

1        **Strong variation in land-use change impacts on tropical avian**  
2        **phylogenetic diversity between ecoregions highlights the need to**  
3        **sample large spatial scales**

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42 **Abstract**

43 Forest conversion for agriculture is a major cause of tropical biodiversity loss, but its impacts  
44 vary with spatial scale. Higher species turnover in forests than in farmland means that land-use  
45 change causes greater biodiversity loss at broader than at local scales, yet broad-scale  
46 assessments are scarce. Phylogenetic diversity is increasingly prioritised in conservation to  
47 protect evolutionary history under global change, yet how deforestation-driven changes in  
48 phylogenetic diversity scale spatially and accumulate in regions of high species turnover  
49 remains unclear. We compiled a large field database from across 13 biogeographically diverse  
50 regions affected by deforestation for cattle farming, covering most of Colombia, a megadiverse  
51 tropical country. Using occupancy models, we estimated bird communities for 1,547 (936  
52 observed plus 611 never-observed) species across ecoregions and nationally in both forest and  
53 pasture habitats to quantify changes in phylogenetic diversity metrics and determine whether  
54 these impacts are dependent on spatial scale. We found an average loss of 2,300 Myr of  
55 phylogenetic diversity at the country scale, with most species negatively affected across the  
56 phylogeny. Although single regional-scale relative loss was on average comparable to broader  
57 scales, there was high variability between regional units. The latter was especially critical when  
58 evaluating metrics of evolutionary distinctiveness, which are key indicators for biodiversity  
59 conservation planning. Such underestimation of national-scale impacts highlights the  
60 importance of sampling across multiple regions. Immediate conservation action is needed to  
61 safeguard evolutionarily unique species and prevent phylogenetic homogenisation driven by  
62 agricultural expansion across spatial scales—a threat often underestimated due to assessments  
63 limited to single biogeographic regions.

64 **Keywords:** Land-use change, Habitat loss, Cattle farming, Occupancy models, Evolutionary  
65 distinctiveness, Colombia.

## 66 **Introduction**

67 Tropical forests are invaluable for conservation, covering approximately one-fifth of the Earth's  
68 terrestrial area and hosting more than half of global biodiversity (Cronan, 2023), including 62%  
69 of vertebrate species (Pillay et al., 2022). However, tropical forests are threatened by land-use  
70 change, with more than 90% of tropical deforestation caused by farming between 2011 and  
71 2015 (Pendrill et al., 2022) and over 219 million hectares converted between 1990-2019  
72 (Vancutsem et al., 2021). Forest conversion to agriculture is therefore considered a major driver  
73 of global biodiversity loss and has been linked to elevated extinction risk, with species in  
74 deforested areas more likely to be classified as threatened by the IUCN (Betts et al., 2017).  
75 However, both field studies (Mills et al., 2023; Parra-Sanchez & Edwards, 2024) and meta-  
76 analysis (Davison et al., 2021; Gibson et al., 2011; Newbold et al., 2015) that quantify the  
77 severity of species loss are limited by problems of spatial scale.

78 Land-use change erodes the diversity of niches available to species and drives conditions that  
79 are more uniform across otherwise ecologically unique areas. There is a set of large-ranged  
80 species that tend to thrive within converted habitats, wherever they are located; concurrently  
81 small-ranged forest-dwelling species are lost across large scales (Socolar et al., 2016). Habitat  
82 conversion thus results in biotic homogenisation, with increasing compositional similarity  
83 across spatially disparate communities (Arce-Peña et al., 2022; Jones et al., 2021; Newbold et  
84 al., 2018). Such spatial decoupling can only be detected where studies work across spatial  
85 scales, and yet the majority of field-based studies are based in one (Birch et al., 2024; Cardoso  
86 et al., 2021; Edwards et al., 2021; Gilroy et al., 2014), or at best 2-3 (Barlow et al., 2016;  
87 Dinerstein et al., 2019; Karp et al., 2012) ecoregions. In turn, global meta-analyses average  
88 across studies to generate global effect sizes of the severity of biodiversity loss, but these  
89 overlook regional-scale impacts (Gibson et al., 2011). Although the latter provide valuable  
90 ecological and conservation information, without direct regional-scale measurements, it

91 remains uncertain whether biodiversity change is less severe within single ecoregions than  
92 across multiple ones. Focusing on birds in Colombia, Socolar et al. (2025) sampled across 13  
93 ecoregions to reveal that diversity losses are 60% worse at national scale compared to losses  
94 detected when focusing on a single biogeographic unit, and 28% more severe than two-  
95 ecoregion losses. This raises the important question of whether other dimensions of  
96 biodiversity loss are similarly underestimated due to the predominance of studies conducted at  
97 local scales.

98 Understanding how evolutionary history is impacted by land-use change across scales is key  
99 (Gumbs, Gray, et al., 2023). Phylogenetically diverse communities and evolutionarily unique  
100 species tend to play important functional roles, have high potential value for human use, and  
101 offer adaptability under global change (Molina-Venegas, 2021; Palmer & Fischer, 2022).  
102 Conservation prioritisation thus increasingly seeks to maximise evolutionary lineage diversity  
103 (i.e., phylogenetic diversity) and associated ecological functions, alongside species rarity  
104 (Gumbs et al., 2024; McClure et al., 2023; Owen et al., 2019; Pollock et al., 2020). There is  
105 growing evidence that land-use change for farming drives major losses of phylogenetic  
106 diversity. For example, in the tropical Andes, forest conversion to cattle pasture led to the loss  
107 of over 650 million years of avian evolutionary history, with phylogenetic diversity 30% lower  
108 than expected ( $\text{expPD} = -0.3$ ) given species richness (Edwards et al., 2015), in Borneo, oil  
109 palm harboured 50% less avian Faith's phylogenetic diversity than forest (Chapman et al.,  
110 2018), while a global meta-analysis revealed that, forest conversion to agriculture, resulted in  
111 the loss of 139 million years of amphibian evolutionary history (Nowakowski et al., 2018).  
112 Similar to the challenges faced with species richness metrics, the issue of scale persists when  
113 local studies are combined via meta-analysis to make global inferences about the severity of  
114 phylogenetic losses from farming (Li et al., 2020). Although phylogenetic diversity increases  
115 with area less rapidly than taxonomic diversity, this scaling limits the interpretation of land-

116 use impacts (Dias et al. 2020). In the tropics, hyperdiversity often reflects recent radiations near  
117 the tips of phylogenies, which frequently produce species with restricted ranges, particularly  
118 in topographically complex landscapes (Jetz et al. 2012). Given widespread forest conversion,  
119 the potential loss of these species may lead to cumulative, scale-dependent impacts on  
120 phylogenetic diversity that may not be captured by local patterns alone. A key question  
121 therefore is understanding the impacts of land-use change on phylogenetic diversity across  
122 spatial scales.

123 In this study, we evaluate the effects of forest conversion on phylogenetic diversity by focusing  
124 on Colombia, a highly biodiverse nation with sharp environmental gradients and high numbers  
125 of range-restricted species. We focus on birds, because they are one of the best studied taxa,  
126 with good data on their distributions (Birdlife International, 2024; Vélez et al., 2021),  
127 functional traits (Tobias et al., 2022), and evolutionary relationships (Jetz et al., 2012). Birds  
128 are also good indicators of the response of biodiversity to land-use change in other taxa (Barlow  
129 et al., 2018; Edwards et al., 2014; Fraixedas et al., 2020). We utilise an unprecedented dataset  
130 derived from extensive field surveys spanning forest and cattle pastures from across 13  
131 ecoregions. Species-specific responses to forest conversion for 1,547 bird species (including  
132 611 never-detected species) were modeled using a multispecies biogeographic occupancy  
133 modeling framework that accounts for imperfect detection while incorporating detailed range  
134 and trait information for all species (Socolar et al., 2022). This allows predicting within-range  
135 occupancy for each species at 2-km resolution across the 13 biogeographic regions and entire  
136 study region in both forest and pasture from which we are then able to estimate avian  
137 communities and derive phylogenetic and evolutionary metrics. We use this approach to  
138 address three core objectives: 1) quantify the effects of forest conversion on phylogenetic  
139 composition; 2) determine impacts on phylogenetic diversity and evolutionary distinctiveness  
140 at individual ecoregion and national scales; and 3) determine whether the impacts of forest-to-

141 pasture transitions on phylogenetic diversity metrics are scale-dependent. Substantial regional  
142 variation in community responses is expected due to differences in baseline assemblages across  
143 ecoregions. For example, effects may be less pronounced in habitats that naturally exhibit  
144 characteristics typical of degraded systems, such as canopy gaps, open areas, and natural  
145 disturbances (e.g. landslides), as is often the case in highland ecoregions. However, we  
146 hypothesise that, owing to the well-established correlation between species richness and  
147 phylogenetic diversity, losses of phylogenetic diversity are likely to be less pronounced within  
148 individual ecoregions (local scale) than across multiple ecoregions (regional scale).

149

## 150 **Methods**

### 151 *Study area and Sampling*

152 Large-scale agriculture, especially cattle pasture, has driven widespread forest conversion in  
153 Colombia, causing half of all deforestation and continuing to expand (Guerrero-Pineda et al.,  
154 2022; Murillo-Sandoval et al., 2020). Decades of conflict have also enabled land-grabbing and  
155 the clearing of over 1 million hectares, mainly for legal and illegal cattle farming, now rapidly  
156 encroaching on protected areas (Baptiste et al., 2017; Murillo-Sandoval et al., 2023). As a  
157 result, landscapes consist of a mix of primary and regenerating forests alongside widespread  
158 pastureland.

159 To capture biogeographic variation in how species assemblages respond to deforestation, we  
160 conducted sampling across thirteen ecoregions (Fig. 1). These are units containing  
161 geographically distinct assemblages of species, natural communities, and environmental  
162 conditions that share similar ecological processes, as defined by the World Wildlife Fund  
163 (WWF) Terrestrial Ecoregions of the World (Dinerstein et al., 2017). We define the national  
164 scale as the combination of all ecoregions, although it does not encompass the entire country.

165 Full ecoregion names are listed below with short names in brackets; only short names are used  
166 hereafter: Eastern Cordillera real montane forests (CC montane), Magdalena-Urabá moist  
167 forests (Magdalena-Urabá moist), Apure-Villavicencio dry forests (Villavicencio dry), Napo  
168 moist forests (Napo moist), Cordillera Oriental montane forests (EC montane), Llanos  
169 (Llanos), Santa Marta montane forests (Santa Marta montane), Magdalena Valley montane  
170 forests (Magdalena montane), Northern Andean páramo (Andean páramo), Caquetá moist  
171 forests (Caquetá moist), Magdalena Valley dry forests (Magdalena dry), Cauca Valley montane  
172 forests (Cauca montane), Northwestern Andean montane forests (WC montane).

173 Site selection was made so that there would be forest and pastures within a few kilometres. In  
174 selected sites, clusters of three points (rarely two) were arranged within a minimum distance  
175 of 200 m, for a total of 848 points in 287 clusters. Special care was taken to ensure that forests  
176 and pastures had comparable geographic and elevational distributions and were sampled within  
177 the same biogeographic unit. Forest points were located at least 200 m inside continuous tracks  
178 of primary or late secondary protected forests to minimise edge effects. Pasture points were  
179 located within cleared pastures in cattle farms. Remnant habitat features such as scrubland  
180 vegetation, hedgerows and isolated trees were estimated visually within the 100 m radius in  
181 pasture points following Gilroy et al. (2014). Species detections by sight or hearing were  
182 registered within 100 m radius points via 10 minute repeat-visits (excluding individuals  
183 detected flying over or at distances >100 meters) on four consecutive days, varying the daily  
184 time of visit between 06:00 and 12:00 and in appropriate weather conditions only. Continuous  
185 sound recording was performed for later identification of unknown vocalisations. A total of  
186 3,357 point-visits were conducted, representing 33,570 minutes of field observation with  
187 24,981 individual detections.

188

190 A multispecies biogeographic occupancy modelling framework was used to estimate species-  
191 specific occupancy probabilities for 1,547 bird species, including 936 observed during field  
192 sampling and 611 never observed; the latter were included to account for imperfect detection,  
193 which can mask the presence of rare, cryptic, or locally extirpated taxa from past forest loss,  
194 while recognising that such species may still contribute to community composition. We used  
195 the model described in Socolar et al. (2025); model description is provided in the  
196 supplementary materials text S1. Essentially, these models account for imperfect detection  
197 while including detailed geographical and elevational range covariates for all species, which  
198 indicate whether a species is within its known geographic range or outside it at the sampling  
199 points (i.e. biogeographic clipping). This approach avoids spatial biases in predictions  
200 compared to the traditional multispecies occupancy framework while retaining its advantages,  
201 such as species-specific inference even for never-observed species. (Socolar et al., 2022). The  
202 occupancy model was fitted within a Bayesian framework using the Stan engine (Stan  
203 Development Team, 2023) implemented through the R package *flocker* (Socolar and Mills,  
204 2022).

205 The model was used to estimate the posterior occupancy probability of 1,547 species within  
206 each cell of a 2x2 km<sup>2</sup> grid across the study area. This grid incorporated predictor variables  
207 representing spatial features (elevation, distance to range, distance to mountains, and valleys)  
208 and species traits (forest dependency, diet, and family). Predictions were generated separately  
209 for forest and pasture habitats, assuming continuous habitat regardless of current land use.  
210 Next, community composition was estimated for each ecoregion using a threshold criterion: a  
211 species was considered present if its predicted occupancy probability was  $\geq 0.3$  in at least one  
212 grid cell and absent otherwise. At the national scale, a species was considered present if it was  
213 estimated present in the previous step in at least one ecoregion. We used the maximum

214 occupancy in the grid within each ecoregion as the value to compare against the threshold,  
215 rather than a central tendency measure like the median, to avoid underestimating presence for  
216 range-restricted species (e.g., endemics). This approach ensured our community estimates were  
217 independent of ecoregion size. The entire process was repeated across 100 posterior draws of  
218 the occupancy model.

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

227

### 228 *Phylogenetic Diversity metrics*

229 Bird phylogenies (n = 1,000) were downloaded from [vertlife.org](http://vertlife.org), using the most recent Hackett  
230 backbone, however using different backbones tend to produce consistent results and have small  
231 differences (Rubolini et al., 2015). To account for phylogenetic uncertainty, each metric (see  
232 below) was computed for each of the 100 posterior predicted communities, each evaluated  
233 across 100 trees randomly sampled from the downloaded pool.

