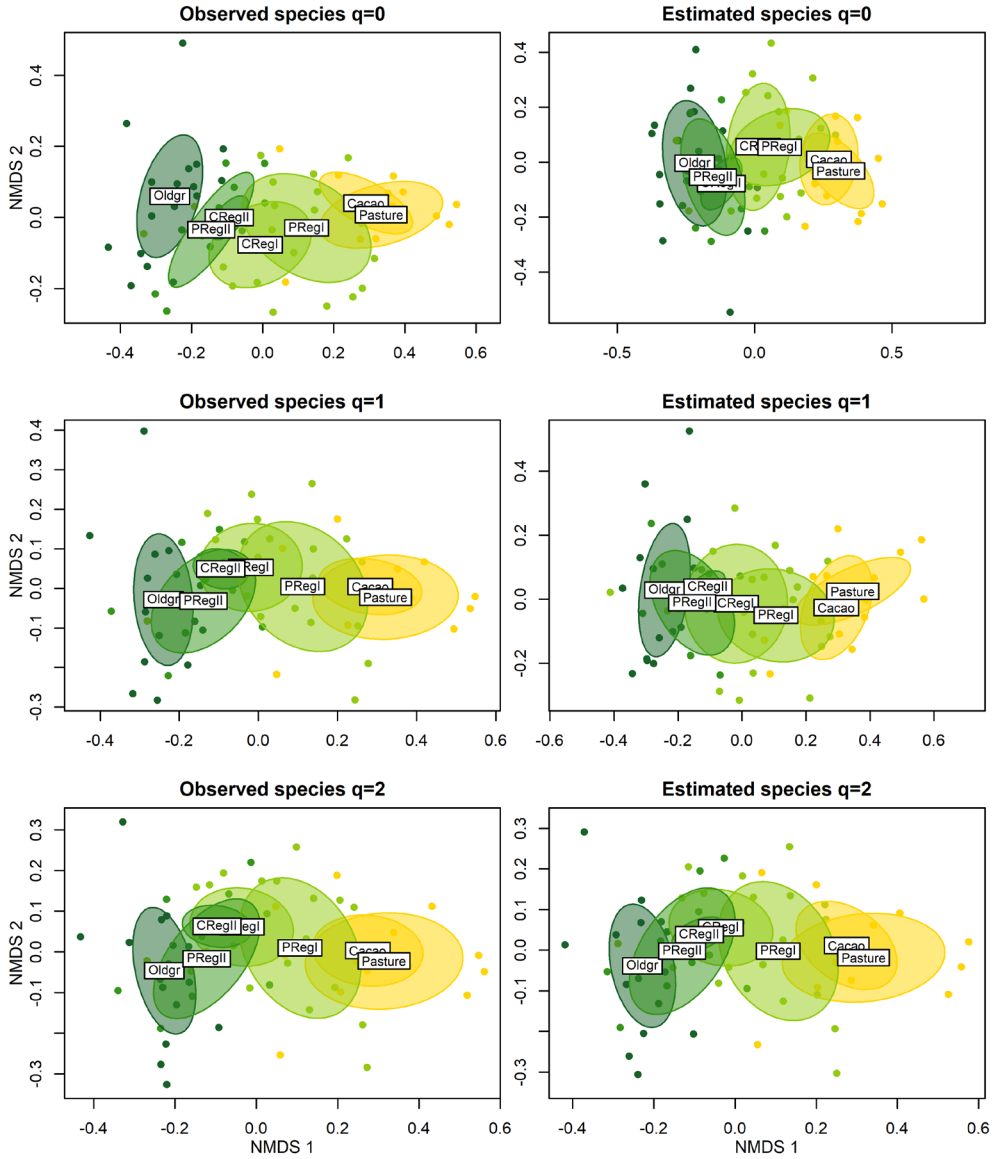


FIGURE 3 Non-metric multidimensional scaling (NMDS) ordination of the studied bird community along a regrowth gradient with managed pasture and cacao, forest regrowth and old-growth in the Ecuadorian Chocó from 2021 and 2022. Results cover different Hill numbers from top to bottom focusing on infrequent ($q = 0$), frequent ($q = 1$) and highly frequent ($q = 2$) bird species. Estimated dissimilarities are standardized for a sample coverage of 90%, the maximum value for which we can reliably extrapolate dissimilarities. Different habitat types are separated by ellipses (pasture, cacao, secondary forest on former pasture 1–20 years old (PRegI), secondary forest on former cacao 1–20 years old (CRegI), secondary forest on former pasture 21–38 years old (PRegII), secondary forest on former cacao 21–38 years old (CRegII) and old-growth forest (Oldgr)).

