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RESEARCH ARTICLE

The effects of tropical secondary forest regeneration on avian phylogenetic diversity

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Abstract

1. The conversion of tropical forests to farmland is a key driver of the current extinction crisis. With the present rate of deforestation unlikely to subside, secondary forests that regenerate on abandoned agricultural land may provide an option for safeguarding biodiversity. While species richness (SR) may recover as secondary forests get older, the extent to which phylogenetic diversity (PD)—the total amount of evolutionary history present in a community—is conserved is less clear. Maximizing PD has been argued to be important to conserve both evolutionary heritage and ecosystem function.

2. Here, we investigate the effects of secondary forest regeneration on PD in birds. The regeneration of secondary forests could lead to a community of closely related species, despite maintaining comparable SR to primary forests, and thus have diminished biodiversity value with reduced evolutionary heritage.

3. We use a meta-dataset of paired primary and secondary forest sites to show that, over time, forest specialist species returned across all sites as secondary forest age increased. Forest specialists colonize secondary tropical forests in both the Old World and the New World, but recovery of PD and community composition with time is only evident in the Old World.

4. *Synthesis and applications*. While preserving primary tropical forests remains a core conservation goal, our results emphasize the important role of secondary forest in maintaining tropical forest biodiversity. Biodiversity recovery differs between Old and New World secondary forests and with proximity to primary forest, highlighting the need to consider local or regional differences in landscape composition and species characteristics, especially resilience to forest degradation and dispersal capability. While farmland abandonment is increasing across marginal areas in the tropics, there remains a critical need to provide long-term management and protection from reconversion to maximize conservation benefits of secondary forests. Our study suggests such investments should be focused on land in close proximity to primary forests.

KEYWORDS
avian biodiversity, community composition, land-use change, secondary forest regrowth, tropical forest

1 | INTRODUCTION

The biggest driver of the current extinction crisis is the conversion of tropical forest to farmland (Laurance, Sayer, & Cassman, 2014). Over 150 million hectares of tropical forest were converted to farmland between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013). However, in many areas, agricultural land has been abandoned resulting in the regeneration of secondary forests (Aide et al., 2013). These secondary forests could help to reduce biodiversity loss (Chazdon, 2014) by providing an alternative to primary forests for species that would otherwise go extinct (Wright & Muller-Landau, 2006). Species richness (SR) often recovers with secondary forest age (Acevedo-Charry & Aide, 2019; Barlow, Mestre, Gardner, & Peres, 2007; Gilroy et al., 2014), and many forest specialists that are threatened by forest loss may also recolonize secondary forests (Basham et al., 2016; Gilroy et al., 2014). However, our understanding of how biodiversity metrics other than SR differ between primary and secondary forests is limited.

One such gap in our knowledge is whether secondary forests conserve or support recovery of phylogenetic diversity (PD)—the total amount of evolutionary history present in a community (Faith, 1992). PD is potentially important for several reasons. First, while functional diversity—the range of functional roles occupied by species within a community (Petchey & Gaston, 2006)—and PD may not be perfectly correlated, prioritizing the conservation of PD is also expected to conserve functional diversity (Faith, 1992; Mazel, Mooers, Riva, & Pennell, 2017; Mazel et al., 2018; Pavoine, Gasc, Bonsall, & Mason, 2013). Functional redundancy increases as secondary forest age increases, potentially leading to greater resilience in ecosystem services (Sayer, Bullock, & Martin, 2017). Moreover, it has been argued that conservation objectives focused on a narrow set of functional traits could lead to the loss of PD. This is because there are many potential axes of functional diversity that are typically condensed to a subset of traits that are easy to measure and/or widely available. Instead, PD may more effectively capture a wide suite of traits encapsulated under the concept of feature diversity, defined broadly as the different evolutionary features of diversity (Faith, 1992; Owen, Gumbs, Gray, & Faith, 2019). Second, phylogenetically diverse communities are more likely to hold evolutionarily distinct or relict species with few close relatives (Jetz et al., 2014) and so harbour a disproportionately large amount of evolutionary history. Third, there is intrinsic value in conserving as much of the world's evolutionary heritage as possible (Winter, Devictor, & Schweiger, 2013). Therefore, understanding how PD recovers and the mechanisms that drive this recovery is critical to understanding the conservation potential of secondary tropical forests.

Recovery of SR alone is unlikely to be an informative guide to the conservation value of secondary forests as SR (i.e. alpha diversity) tells us nothing about community composition. Conversion of forest to agriculture could result in the loss of forest-dependent or disturbance-sensitive species, and the gain of disturbance-tolerant species or species adapted to more open habitats. As such, whilst SR may recover rapidly following abandonment, it may markedly differ in community structure, phylogenetic composition, and ecosystem function. However, subsequent succession towards secondary forest may allow the return of forest-dependent species. Large frugivores and understorey insectivores, for example, are particularly forest dependent and sensitive to disturbance (Powell et al., 2015; Şekercioğlu, 2012; Şekercioğlu et al., 2002) so may require time for secondary forest to mature before returning. In addition, species with low dispersal abilities may have a reduced ability to recolonize secondary forests (Laurance & Gomez, 2005; Moore, Robinson, Lovette, & Robinson, 2008), particularly if secondary forest patches are far from the remaining primary forest source pool.