234 Phylogenetic diversity metrics used were: Faith's Phylogenetic diversity (Faith, 1992) which  
235 sums the branch lengths in the phylogenetic tree for all species in a community; Mean Pairwise  
236 Distance, the average branch distance between all species pairs in the tree; and Mean Nearest  
237 Taxon Distance, the average branch distance between immediate sister species pairs (Webb et

238 al., 2002). Additionally, we calculated total Evolutionary distinctiveness (ED) and  
239 Evolutionary Distinct Globally Endangered (EDGE) metrics. Communities with higher values  
240 of these metrics hold species of conservation interest because they are both isolated in the  
241 evolutionary tree and under risk of extinction according to their red list categories (Gumbs et  
242 al., 2024; Isaac et al., 2007). We used the mean of ED computed for 10000 trees with the fair  
243 proportions method (Kembel et al., 2010). EDGE values for each species were retrieved from  
244 (Gumbs et al., 2024). Handling of phylogenetic information and computation of metrics were  
245 performed with the packages *Phylomeasures* (Tsirogiannis & Sandel, 2016) and *treedataverse*  
246 (Yu, 2023) in the *R* software (R Core Team, 2023).

247

248 *Computing the impacts and scale dependence of phylogenetic diversity loss.*

249 We estimated impacts by predicting for the entire study area as either forest or pasture,  
250 effectively simulating complete deforestation across the nation. Impacts were calculated as the  
251 pairwise subtraction of metrics in forest minus pasture within each ecoregion and Colombia.  
252 Next, the relative impacts were computed as the division of each ecoregion's impact by the  
253 impact at the national scale, therefore relative impacts higher than 1 reveal an overestimation  
254 (impact in single ecoregion higher than national), and relative impacts lower than 1 show  
255 underestimation of metrics in comparison to national scale estimates. Additionally, we  
256 computed the Standardised Effect Size (SES) of the differences between metrics in forest and  
257 pasture habitats to assess whether the impacts represent a systematic loss or merely reflect  
258 inherent differences in species richness between habitats. This was achieved by randomising  
259 species presences in the predicted forest and pasture communities, then computing the metrics  
260 and their difference. Repeating the procedure 1,000 times generated a null distribution, which  
261 was compared with the observed value for each posterior predicted draw.

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

269

## 270 **Results**

### 271 *Forest conversion impacts on phylogenetic composition*

272 In Colombia, the total phylogenetic diversity represented by all species included in this study  
273 is 19,300 million years (Myr; Fig. 2). Of this, estimated forest communities equate to around  
274 18,200 Myr, whereas pastures account for 15,900 Myr—indicating that habitat conversion  
275 results in the loss of ~ 2,300 Myr (~12%) of evolutionary history. For context, each species  
276 contributes an average of 12.5 Myr (range: 2.7 – 81.6 Myr).

277 Species predicted to be present in each habitat are distributed broadly across the phylogeny,  
278 with no systematic loss of entire lineages observed in the phylogenetic reconstructions,  
279 although certain monophyletic groups are disproportionately affected by habitat conversion  
280 (Fig. 2). A higher proportion of species are predicted to occupy only forest habitats, both at the  
281 national scale and across the 13 specific ecoregions (Fig. 2; blue). This trend is particularly  
282 evident in EC montane (Fig. S1D), CC montane (Fig. S1E), and Napo moist (Fig. S1J)  
283 ecoregions, suggesting that these may be more vulnerable to forest conversion due to their  
284 species' higher reliance on forest habitats. By contrast, species predicted to exclusively occupy  
285 pastures are less common overall and tend to come from the same lineages (e.g. Gruiformes,

286 Charadriiformes, Fringillidae) (Fig. 2; red). These species are more prevalent within ecoregions  
287 with lower species richness values, such as the Magdalena dry (Fig. S1G), Magdalena-Urabá  
288 moist (Fig. S1J), and Santa Marta montane (Fig. S1M) ecoregions, therefore these appear to  
289 have a lower impact from forest loss. Species predicted to persist in both habitats (Fig. 2;  
290 yellow) are more evenly distributed across ecoregions and clades.

291 Based on the average community only, we predict 1,377 species to be present in at least one  
292 habitat, including 1,146 species classified as losers and 231 as winners from deforestation  
293 (Table S1). All ecoregions had a higher number of loser species (1.5 to 3 times more) compared  
294 to winner species, especially the EC montane (842 losers, 199 winners) and Magdalena  
295 montane (743 losers, 208 winners) ecoregions. Lower proportions of losers compared to  
296 winners occurred in Magdalena-Urabá moist (377 losers, 155 winners) and Santa Marta  
297 montane (272 losers, 139 winners) ecoregions. Losers from deforestation thus accounted for  
298 66.2% to 82.4% (mean =  $77.0 \pm 4.5$  %) of species across ecoregions. Overall, greater losses are  
299 observed in hyperdiverse lowland ecoregions (e.g. Napo moist) and along elevational gradients  
300 (e.g. EC montane, CC montane). The top five clades with the highest loser/winner ratio,  
301 indicating more losers, included: Thamnophilidae (13, number of ecoregions in which present),  
302 Ramphastidae (10), Cotingidae (7), Cuculidae (6), Grallaridae, and Bucconidae (both 5). These  
303 represent the lineages most significantly impacted; however, we found no evidence for the  
304 complete loss of any entire lineage based on the metrics (see section below). Alternatively,  
305 clades with more winners from deforestation were: Ardeidae (13), Hirundinidae (13),  
306 Scolopaci (12), Threskiornithidae (12), and Corvidae (7), which are more likely to exhibit  
307 homogeneity of species across ecoregions after conversion.

308

309

310 *Impacts of deforestation on phylogenetic diversity metrics across ecoregions*

311 There was considerable regional variation in the impacts of land-use change on phylogenetic  
312 diversity metrics. Faith's Phylogenetic diversity was lower in pasture than forest, with median  
313 loss at the national scale of 2,313.25 with a 95% highest density interval (HDI) of 1,518.16 –  
314 3,214.37 Myr, and losses in ecoregions varying substantially from 729.24 to 2,516.07 Myr.  
315 (Fig. 3a). Differences in predicted mean pairwise distance between forest and pasture habitats  
316 were 1.02; HDI: -0.60 – 2.91 Myr nationally and between 0.26 to 2.29 Myr across ecoregions  
317 (Fig. 3d). By contrast, mean nearest taxon distance was higher in pasture than forest across  
318 ecoregions, leading to negative differences of -1.40; HDI: -2.03 – -0.71 at the national scale  
319 and from -1.88 to -3.73 across ecoregions (Fig. 3g).

320 The extent of phylogenetic diversity change relative to national estimates varied highly by  
321 ecoregion (median differences in metrics and 95% HDIs for all ecoregions are provided in  
322 Table S2). Nine ecoregions showed median relative impacts ranging from 0.32 to 0.97 times  
323 the national estimate (i.e. 68% to 3% lower) across ecoregions, suggesting an underestimation  
324 of Faith's Phylogenetic Diversity loss in comparison to the national scale, which is particularly  
325 high in regions like Santa Marta montane and Magdalena-Urabá moist (Fig. 3b). By contrast,  
326 four ecoregions had relative impacts greater than one, showing that impacts might be  
327 overestimated, particularly in the CC montane, EC montane and Napo moist ecoregions.  
328 Relative impacts on mean pairwise distance were minimal, although highly variable, with some  
329 ecoregions showing a tendency towards underestimation (e.g., CC Montane, Napo moist) and  
330 others to overestimation (e.g., Andean páramo, Fig. 3e). Relative impacts on mean nearest  
331 taxon distance were on average 1.28 to 2.57 times higher than the national estimate (i.e. 28%  
332 to 157% higher). However due to the limited change in raw metrics, this indicates only a slight  
333 overestimation of impacts within individual ecoregions compared to the national scale (Fig.  
334 3h).

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

342 Forest loss reduces both ED and EDGE (Fig. 4). At the national level, ED loss was estimated  
343 at 3,353.50; HDI: 2,319.66 – 4,368.98 Myr, with median regional losses ranging from 671.33  
344 to 3,219.54 Myr (Fig. 4a), highlighting marked variation across ecoregions. The magnitude of  
345 ED loss differs substantially among regions: while the EC montane, CC montane, and Napo  
346 moist ecoregions show losses comparable to national levels, others—such as the Andean  
347 páramo, Magdalena-Urabá moist, and Santa Marta montane ecoregions—exhibit losses less  
348 than half the national estimate. Specifically, relative ED losses across ecoregions ranged from  
349 0.20 to 0.95 (i.e. 80% to 5% lower) times the national value (Fig. 4b). EDGE followed similar  
350 trends, with a national decline of 74; HDI 49 – 98 and median regional losses ranging from 18  
351 to 55 (Fig. 4c). Underestimation of EDGE was more pronounced, with median regional impacts  
352 ranging from 0.25 to 0.76 times the national estimate (i.e. 75% to 24% lower), particularly in  
353 ecoregions showing low ED losses as well as additional regions such as the Llanos, WC  
354 montane, and Magdalena dry (Fig. 4d). Overall, results indicate that estimates from individual  
355 ecoregions differ markedly from national-level losses, with local assessments underestimating  
356 the broader impact of forest loss on evolutionary uniqueness.

357

358

359 *Are impacts of deforestation on phylogenetic diversity scale dependent?*

360 The impacts of forest conversion on phylogenetic diversity appear largely scale-independent.  
361 Increasing spatial scale by randomly pooling ecoregions did not substantially alter the  
362 magnitude of impacts, which remained close to 1 on median average relative to national  
363 estimates (Fig. 5). This general stability was consistent across PD metrics, although some  
364 differences emerged. Considering single ecoregion assessments of Faith's PD, national impacts  
365 are underestimated by a median of 17%, with a broad range of values. Credible intervals span  
366 approximately from 0.53 to 2.55, indicating that single-ecoregion estimates can overestimate  
367 national impacts by up to 50% or underestimate them by up to 150%. This wide range reflects  
368 a high likelihood of misestimating broad-scale impacts when relying solely on single ecoregion  
369 data. Increasing the number of ecoregions greatly reduced the associated uncertainty (i.e.  
370 confidence intervals), leading to greater precision at broader spatial scales. Mean pairwise  
371 distance (MPD) showed minimal variation with increasing scale, suggesting more stable  
372 responses across spatial extents. In contrast, mean nearest taxon distance (MNTD) showed that  
373 national loss estimates were 46% lower than those from single-ecoregion assessments (median  
374 ratio = 0.54) but only 32% lower than estimates based on aggregations of five ecoregions  
375 (median ratio = 0.68). This indicates that including more ecoregions improves accuracy, and  
376 assessments need to aggregate multiple ecoregions to approach the national-scale impact (Fig.  
377 5c). Forest conversion disproportionately increases MNTD within ecoregions, confirming that  
378 phylogenetic diversity loss is primarily driven by the loss of closely related species within taxa  
379 (i.e. sister taxa).

380 For metrics of evolutionary uniqueness (ED and EDGE), the effect of spatial scale was evident  
381 only when sampling a single ecoregion. In these cases, national-level impacts were consistently  
382 58% greater for ED (median ratio = 1.58) and 82% greater for EDGE (median ratio = 1.82)  
383 than those estimated at the ecoregion scale, indicating that regional assessments underestimate

384 national losses (Fig. 5g,h). However, this pattern of scale dependence largely disappeared when  
385 aggregating two or more ecoregions, with estimates based on two ecoregions converging  
386 toward national values and national impacts being a median of 7% greater for ED (median ratio  
387 = 1.07) and 30% greater for EDGE (median ratio = 1.3) than regional estimates, along with  
388 narrower confidence intervals, indicating reduced uncertainty. Despite variation and wide  
389 confidence intervals, underestimation dominated at the single-ecoregion scale. Sampling at  
390 least two ecoregions is therefore essential to accurately assess national-scale loss of  
391 evolutionary uniqueness from forest conversion.

392

## 393 **Discussion**

### 394 *Forest conversion threatens evolutionary history*

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

405 A significant proportion of taxa are expected to be lost following forest conversion to  
406 agriculture, both at the national level and within single ecoregions. Despite this, evolutionary  
407 lineages (clades) are still represented within altered communities, albeit composed of fewer

408 species. Habitat association, whether forest or non-forest, is a crucial factor influencing bird  
409 responses to agriculture (Newbold et al., 2013) and often aligns with ecological traits such as  
410 insectivory or poor long-distance dispersal capacity (Sherry, 2021). Species that benefit from  
411 pasture habitats are usually non-forest species and play a key role in preserving evolutionary  
412 diversity across fragmented landscapes (Morante-Filho et al., 2018). Similarly, we observe an  
413 extirpation of species and the prevalence of others based on their forest dependency. This  
414 phenomenon may lead to increased phylogenetic homogenisation across ecoregions, along  
415 with the depletion of other correlated ecological traits. Our findings partially align with the  
416 global analysis of amphibians by Nowakowski et al., (2018) that found species' responses to  
417 habitat conversion are strongly shaped by their phylogenetic relationships. In their study,  
418 closely related species exhibited similar responses to environmental changes, resulting in the  
419 dominance of certain lineages while others were excluded from local assemblages. This process  
420 ultimately contributed to a significant loss of global phylogenetic diversity.

421 Forest conversion is particularly severe for evolutionarily unique taxa (Fig. 4), a major issue  
422 since Colombia is the country with the second highest avian evolutionary history globally  
423 (McClure et al., 2023). Reductions in Phylogenetic Diversity are driven by a marked decline  
424 of terminal branches within clades (increased Mean Nearest Taxon Distance), without the loss  
425 of deep evolutionary relationships (Mean Pairwise Distance mostly unchanged). These  
426 reductions lead to a loss of 10% to 30% in Faith's Phylogenetic diversity. Ecoregions  
427 experiencing greater losses are typically located along elevational gradients (e.g., EC Montane,  
428 CC Montane) or in hyperdiverse lowland (e.g., Napo moist) areas where disturbance tolerance  
429 is generally low (Weeks et al., 2023). In contrast, less impacted ecoregions are located in more  
430 environmentally homogeneous (e.g., Magdalena-Urabá moist, Magdalena dry) or isolated (e.g.,  
431 Santa Marta montane, Andean páramo) areas, often supporting more open-habitat or  
432 disturbance-tolerant species (Ausprey et al., 2023; Mills et al., 2023). Despite these differences,

433 it is crucial not to overlook the importance of forests in areas with lower relative impacts. Forest  
434 loss also led to reduced phylogenetic diversity and evolutionary uniqueness in such ecoregions.  
435 For instance, the median loss in the least-sensitive Santa Marta montane ecoregion was 729.24  
436 Myr, an area that hosts over 30% of Colombia's endemic avifauna (Chaparro-Herrera et al.,  
437 2024).