former pastures. We suggest that this might be due to the forest-like character of cacao plantations formed by cacao trees. In contrast, former pastures are characterized by a dense herb layer and maintain open patches and low shrubs during forest recovery. This pattern changes only in later succession after about 20–30 years. Especially for highly frequent species, bird community composition in late succession on former pastures is more similar to that of old-growth patches than in late succession on former cacao patches (in contrast to early succession). This indicates that former pastures and cacao patches differ in their regeneration dynamics and that these differences can persist for several decades.

4.1 | Sample coverage follows the recovery gradient

Our results showed that sample coverage decreased significantly along the recovery gradient (Figure 4). With a constant sampling effort, fewer members of the bird community are recorded in forests of higher age. More specifically, there were more calls or songs per minute in agricultural compared to forest sites, indicating a higher activity and hence detectability of birds in agricultural land (Müller et al., 2023). Therefore, controlling for differences in sample coverage directly affected some of the diversity measures along the

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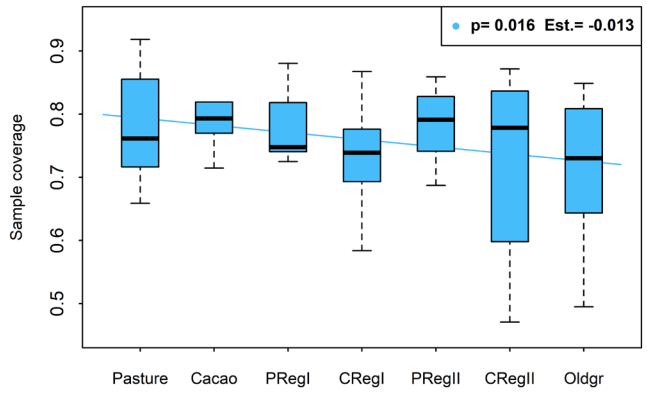


FIGURE 4 Boxplots of sample coverage per habitat type. The line indicates the results of the linear model with the seven habitat types as ordered factor (pasture, cacao, secondary forest on former pasture 1–20 years old (PRegI), secondary forest on former cacao 1–20 years old (CRegI), secondary forest on former pasture 21–38 years old (PRegII), secondary forest on former cacao 21–38 years old (CRegII) and old-growth forest (Oldgr)). Sample coverage decreased significantly with ongoing succession.

recovery gradient. In our study, the raw taxon counts were affected by the sample success within the different habitat types, and hence produced overestimated effects. Note that in our study the direction of the observed trends did not change after sample coverage standardization. Negative trends remained negative. Still, the effect strength decreased (Figure 5) and significant effects disappeared after standardization. Such an overestimation of sample-coverage-biased effects can lead to misinterpretations of diversity trends. These results underscore the importance of controlling for sample coverage across ecological gradients (Chao & Jost, 2012; Chazdon et al., 2023; Gotelli & Colwell, 2001).

4.2 | Taxonomic diversity

After controlling for sample coverage, taxonomic diversity did not show a significant response along the second-growth gradient. Although the bird community shifted along the gradient, taxonomic diversity only showed a weak response, even when infrequent, frequent and highly frequent species were analysed separately (Figure 5). Note that Hill numbers in our study are based on incidence data and do not represent numbers of individuals, but the number of audio files in which a bird species was detected, hence representing vocal activity levels.

Previous ecological studies showed that by analysing only overall taxonomic diversity, we can miss more specific changes in species communities (Roth et al., 2021; Staab et al., 2023). For example, a study from subtropical forests in China showed that species richness of forest spider communities decreased with increasing plant richness, while functional dissimilarity increased (Schuldt et al., 2014). Furthermore, the weak response of taxonomic alpha diversity along the gradient in our study does not indicate that the same bird communities are present in all habitats. There are clear community shifts along the recovery gradient, as shown by our ordinations (Figure 3). The results show that we have high taxonomic diversity values in agricultural areas, but communities in these habitats contain different species than in old-growth forests, which is consistent with a study of tree species from more than 50 Neotropical lowland forests (Rozendaal et al., 2019). A previous study in the same study area also showed that bird communities in active pastures and cacao plantations were very different from those in forest patches (Müller et al., 2023).