At one extreme, the same set of species originally found in the primary forest prior to conversion to agriculture could recolonize the secondary forest resulting in the simultaneous recovery of SR, community composition, and PD. At the other extreme, community intactness may be substantially degraded. PD in intact primary forest tends to be greater than expected by chance and rapid land-use change results in phylogenetic clustering of communities as PD is lost rapidly with increasing agricultural intensification (Frishkoff et al., 2014; Prescott et al., 2016). This leads to the prediction that young secondary forests should have low PD compared to primary forests whereas differences in SR may be comparatively minor. If secondary forest provides a viable alternative habitat for primary forest species, then PD should increase with age as the forest matures (e.g. Edwards, Massam, Haugaasen, & Gilroy, 2017). The effect of variability in species traits and of the landscape matrix is that recovery of SR, community composition and PD may be further mediated by the degree of isolation of secondary forest patches, with stalled or slow recovery in the most isolated secondary forests.

Here, we conduct the first pan-tropical assessment of change in PD with secondary forest age. We focus on birds, because they are functionally important components of ecosystems (Şekercioğlu, Wenny, & Whelan, 2016). Specifically, we assess if SR and PD vary between primary and secondary forests and whether the secondary forest communities attain comparable SR and PD to paired primary forest communities as time since abandonment increases. We further assess how distance to primary forest, biogeography (Old World vs. New World) and climate mediate variation in the recovery of tropical forest bird communities.

2 | MATERIALS AND METHODS

2.1 | Data collation

A total of 20 pan-tropical studies containing 35 paired secondary and primary forest sites were selected from a review by Sayer et al. (2017; see Data Sources and Table S1). Seven sites included by Sayer et al. (2017) were considered unsuitable for the present study (i.e. due to incomplete species lists, ambiguous secondary forest ages, etc.) and were excluded (Appendix S1). All sites included were in the tropics and subtropics with 21 in the New World and 14 in the Old World (Figure 1). Primary forest sites are native forests with no evidence of previous deforestation and degradation. Secondary forest sites are defined as areas undergoing succession after all or nearly all trees had been removed to make way for agriculture (Corlett, 1994). Forests recovering after fires
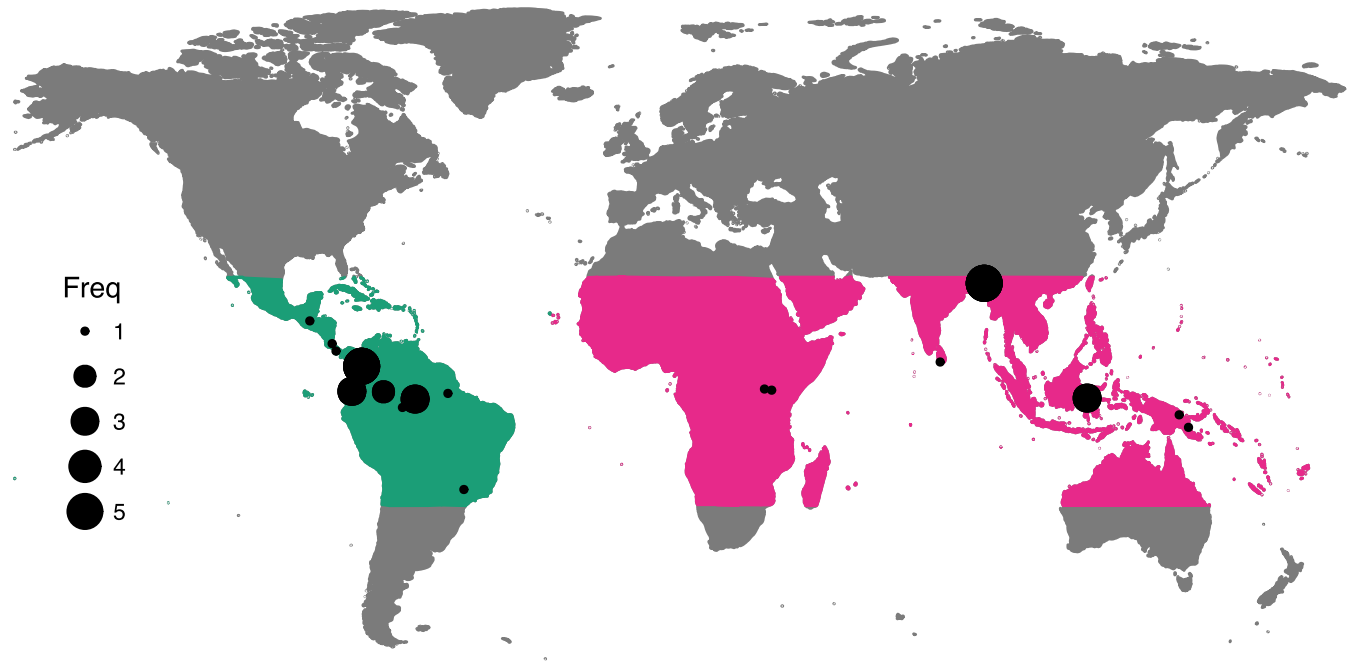
FIGURE 1 The distribution of the 35 paired sites in this study. Sites were chosen within 24 degrees of latitude from the equator. The number of paired sites per study area is indicated by circle size. The New World is coloured green and the Old World is coloured pink

or sites that had been selectively logged were not included in this definition.

The ages of secondary forest sites were given in each study as single ages or age ranges where similarly aged stands were grouped together. In the latter instance, the median values of secondary forest patches were calculated (Sayer et al., 2017). Where available, we extracted the distances between paired primary and secondary forest sites from measured values, or qualitative descriptions given in the studies considered (n = 31; Table S1). Each of the chosen studies sampled the entire local avian community in both primary and secondary forest patches using consistent methods within studies, but which varied between studies (i.e. point counts, mist netting, transects). Specific information regarding how each species observed used the habitat (e.g. foraging, breeding, etc.) were not described.