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

450

#### 451 *Scale dependence of phylogenetic diversity*

452 The analysis of relative impacts at increasing scales shows no average differences between  
453 habitats, primarily due to the significant variability among ecoregions. Sampling only one  
454 ecoregion tends to result in a slight underestimation of Faith's Phylogenetic Diversity, ED, and  
455 EDGE values. However, adding a second and third ecoregion leads to relative impacts close to  
456 one, although with slightly overestimated medians, suggesting scale-independence in

457 estimating impacts on phylogenetic diversity. This contrasts with findings in Socolar et al.  
458 (2025), who found that six or more different ecoregions are needed to avoid underestimating  
459 national impacts of forest conversion on taxonomic diversity (species richness) derived from  
460 local-scale data. This apparent divergence arises because phylogenetic similarity between  
461 communities declines with geographic distance more slowly than does taxonomic species  
462 composition (Morlon et al., 2011). Biodiversity-area relationships reveal that taxonomic  
463 diversity increases more rapidly with area than functional diversity, which in turn, accumulates  
464 faster than phylogenetic diversity (Dias et al., 2020). Namely, ecoregions share more  
465 phylogenetic diversity—in terms of evolutionary time in the backbone branches of lineages—  
466 than species diversity, making fewer areas more effective at preserving it and requiring fewer  
467 ecoregions to estimate phylogenetic diversity loss at a national level.

468

#### 469 *Study caveats*

470 Using a threshold to determine species presence/absence introduces a notable limitation, as it  
471 might overlook differences in species occupancy between forest and pasture. For example, a  
472 species with an occupancy probability of 0.9 in forest and 0.4 in pasture would be considered  
473 present with our threshold of 0.3, despite the 0.5 considerable difference in occupancy  
474 probability. Consequently, they would contribute equally to metric computations (branch  
475 lengths) potentially masking the true differences between habitats. This limitation is partially  
476 mitigated by incorporating uncertainty in occupancy probabilities throughout the analysis,  
477 using 100 posterior draws from the model to calculate the metrics. Ideally, collapsing  
478 occupancy data into presence–absence can be avoided by using a phylogeny-weighted  
479 conservation metric based on species abundances. For example, unique species may decline

480 more than common ones without going extinct, a pattern often overlooked and a promising  
481 avenue for future research.

482 Although we focus on birds, the widespread impacts observed here are likely to be even more  
483 drastic for other taxa, particularly understudied groups (Eisenhauer et al., 2019; Pollock et al.,  
484 2020). For instance, the average loss of evolutionary history per amphibian species is more  
485 than double that of birds (Gumbs et al., 2024). Finally, the effect of time was not accounted  
486 for, which may have concealed the magnitude of observed differences due to temporal inertia  
487 and extinction debt. Our sampling design used a space-for-time substitution, preventing us  
488 from directly inferring temporal changes caused by impacts. Future research should further  
489 explore these dynamics by incorporating estimates of beta diversity, functional diversity, and  
490 the effects of time, as well as focusing on different taxa and groups within them; for instance,  
491 we observed that pastures often retain wetland species from long-branched lineages, whose  
492 disproportionate contribution of evolutionary time can inflate phylogenetic diversity values and  
493 bias estimates of loss, suggesting that wetland species be evaluated separately to improve  
494 accuracy (Supplementary results S1). The actual situation may be more severe than predicted,  
495 due to additional factors not fully captured in this study such as the effect of past ecological  
496 filtering (Hua et al., (2024). Our results likely represent the minimum expected impacts of  
497 forest conversion on phylogenetic diversity, given the study's assumptions and limitations.

498

## 499 **Conclusions and management implications**

500 We aimed to quantify the impacts of forest conversion on avian phylogenetic diversity in  
501 Colombia from local to a national scale. Our findings indicate that the impacts are primarily  
502 driven by the loss of terminal branches in the phylogenetic tree, particularly evolutionarily  
503 unique taxa (e.g. Antbirds, Cotingas, Antpittas). Contrary to expectations, the scaling analysis

504 revealed that aggregating two or more ecoregions did not significantly alter the estimated  
505 impacts compared to the national level, challenging our hypothesis that aggregating several  
506 ecoregions would be necessary to comprehensively quantify the severity of phylogenetic  
507 diversity loss from land-use change. This suggests that estimates of phylogenetic diversity loss  
508 at the single ecoregion level may reliably reflect impacts at larger spatial scales.

509 Conserving optional value (i.e. value of biodiversity for yet-unknown future uses) and nature's  
510 contributions to people is central to the grand objective of addressing the environmental crises  
511 and ensuring a stable and healthy future (Gumbs, Gray, et al., 2023). As outlined in the  
512 Kunming-Montreal Global Biodiversity Framework and Paris Agreement, maximising  
513 phylogenetic diversity is an effective strategy for preserving future option and retaining current  
514 benefits for human well-being, including physical, mental, cultural and spiritual benefits that  
515 may be overlooked when focusing solely on avoiding species extinction (Gumbs, Gray, et al.,  
516 2023; Hayward et al., 2022). Both Faith's phylogenetic diversity and EDGE are key indicators  
517 towards these goals (Secretariat of the Convention on Biological Diversity, 2022). Tracking  
518 these indicators at national levels is essential to capture the broad value of biodiversity,  
519 particularly since conservation efforts often overlook evolutionarily unique species (Owen et  
520 al., 2019). Many of these cannot be assessed for evolutionary history metrics, or remain  
521 unknown to science, and may be substantially more sensitive than the bird species used here.  
522 The loss and homogenisation of diversity across ecoregions leads to a similar subset of species  
523 to occur in pastures (Socolar et al., 2016), which can have broad negative effects such as  
524 reduced ecosystem stability (Gumbs, Chaudhary, et al., 2023). While losses of phylogenetic  
525 diversity did not increase with spatial scale, the losses incurred within each ecoregion are  
526 substantial. These losses point towards an erosion of overall biodiversity and the evolutionary  
527 values critical for ecosystem resilience and future adaptation.

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

545

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555

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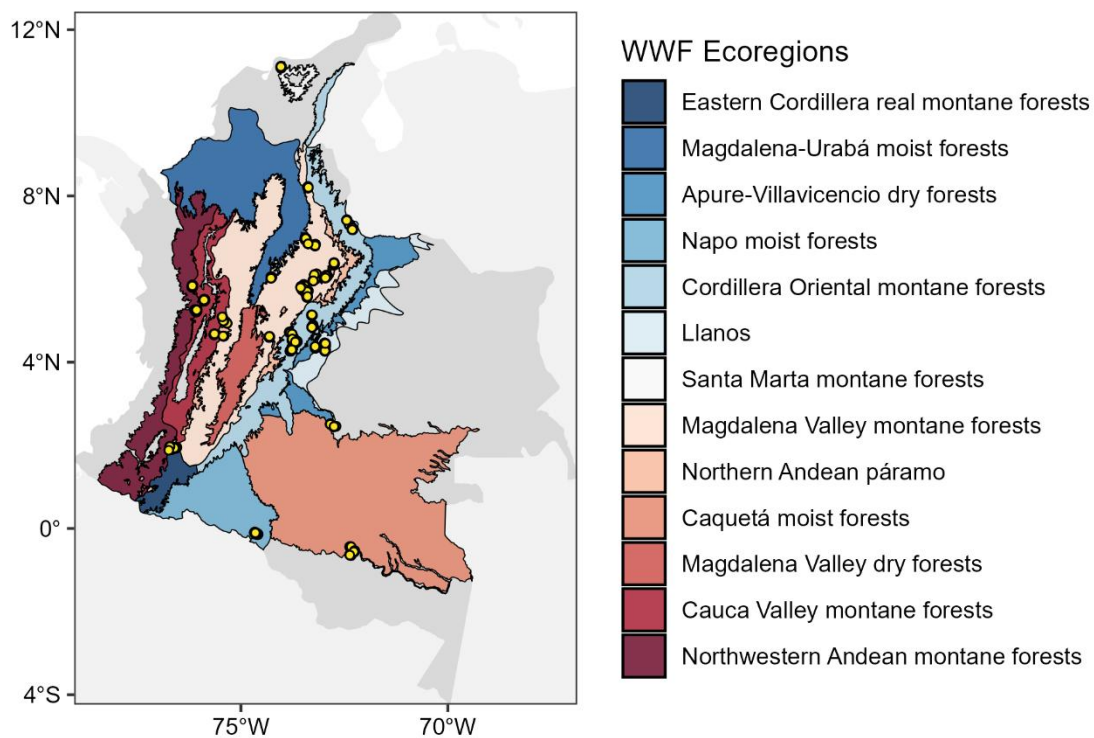
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847 **Figure Captions**

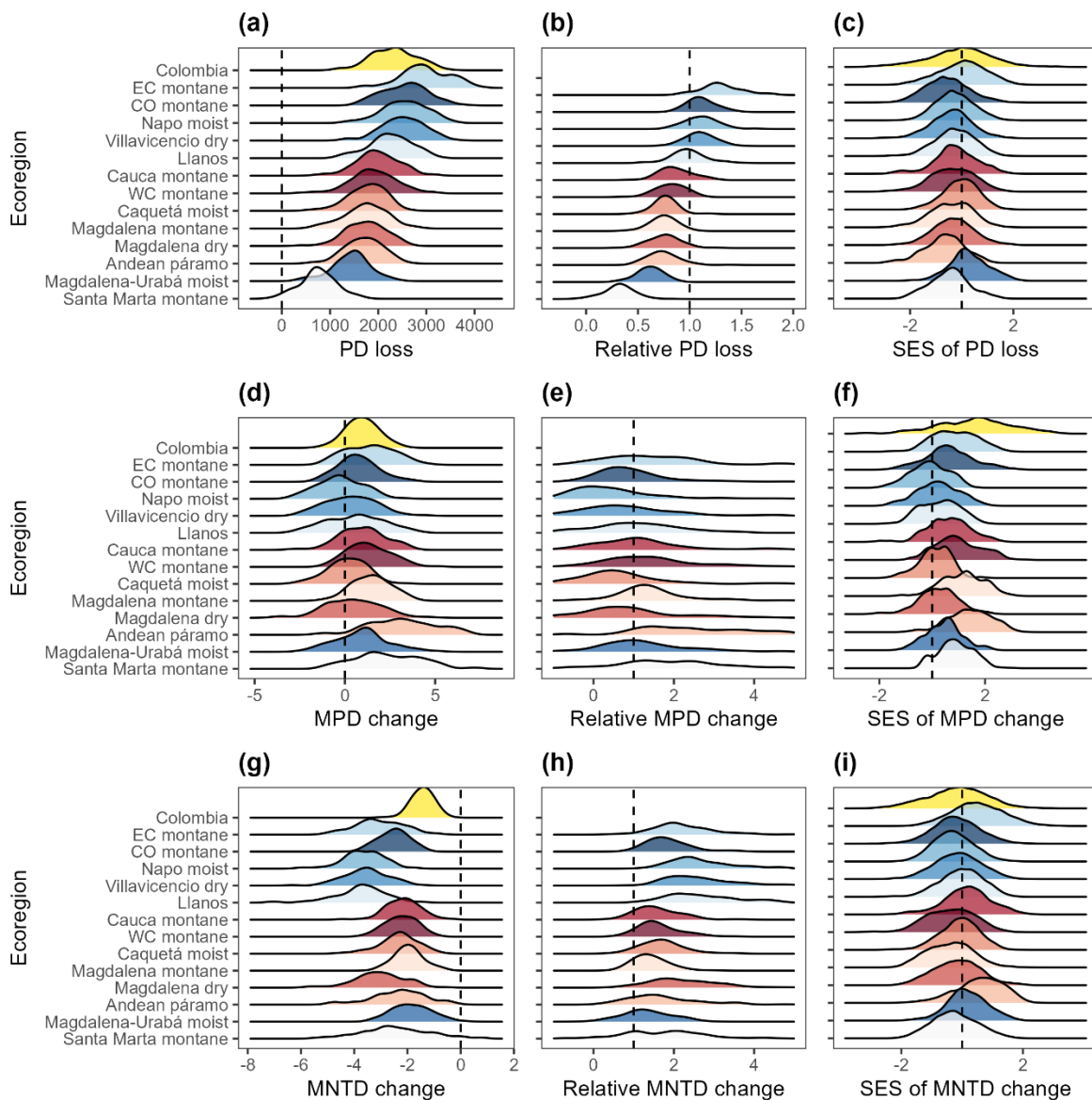


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849 Figure 1. Map of the study area. Yellow dots indicate sampling points. The background colour  
850 gradient (blue to red) represents the 13 sampled ecoregions. Areas of mainland Colombia that  
851 were not included in the study are in grey. Ecoregions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