A key question is whether the low taxonomic diversity observed in our old-growth plots results from species loss due to forest fragmentation within the study area. However, our study area is part of the largest remaining patch of Chocó Forest in Ecuador, spanning over 300,000 ha. This expanse is sufficient to support viable populations of old-growth specialists. Furthermore, our records include typical forest specialists, particularly from the understory guild of insectivores, which are highly sensitive to changes in forest structure and composition. These species include the Bicolored Antbird (*Gymnopithys bicolor*), Ocellated Antbird (*Phaenostictus mcleannani*) and Banded Ground Cuckoo (*Neomorphus radiolosus*), as well as the Lita Woodpecker (*Piculus litae*).

4.3 | Contrasts in phylogenetic and functional diversity

In contrast to taxonomic and phylogenetic diversity, functional diversity showed a significant decline as forest recovery progressed, indicating that communities in all analysed habitat types comprised a similar number of phylogenetic lineages, but agricultural sites showed a significant increase in functionality compared to forest sites (Figure 5). Conversely, this implies that the decline in functionality in forest habitats occurs among close relatives and does not affect highly conserved traits (Cavender-Bares et al., 2009; Večeřa et al., 2023). Likewise, the additional species found in open patches are not confined to specific lineages but are evenly distributed across the phylogenetic tree (Falconí-Lopez et al., 2024). Because the open habitat patches in our study area result from logging and land use, the higher functional diversity observed in these patches represents an artificial increase compared to old-growth patches. This increase likely stems from the inclusion of additional open-land species from more southern areas of South America (Falconí-Lopez et al., 2024) alongside forest species (Figures S1.2 and S1.4).

Our results for gamma diversity were similar to the results for alpha diversity. Taxonomic, phylogenetic and functional gamma diversity decreased along the recovery gradient. But, while taxonomic diversity in early regeneration was similarly high as in agricultural sites, phylogenetic and functional diversity were significantly lower (Figure S1.1). Differences between habitat types were also more pronounced for frequent, and highly frequent species than for infrequent species. The observed responses stress the fact that it is essential to focus on species frequencies in ecological studies.

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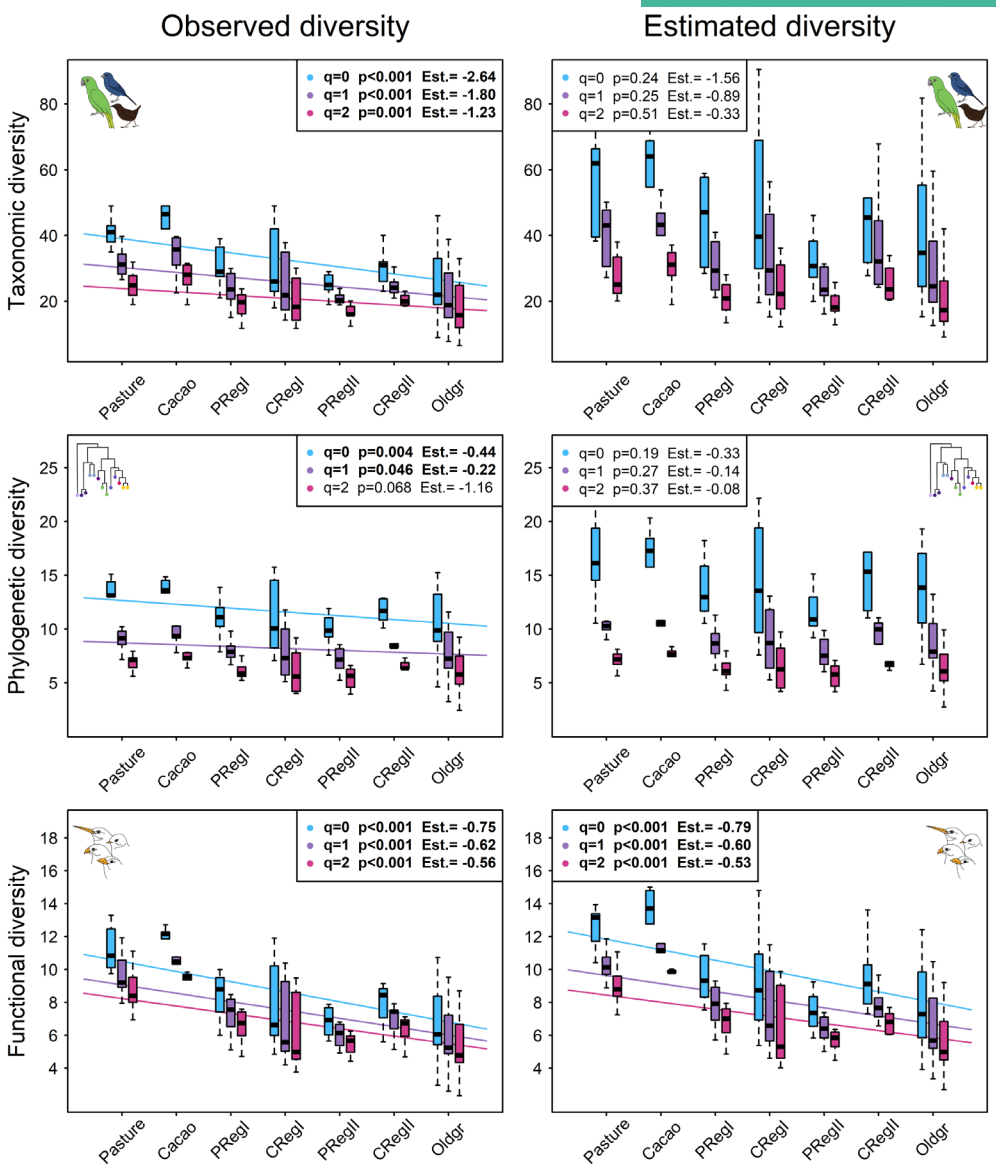