We also collected data for three environmental variables at each site. Elevation (metres above sea level) for each site was obtained from the GTOP030 global digital elevation model (GTOPO30 DEM, 1996) using Google Earth Engine (Gorelick et al., 2017). Mean annual temperature and mean annual precipitation were extracted for each site from the WorldClim database (Fick & Hijmans, 2017). Elevation, precipitation and temperature were log-transformed prior to analysis.

2.2 | Measures of species richness and phylogenetic diversity

For each study site, we calculated the number of different species present in each community (SR), and beta diversity (βTD; Whittaker, 1960, 1972), and phylogenetic beta diversity (βPD; Bryant et al., 2008; Graham & Fine, 2008) as measures of community intactness, for each

paired primary and secondary forest site. We calculated the Sørenson index in the R package VEGAN (version 1.4-2: Oksanen et al., 2008) as a measure of βTD, to assess the losses of species from each secondary forest site compared to the corresponding paired primary site. βPD was measured as a fraction of the phylogenetic branch lengths present in secondary forest communities that were also present in paired primary forest communities using the *phylosor* function in the R package PICANTE (version 1.6-2: Kembel et al., 2010).

We also calculated three PD metrics and their standardized effect sizes using the R package PICANTE (version 1.6-2: Kembel et al., 2010). These were: phylogenetic diversity (PD, the total amount of evolutionary history represented by a community; Faith, 1992); mean pairwise difference (MPD, average phylogenetic distance between every combination of paired individuals in a community; Webb, Ackerly, McPeek, & Donoghue, 2002); and the mean nearest taxon distance (MNTD, average phylogenetic distance between an individual and its closest relative in the community; Webb et al., 2002). Because PD, MPD and MNTD can all scale with SR (Webb et al., 2002) we calculated standardized effect sizes for each raw PD measure using the 'richness' algorithm in PICANTE. This maintains SR for each site but allows the random selection of species from a wider species pool (Webb et al., 2002). We refer to these metrics as ses.PD, ses.MPD and ses.MNTD respectively. A full description of the metrics, including the equations used, is available in the Table S2.

Species pools were generated by downloading species lists from http://mol.org/ (Map of Life, 2017) for a 50-km radius around each study site. Map of Life uses species range maps (e.g. BirdLife International), as well as data from additional sources such as point count data from published studies. A 50-km radius was chosen for three reasons. Firstly, it allows the inclusion of all species that are likely to occur at each site. Secondly, previous studies have shown

that finer spatial resolutions are not practical given the quality of range maps, and can give an inaccurate representation of observed species pools (Hurlbert & Jetz, 2007). Thirdly, the Map of Life database only allows for a radius of 50 km to be selected. Including all species within a 50-km radius of each site could result in species appearing that would never occur at our sites, particularly in areas that are topographically diverse or at the margins of distinct biomes. To investigate the impact of changing species pools, we ran analyses on subsets of our species pools (all species, and forest only species), and found similar results in both instances (Tables S5 and S6).

We downloaded 500 phylogenetic trees based on the Hackett backbone (Hackett et al., 2008) from http://birdtree.org/ (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) and calculated all metrics on every tree to account for phylogenetic uncertainty. For each measure of PD and for βPD, the 500 values were found to be normally distributed and an arithmetic mean value was taken for each site or paired site community.

2.3 | Statistical analysis

We used linear mixed-effects models in the LME4 R package (version 1.1-13: Bates, Mächler, Bolker, & Walker, 2014) with RStudio version 1.0.136 (RStudio Team, 2016) and R version 3.3.2 (R Core Team, 2016). We included study identity as a random effect in all models because study areas included multiple secondary forest sites with a single primary forest site (Table S1). As differing evolutionary histories and biogeographic variation in dispersal may influence PD recovery patterns, we compared New World and Old World sites. For each analysis, models were constructed with either the fixed effect of forest type (primary or secondary), or secondary forest age and distance between primary and secondary sites, as well as the random effect of study identity. Secondary forest age and distance between primary and secondary sites were log-transformed. These models were compared to a null intercept only model, with study identity as a random intercept. Residuals for each model were checked for normality and homoscedasticity. Likelihood ratio tests (LRTs) were used to compare models. We added our three climatic predictors in turn to the best-fitting age and distance models for each response variable and region combination.

2.3.1 | Primary versus secondary forests

We analysed the effect of forest type on SR and each of the raw PD metrics.

2.3.2 | Species and phylogenetic community composition

We tested the effect of secondary forest age, and distance between paired primary and secondary forest sites, on community

intactness. We calculated community intactness for βTD and βPD between paired primary and secondary forest sites using a restricted species pool containing just primary forest species (n = 1,179).

2.3.3 | Species and phylogenetic diversity

We next examined changes in PD with time since secondary forest abandonment. We calculated our metrics on all species (n = 1,519), and also on a reduced subset, excluding species that were defined by BirdLife International as 'Non-forest' (does not normally occur in forested habitat). The remaining 1,478 species were categorized as having either 'High' (forest specialists, always or nearly always recorded in primary forest), 'Medium' (largely found in primary forest, but often occurs and can breed, in degraded habitat) or 'Low' (can occur in primary forest, but more often found and breeds, in degraded habitat) forest dependency (Birdlife International, 2017; Buchanan et al., 2008; Figure S1). When considering only forest species in our analyses, we likewise reduced the species pools used for calculating standardized effect sizes by removing species that were defined as not dependent on forests (Birdlife International, 2017).

