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Strong Variation in Land-Use Change Impacts on Tropical Avian Phylogenetic Diversity Between Ecoregions Highlights the Need to Sample Large Spatial Scales

Giovanny Pérez[1,2] | Simon C. Mills[1,3] | Jacob B. Socolar[4,5] | Jose M. Ochoa Quintero[6,7] | Robert P. Freckleton[1] | Torbjørn Haugaasen[5] | James J. Gilroy[3] | David P. Edwards[2,8]

[1]Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, UK | [2]Department of Plant Sciences and Centre for Global Wood Security, University of Cambridge, Cambridge, UK | [3]Rainforest Builder, London, UK | [4]BeZero Carbon, Ltd, London, UK | [5]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway | [6]Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, Colombia | [7]Universidade Federal de Mato Grosso do Sul, Campo Grande, Brazil | [8]Conservation Research Institute, University of Cambridge, Cambridge, UK

Correspondence: Giovanny Pérez (gapz01@gmail.com)

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ABSTRACT

Forest conversion for agriculture is a major cause of tropical biodiversity loss, but its impacts vary with spatial scale. Higher species turnover in forests than in farmland means that land-use change causes greater biodiversity loss at broader than at local scales, yet broad-scale assessments are scarce. Phylogenetic diversity is increasingly prioritised in conservation to protect evolutionary history under global change, yet how deforestation-driven changes in phylogenetic diversity scale spatially and accumulate in regions of high species turnover remains unclear. We compiled a large field database from across 13 biogeographically diverse regions affected by deforestation for cattle farming, covering most of Colombia, a megadiverse tropical country. Using occupancy models, we estimated bird communities for 1547 (936 observed plus 611 never-observed) species across ecoregions and nationally in both forest and pasture habitats to quantify changes in phylogenetic diversity metrics and determine whether these impacts are dependent on spatial scale. We found an average loss of 2300 Myr of phylogenetic diversity at the country scale, with most species negatively affected across the phylogeny. Although single regional-scale relative loss was on average comparable to broader scales, there was high variability between regional units. The latter was especially critical when evaluating metrics of evolutionary distinctiveness, which are key indicators for biodiversity conservation planning. Such underestimation of national-scale impacts highlights the importance of sampling across multiple regions. Immediate conservation action is needed to safeguard evolutionarily unique species and prevent phylogenetic homogenisation driven by agricultural expansion across spatial scales—a threat often underestimated due to assessments limited to single biogeographic regions.

1 | Introduction

Tropical forests are invaluable for conservation, covering approximately one-fifth of the Earth's terrestrial area and hosting more than half of global biodiversity (Cronan 2023), including 62% of vertebrate species (Pillay et al. 2022). However, tropical forests are threatened by land-use change, with more than 90% of tropical deforestation caused by farming between 2011 and 2015 (Pendrill et al. 2022) and over 219 million hectares converted between 1990 and 2019 (Vancutsem et al. 2021). Forest conversion to agriculture is therefore considered a major driver of global biodiversity loss and has been linked to elevated extinction risk,

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with species in deforested areas more likely to be classified as threatened by the IUCN (Betts et al. 2017). However, both field studies (Mills et al. 2023; Parra-Sanchez and Edwards 2024) and meta-analysis (Davison et al. 2021; Gibson et al. 2011; Newbold et al. 2015) that quantify the severity of species loss are limited by problems of spatial scale.

Land-use change erodes the diversity of niches available to species and drives conditions that are more uniform across otherwise ecologically unique areas. There is a set of large-ranged species that tend to thrive within converted habitats, wherever they are located; concurrently, small-ranged forest-dwelling species are lost across large scales (Socolar et al. 2016). Habitat conversion thus results in biotic homogenisation, with increasing compositional similarity across spatially disparate communities (Arce-Peña et al. 2022; Jones et al. 2021; Newbold et al. 2018). Such spatial decoupling can only be detected where studies work across spatial scales, and yet the majority of field-based studies are based in one (Birch et al. 2024; Cardoso et al. 2021; Edwards et al. 2021; Gilroy et al. 2014), or at best 2–3 (Barlow et al. 2016; Dinerstein et al. 2019; Karp et al. 2012) ecoregions. In turn, global meta-analyses average across studies to generate global effect sizes of the severity of biodiversity loss, but these overlook regional-scale impacts (Gibson et al. 2011). Although the latter provide valuable ecological and conservation information, without direct regional-scale measurements, it remains uncertain whether biodiversity change is less severe within single ecoregions than across multiple ones. Focusing on birds in Colombia, Socolar et al. (2025) sampled across 13 ecoregions to reveal that diversity losses are 60% worse at national scale compared to losses detected when focusing on a single biogeographic unit, and 28% more severe than two-ecoregion losses. This raises the important question of whether other dimensions of biodiversity loss are similarly underestimated due to the predominance of studies conducted at local scales.

Understanding how evolutionary history is impacted by land-use change across scales is key (Gumbs, Gray, et al. 2023). Phylogenetically diverse communities and evolutionarily unique species tend to play important functional roles, have high potential value for human use, and offer adaptability under global change (Molina-Venegas 2021; Palmer and Fischer 2022). Conservation prioritisation thus increasingly seeks to maximise evolutionary lineage diversity (i.e., phylogenetic diversity) and associated ecological functions, alongside species rarity (Gumbs et al. 2024; McClure et al. 2023; Owen et al. 2019; Pollock et al. 2020). There is growing evidence that land-use change for farming drives major losses of phylogenetic diversity. For example, in the tropical Andes, forest conversion to cattle pasture led to the loss of over 650 million years of avian evolutionary history, with phylogenetic diversity 30% lower than expected (expPD = −0.3) given species richness (Edwards et al. 2015), in Borneo, oil palm harboured 50% less avian Faith's phylogenetic diversity than forest (Chapman et al. 2018), while a global meta-analysis revealed that forest conversion to agriculture resulted in the loss of 139 million years of amphibian evolutionary history (Nowakowski et al. 2018). Similar to the challenges faced with species richness metrics, the issue of scale persists when local studies are combined via meta-analysis to make global inferences about the severity of phylogenetic losses from farming (Li et al. 2020). Although phylogenetic diversity increases with area less rapidly than taxonomic diversity, this scaling limits the interpretation of land-use impacts (Dias et al. 2020). In the tropics, hyperdiversity often reflects recent radiations near the tips of phylogenies, which frequently produce species with restricted ranges, particularly in topographically complex landscapes (Jetz et al. 2012). Given widespread forest conversion, the potential loss of these species may lead to cumulative, scale-dependent impacts on phylogenetic diversity that may not be captured by local patterns alone. A key question therefore is understanding the impacts of land-use change on phylogenetic diversity across spatial scales.