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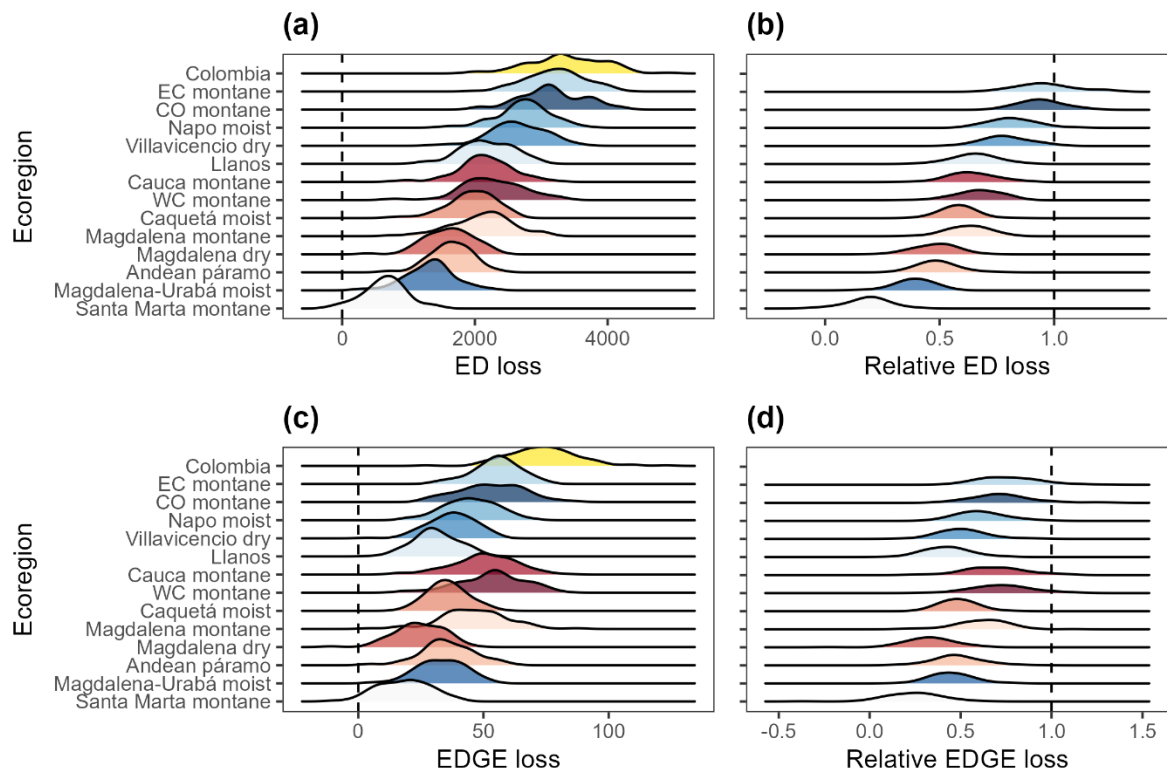


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862 Figure 3: Impacts of forest conversion to pasture on phylogenetic diversity metrics across  
 863 ecoregions and at the national scale (y-axis). Ridgeline plots show the distribution of the  
 864 difference in predicted metrics between forest and pasture across 100 posterior draws. A value  
 865 of zero (dashed lines in A, D, G) indicates no difference between forest and pasture. Relative  
 866 impacts compare regional loss to national loss for each ecoregion: values  $< 1$  show less severe  
 867 regional impacts compared to the national scale, while values  $> 1$  show greater impacts. A  
 868 relative impact value of 1 (dashed lines in B, E, H) represents no difference between an  
 869 ecoregion and the national estimate. Panels C, F, and I show standardised effect sizes (SES) of

870 the difference in predicted metrics. Metrics: PD (Faith's phylogenetic diversity), MPD (Mean  
871 Pairwise Distance), and MNTD (Mean Nearest Taxon Distance). Colours represent ecoregions  
872 from Fig. 1.

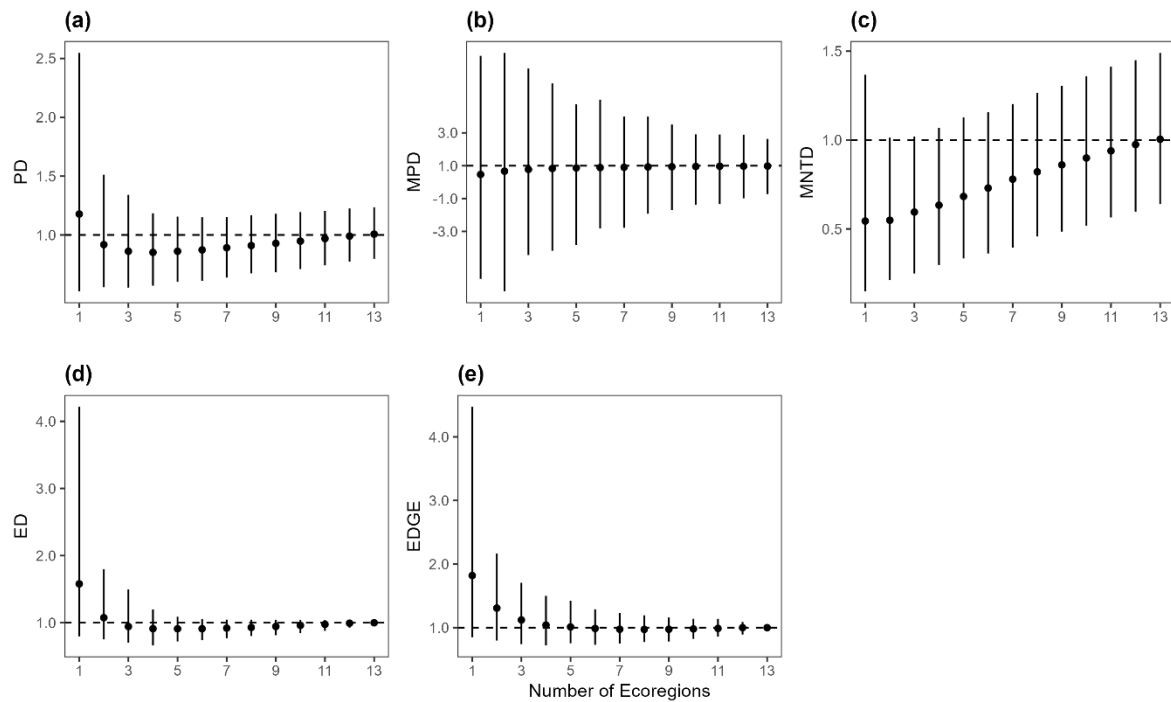
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875 Figure 4: Impacts of forest conversion to pasture on Evolutionary Distinctness (ED) and  
 876 Evolutionary distinct and globally endangered (EDGE) metrics across ecoregions and at the  
 877 national scale (y-axis). Ridgeline plots show the distribution of the difference in predicted  
 878 metrics for forest minus pasture across 100 posterior draws. A value of zero (dashed lines in A  
 879 and B) implies no difference between forest and pasture. Relative impacts compare the regional  
 880 loss to the national loss for each ecoregion. Values  $< 1$  indicate that the difference in diversity  
 881 between forest and pasture in a region is less severe than national while values  $> 1$  indicate  
 882 higher impacts. A relative impact value of 1 (dashed lines in D and E) indicates no difference  
 883 between an ecoregion and the country level estimate. Colours represent ecoregions from Fig.  
 884 1.

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887 Figure 5. Relative impacts of forest conversion on phylogenetic diversity metrics across  
 888 increasing spatial scales (x-axis). Values represent the national loss divided by the loss from  
 889 aggregated ecoregions (1 to 13). A ratio of 1.0 (dashed line) indicates no difference. Values  
 890 above 1.0 mean national loss exceeds regional loss (e.g. 1.5 = 50% greater), while values below  
 891 1.0 indicate overestimation by regional assessments. Point range lines show median ratios with  
 892 95% Highest Density Credible Intervals. Metrics: A. Faith's Phylogenetic Diversity (PD), B.  
 893 Mean Pairwise Distance (MPD), C. Mean Nearest Taxon Distance (MNTD), D. Evolutionary  
 894 Distinctiveness (ED), E. Evolutionarily Distinct and Globally Endangered (EDGE).

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902 **Supplementary materials**

903

904 **Strong variation in land-use change impacts on tropical avian phylogenetic diversity**  
 905 **between ecoregions highlights the need to sample large spatial scales**

906 **Authors:** Giovanni Pérez\*<sup>1,2</sup>, Simon C. Mills<sup>1,3</sup>, Jacob B. Socolar<sup>4,5</sup>, Jose M. Ochoa  
 907 Quintero<sup>6,7</sup>, Robert P. Freckleton<sup>1</sup>, Torbjørn Haugaasen<sup>5</sup>, James. J. Gilroy<sup>3</sup>, David P.  
 908 Edwards<sup>2,8</sup>

909 **Table S1:** Number of species predicted per ecoregion and habitat, along with losers and  
 910 winners from deforestation. Losers have lower occupancy in pasture than forest, while winners  
 911 have lower occupancy in forest than pasture. Values are based on the averaged community  
 912 across 100 posterior draws of the occupancy model.

<b>Ecoregion</b>	<b>Species</b>	<b>Forest</b>	<b>Pasture</b>	<b>Both</b>	<b>Loser</b>	<b>Winner</b>
Colombia	1377	691	73	613	1146	231
Cordillera Oriental montane forests	1041	530	77	434	842	199
Magdalena Valley montane forests	951	450	72	429	743	208
Northwestern Andean montane forests	895	422	74	399	697	198
Eastern Cordillera real montane	837	452	64	321	688	149
Cauca Valley montane forests	813	383	67	363	631	182
Apure-Villavicencio dry forests	781	446	81	254	619	162
Napo moist forests	761	455	61	245	627	134
Caquetá moist forests	700	424	69	207	567	133
Northern Andean páramo	669	321	68	280	508	161
Magdalena Valley dry forests	605	286	72	247	439	166
Llanos	584	335	73	176	448	136
Magdalena-Urabá moist forests	532	249	72	211	377	155
Santa Marta montane forests	411	150	56	205	272	139

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914 Table S2: Median differences and 95% highest density credible intervals for phylogenetic  
 915 diversity metrics comparing predicted avian communities in forests versus pastures, reported  
 916 for each ecoregion and for Colombia.

<b>Ecoregion</b>	<b>Metric</b>	<b>Median</b>	<b>Lower HDI</b>	<b>Upper HDI</b>
Apure-Villavicencio dry forests	SR	228,50	186,00	281,00
Apure-Villavicencio dry forests	PD	2516,07	1728,86	3324,65
Apure-Villavicencio dry forests	MPD	0,35	-2,49	2,46
Apure-Villavicencio dry forests	MNTD	-3,54	-5,05	-1,88
Apure-Villavicencio dry forests	SES.PD	-0,69	-2,32	1,99
Apure-Villavicencio dry forests	SES.MPD	0,35	-1,89	2,09
Apure-Villavicencio dry forests	SES.MNTD	-0,34	-2,54	1,61
Apure-Villavicencio dry forests	ED	2628,83	2008,57	3601,35
Apure-Villavicencio dry forests	EDGE	38,00	21,00	55,00
Caquetá moist forests	SR	158,00	119,50	200,00
Caquetá moist forests	PD	1816,23	940,39	2462,79
Caquetá moist forests	MPD	0,16	-1,87	2,31
Caquetá moist forests	MNTD	-2,28	-3,85	-1,00
Caquetá moist forests	SES.PD	-0,05	-1,93	1,68
Caquetá moist forests	SES.MPD	0,23	-1,51	1,63
Caquetá moist forests	SES.MNTD	0,15	-1,37	2,10
Caquetá moist forests	ED	1990,98	1323,82	2596,83
Caquetá moist forests	EDGE	35,00	22,00	51,00
Cauca Valley montane forests	SR	189,00	135,00	239,00
Cauca Valley montane forests	PD	1942,10	979,15	2769,82
Cauca Valley montane forests	MPD	1,08	-1,14	3,32
Cauca Valley montane forests	MNTD	-2,12	-3,17	-0,63
Cauca Valley montane forests	SES.PD	-0,51	-3,14	1,83
Cauca Valley montane forests	SES.MPD	-0,57	-2,59	1,64
Cauca Valley montane forests	SES.MNTD	-0,43	-2,04	2,07
Cauca Valley montane forests	ED	2153,04	1433,05	3080,53
Cauca Valley montane forests	EDGE	51,00	25,00	76,00
Colombia	SR	274,00	205,00	342,00
Colombia	PD	2313,25	1518,16	3214,37
Colombia	MPD	1,02	-0,60	2,91
Colombia	MNTD	-1,40	-2,03	-0,71
Colombia	SES.PD	-2,63	-5,89	1,94
Colombia	SES.MPD	-1,95	-5,54	1,49
Colombia	SES.MNTD	-1,90	-4,99	1,08
Colombia	ED	3353,50	2319,66	4368,98
Colombia	EDGE	74,00	49,00	98,00
Cordillera Oriental montane forests	SR	272,50	220,50	340,00
Cordillera Oriental montane forests	PD	2580,18	1719,29	3502,27
Cordillera Oriental montane forests	MPD	0,64	-1,45	2,78
Cordillera Oriental montane forests	MNTD	-2,50	-3,58	-1,53
Cordillera Oriental montane forests	SES.PD	-1,25	-3,56	0,91
Cordillera Oriental montane forests	SES.MPD	-0,46	-2,93	1,59