We calculated the log response ratio (Hedges, Gurevitch, & Curtis, 1999) as the log proportional difference between the means of each metric (SR, PD, MPD, MNTD) in secondary forest sites and primary forest sites. Values of ses.PD, ses.MPD and ses.MNTD can be negative, and so raw differences between paired secondary and primary forest were calculated.

2.3.4 | Forest-dependent species

We investigated whether the proportion of forest-dependent species at each site became more equal as secondary forest age increased. For each site, we calculated the percentage of the avian community that were classed by Birdlife International (2017) as having 'High' forest dependency, before calculating the difference between those percentages for each paired secondary and primary forest sites.

3 | RESULTS

Across all study sites, 1,519 unique species were recorded spanning 87 avian clades (Figure 2). We found large clades in Old World sites with similar numbers of species found in both primary and secondary forest types (i.e. Shrikes and Monarchs, Pigeons and Doves, Cuckoos), with the exception of the Chats and Old World Flycatchers with higher SR in secondary forest sites. Some families with only a single species represented across all study sites were present in primary but not secondary forests (e.g. Whipbirds and Allies: *Ptilorrhoa caerulescens*, Bowerbirds: *Ailuroedus buccoides*).
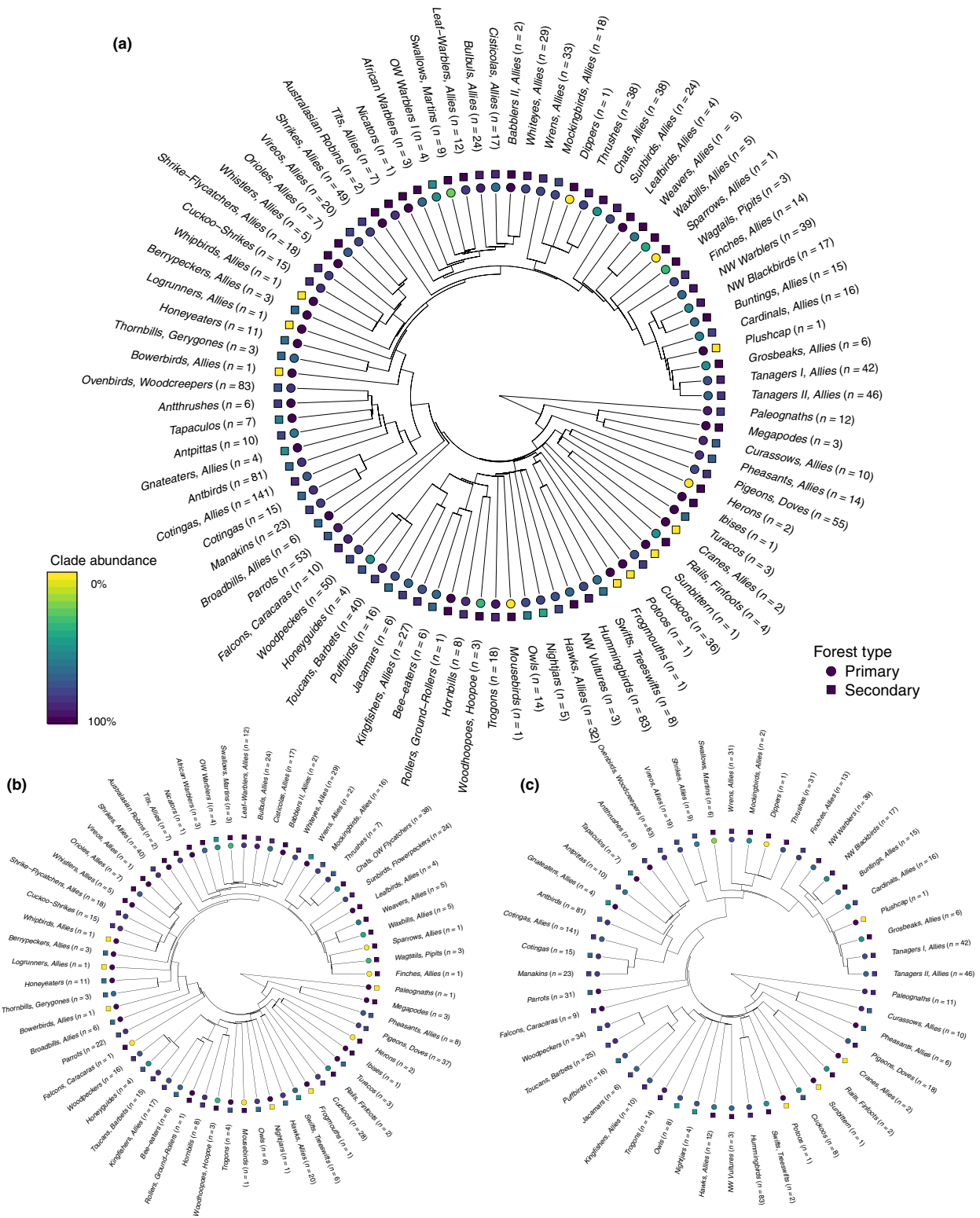
FIGURE 2 Phylogenetic distribution of avian clades in secondary and primary forests across (a) all study sites, (b) Old World sites and (c) New World sites. Spots and squares show a clade's presence in primary and secondary forest respectively. The colour scale bar shows the proportion of species in a clade which is found in that particular habitat type

In the New World, many avian clades were species rich in both primary and secondary forests (e.g. Woodpeckers, Trogons, Manakins and Cotingas; Figure 2c). Some very small clades were present in only primary (Potoos and Sunbittern) or only secondary forest

sites (e.g. Sparrows and Dippers). Several young passerine clades (e.g. Tanagers, Grosbeaks, Cardinals, Buntings, New World Blackbirds, New World Warblers) were more species rich in secondary than primary forests.