In this study, we evaluate the effects of forest conversion on phylogenetic diversity by focusing on Colombia, a highly biodiverse nation with sharp environmental gradients and high numbers of range-restricted species. We focus on birds, because they are one of the best studied taxa, with good data on their distributions (Birdlife International 2024; Vélez et al. 2021), functional traits (Tobias et al. 2022) and evolutionary relationships (Jetz et al. 2012). Birds are also good indicators of the response of biodiversity to land-use change in other taxa (Barlow et al. 2018; Edwards et al. 2014; Fraixedas et al. 2020). We utilise an unprecedented dataset derived from extensive field surveys spanning forest and cattle pastures from across 13 ecoregions. Species-specific responses to forest conversion for 1547 bird species (including 611 never-detected species) were modelled using a multispecies biogeographic occupancy modelling framework that accounts for imperfect detection while incorporating detailed range and trait information for all species (Socolar et al. 2022). This allows predicting within-range occupancy for each species at 2-km resolution across the 13 biogeographic regions and entire study region in both forest and pasture from which we are then able to estimate avian communities and derive phylogenetic and evolutionary metrics. We use this approach to address three core objectives: (1) quantify the effects of forest conversion on phylogenetic composition; (2) determine impacts on phylogenetic diversity and evolutionary distinctiveness at individual ecoregion and national scales; and (3) determine whether the impacts of forest-to-pasture transitions on phylogenetic diversity metrics are scale-dependent. Substantial regional variation in community responses is expected due to differences in baseline assemblages across ecoregions. For example, effects may be less pronounced in habitats that naturally exhibit characteristics typical of degraded systems, such as canopy gaps, open areas and natural disturbances (e.g., landslides), as is often the case in highland ecoregions. However, we hypothesise that, owing to the well-established correlation between species richness and phylogenetic diversity, losses of phylogenetic diversity are likely to be less pronounced within individual ecoregions (local scale) than across multiple ecoregions (regional scale).

2 | Methods

2.1 | Study Area and Sampling

Large-scale agriculture, especially cattle pasture, has driven widespread forest conversion in Colombia, causing half of all deforestation and continuing to expand (Guerrero-Pineda

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et al. 2022; Murillo-Sandoval et al. 2020). Decades of conflict have also enabled land grabbing and the clearing of over 1 million hectares, mainly for legal and illegal cattle farming, now rapidly encroaching on protected areas (Baptiste et al. 2017; Murillo-Sandoval et al. 2023). As a result, landscapes consist of a mix of primary and regenerating forests alongside widespread pastureland.

To capture biogeographic variation in how species assemblages respond to deforestation, we conducted sampling across thirteen ecoregions (Figure 1). These are units containing geographically distinct assemblages of species, natural communities and environmental conditions that share similar ecological processes, as defined by the World Wildlife Fund (WWF) Terrestrial Ecoregions of the World (Dinerstein et al. 2017). We define the national scale as the combination of all ecoregions, although it does not encompass the entire country. Full ecoregion names are listed below with short names in brackets; only short names are used hereafter: Eastern Cordillera real montane forests (CC montane), Magdalena-Urabá moist forests (Magdalena-Urabá moist), Apure-Villavicencio dry forests (Villavicencio dry), Napo moist forests (Napo moist), Cordillera Oriental montane forests (EC montane), Llanos (Llanos), Santa Marta montane forests (Santa Marta montane), Magdalena Valley montane forests (Magdalena montane), Northern Andean páramo (Andean páramo), Caquetá moist forests (Caquetá moist), Magdalena Valley dry forests (Magdalena dry), Cauca Valley montane forests (Cauca montane), Northwestern Andean montane forests (WC montane).

Site selection was made so that there would be forest and pastures within a few kilometres. In selected sites, clusters of three points (rarely two) were arranged within a minimum distance of 200 m, for a total of 848 points in 287 clusters. Special care was taken to ensure that forests and pastures had comparable geographic and elevational distributions and were sampled within the same biogeographic unit. Forest points were located at least 200 m inside continuous tracks of primary or late secondary protected forests to minimise edge effects. Pasture points were located within cleared pastures in cattle farms. Remnant habitat features such as scrubland vegetation, hedgerows and isolated trees were estimated visually within the 100 m radius in pasture points following Gilroy et al. (2014). Species detections by sight or hearing were registered within 100 m radius points via 10 min repeat-visits (excluding individuals detected flying over or at distances > 100 m) on four consecutive days, varying the daily time of visit between 06:00 and 12:00 and in appropriate weather conditions only. Continuous sound recording was performed for later identification of unknown vocalisations. A total of 3357 point-visits were conducted, representing 33,570 min of field observation with 24,981 individual detections.

2.2 | Estimating Avian Communities Across Ecoregions

A multispecies biogeographic occupancy modelling framework was used to estimate species-specific occupancy probabilities for 1547 bird species, including 936 observed during field sampling and 611 never observed; the latter were included to account for imperfect detection, which can mask the presence of rare, cryptic, or locally extirpated taxa from past forest loss, while recognising that such species may still contribute to community composition. We used the model described in Socolar et al. (2025); model description is provided in the Text S1. Essentially, these models account for imperfect detection while including detailed geographical and elevational range covariates for all species, which indicate whether a species is within its known geographic range or outside it

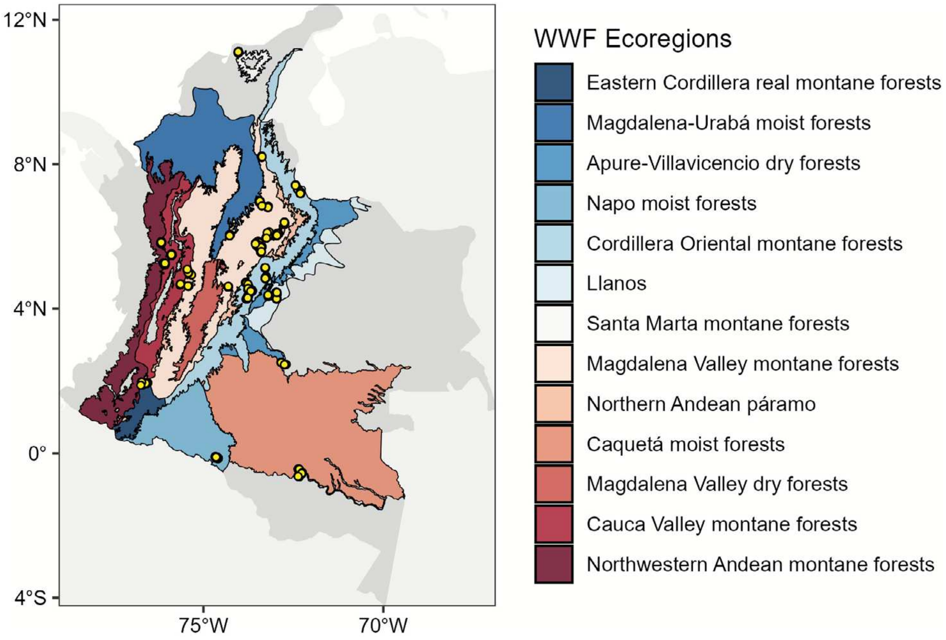

FIGURE 1 | Map of the study area. Yellow dots indicate sampling points. The background colour gradient (blue to red) represents the 13 sampled ecoregions. Areas of mainland Colombia that were not included in the study are in grey. Ecoregions are defined according to (Dinerstein et al. 2017). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

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at the sampling points (i.e., biogeographic clipping). This approach avoids spatial biases in predictions compared to the traditional multispecies occupancy framework while retaining its advantages, such as species-specific inference even for never-observed species (Socolar et al. 2022). The occupancy model was fitted within a Bayesian framework using the Stan engine (Stan Development Team 2023) implemented through the R package flocker (Socolar and Mills 2022).