Cordillera Oriental montane forests	SES.MNTD	-0,92	-3,13	1,17
Cordillera Oriental montane forests	ED	3135,56	2014,47	3933,80
Cordillera Oriental montane forests	EDGE	53,00	26,00	74,00
Eastern Cordillera real montane forests	SR	268,50	219,00	319,00
Eastern Cordillera real montane forests	PD	2977,53	2061,21	3966,09
Eastern Cordillera real montane forests	MPD	1,44	-0,99	3,74
Eastern Cordillera real montane forests	MNTD	-3,11	-5,05	-1,65
Eastern Cordillera real montane forests	SES.PD	-0,01	-3,06	2,27
Eastern Cordillera real montane forests	SES.MPD	-0,30	-2,15	1,57
Eastern Cordillera real montane forests	SES.MNTD	0,13	-2,15	2,79
Eastern Cordillera real montane forests	ED	3219,54	2438,83	4052,81
Eastern Cordillera real montane forests	EDGE	55,00	34,00	73,00
Llanos	SR	184,00	140,00	228,00
Llanos	PD	2245,09	1362,37	3082,75
Llanos	MPD	0,68	-2,45	3,39
Llanos	MNTD	-3,73	-5,99	-2,10
Llanos	SES.PD	-0,37	-2,58	1,06
Llanos	SES.MPD	0,65	-1,45	2,14
Llanos	SES.MNTD	0,15	-1,82	1,74
Llanos	ED	2164,15	1594,70	2981,37
Llanos	EDGE	30,50	15,00	47,00
Magdalena Valley dry forests	SR	150,00	103,00	182,00
Magdalena Valley dry forests	PD	1752,44	1002,86	2503,30
Magdalena Valley dry forests	MPD	0,36	-2,08	4,09
Magdalena Valley dry forests	MNTD	-3,05	-5,22	-1,46
Magdalena Valley dry forests	SES.PD	-0,51	-2,86	1,71
Magdalena Valley dry forests	SES.MPD	-0,31	-2,31	1,87
Magdalena Valley dry forests	SES.MNTD	-0,39	-2,72	1,44
Magdalena Valley dry forests	ED	1621,40	959,60	2223,48
Magdalena Valley dry forests	EDGE	24,00	7,00	41,00
Magdalena Valley montane forests	SR	183,00	142,00	245,00
Magdalena Valley montane forests	PD	1747,64	802,65	2607,41
Magdalena Valley montane forests	MPD	1,52	-0,40	3,43
Magdalena Valley montane forests	MNTD	-1,94	-2,94	-0,76
Magdalena Valley montane forests	SES.PD	-0,70	-3,24	1,59
Magdalena Valley montane forests	SES.MPD	0,60	-1,01	2,69
Magdalena Valley montane forests	SES.MNTD	-0,80	-2,91	1,05
Magdalena Valley montane forests	ED	2164,09	1304,90	3093,14
Magdalena Valley montane forests	EDGE	45,50	17,00	70,00
Magdalena-Urabá moist forests	SR	107,00	73,00	153,00
Magdalena-Urabá moist forests	PD	1486,62	555,92	2247,01
Magdalena-Urabá moist forests	MPD	1,06	-1,79	3,97
Magdalena-Urabá moist forests	MNTD	-1,88	-3,25	-0,42
Magdalena-Urabá moist forests	SES.PD	0,43	-1,34	2,84
Magdalena-Urabá moist forests	SES.MPD	0,70	-1,03	2,52
Magdalena-Urabá moist forests	SES.MNTD	0,40	-1,53	2,36

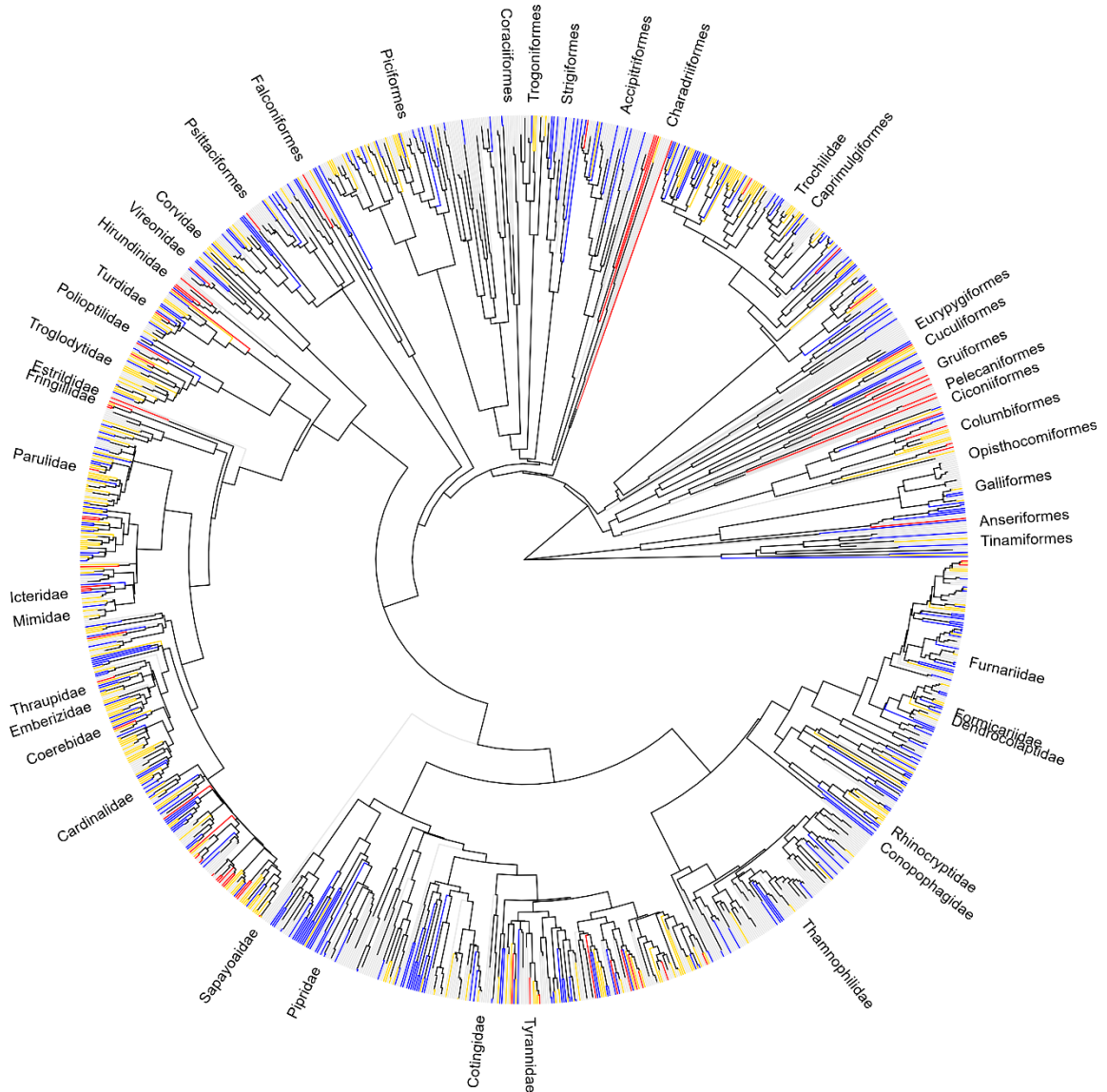
Magdalena-Urabá moist forests	ED	1367,83	765,75	2288,08
Magdalena-Urabá moist forests	EDGE	34,00	18,50	53,00
Napo moist forests	SR	235,00	173,00	273,00
Napo moist forests	PD	2557,82	1692,55	3460,30
Napo moist forests	MPD	-0,26	-2,89	1,70
Napo moist forests	MNTD	-3,68	-5,39	-2,43
Napo moist forests	SES.PD	-0,53	-2,13	1,52
Napo moist forests	SES.MPD	-0,53	-2,63	0,88
Napo moist forests	SES.MNTD	-0,27	-2,00	1,55
Napo moist forests	ED	2738,26	2037,43	3530,83
Napo moist forests	EDGE	45,00	20,00	62,00
Northern Andean páramo	SR	147,50	118,00	188,00
Northern Andean páramo	PD	1727,37	1053,26	2428,11
Northern Andean páramo	MPD	3,18	0,49	6,78
Northern Andean páramo	MNTD	-2,29	-4,73	-0,51
Northern Andean páramo	SES.PD	-0,83	-3,42	1,01
Northern Andean páramo	SES.MPD	0,54	-1,67	2,67
Northern Andean páramo	SES.MNTD	-0,71	-3,06	1,24
Northern Andean páramo	ED	1629,64	1132,40	2306,89
Northern Andean páramo	EDGE	35,00	16,00	56,00
Northwestern Andean montane forests	SR	191,00	153,00	263,00
Northwestern Andean montane forests	PD	1892,22	793,04	2808,84
Northwestern Andean montane forests	MPD	1,20	-0,95	3,33
Northwestern Andean montane forests	MNTD	-2,23	-3,28	-1,04
Northwestern Andean montane forests	SES.PD	-0,76	-3,14	1,73
Northwestern Andean montane forests	SES.MPD	0,07	-1,65	2,14
Northwestern Andean montane forests	SES.MNTD	-0,94	-2,67	1,23
Northwestern Andean montane forests	ED	2237,58	1641,74	3341,43
Northwestern Andean montane forests	EDGE	54,00	26,00	77,00
Santa Marta montane forests	SR	62,00	35,50	102,00
Santa Marta montane forests	PD	729,24	-23,45	1479,28
Santa Marta montane forests	MPD	2,29	-1,04	5,38
Santa Marta montane forests	MNTD	-2,48	-5,03	0,11
Santa Marta montane forests	SES.PD	-0,65	-2,69	1,32
Santa Marta montane forests	SES.MPD	1,00	-0,78	2,47
Santa Marta montane forests	SES.MNTD	-0,69	-2,45	1,47
Santa Marta montane forests	ED	671,33	-60,24	1290,15
Santa Marta montane forests	EDGE	18,50	2,00	39,00

917

918







929

930 Figure S1C: Phylogenetic tree of predicted avian communities in the Cauca Valley montane

931 forests ecoregion. Terminal branches are coloured according to predicted presence in forest

932 (blue), pasture (red), both habitats (yellow), or absence (light grey); a species is considered

933 present when its mean occupancy probability  $\geq 0.3$ .