3.1 | Primary versus secondary forests

Primary forests had a similar SR to secondary forests across the tropics (LRT: $\chi^2 = 1.01$, $p = 0.315$), in the New World (LRT: $\chi^2 = 0.26$, $p = 0.609$), and in the Old World (LRT: $\chi^2 = 1.43$, $p = 0.232$). PD did not differ between primary forests and secondary forests across all sites (LRT: $\chi^2 = 2.45$, $p = 0.118$), Old World sites (LRT: $\chi^2 = 2.63$, $p = 0.105$) or New World sites (LRT: $\chi^2 = 0.52$, $p = 0.469$). Similarly, we found no differences in ses.PD, MPD, ses.MPD, MNTD or ses.MNTD between primary and secondary forests, in the New World, Old World and across all sites (Table S3).

3.2 | Species and phylogenetic community composition

Avian communities in paired secondary and primary forest sites in the Old World became increasingly similar in both species (βTD; Figure 3a; Table S4; LRT: $\chi^2 = 17.71$, $p < 0.001$) and phylogenetic (βPD; Figure 3b; Table S4; LRT: $\chi^2 = 19.51$, $p < 0.001$) composition with increasing time since abandonment. Based on estimated slopes, secondary forest species and phylogenetic composition would equal that of primary forests after 97 and 92 years respectively. In the Old World, distance between secondary and primary forest sites did not influence phylogenetic (LRT: $\chi^2 = 0.16$, $p = 0.685$) or species community intactness (LRT: $\chi^2 = 0.19$, $p = 0.665$; Figure 3c,d; Table S4). We also found a significant interaction with distance for both βTD and βPD where recovery appeared to be more rapid in more isolated sites (Table S4). We

suggest that the counterintuitive result may be spurious because only three Old World sites are isolated from primary forest, and in those sites, distance and age have a perfect rank correlation.

We found no change in βTD (LRT: $\chi^2 = 0.01$, $p = 0.923$) or βPD (LRT: $\chi^2 = 0.05$, $p = 0.827$) between paired primary and secondary forest communities in the New World as time since disturbance increases (Figure 3a,b; Table S4). Indeed, soon after land abandonment, New World communities retained around 72% of species and 79% of phylogenetic intactness compared to primary forest communities, and this did not significantly change across the 50-year study period. However, we found that as distance between sites increases, the number of primary forest species that are found in New World secondary forest sites decreases (LRT: $\chi^2 = 5.43$, $p = 0.020$), but that phylogenetic intactness (LRT: $\chi^2 = 3.30$, $p = 0.069$) did not change (Figure 3c,d; Table S4). We found no effect of any of the climatic predictors on species or phylogenetic community intactness (Table S8).

3.3 | Species and phylogenetic diversity

Across all sites, relative SR did not increase with secondary forest age (LRT: $\chi^2 = 2.22$, $p = 0.137$). However, in the Old World, as secondary forest age increased relative SR recovered (LRT: $\chi^2 = 6.39$, $p = 0.011$) and reached primary forest levels in ~46 years (Figure 4a; Table S5). As with our analysis of community intactness above, we found a significant but weak interaction between age and distance. Secondary forest age did not have a significant effect on SR in the New World (LRT: $\chi^2 = 0.01$, $p = 0.928$). We found a positive effect of secondary forest age on PD recovery in the Old World (LRT: $\chi^2 = 4.01$, $p = 0.045$),
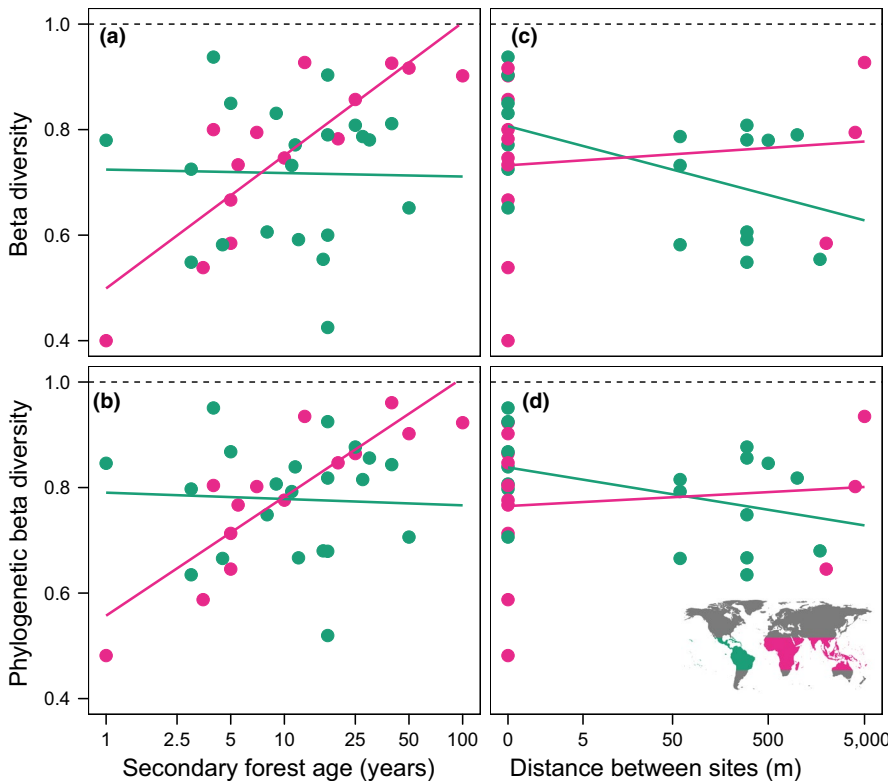
FIGURE 3 The effect of secondary forest age on (a) βTD and (b) βPD and the distance between primary and secondary forest sites on (c) βTD and (d) βPD in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. On both *y*-axes, values fall between 0 (primary and secondary forests are dissimilar) and 1 (primary and secondary forests are similar). Lines of best fit were plotted from the fixed effects output of our mixed-effects models. The dotted line represents the value at which primary and secondary forests are identical