The model was used to estimate the posterior occupancy probability of 1547 species within each cell of a $2 \times 2\,\text{km}^2$ grid across the study area. This grid incorporated predictor variables representing spatial features (elevation, distance to range, distance to mountains and valleys) and species traits (forest dependency, diet and family). Predictions were generated separately for forest and pasture habitats, assuming continuous habitat regardless of current land use. Next, community composition was estimated for each ecoregion using a threshold criterion: a species was considered present if its predicted occupancy probability was ≥ 0.3 in at least one grid cell and absent otherwise. At the national scale, a species was considered present if it was estimated present in the previous step in at least one ecoregion. We used the maximum occupancy in the grid within each ecoregion as the value to compare against the threshold, rather than a central tendency measure like the median, to avoid underestimating presence for range-restricted species (e.g., endemics). This approach ensured our community estimates were independent of ecoregion size. The entire process was repeated across 100 posterior draws of the occupancy model.

Estimated communities were used for two purposes: (1) to plot the phylogenetic relationships of species and (2) to compute phylogenetic diversity metrics across ecoregions. For (1), we used the averaged community across 100 posterior draws to map species presence/absence in each habitat and ecoregion onto a phylogenetic tree. Additionally, species were also classified as *winners* or *losers* from deforestation: *winners* had higher mean occupancy in pasture than in forest, while *losers* had lower mean occupancy in pasture. For (2), we used each of the 100 posterior predicted communities to calculate phylogenetic diversity metrics for forest and pasture habitats separately at the ecoregion and national scales.

2.3 | Phylogenetic Diversity Metrics

Bird phylogenies ($n = 1000$) were downloaded from vertlife.org, using the most recent Hackett backbone; however, using different backbones tends to produce consistent results and have small differences (Rubolini et al. 2015). To account for phylogenetic uncertainty, each metric (see below) was computed for each of the 100 posterior predicted communities, each evaluated across 100 trees randomly sampled from the downloaded pool.

Phylogenetic diversity metrics used were: Faith's Phylogenetic diversity (Faith 1992) which sums the branch lengths in the phylogenetic tree for all species in a community; Mean Pairwise Distance, the average branch distance between all species pairs in the tree; and Mean Nearest Taxon Distance, the average branch distance between immediate sister species pairs (Webb et al. 2002). Additionally, we calculated total Evolutionary distinctiveness (ED) and Evolutionary Distinct Globally Endangered (EDGE) metrics. Communities with higher values of these metrics hold species of conservation interest because they are both isolated in the evolutionary tree and under risk of extinction according to their red list categories (Gumbs et al. 2024; Isaac et al. 2007). We used the mean of ED computed for 10,000 trees with the fair proportions method (Kembel et al. 2010). EDGE values for each species were retrieved from (Gumbs et al. 2024). Handling of phylogenetic information and computation of metrics were performed with the packages *Phylomeasures* (Tsirogiannis and Sandel 2016) and *treedataverse* (Yu 2023) in the *R* software (R Core Team 2023).

2.4 | Computing the Impacts and Scale Dependence of Phylogenetic Diversity Loss

We estimated impacts by predicting for the entire study area as either forest or pasture, effectively simulating complete deforestation across the nation. Impacts were calculated as the pairwise subtraction of metrics in forest minus pasture within each ecoregion and Colombia. Next, the relative impacts were computed as the division of each ecoregion's impact by the impact at the national scale; therefore, relative impacts higher than 1 reveal an overestimation (impact in single ecoregion higher than national), and relative impacts lower than 1 show underestimation of metrics in comparison to national scale estimates. Additionally, we computed the Standardised Effect Size (SES) of the differences between metrics in forest and pasture habitats to assess whether the impacts represent a systematic loss or merely reflect inherent differences in species richness between habitats. This was achieved by randomising species presences in the predicted forest and pasture communities, then computing the metrics and their difference. Repeating the procedure 1000 times generated a null distribution, which was compared with the observed value for each posterior predicted draw.

Finally, to assess the cumulative impacts of forest-to-pasture conversion across scales, we computed phylogenetic diversity metrics for randomly aggregated communities. Metrics were first calculated for individual ecoregions, then for combinations of two, three and so on, up to all thirteen ecoregions. At each step, we calculated the relative impact as the national loss divided by the corresponding regional loss, providing a scale-dependent comparison of diversity loss. This procedure was repeated for 100 random ecoregion aggregations, each analysed across 100 posterior draws of predicted communities.

3 | Results

3.1 | Forest Conversion Impacts on Phylogenetic Composition

In Colombia, the total phylogenetic diversity represented by all species included in this study is 19,300 million years (Myr; Figure 2). Of this, estimated forest communities equate to around 18,200 Myr, whereas pastures account for 15,900 Myr—indicating that habitat conversion results in the loss of ~2300

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Myr (~12%) of evolutionary history. For context, each species contributes an average of 12.5 Myr (range: 2.7–81.6 Myr).

Species predicted to be present in each habitat are distributed broadly across the phylogeny, with no systematic loss of entire lineages observed in the phylogenetic reconstructions, although certain monophyletic groups are disproportionately affected by habitat conversion (Figure 2). A higher proportion of species are predicted to occupy only forest habitats, both at the national scale and across the 13 specific ecoregions (Figure 2; blue). This trend is particularly evident in EC montane (Figure S1D), CC montane (Figure S1E) and Napo moist (Figure S1J) ecoregions, suggesting that these may be more vulnerable to forest conversion due to their species' higher reliance on forest habitats. By contrast, species predicted to exclusively occupy pastures are less common overall and tend to come from the same lineages (e.g., Gruiformes, Charadriiformes, Fringillidae) (Figure 2; red). These species are more prevalent within ecoregions with lower species richness values, such as the Magdalena dry (Figure S1G), Magdalena-Urabá moist (Figure S1J) and Santa Marta montane (Figure S1M) ecoregions; therefore, these appear to have a lower impact from forest loss. Species predicted to persist in both habitats (Figure 2; yellow) are more evenly distributed across ecoregions and clades.

Based on the average community only, we predict 1377 species to be present in at least one habitat, including 1146 species classified as losers and 231 as winners from deforestation (Table S1). All ecoregions had a higher number of loser species (1.5–3 times more) compared to winner species, especially the EC montane (842 losers, 199 winners) and Magdalena montane (743 losers, 208 winners) ecoregions. Lower proportions of losers compared to winners occurred in Magdalena-Urabá moist (377 losers, 155 winners) and Santa Marta montane (272 losers, 139 winners) ecoregions. Losers from deforestation thus accounted for 66.2%–82.4% (mean = 77.0% ± 4.5%) of species across ecoregions. Overall, greater losses are observed in hyperdiverse lowland ecoregions (e.g., Napo moist) and along elevational gradients (e.g., EC montane, CC montane). The top five clades with the highest loser/winner ratio, indicating more losers, included: Thamnophilidae (13, number of ecoregions in which present), Ramphastidae (10), Cotingidae (7), Cuculidae (6), Grallaridae and Bucconidae (both 5). These represent the lineages most significantly impacted; however, we found no evidence for the complete loss of any entire lineage based on the metrics (see section below). Alternatively, clades with more winners from deforestation were: Ardeidae (13), Hirundinidae (13), Scolopaci (12), Threskiornithidae (12) and Corvidae (7), which are more likely to exhibit homogeneity of species across ecoregions after conversion.