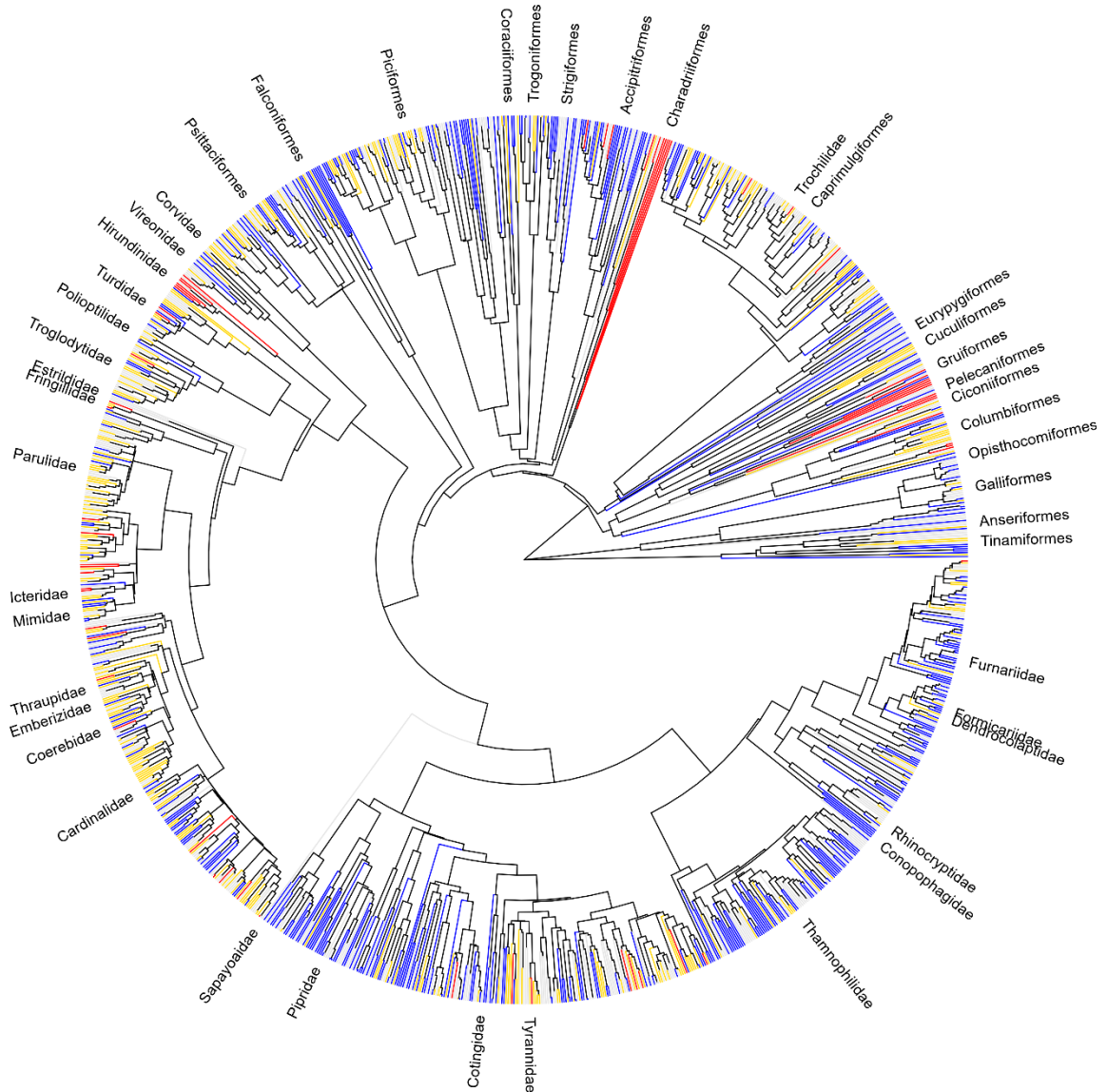






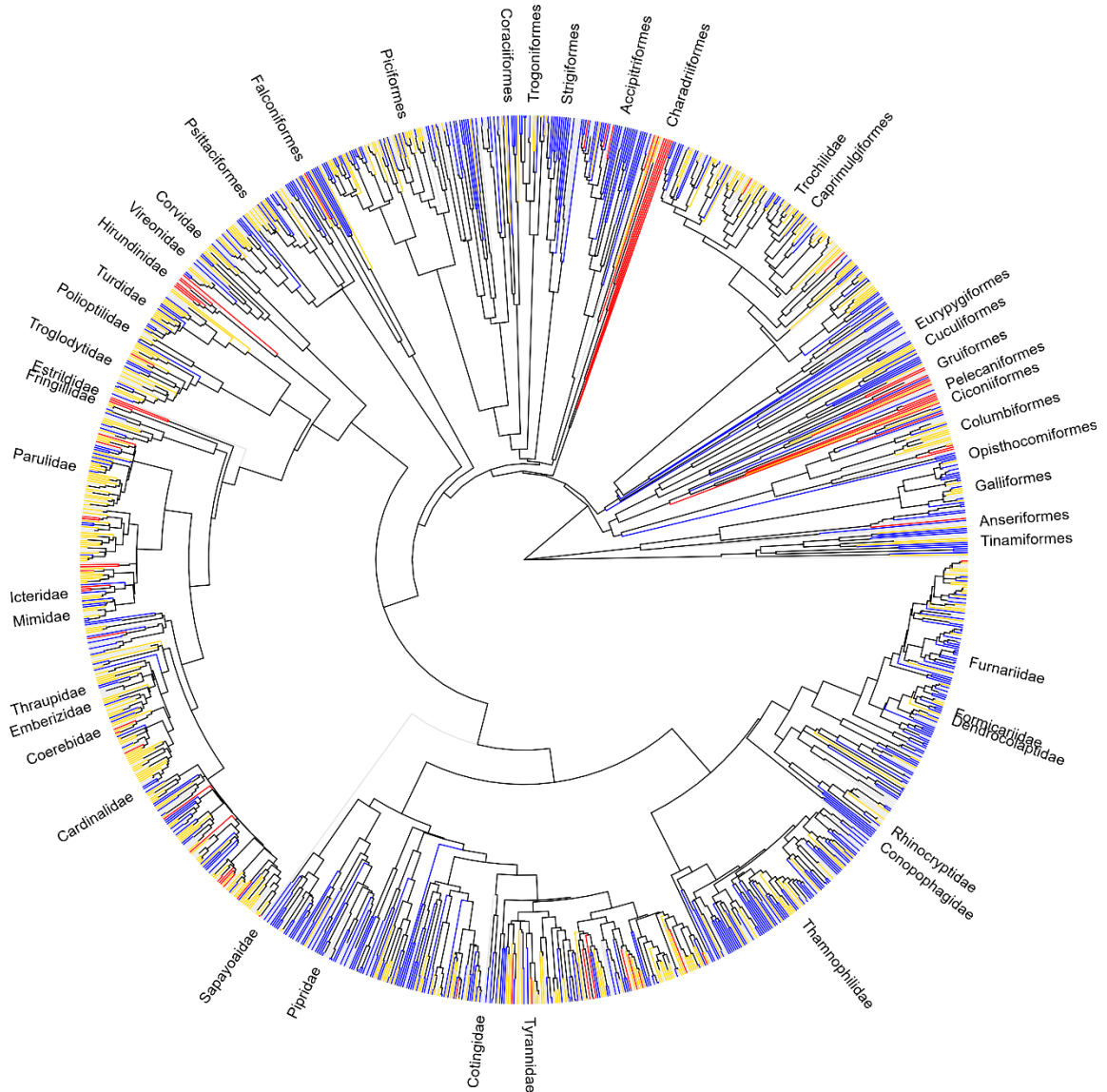






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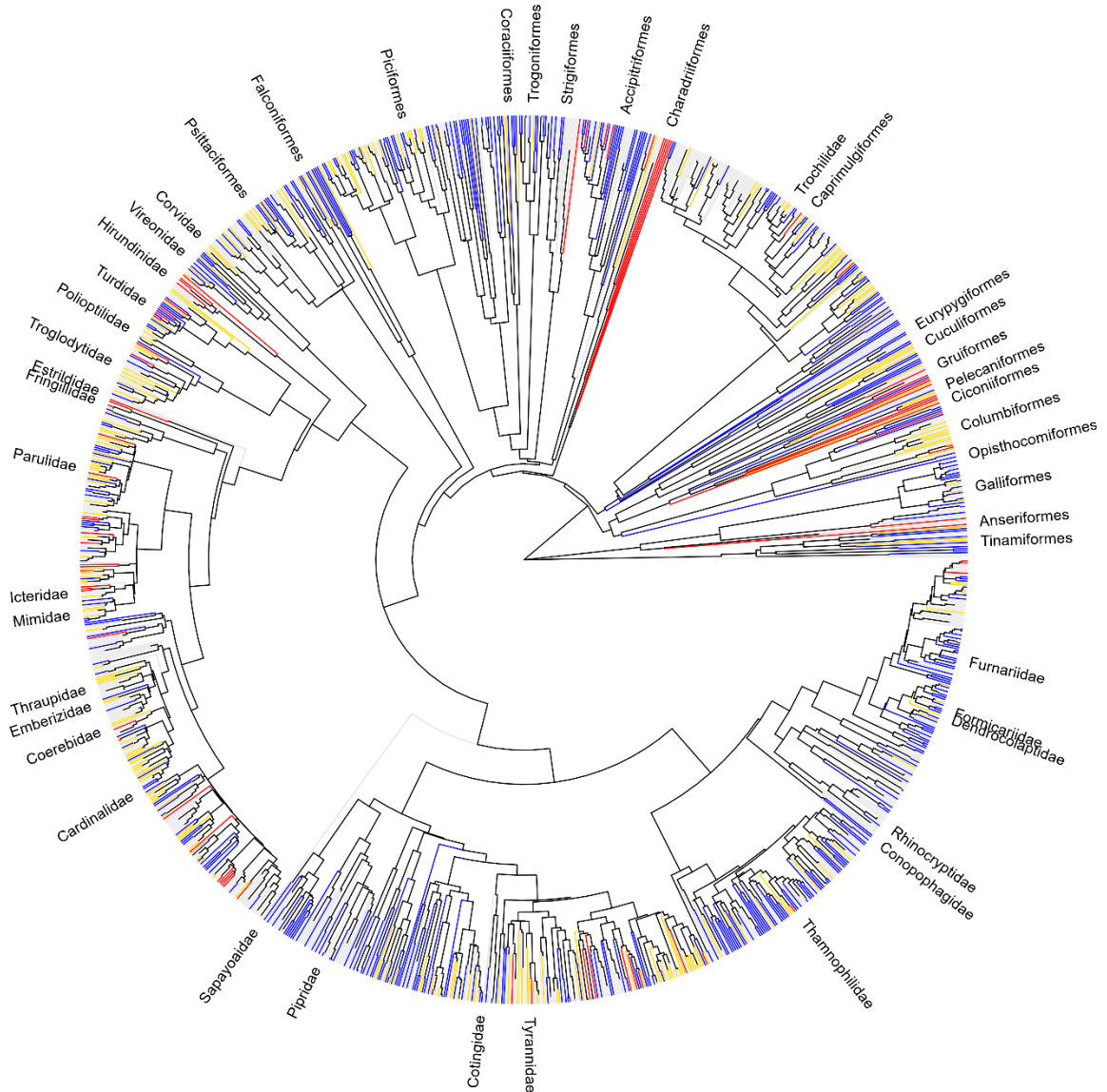
960 Figure S11: Phylogenetic tree of predicted avian communities in the Magdalena Urabá moist  
 961 forests ecoregion. Terminal branches are coloured according to predicted presence in forest  
 962 (blue), pasture (red), both habitats (yellow), or absence (light grey); a species is considered  
 963 present when its mean occupancy probability  $\geq 0.3$ .



964  
 965 Figure S1J: Phylogenetic tree of predicted avian communities in the Napo moist forests  
 966 ecoregion. Terminal branches are coloured according to predicted presence in forest (blue),  
 967 pasture (red), both habitats (yellow), or absence (light grey); a species is considered present  
 968 when its mean occupancy probability  $\geq 0.3$ .

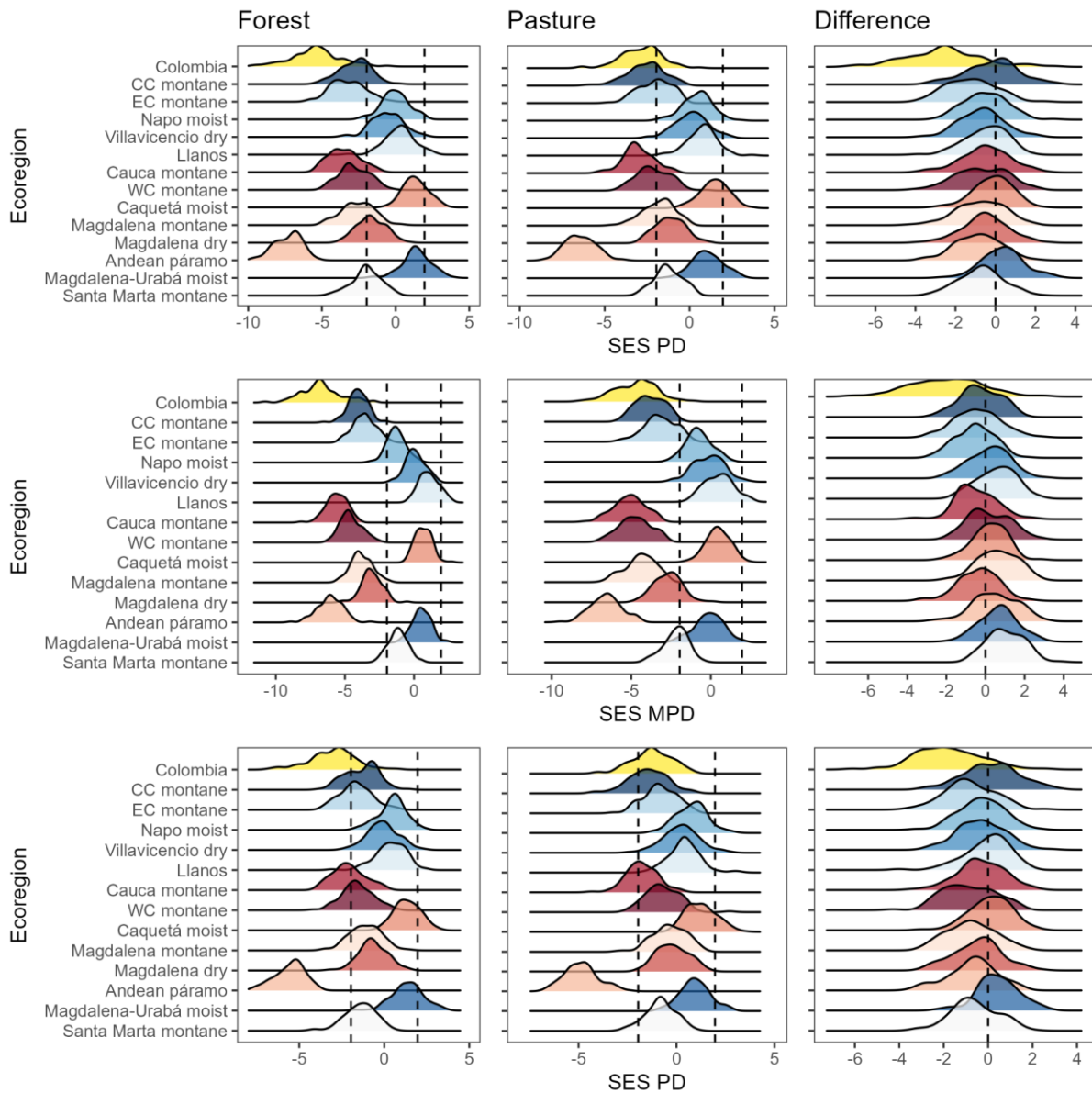






979

980 Figure S1M: Phylogenetic tree of predicted avian communities in the Santa Marta montane  
 981 forests ecoregion. Terminal branches are coloured according to predicted presence in forest  
 982 (blue), pasture (red), both habitats (yellow), or absence (light grey); a species is considered  
 983 present when its mean occupancy probability  $\geq 0.3$ .



984

985 Figure S2: Standardised effect size (SES) of phylogenetic diversity metrics in forest, pasture,  
 986 and their difference across ecoregions and at the national scale. Dashed lines at forest and  
 987 pasture plots represent thresholds for change in phylogenetic assembly: values below -1.96  
 988 indicate phylogenetic clustering, while values between -1.96 and 1.96 indicate random  
 989 assembly. Dashed lines in difference plots represent no change between habitats. Metrics: PD  
 990 (Faith's Phylogenetic Diversity), MPD (Mean Pairwise Distance), and MNTD (Mean Nearest  
 991 Taxon Distance).

992

993 **Text S1. Supplementary methods: Model description**

994 A full detailed description of the modelling approach is found in Socolar et. al., (2025) and  
995 their supplementary materials, which we partially reproduce in here with permission:

996

997 *Species-distribution modelling*

998 Occupancy was modelled across the entire study area using a biogeographically constrained  
999 multi-species occupancy framework. The occupancy component included species-standardised  
1000 elevation (linear and quadratic terms, estimated separately for species with elevational minima  
1001 at zero and those above zero), a monotonic effect of distance to range, habitat (forest or  
1002 pasture), functional and biogeographic traits, and interactions between habitat and all species  
1003 traits. To account for phylogenetic and species-level variation, random intercepts grouped by  
1004 species and family were included, along with random slopes for elevation by species, and  
1005 random slopes for habitat by both family and species. Spatial autocorrelation was addressed by  
1006 including random intercepts grouped by species within cluster and by species within ecoregion.

1007 The detection component was modelled as a function of time after sunrise, observer, habitat,  
1008 and five species traits. Random intercepts were included for species, family, and species-by-  
1009 observer, along with random slopes for time after sunrise by species and for land use by both  
1010 species and family.

1011 Prior specifications are provided in the table below. Bayesian modelling was conducted using  
1012 Stan via the R package flocker, which serves as an occupancy-modelling front end for the R  
1013 package brms. Four chains were run, each with 1,000 warm-up iterations followed by 1,000  
1014 sampling iterations. All chains completed without post-warm-up divergences. Across all  
1015 chains, all parameters had R-hat values (split, folded, rank-normalised) below 1.02 and bulk  
1016 effective sample sizes greater than 100. The final model was developed through iterative

1017 refinement informed by posterior predictive checks. Details of model refinement and adequacy  
 1018 are provided in Appendices S2 and S3 of Socolar et al. (2025).