FIGURE 4 The effect of secondary forest age on (a) relative species richness (SR), (b) relative phylogenetic diversity (PD), (c) relative mean nearest taxon distance (MNTD) and (d) relative ses. MPD in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. If SR, PD, MNTD or ses.MPD is lower in secondary forests compared to primary forests, values on the y-axis will be negative and vice versa. Lines of best fit were plotted from the fixed effects output of our mixed-effects models. The dotted line highlights where SR, PD, MNTD and ses.MPD are equal in both primary and secondary forests
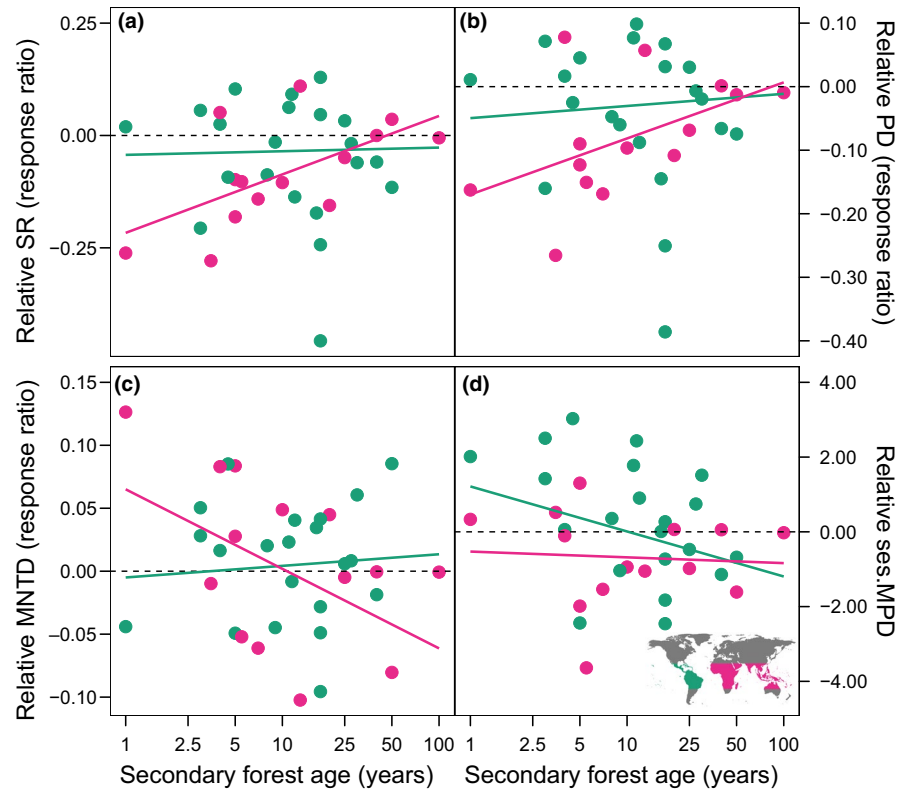

with PD reaching primary forest levels ~84 years after disturbance (Figure 4b; Table S5). Secondary forest age did not have a significant effect on PD in the New World (LRT: $\chi^2 = 0.08$, $p = 0.782$). Secondary forest regeneration time had no effect on ses.PD levels in the New World, Old World or across all sites (Table S5).

Across New World sites, relative ses.MPD decreased as secondary forest age increased (LRT, $\chi^2 = 4.40$, $p = 0.040$; Figure 4c; Table S5). This indicates that species within communities become more closely related to each other as secondary forest age increases. We found no effect of secondary forest age on ses.MPD in the Old World or across all sites (Table S5). Relative MNTD decreased in the Old World as secondary forests get older (LRT, $\chi^2 = 4.31$, $p = 0.038$; Figure 4d; Table S5). No change in relative MNTD was found in the New World or across all sites (Table S5). Secondary forest age did not predict relative MPD, MNTD or ses.MNTD in the New World, Old World and across all sites, with models containing secondary forest age not significantly explaining the data better than null models. Adding climatic variables to our best-fitting age and distance models did not improve model fit for any metric of richness or PD (Table S8).