FIGURE 5 Boxplots of different diversity metrics per habitat type (pasture, cacao, secondary forest on former pasture 1–20 years old (PRegI), secondary forest on former cacao 1–20 years old (CRegI), secondary forest on former pasture 21–38 years old (PRegII), secondary forest on former cacao 21–38 years old (CRegII) and old-growth forest (Oldgr)). Lines indicate significant results ($p < 0.05$) of linear models with habitat types as ordered factors. Left side shows results for observed taxonomic, phylogenetic and functional diversity. Right side shows results for the estimated diversity metrics for a standardized sample coverage of 90% (based on the mean sample coverage of all study plots).

Although abundant species can define ecosystems and functions, rare species are mostly of greater conservation concern and can also play key roles in ecosystems (Hsieh & Chao, 2017 and references within).

Our results on phylogenetic diversity are in line with other studies that reported comparable levels of standardized functional diversity in forests, pastures and oil palm plantations (Chapman et al., 2018; Edwards et al., 2013; Prescott et al., 2016). In contrast, Edwards et al. (2017), who compared phylogenetic bird diversity between pasture, a second-growth gradient and primary forest in the Colombian Chocó-Andes, found an increase with ongoing succession.

Overall, the high values of taxonomic, phylogenetic and functional diversity in agricultural and former agricultural sites indicate that within a small-scale matrix such as our study region, these habitats could have relatively high ecosystem productivity and stability or resilience.

4.4 | Spillover in a small-scale habitat matrix and ecological value of second-growth

We found high bird diversity in early successional stages or in active agriculture. In contrast, a study from the northeastern Brazilian

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Amazon reported lower alpha diversity in second growth than in primary forest. The study analysed large disturbed patches of over 1000 ha (Barlow et al., 2007), whereas our study area is very heterogeneous with small agricultural areas embedded in a forest matrix. Similar to our results, a study of small-scale agroecosystems in Kenya (tropical Africa) also found high species richness in agricultural areas (Mulwa et al., 2012). In addition, the pastures in our study are extensively used and often contain individual shrubs or remnant trees from the original forest (see Figures S3.2 and S3.3). Within this matrix, mobile species, such as birds, can also occur in patches that are used secondarily for foraging, and old-growth patches can serve as stepping stones or refugia (Chazdon et al., 2009). In our study, an average of 90% of the species found in old-growth sites were also found in at least some of the agricultural sites. In contrast, on average only 43% of the species occurring in agricultural sites were also found in old-growth sites (Figure S1.2). In addition, only five species could be classified as old-growth specialists (Figure S1.4). Thus, there is a regular spillover from forests to agricultural sites. This has also been shown in studies from Costa Rica and Panama, where second-growth was in close proximity to old-growth and contained high numbers of bird species found in old-growth sites (Blake & Loiselle, 2001; Mayhew et al., 2019). A spillover from old-growth to second growths can also occur for endemic species such as the Berlepsch's tinamou (*Crypturellus berlepschi*, Rothschild, 1897) or the purple quail-dove (*Geotrygon purpurata*, Salvin, 1878) which were also found in recovery plots in our study. The combination of species associated with forests and additional species associated with more open woodland or grassland can lead to high taxonomic diversity values in small agricultural sites.