1019 Table: Occupancy model parameters, priors, and posterior margins

Model component	Parameter class	Parameter	Prior	Posterior 90% CI	
				.05 quantile	.95 quantile
Occupancy	intercept	intercept	normal(-7, 2.5)	-9.57	-7.36
	slope	point is pasture	normal(0,1)	-1.23	0.19
		relative elevation	normal(0,5)	-1.08	-0.46
		relative elevation squared	normal(0,5)	-6.27	-5.42
		species reaches lowlands	normal(0,1)	-0.76	-0.06
		[relative elevation] x [species reaches lowlands]	normal(0,5)	-2.02	-1.48
		[relative elevation squared] x [species reaches lowlands]	normal(0,5)	0.62	1.22
		species elevational breadth	normal(0,1)	0.40	0.86
		[species elevational breadth] x [point is pasture]	normal(0,1)	0.42	0.78
		species elevational median	normal(0,1)	-0.19	0.42
		[species elevational median] x [point is pasture]	normal(0,1)	-0.56	-0.18
		species is migratory	normal(0,1)	-2.12	-1.05
		[species is migratory] x [point is pasture]	normal(0,1)	-0.33	0.34
		species body mass	normal(0,0.5)	-0.75	-0.06
[species body mass] x [point is pasture]	normal(0,0.5)	-0.33	0.09		

		species occurs in arid biomes	normal(0,1)	-0.48	0.39
		[species occurs in arid biomes] x [point is pasture]	normal(0,1)	-0.14	0.43
		species occurs in dry forest biome	normal(0,1)	0.27	0.75
		[species occurs in dry forest biome] x [point is pasture]	normal(0,1)	0.06	0.41
		species occurs in forest biomes	normal(0,1)	0.61	1.29
		[species occurs in forest biomes] x [point is pasture]	normal(0,1)	-0.70	-0.21
		[species occurs in forest biomes] x [species elevational median]	normal(0,1)	-0.37	0.15
		[species occurs in forest biomes] x [species elevational median] x [point is pasture]	normal(0,1)	0.08	0.47
		species is restricted to forest biomes	normal(0,1)	-0.30	0.32
		[species is restricted to forest biomes] x [point is pasture]	normal(0,1)	-1.21	-0.81
		[species is restricted to forest biomes] x [species elevational median]	normal(0,1)	0.11	0.57
		[species is restricted to forest biomes] x [species elevational median] x [point is pasture]	normal(0,1)	-0.25	0.06
		species is restricted to dry forest biomes and/or is a floodplain specialist in Amazonia	normal(0,1)	-0.67	0.21
		[species is restricted to dry forest biomes and/or is a floodplain specialist in Amazonia] x [point is pasture]	normal(0,1)	0.13	0.79
		species is restricted to terra firme in Amazonia	normal(0,1)	-0.43	-0.01
		[species is restricted to terra firme in Amazonia] x [point is pasture]	normal(0,1)	-0.32	-0.01

		species is limited by a mountain barrier	normal(0,1)	-0.18	0.29
		[species is limited by a mountain barrier] x [point is pasture]	normal(0,1)	-0.41	-0.05
		species is limited by a valley barrier	normal(0,1)	-0.36	0.25
		[species is limited by a valley barrier] x [point is pasture]	normal(0,1)	-0.51	-0.12
		species is a carnivore	normal(0,0.5)	-0.94	0.11
		[species is a carnivore] x [point is pasture]	normal(0,0.5)	-0.65	0.05
		species is a frugivore or nectivore	normal(0,0.5)	0.22	0.79
		[species is a frugivore or nectivore] x [point is pasture]	normal(0,0.5)	-0.13	0.28
		species is a granivore	normal(0,0.5)	-0.65	0.14
		[species is a granivore] x [point is pasture]	normal(0,0.5)	-0.08	0.43
		species is an insectivore	normal(0,0.5)	-0.55	-0.02
		[species is an insectivore] x [point is pasture]	normal(0,0.5)	-0.33	0.03
	monotonic effect <sup>1</sup>	distance from range	flat	-0.88	-0.66
	random effect standard deviations	intercept: by species	half-normal(0,2)	2.32	2.82
		intercept: by family	half-normal(0,2)	1.24	2.28
		intercept: by species-cluster	half-normal(0,3)	2.07	2.29
		intercept: by species-subregion	half-normal(0,3)	2.79	3.08
		slope, point is pasture: by species	half-normal(0,1)	1.56	1.92
		slope, point is pasture: by family	half-normal(0,1)	0.43	1.09

		slope, relative elevation: by species	half-normal(0,2)	2.91	3.90
		slope, relative elevation squared: by species	half-normal(0,2)	2.53	3.12
	random effect covariances	all	LKJ(1)		
Detection	intercept	intercept	normal(-3,1)	-3.63	-2.71
	slope	point is pasture	normal(0,0.75)	-0.04	0.34
		species body mass	normal(0,0.5)	-0.30	-0.01
		species elevational median	normal(0,0.5)	0.03	0.19
		species is migratory	normal(0,1)	-1.05	-0.52
		species is a carnivore	normal(0,0.5)	-0.46	0.15
		count time of day	normal(0,0.5)	-0.30	-0.24
		[count time of day] x [point elevation]	normal(0,0.5)	-0.02	0.02
		observer is SM	normal(0,0.25)	-0.05	0.08
		observer is JG	normal(0,0.25)	0.17	0.29
		observer is DPE	normal(0,0.25)	0.09	0.21
	random effect standard deviations	intercept: by species	half-normal(0,2)	0.66	0.89
		intercept: by family	half-normal(0,2)	0.49	0.99
		intercept: by [species x observer]	student_t(3, 0, 2.5)	0.65	0.77
		slope, point is pasture: by species	half-normal(0,1)	0.66	0.83
		slope, point is pasture: by family	half-normal(0,1)	0.19	0.57
slope, count time: by species		half-normal(0,1)	0.20	0.25	

	random effect covariances	all	LKJ(1)		
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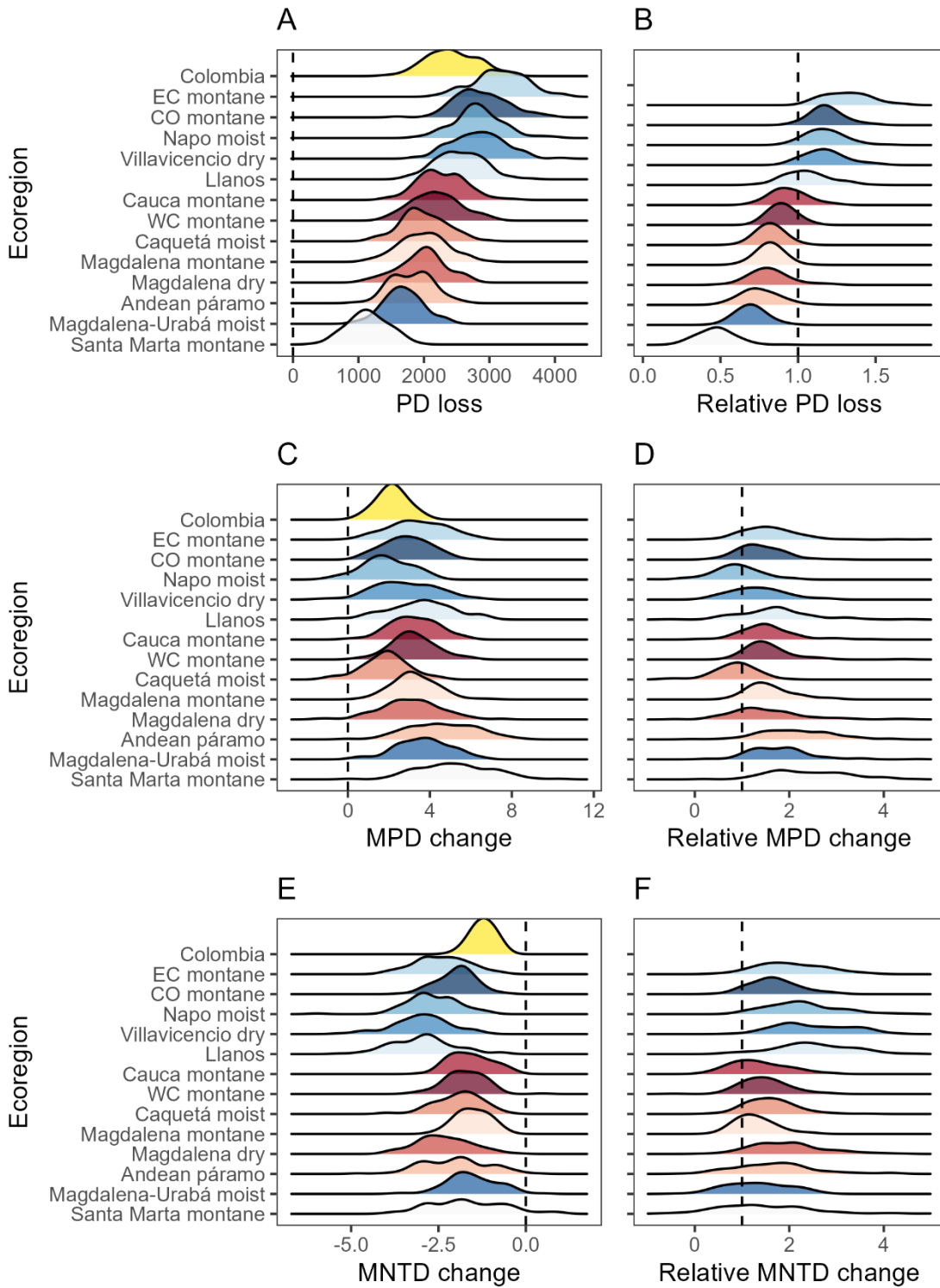
1020

1021

1022 **Supplementary Results S1**

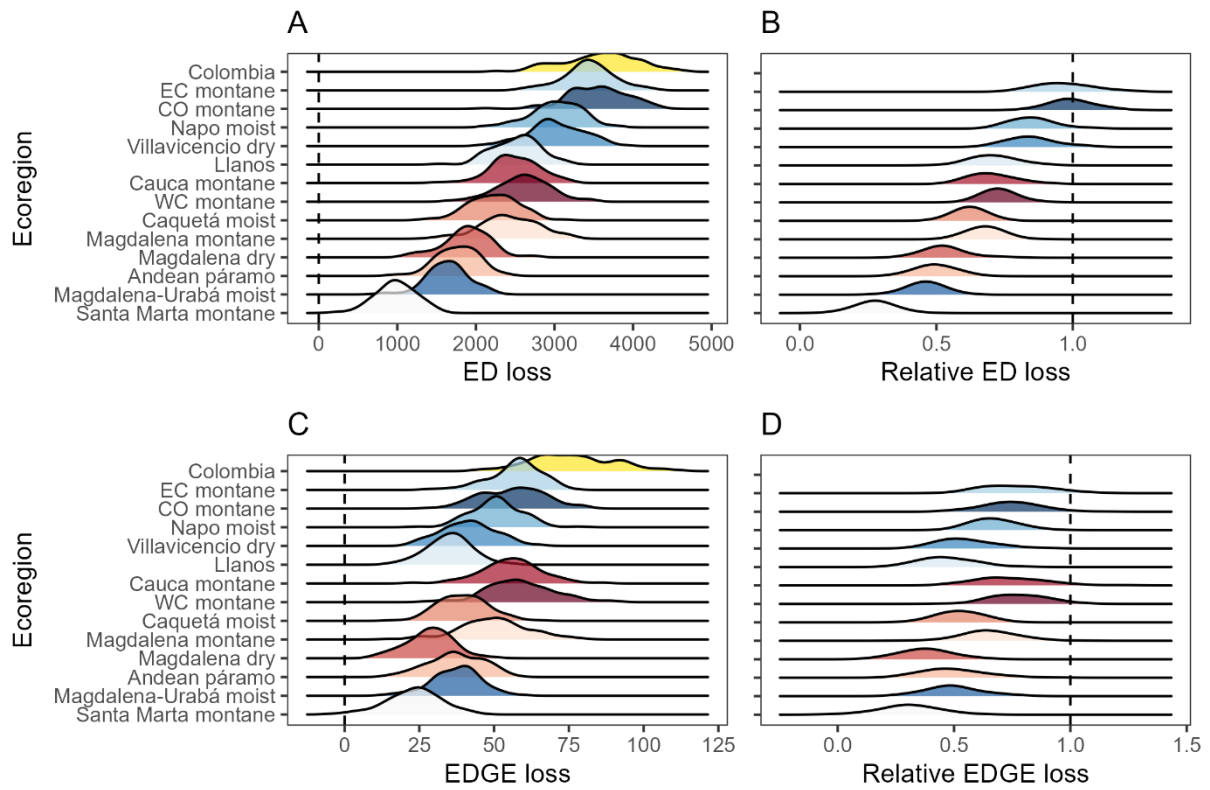
1023 During the review process, we were asked to examine the effect of excluding wetland species  
1024 from the analysis. Pasture expansion in tropical regions typically begins in wetter areas, which  
1025 provide better grazing conditions and flood regularly, offering suitable habitat for wetland non-  
1026 forest bird species. As a result, agricultural areas tend to retain relatively high PD values  
1027 because they are often occupied by wetland species, many of which belong to older lineages  
1028 and therefore contribute disproportionately to phylogenetic metrics.

1029 To assess this, we reproduced Figures 3, 4, and 5 from the main text after excluding wetland  
1030 species. We identified wetland species using the “habitat” category in the AVONET dataset  
1031 (Tobias et al. 2022) and excluded those classified as wetland, resulting in the removal of 112  
1032 species. SES metrics were omitted for brevity. The results closely mirror our main findings,  
1033 although the magnitude of biodiversity loss is slightly larger. Given this similarity and to avoid  
1034 overextending the discussion, we do not provide further interpretation.



1035

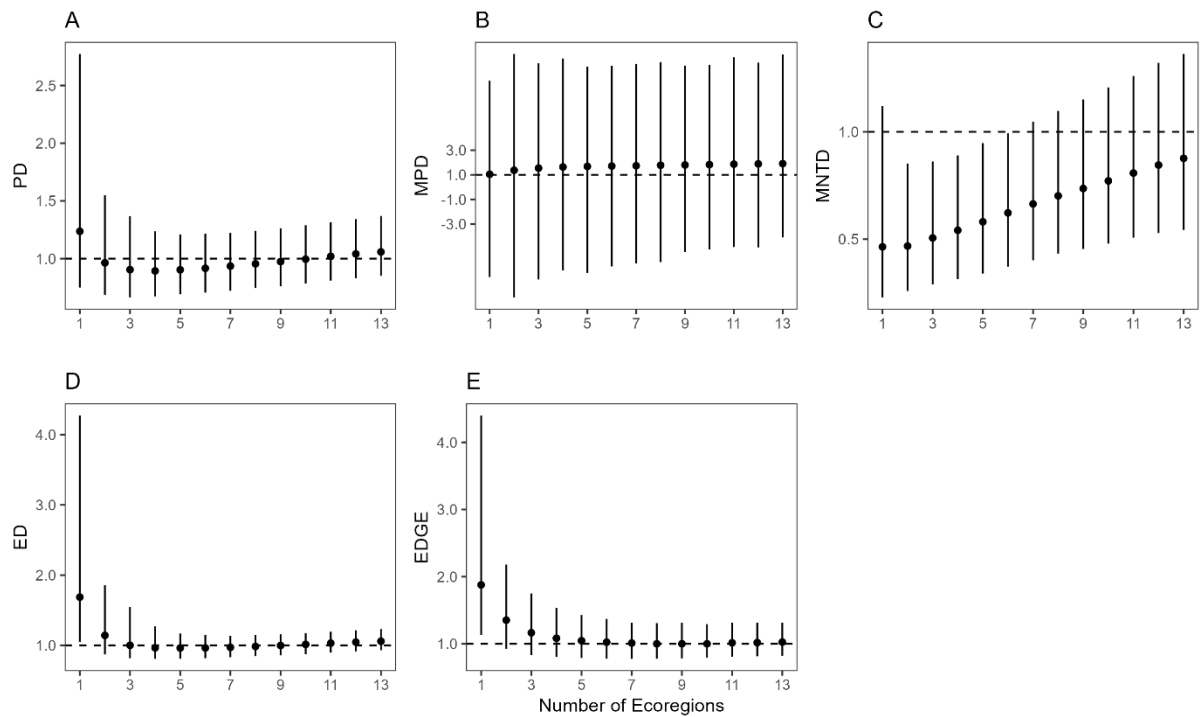
1036 Supplementary Result S1 Figure 3, Excluding wetland species. Impacts of forest conversion to  
 1037 pasture on phylogenetic diversity metrics across ecoregions and at the national scale (y-axis).