3.4 | Forest-dependent species

We found that the relative proportion of forest-dependent species increased with secondary forest age across all sites (LRT: $\chi^2 = 9.55$, $p = 0.002$), New World (LRT: $\chi^2 = 4.12$, $p = 0.043$) and Old World sites (LRT: $\chi^2 = 7.02$, $p = 0.008$; Figure 5; Table S7). Indeed, there were an equal percentage of forest-dependent species in paired primary and secondary forest sites in the Old World after 45 years. However,
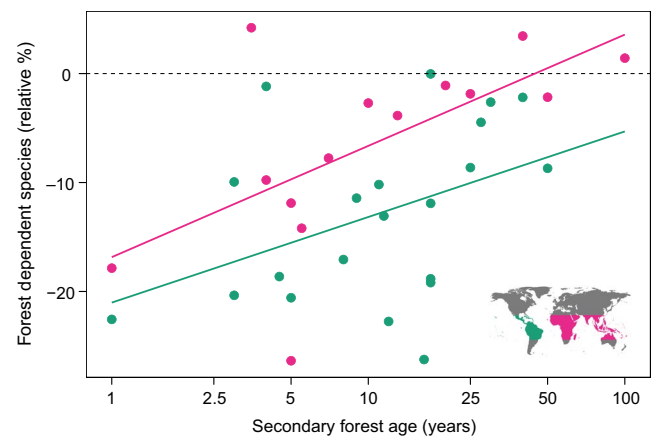
FIGURE 5 The effect of secondary forest age on the proportion of highly dependent forest species found in secondary forest communities when compared to the paired primary forest site in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. Lines of best fit were plotted from the fixed effects output of our mixed-effects models. The dotted line highlights where the proportion of highly dependent forest species in a community is equal in both primary and secondary forests

after 50 years of secondary recovery in the New World, there were still 7.7% fewer forest-dependent species in secondary forests, compared to primary forests. The proportion of forest-dependent species declined with increasing temperature when temperature was added to the best-fitting age and distance model, but only for the New World and global analyses. No other climatic variables improved model fit (Table S8).

4 | DISCUSSION

Our study represents the first global assessment of recovery of avian PD in secondary tropical forests. Our results confirm that secondary forests can act as important reservoirs of PD, particularly in landscapes with little remaining natural forest (Frishkoff et al., 2014). Overall, we find that avian PD recovers towards primary forest levels as Old World secondary forests become older, reaching equivalence at around 100 years, but that this level of recovery is not evident in New World secondary forest. Importantly, this pattern is not driven by the colonization of a closely related set of species, but by the same set of species found in primary forests returning to Old World secondary forests sites over time (as highlighted by increasing community intactness with age). This suggests that, at least in the Old World, forest specialist species that are threatened by forest loss are returning to secondary forests. In New World secondary forests, previous work has shown that both SR (Dunn, 2004) and PD (Edwards et al., 2017) recover as secondary forest age increases. Our findings from the Old World support the hypothesis that secondary forest regeneration can lead to comparable biodiversity to those found in primary forests and that PD recovers concomitantly with SR as the set of species that colonize secondary forest during recovery is drawn from the primary forest pool.

Previous studies (e.g. Edwards et al., 2017; Frishkoff et al., 2014) found that the conversion of primary forest to agricultural land can initially lead to phylogenetic clustering, with the avian community containing species that are on average much more closely related to each other in evolutionary time. If secondary forest allows recovery of avian communities, then we might expect to see the trend reversed with increasing PD and decreasing clustering through time. Our results are partially consistent with this prediction, but suggest a more nuanced dynamic of gains of forest species alongside loss of non-forest, open habitat species. In both the Old and New World, the proportion of forest-dependent species increases with secondary forest age, although the effect appears to be weaker in the New World, at least with respect to our sampled sites. In the Old World, this is concomitant with increases in SR and PD. In the New World, neither SR nor PD increases with age.

The degree of phylogenetic clustering, however, appears to increase with age in both the Old World and the New World. This result is best explained by the gradual shift from open/agricultural habitats to mature forest, as opposed to the abrupt change associated with deforestation in the reverse direction. Avian communities in the early stages of recovery are likely to consist of resilient open habitat species (Acevedo-Charry & Aide, 2019), those from younger clades (Edwards et al., 2017; Frishkoff et al., 2014), species with wide diet breadths (e.g. granivores; Frishkoff et al., 2014) and the most resilient forest-dependent species. Over time, the gain of forest species seems to outweigh the loss of open habitat species, leading to net gains in SR and total PD (although this was only observed in the Old World in our data). However, the community becomes increasingly dominated by a more closely related set of forest specialists returning and becoming more common (e.g. understorey insectivores: Acevedo-Charry & Aide, 2019; Stratford & Stouffer, 2015). This turnover-driven pattern is borne-out by considering analyses using species pools including all species compared to species pools with only forest-dependent species: the clustering trends are much weaker or absent in analyses including only forest-dependent species. If this pattern of recovery continues steadily over time, then we would expect to observe trends that eventually lead to clustering patterns that are similar to those in primary forests. The absence of this pattern in our data suggests that secondary forest may take a longer period of time than that captured in our dataset for to mature. If so, then some of the most forest-dependent species may have not yet returned, and indeed may never return (Acevedo-Charry & Aide, 2019; Sayer et al., 2017). In both our Old and New World samples, species from some clades represented in primary forest do not appear in secondary forest sites and are also among the most phylogenetically distinct, such as Potoos and Sunbittern in the New World and the Nightjars and Frogmouths in the Old World.