3.2 | Impacts of Deforestation on Phylogenetic Diversity Metrics Across Ecoregions

There was considerable regional variation in the impacts of land-use change on phylogenetic diversity metrics. Faith's Phylogenetic diversity was lower in pasture than forest, with median loss at the national scale of 2313.25 with a 95% highest density interval (HDI) of 1518.16–3214.37 Myr, and losses in ecoregions varying substantially from 729.24–2516.07 Myr (Figure 3a). Differences in predicted mean pairwise distance between forest and pasture habitats were 1.02; HDI: −0.60 to 2.91 Myr nationally and between 0.26 and 2.29 Myr across ecoregions (Figure 3d). By contrast, mean nearest taxon distance was higher in pasture than forest across ecoregions, leading to negative differences of −1.40; HDI: −2.03 to −0.71 at the national scale and from −1.88 to −3.73 across ecoregions (Figure 3g).

The extent of phylogenetic diversity change relative to national estimates varied highly by ecoregion (median differences in metrics and 95% HDIs for all ecoregions are provided in Table S2). Nine ecoregions showed median relative impacts ranging from 0.32 to 0.97 times the national estimate (i.e., 68%–3% lower) across ecoregions, suggesting an underestimation of Faith's Phylogenetic Diversity loss in comparison to the national scale, which is particularly high in regions like Santa Marta montane and Magdalena-Urabá moist (Figure 3b). By contrast, four ecoregions had relative impacts greater than one, showing that impacts might be overestimated, particularly in the CC montane, EC montane and Napo moist ecoregions. Relative impacts on mean pairwise distance were minimal, although highly variable, with some ecoregions showing a tendency towards underestimation (e.g., CC Montane, Napo moist) and others to overestimation (e.g., Andean páramo, Figure 3e). Relative impacts on mean nearest taxon distance were on average 1.28–2.57 times higher than the national estimate (i.e., 28%–157% higher). However, due to the limited change in raw metrics, this indicates only a slight overestimation of impacts within individual ecoregions compared to the national scale (Figure 3h).

Values for the SES of differences in metrics between forest and pasture fell consistently within the ±1.96 range across ecoregions and the national scale, indicating that impacts align with random expectations rather than in a systematic way (Figure 3c,f,i). For further insight, we computed the SES of phylogenetic diversity metrics for each habitat separately (rather than their differences, Figure S2). This revealed that, while ecoregions vary in their phylogenetic assembly (e.g., phylogenetic clustering or random assembly), the conversion of forest to pasture does not alter such assembly patterns.

Forest loss reduces both ED and EDGE (Figure 4). At the national level, ED loss was estimated at 3353.50; HDI: 2319.66–4368.98 Myr, with median regional losses ranging from 671.33 to 3219.54 Myr (Figure 4a), highlighting marked variation across ecoregions. The magnitude of ED loss differs substantially among regions: while the EC montane, CC montane and Napo moist ecoregions show losses comparable to national levels, others—such as the Andean páramo, Magdalena-Urabá moist and Santa Marta montane ecoregions—exhibit losses less than half the national estimate. Specifically, relative ED losses across ecoregions ranged from 0.20 to 0.95 (i.e., 80%–5% lower) times the national value (Figure 4b). EDGE followed similar trends, with a national decline of 74; HDI 49–98 and median regional losses ranging from 18 to 55 (Figure 4c). Underestimation of EDGE was more pronounced, with median regional impacts ranging from 0.25 to 0.76 times the national estimate (i.e., 75%–24% lower), particularly in ecoregions showing low ED losses as well as additional regions such as the Llanos, WC montane and Magdalena dry (Figure 4d). Overall, results indicate that estimates from individual ecoregions differ markedly from national-level losses, with local

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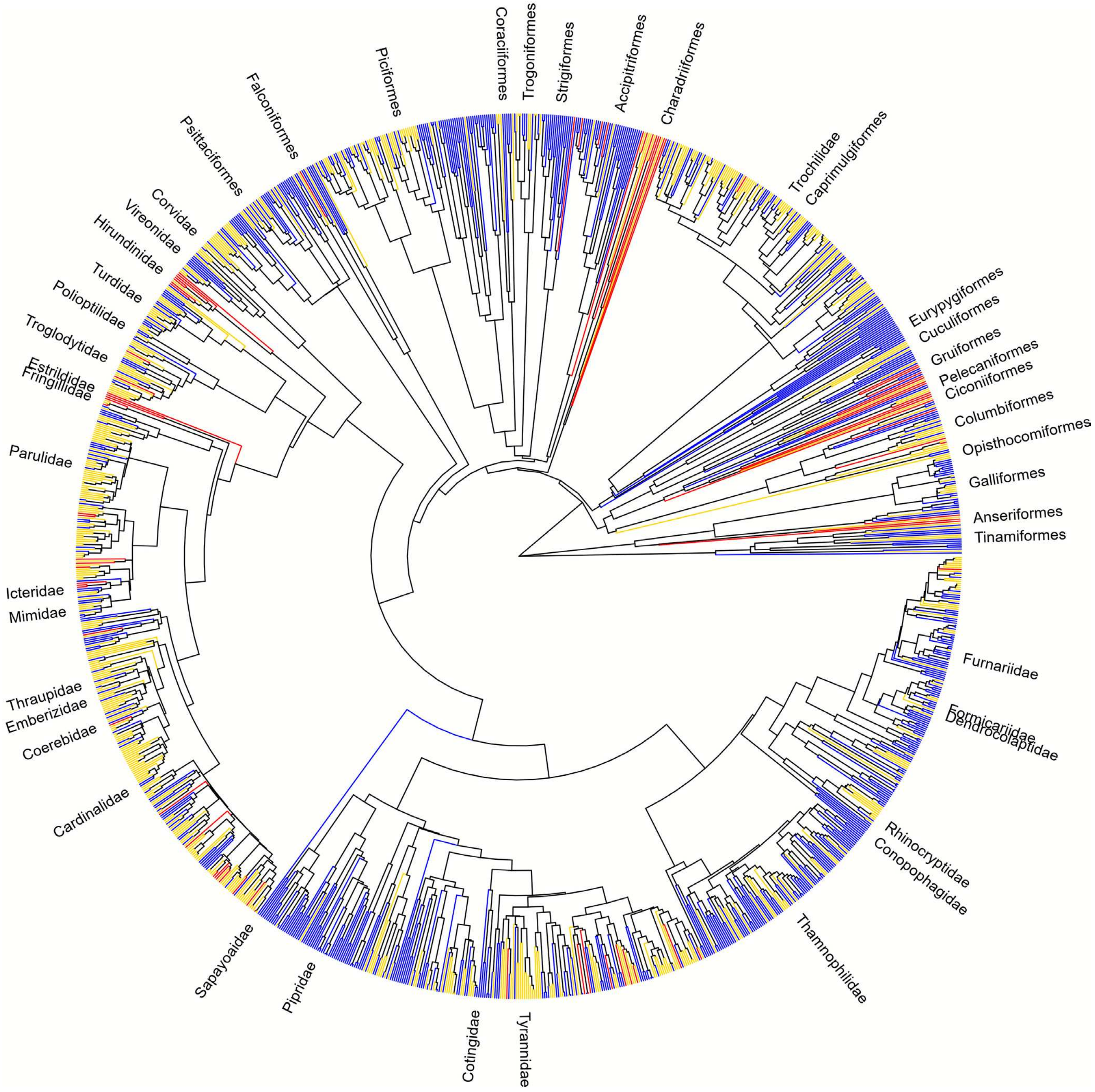