1038

1039 Supplementary Result S1 Figure 4, Excluding wetland species. Impacts of forest conversion to  
 1040 pasture on Evolutionary Distinctness (ED) and Evolutionary distinct and globally endangered  
 1041 (EDGE) metrics across ecoregions and at the national scale (y-axis).

1042



1043

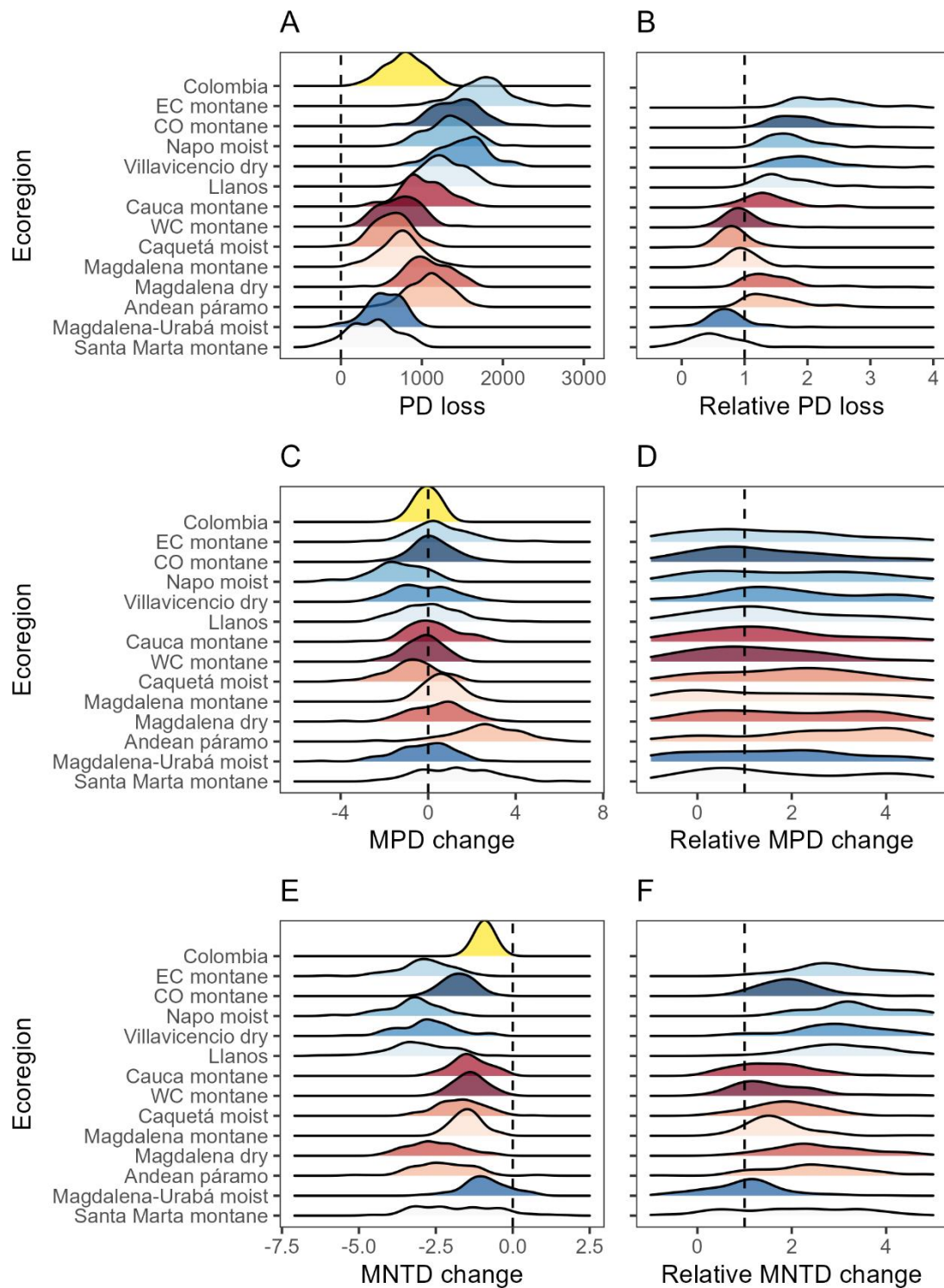
1044 Supplementary Result Figure 4, Excluding wetland species. Relative impacts of forest  
 1045 conversion on phylogenetic diversity metrics across increasing spatial scales (x-axis). Values  
 1046 represent the national loss divided by the loss from aggregated ecoregions (1 to 13). A ratio of  
 1047 1.0 (dashed line) indicates no difference. Values above 1.0 mean national loss exceeds regional  
 1048 loss (e.g. 1.5 = 50% greater), while values below 1.0 indicate overestimation by regional  
 1049 assessments.

1050

1051 **Supplementary Results S2**

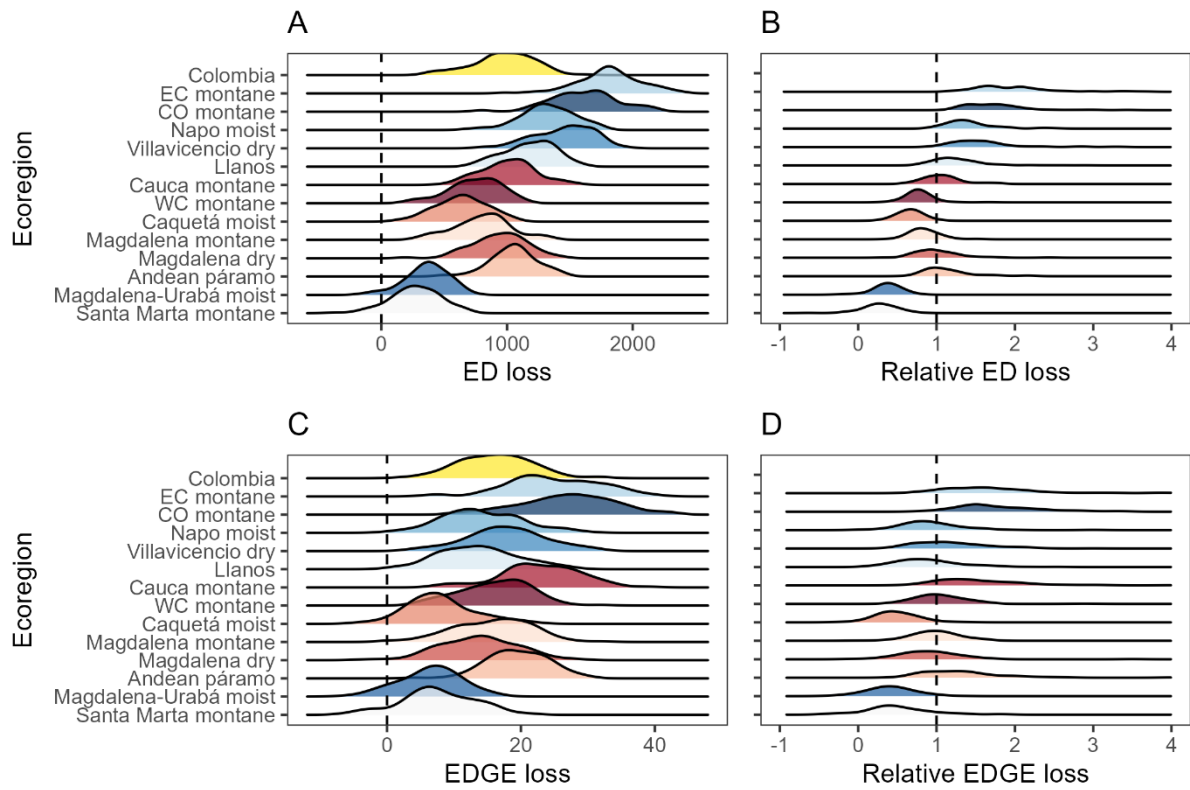
1052 To examine the potential effects of taxonomic extrapolation arising from the inclusion of  
1053 never-observed species in our model, we repeated most analyses after excluding these  
1054 species, that is, we included only species with at least one confirmed field detection. We  
1055 reproduced Figures 3, 4, and 5 from the main text after excluding never-observed species,  
1056 resulting in the removal of 611 species and the retention of 936 observed species. SES  
1057 metrics were omitted for brevity. The analysis of models including only species that were both  
1058 observed and included in the model confirms our main conclusion, although differences in  
1059 phylogenetic diversity metrics were reduced. National PD loss amounted to 1,450 Myr,  
1060 compared with 2,300 Myr in the main text, and ranged from 400 to 1,760 Myr across  
1061 ecoregions, compared with 730 to 2,500 Myr previously. Similarly, national ED loss was 900  
1062 Myr, compared with 3,350 Myr in the main text. As reported previously, other phylogenetic  
1063 diversity metrics showed minimal variation. These changes are expected, as the species  
1064 excluded from this analysis (never-observed species) tend to be those that are sensitive—rare,  
1065 cryptic, range-restricted, and forest-dependent. Given the similarity in overall patterns and to  
1066 avoid overextending the discussion, we do not provide further interpretation.

1067



1068

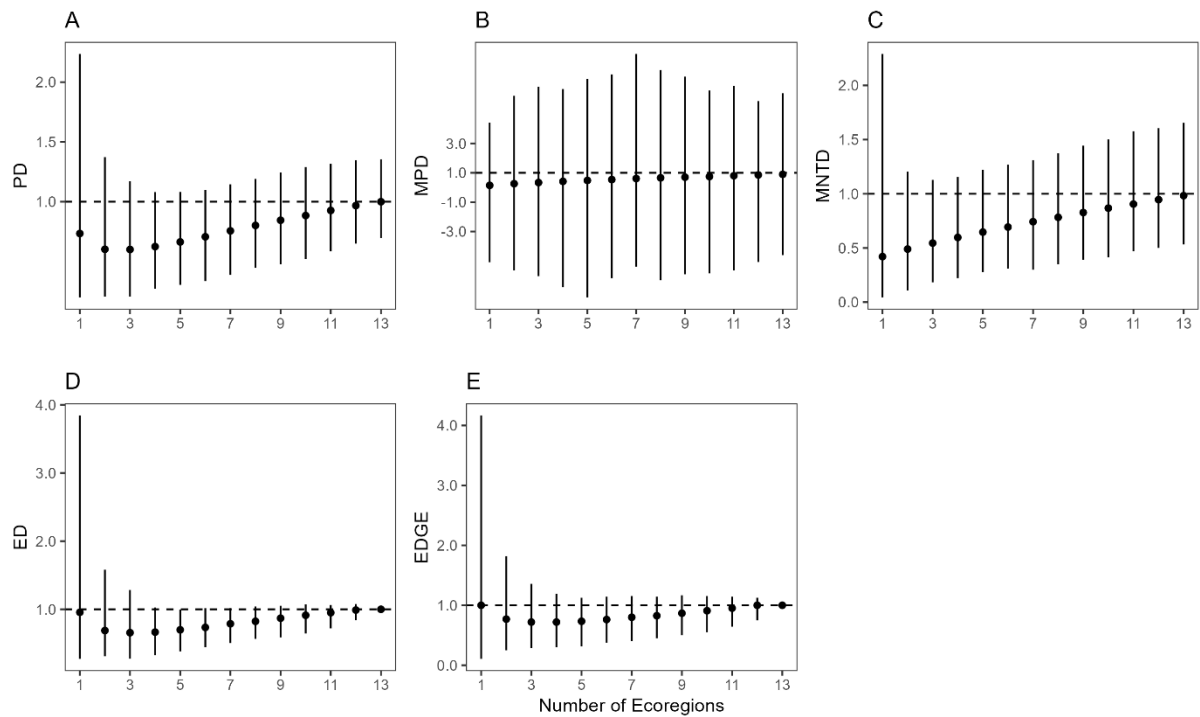
1069 Supplementary Result S2 Figure 3, Excluding never-observed species. Impacts of forest  
 1070 conversion to pasture on phylogenetic diversity metrics across ecoregions and at the national  
 1071 scale (y-axis).



1072

1073 Supplementary Result S2 Figure 4, Excluding wetland species. Impacts of forest conversion to  
 1074 pasture on Evolutionary Distinctness (ED) and Evolutionary distinct and globally endangered  
 1075 (EDGE) metrics across ecoregions and at the national scale (y-axis).

1076



1077

1078 Supplementary Result S2 Figure 4, Excluding wetland species. Relative impacts of forest  
 1079 conversion on phylogenetic diversity metrics across increasing spatial scales (x-axis). Values  
 1080 represent the national loss divided by the loss from aggregated ecoregions (1 to 13). A ratio of  
 1081 1.0 (dashed line) indicates no difference. Values above 1.0 mean national loss exceeds regional  
 1082 loss (e.g. 1.5 = 50% greater), while values below 1.0 indicate overestimation by regional  
 1083 assessments.

1084

1085