While forest species appear to increasingly colonize secondary forest communities over time in both the Old and New World, community composition recovers with age in the Old World but not the New World where paired primary and secondary forests hold 72% of the same species, and this does not significantly change across the 50-year study period. This could be interpreted as evidence for hemispheric differences in the response of species and such differences could be the result of largely independent evolutionary histories. However, we suggest a more parsimonious explanation due to differences in the sites included in our meta-dataset. Specifically, in the Old World, the majority of paired sites are contiguous such that secondary forest abuts primary forest. Only three sites in our Old World data are not connected (and are also the most distant sites within the entire dataset). Effectively, and by chance, this controls for potential confounding effects of distance and the role of species-specific dispersal in determining patterns of recovery. In contrast, New World sites are rarely contiguous and distances between secondary and primary forest sites are highly variable (ranging from 0 to 1,725 m). Indeed, our models including distance between sites suggested lower recovery as distance increases. That is, in the New World recovery by distance may mask any effect of recovery by age. We are cautious in our interpretation because the distance data are incomplete and, in some cases, qualitative rather than quantitative.

An alternative explanation for our finding that PD recovery differs in the Old and New World could be a difference in species dispersal potential. Moore et al. (2008) found that some Neotropical species in Panama were unable to fly 100 m, and similarly, passerines from the families Formicariidae and Thamnophilidae in the Brazilian Amazon failed to cross 250 m over farmland to reach their territories (Laurance & Gomez, 2005). While bird groups with poor dispersal ability, such as the wren-babblers (Timallidae), do occur in the Old World, there may be disproportionately more poorly dispersing species in the New World. At present, detailed data on the dispersal ability of many tropical birds are lacking. Nonetheless, identifying whether New World species share any dispersal, or colonization, limiting traits could suggest that region- and ecology-specific conservation strategies are required for secondary forest management.

5 | CONCLUSIONS

5.1 | Management implications

The rate of deforestation of primary tropical forests is unlikely to slow. In some regions that have experienced high levels of primary forest loss in agriculturally suitable areas, the area of space occupied by secondary forests is increasing as farmland is abandoned. For instance, in Latin America and the Caribbean, >360,000 km^2 of new secondary growth occurred between 2001 and 2010 (Aide et al., 2013). Furthermore, each year around 290,000 km^2 of secondary forest regrowth occurs on abandoned land globally (Hurtt et al., 2017). Abandonment is most likely to happen in marginal areas that are too dry or steep for more modern farming methods (de Rezende, Uezu, Scarano, & Araujo, 2015; Sloan, Goosem, & Laurance, 2016), and it is these marginal areas that perhaps pose the biggest opportunities for conservation gains (Edwards et al., 2017; Gilroy et al., 2014).

Forest connectivity, the sizes of primary forest patches and human activity could influence the rate at which species can re-colonize secondary forests following abandonment (Banks-Leite, Ewers, & Metzger, 2012; Maldonado-Coelho & Marini, 2000; Prugh, Hodges, Sinclair, & Brashares, 2008). The majority of secondary forests are reportedly found in close proximity to remnant forest across the tropics (Crk, Uriarte, Corsi, & Flynn, 2009; Edwards et al., 2017; Sloan et al., 2016), and it is therefore likely that primary forest patches acted as sources of colonizing dispersers to secondary forest patches across all sites in our study (Gilroy & Edwards, 2017). Indeed, in the Old World, the majority of secondary forest sites are contiguous with primary forest sites.

Although secondary forest regeneration is likely to occur in areas that are unsuitable for modern farming practices, they still face the threat of deforestation. Indeed, in Costa Rica, 50% of secondary forests were found to have been cleared within 20 years, and 84% within 54 years (Reid, Fagan, Lucas, Slaughter, & Zahawi, 2018). In both the Old and New World, using carbon-based payments for ecosystem services under REDD+ to protect these new forests from deforestation or to enhance the rate with which land is abandoned and returned to secondary forest (Gilroy et al., 2014) represents a key conservation opportunity. Furthermore, the emerging global Forest and Landscape Restoration agenda, in which nations have targeted 350 million hectares of restoration by 2030 (Bonn Challenge, n.d.; GPFLR, 2003), represents another policy driver for the recovery of secondary forests. Such investments should be focused on land in close proximity to primary forests, which our study suggests would enhance the rate of recovery of diversity. In addition, regenerating forests tend to be poorly protected, with laws, policies and socioeconomic conditions that can work against long-term persistence. In Costa Rica, for example, the laws that protect forests exclude young, regenerating sites; in fact, they are often targeted for clearing to prevent them being reclassified as forest (Sierra & Russman, 2006). We thus need to focus our attention on legal frameworks to remove disincentives to the longer term persistence of secondary forests.

Taken together, our results not only point to an important role of secondary forest in maintaining tropical forest biodiversity but also suggest the critical need to provide long-term management and protection to maximize conservation benefits. We also highlight the importance of integrating local and regional patterns of fragmentation and landscape ecology when investigating the potential of secondary forests to safeguard biodiversity (Arroyo-Rodríguez et al., 2017). Secondary forests are likely to be at constant threat of reconversion to farmland (Reid et al., 2018; Sánchez-Cuervo & Aide, 2013; Sodhi et al., 2010) and given that agricultural land has far lower SR and PD than does secondary forest (Edwards et al., 2017), protection of secondary forests should be seen as a priority for the conservation of tropical biodiversity.

AUTHORS' CONTRIBUTIONS

E.C.H., D.P.E. and G.H.T. conceived the ideas and designed methodology; E.C.H., C.A.S. and P.A.M. collected the data; E.C.H. analysed the data; E.C.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

This paper brings together data from a number of published studies which are referenced in the Data Sources section below, and outlined in Table S1. C. Banks-Leite, D. Becker, S.H. Borges and B. Maas, provided access and permission to use additional data for this study. Our generated data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.0p2ngf1ww (Hughes, Edwards, Sayer, Martin, & Thomas, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.