FIGURE 2 | Phylogenetic tree for predicted species at the national scale in Colombia. Terminal branches are coloured according to predicted presence of each species in forest (blue), pasture (red), both habitats (yellow) or absent (light grey); a species is present when its mean occupancy probability ≥ 0.3. Ecoregion phylogenies in Figure S1.

assessments underestimating the broader impact of forest loss on evolutionary uniqueness.

3.3 | Are Impacts of Deforestation on Phylogenetic Diversity Scale Dependent?

The impacts of forest conversion on phylogenetic diversity appear largely scale-independent. Increasing spatial scale by randomly pooling ecoregions did not substantially alter the magnitude of impacts, which remained close to 1 on median average relative to national estimates (Figure 5). This general stability was consistent across PD metrics, although some differences emerged. Considering single ecoregion assessments of Faith's PD, national impacts are underestimated by a median of 17%, with a broad range of values. Credible intervals span approximately from 0.53 to 2.55, indicating that single-ecoregion estimates can overestimate national impacts by up to 50% or underestimate them by up to 150%. This wide range reflects a high likelihood of misestimating broad-scale impacts when relying solely on single ecoregion data. Increasing the number of ecoregions greatly reduced the associated uncertainty (i.e., confidence intervals), leading to greater precision at broader spatial scales. Mean pairwise distance (MPD) showed minimal variation with

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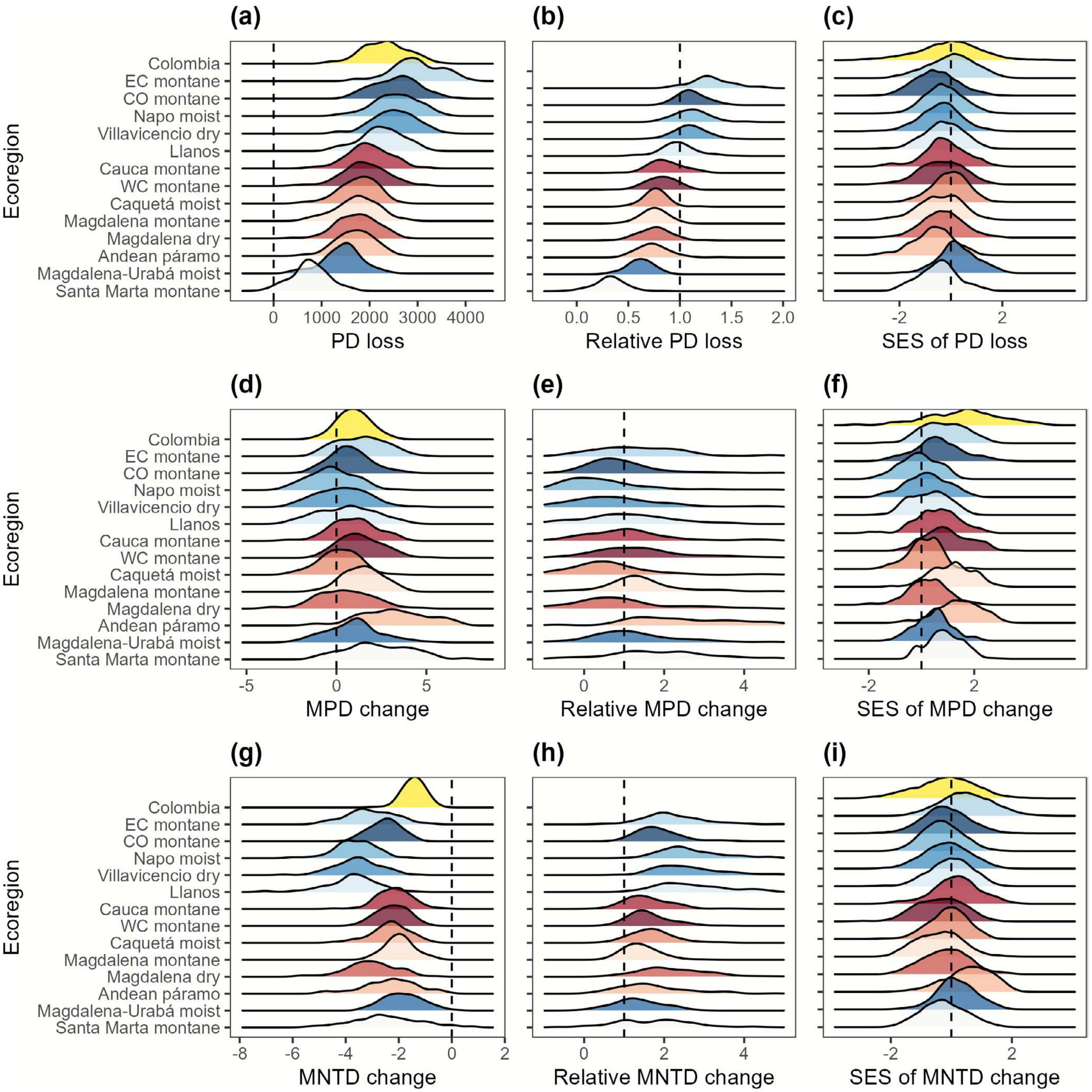

FIGURE 3 | Impacts of forest conversion to pasture on phylogenetic diversity metrics across ecoregions and at the national scale (y-axis). Ridgeline plots show the distribution of the difference in predicted metrics between forest and pasture across 100 posterior draws. A value of zero (dashed lines in a, d, g) indicates no difference between forest and pasture. Relative impacts compare regional loss to national loss for each ecoregion: Values < 1 show less severe regional impacts compared to the national scale, while values > 1 show greater impacts. A relative impact value of 1 (dashed lines in b, e, h) represents no difference between an ecoregion and the national estimate. Panels c, f and i show standardised effect sizes (SES) of the difference in predicted metrics. Metrics: PD (Faith's phylogenetic diversity), MPD (Mean Pairwise Distance) and MNTD (Mean Nearest Taxon Distance). Colours represent ecoregions from Figure 1.

increasing scale, suggesting more stable responses across spatial extents. In contrast, mean nearest taxon distance (MNTD) showed that national loss estimates were 46% lower than those from single-ecoregion assessments (median ratio = 0.54) but only 32% lower than estimates based on aggregations of five ecoregions (median ratio = 0.68). This indicates that including more ecoregions improves accuracy, and assessments need to aggregate multiple ecoregions to approach the national-scale impact (Figure 5c). Forest conversion disproportionately increases MNTD within ecoregions, confirming that phylogenetic diversity loss is primarily driven by the loss of closely related species within taxa (i.e., sister taxa).