Nevertheless, we need to consider the possibility of a source-sink dynamic, where (former) agricultural sites are of low quality and act as biodiversity sinks, whereas old-growth sites act as biodiversity sources. In this scenario, agricultural and recovering forest patches would have negative long-term effects on bird communities on the landscape scale. However, testing this would require additional data, like reproductive success or long-term population trends on species level. Based on our results, secondary growth on abandoned agricultural sites shows high potential for conservation, particularly within a small-scale forest matrix.

Because we used acoustic recorders in a small-scale landscape, we cannot rule out the possibility that we may have detected rather noisy bird species from adjacent forest patches with recorders placed in pastures and cacao plantations. However, these noisy species are only present in small numbers and do not appear to have a significant impact on the overall communities (Appendix S1, Figure S1.6).

5 | CONCLUSIONS

We show that despite standardized audio sampling methods, sample coverage can still vary between habitats. Alpha diversity is particularly sensitive to differences in sampling coverage. As incomplete samples are the rule rather than the exception in highly diverse tropical habitats, studies of tropical forest recovery should control whether sample coverage is biased by the patterns or gradients being analysed. If this is the case, sample coverage should be standardized in subsequent analyses of diversity and communities. We also suggest considering patterns of less frequent species, as these are often of high conservation and restoration concern. Furthermore, alpha diversity can be a weak indicator when comparing different habitat types. In our study, alpha diversity showed no difference between agricultural areas and old-growth forests. In contrast, beta diversity was more robust to changes in sample coverage and also showed clear differences along the restoration gradient, although very few bird species could be classified as old-growth specialists. Beta diversity should therefore be included in the monitoring of restoration efforts. In our study, small-scale cacao plantations show high levels of bird diversity, which may be due to spillover from nearby native forests into agricultural areas, as well as the colonization by open habitat species. Secondary forests in a matrix of small-scale agricultural land use associated with old-growth forest appear to have a high potential for natural recovery of taxonomic, phylogenetic and functional diversity. Protection of secondary forests in such landscapes may therefore be particularly effective in promoting natural recovery of tropical forests.

AUTHOR CONTRIBUTIONS

Mareike Kortmann, Anne Chao and Jörg Müller conceived the ideas and elaborated the methods; Jörg Müller, Nico Blüthgen, Constance J. Tremlett and Heike Feldhaar were involved with project management; Rudy Gelis identified the bird species; Annika Busse, Marcel Püls, Sebastian Seibold, Peter Kriegel, Dominik Rabl, Felicity L. Newell, Jörg Müller, Maria de la Hoz and Çağan H. Şekercioğlu collected the data; Sonja Kümmet and Oliver Mitesser curated the data; Mareike Kortmann and Jörg Müller analysed the data; Mareike Kortmann, Anne Chao, H. Martin Schaefer, Matthias Schleuning and Jörg Müller interpreted the results; Mareike Kortmann wrote the first draft; Anne Chao, H. Martin Schaefer, Nico Blüthgen, Rudy Gelis, Constance J. Tremlett, Annika Busse, Çağan H. Şekercioğlu, Matthias Schleuning, Heike Feldhaar, Felicity L. Newell, Marcel K. Peters and Jörg Müller edited the manuscript, all authors were involved in the manuscript review and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available via Zenodo https://doi.org/10.5281/zenodo.14616054 (Kortmann, 2025).

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SUPPORTING INFORMATION

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

Appendix S1: Additional results.

Appendix S2: Bird traits.

Appendix S3: Additional description of the methods.

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