For metrics of evolutionary uniqueness (ED and EDGE), the effect of spatial scale was evident only when sampling a single ecoregion. In these cases, national-level impacts were consistently 58%

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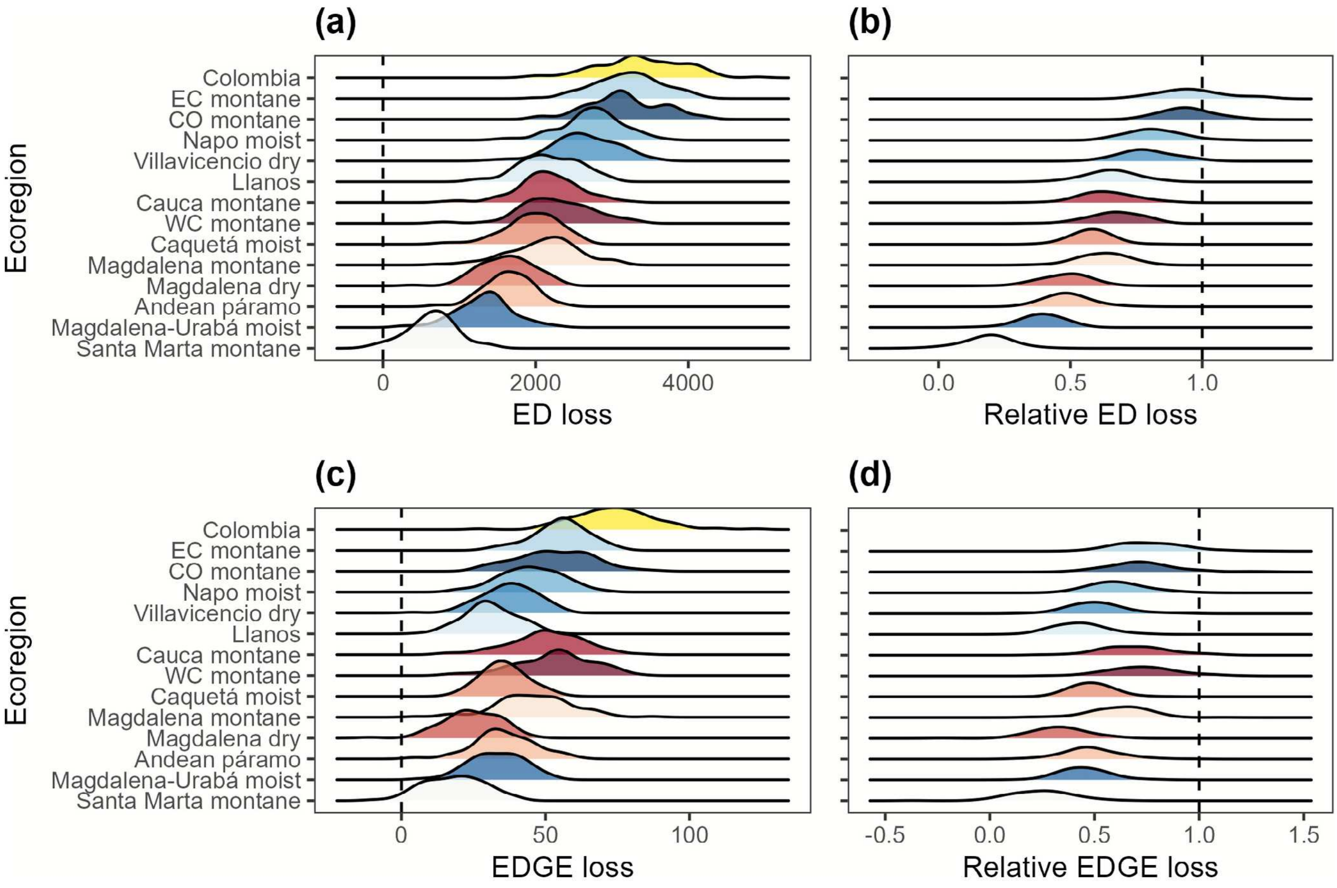

FIGURE 4 | Impacts of forest conversion to pasture on Evolutionary Distinctness (ED) and Evolutionary distinct and globally endangered (EDGE) metrics across ecoregions and at the national scale (y-axis). Ridgeline plots show the distribution of the difference in predicted metrics for forest minus pasture across 100 posterior draws. A value of zero (dashed lines in a and c) implies no difference between forest and pasture. Relative impacts compare the regional loss to the national loss for each ecoregion. Values <1 indicate that the difference in diversity between forest and pasture in a region is less severe than national while values >1 indicate higher impacts. A relative impact value of 1 (dashed lines in b and d) indicates no difference between an ecoregion and the country level estimate. Colours represent ecoregions from Figure 1.

greater for ED (median ratio = 1.58) and 82% greater for EDGE (median ratio = 1.82) than those estimated at the ecoregion scale, indicating that regional assessments underestimate national losses (Figure 5g,h). However, this pattern of scale dependence largely disappeared when aggregating two or more ecoregions, with estimates based on two ecoregions converging towards national values and national impacts being a median of 7% greater for ED (median ratio = 1.07) and 30% greater for EDGE (median ratio = 1.3) than regional estimates, along with narrower confidence intervals, indicating reduced uncertainty. Despite variation and wide confidence intervals, underestimation dominated at the single-ecoregion scale. Sampling at least two ecoregions is therefore essential to accurately assess national-scale loss of evolutionary uniqueness from forest conversion.

4 | Discussion

4.1 | Forest Conversion Threatens Evolutionary History

We present estimates of phylogenetic diversity across Colombia—one of the world's most biodiverse countries—spanning multiple ecoregions characterised by sharp environmental gradients. Our findings reveal notable phylogenetic diversity loss due to forest conversion from agricultural expansion, underscoring the urgent need to address the critical threat to these unique habitats. We found that estimating the loss of phylogenetic diversity due to land-use change is mostly scale-independent, and thus that assessments conducted within single ecoregions can often serve as proxies for broad-scale impacts, although some ecoregions tend to slightly underestimate or overestimate losses relative to national-scale impacts. Therefore, sampling at least two ecoregions, preferably heterogeneous ones such as non-adjacent regions or at different elevations, is likely to yield more reliable estimates.

A significant proportion of taxa are expected to be lost following forest conversion to agriculture, both at the national level and within single ecoregions. Despite this, evolutionary lineages (clades) are still represented within altered communities, albeit composed of fewer species. Habitat association, whether forest or non-forest, is a crucial factor influencing bird responses to agriculture (Newbold et al. 2013) and often aligns with ecological traits such as insectivory or poor long-distance dispersal capacity (Sherry 2021). Species that benefit from pasture habitats are usually non-forest species and play a key role in preserving evolutionary diversity across fragmented landscapes

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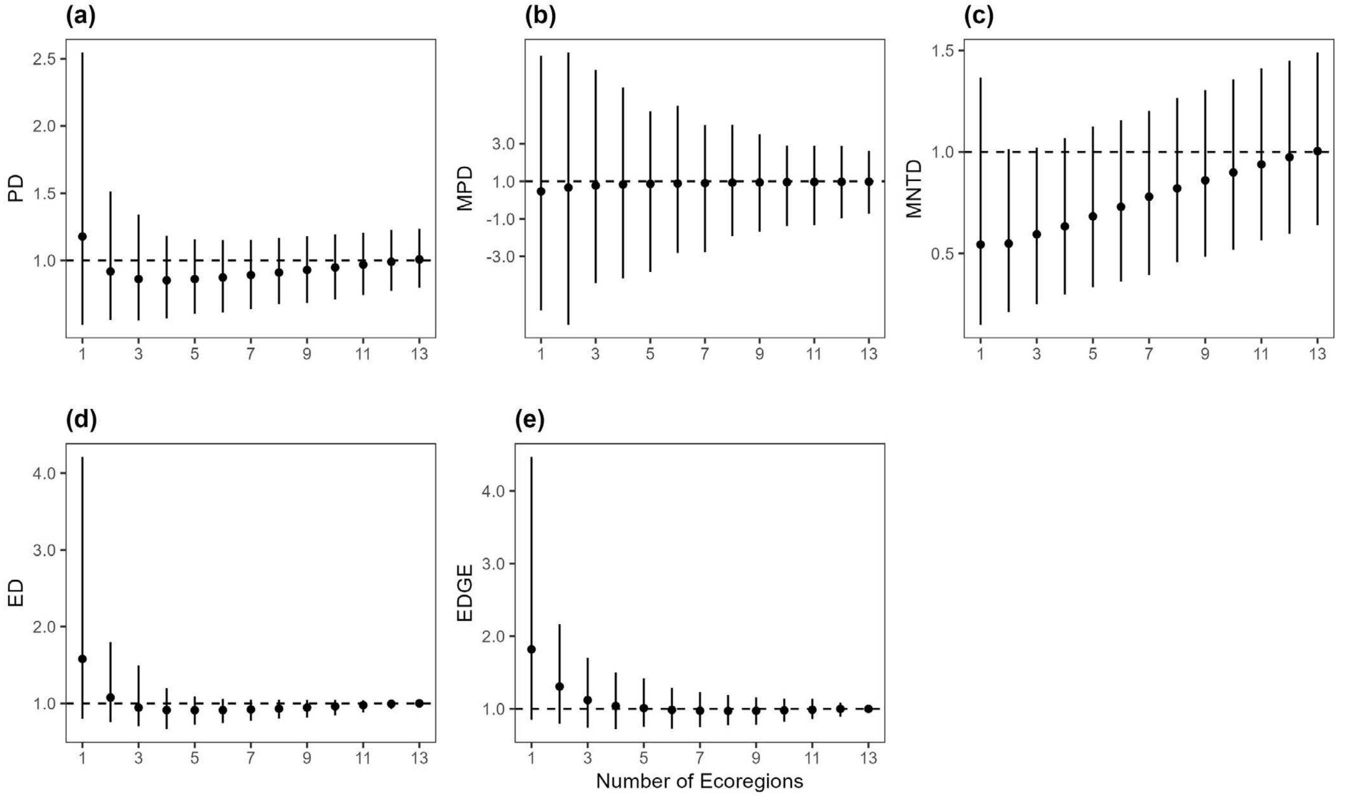

FIGURE 5 | Relative impacts of forest conversion on phylogenetic diversity metrics across increasing spatial scales (x-axis). Values represent the national loss divided by the loss from aggregated ecoregions (1–13). A ratio of 1.0 (dashed line) indicates no difference. Values above 1.0 mean national loss exceeds regional loss (e.g., 1.5 = 50% greater), while values below 1.0 indicate overestimation by regional assessments. Point range lines show median ratios with 95% Highest Density Credible Intervals. Metrics: (a) Faith's Phylogenetic Diversity (PD), (b) Mean Pairwise Distance (MPD), (c) Mean Nearest Taxon Distance (MNTD), (d) Evolutionary Distinctiveness (ED), (e) Evolutionarily Distinct and Globally Endangered (EDGE).

(Morante-Filho et al. 2018). Similarly, we observe an extirpation of species and the prevalence of others based on their forest dependency. This phenomenon may lead to increased phylogenetic homogenisation across ecoregions, along with the depletion of other correlated ecological traits. Our findings partially align with the global analysis of amphibians by Nowakowski et al. (2018) that found species' responses to habitat conversion are strongly shaped by their phylogenetic relationships. In their study, closely related species exhibited similar responses to environmental changes, resulting in the dominance of certain lineages while others were excluded from local assemblages. This process ultimately contributed to a significant loss of global phylogenetic diversity.

Forest conversion is particularly severe for evolutionarily unique taxa (Figure 4), a major issue since Colombia is the country with the second highest avian evolutionary history globally (McClure et al. 2023). Reductions in Phylogenetic Diversity are driven by a marked decline of terminal branches within clades (increased Mean Nearest Taxon Distance), without the loss of deep evolutionary relationships (Mean Pairwise Distance mostly unchanged). These reductions lead to a loss of 10%–30% in Faith's Phylogenetic diversity. Ecoregions experiencing greater losses are typically located along elevational gradients (e.g., EC Montane, CC Montane) or in hyperdiverse lowland (e.g., Napo moist) areas where disturbance tolerance is generally low (Weeks et al. 2023). In contrast, less impacted ecoregions are located in more environmentally homogeneous (e.g., Magdalena-Urabá moist, Magdalena dry) or isolated (e.g., Santa Marta montane, Andean páramo) areas, often supporting more open-habitat or disturbance-tolerant species (Ausprey et al. 2023; Mills et al. 2023). Despite these differences, it is crucial not to overlook the importance of forests in areas with lower relative impacts. Forest loss also led to reduced phylogenetic diversity and evolutionary uniqueness in such ecoregions. For instance, the median loss in the least-sensitive Santa Marta montane ecoregion was 729.24 Myr, an area that hosts over 30% of Colombia's endemic avifauna (Chaparro-Herrera et al. 2024).

Our results align with previous studies showing that shifts in species composition and richness along gradients of forest cover occur either randomly or uniformly across the phylogenetic tree without targeting entire clades (Arroyo-Rodríguez et al. 2012; Morante-Filho et al. 2018). This indicates weak phylogenetic conservatism in traits that determine species' vulnerability to forest loss (Arroyo-Rodríguez et al. 2012). Although certain clades either benefit from or are more negatively impacted by forest conversion, we found no evidence of systematic loss of entire lineages both visually and according to metrics (Figure 2, Figure S2). Deep evolutionary history persists because, although many species are lost, sister species often remain within clades. In addition, metrics balance overall gains and losses, partially offsetting the observed loss of evolutionary history. As a result, the impacts of forest conversion on phylogenetic diversity at regional scales are primarily driven by differences in species

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richness between habitats, rather than by a targeted loss of specific clades.

4.2 | Scale Dependence of Phylogenetic Diversity

The analysis of relative impacts at increasing scales shows no average differences between habitats, primarily due to the significant variability among ecoregions. Sampling only one ecoregion tends to result in a slight underestimation of Faith's Phylogenetic Diversity, ED and EDGE values. However, adding a second and third ecoregion leads to relative impacts close to one, although with slightly overestimated medians, suggesting scale-independence in estimating impacts on phylogenetic diversity. This contrasts with findings in Socolar et al. (2025), who found that six or more different ecoregions are needed to avoid underestimating national impacts of forest conversion on taxonomic diversity (species richness) derived from local-scale data. This apparent divergence arises because phylogenetic similarity between communities declines with geographic distance more slowly than does taxonomic species composition (Morlon et al. 2011). Biodiversity-area relationships reveal that taxonomic diversity increases more rapidly with area than functional diversity, which in turn, accumulates faster than phylogenetic diversity (Dias et al. 2020). Namely, ecoregions share more phylogenetic diversity—in terms of evolutionary time in the backbone branches of lineages—than species diversity, making fewer areas more effective at preserving it and requiring fewer ecoregions to estimate phylogenetic diversity loss at a national level.

4.3 | Study Caveats

Using a threshold to determine species presence/absence introduces a notable limitation, as it might overlook differences in species occupancy between forest and pasture. For example, a species with an occupancy probability of 0.9 in forest and 0.4 in pasture would be considered present with our threshold of 0.3, despite the 0.5 considerable difference in occupancy probability. Consequently, they would contribute equally to metric computations (branch lengths), potentially masking the true differences between habitats. This limitation is partially mitigated by incorporating uncertainty in occupancy probabilities throughout the analysis, using 100 posterior draws from the model to calculate the metrics. Ideally, collapsing occupancy data into presence–absence can be avoided by using a phylogeny-weighted conservation metric based on species abundances. For example, unique species may decline more than common ones without going extinct, a pattern often overlooked and a promising avenue for future research.

Although we focus on birds, the widespread impacts observed here are likely to be even more drastic for other taxa, particularly understudied groups (Eisenhauer et al. 2019; Pollock et al. 2020). For instance, the average loss of evolutionary history per amphibian species is more than double that of birds (Gumbs et al. 2024). Finally, the effect of time was not accounted for, which may have concealed the magnitude of observed differences due to temporal inertia and extinction debt. Our sampling design used a space-for-time substitution, preventing us from directly inferring temporal changes caused by impacts. Future research should further explore these dynamics by incorporating estimates of beta diversity, functional diversity, and the effects of time, as well as focusing on different taxa and groups within them; for instance, we observed that pastures often retain wetland species from long-branched lineages, whose disproportionate contribution of evolutionary time can inflate phylogenetic diversity values and bias estimates of loss, suggesting that wetland species be evaluated separately to improve accuracy (Results S1). The actual situation may be more severe than predicted, due to additional factors not fully captured in this study such as the effect of past ecological filtering (Hua et al. 2024). Our results likely represent the minimum expected impacts of forest conversion on phylogenetic diversity, given the study's assumptions and limitations.

5 | Conclusions and Management Implications

We aimed to quantify the impacts of forest conversion on avian phylogenetic diversity in Colombia from local to a national scale. Our findings indicate that the impacts are primarily driven by the loss of terminal branches in the phylogenetic tree, particularly evolutionarily unique taxa (e.g., Antbirds, Cotingas, Antpittas). Contrary to expectations, the scaling analysis revealed that aggregating two or more ecoregions did not significantly alter the estimated impacts compared to the national level, challenging our hypothesis that aggregating several ecoregions would be necessary to comprehensively quantify the severity of phylogenetic diversity loss from land-use change. This suggests that estimates of phylogenetic diversity loss at the single ecoregion level may reliably reflect impacts at larger spatial scales.

Conserving optional value (i.e., value of biodiversity for yet-unknown future uses) and nature's contributions to people is central to the grand objective of addressing the environmental crises and ensuring a stable and healthy future (Gumbs, Gray, et al. 2023). As outlined in the Kunming-Montreal Global Biodiversity Framework and Paris Agreement, maximising phylogenetic diversity is an effective strategy for preserving future option and retaining current benefits for human well-being, including physical, mental, cultural and spiritual benefits that may be overlooked when focusing solely on avoiding species extinction (Gumbs, Gray, et al. 2023; Hayward et al. 2022). Both Faith's phylogenetic diversity and EDGE are key indicators towards these goals (Secretariat of the Convention on Biological Diversity 2022). Tracking these indicators at national levels is essential to capture the broad value of biodiversity, particularly since conservation efforts often overlook evolutionarily unique species (Owen et al. 2019). Many of these cannot be assessed for evolutionary history metrics, or remain unknown to science, and may be substantially more sensitive than the bird species used here. The loss and homogenisation of diversity across ecoregions leads to a similar subset of species to occur in pastures (Socolar et al. 2016), which can have broad negative effects such as reduced ecosystem stability (Gumbs, Chaudhary, et al. 2023). While losses of phylogenetic diversity did not increase with spatial scale, the losses incurred within each ecoregion are substantial. These losses point towards an erosion of overall biodiversity and the evolutionary values critical for ecosystem resilience and future adaptation.

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The livestock sector contributes nearly 50% of global agricultural GDP but is also a significant source of deforestation and greenhouse gas emissions. A potential solution is to mitigate biodiversity loss through sustainable intensification practices, improved manure management and reduced livestock demand (Herrero et al. 2016). Addressing these inefficiencies is crucial in Colombia, where 42% of grazing land has low suitability for cattle production and 60% of rangelands have low stocking rates (Zuluaga et al. 2021). As part of its commitment to international climate and biodiversity agreements, Colombia must prioritise freeing up pasture for alternative uses and intensifying livestock production in more suitable areas by scaling up sustainable intensification initiatives, such as silvopastoral systems in livestock, that have already shown promising results at local scales (Tapasco et al. 2019). Approaches such as land-sparing, which conserve greater phylogenetic and functional diversity within individual ecoregions (Pérez et al. 2024), are crucial. Although primary forest loss in Colombia decreased by 49% in 2023, deforestation across the tropics remained alarmingly high, with 3.7 million hectares lost in recent years (Global Forest Review 2024). Our findings underscore that only through immediate and bold conservation strategies for the remaining tropical forests can we hope to reverse these trends and safeguard the unparalleled tropical biodiversity for future generations.

Author Contributions

Giovanny Pérez: conceptualization, formal analysis, visualization, writing – original draft, writing – review and editing. **Simon C. Mills:** conceptualization, data curation, formal analysis, methodology. **Jacob B. Socolar:** data curation, formal analysis, methodology. **Jose M. Ochoa Quintero:** data curation. **Robert P. Freckleton:** conceptualization, funding acquisition. **Torbjørn Haugaasen:** conceptualization, funding acquisition. **James J. Gilroy:** conceptualization, supervision, writing – review and editing. **David P. Edwards:** conceptualization, funding acquisition, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.6hdr7srcx.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** gcb70702-sup-0001-AppendixS1.docx.

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