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Dynamics of avian species and functional diversity in secondary tropical forests

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Abstract
Deforestation for agriculture in the tropics, followed by abandonment, has resulted in large areas of secondary forest. Some authors have suggested that this secondary regrowth could help prevent mass extinction in the tropics by providing habitat for forest species. However, there is little generalised understanding of the biodiversity value of secondary forest. To address this knowledge gap, we conducted an analysis of avian responses to secondary forest succession, comparing data from 44 tropical secondary forest sites with nearby primary forest sites and investigating both species and functional diversity based metrics. Total species richness in secondary forests was 12% lower than in primary forests and was not related to secondary forest age. In contrast, forest specialist species richness increased with time since disturbance, reaching 99% of primary forest values after 100 years. In terms of functional diversity, functional dispersion (FDis) and functional divergence (FDiv) were similar in primary and secondary forests. However, functional evenness (FEve) was 5% higher in secondary than in primary forests. The standardized effect size of functional diversity (sesFD) was higher in young secondary forests than primary forests and declined with time since disturbance. Overall, these results suggest that secondary tropical forests can support provision of ecosystem services but that these services may be less stable in young forests. Therefore, secondary tropical forests, particularly older regrowth, have biodiversity value and can support important ecosystem functions. These secondary forests should be protected from further disturbance but preserving primary forest is vital for supporting overall and forest specialist species richness.

Key words: forest recovery; birds; functional diversity; ecosystem functioning; avian biodiversity

Introduction

Agricultural expansion in the tropics has led to large-scale deforestation (Gibbs et al., 2010), causing loss of forest species. Traditionally, protected areas have been seen as the best way to reduce deforestation and limit the resulting loss of biodiversity. These protected areas generally consist of natural or near-natural ecosystems, such as primary forest (Dudley, 2008). In the tropics such primary forests are generally considered to be irreplaceable for their biodiversity value (Gibson et al., 2011), as well as providing numerous ecosystem services. However, biodiversity declines continue in many tropical forest protected areas (Curran, 2004; Laurance et al., 2012). Additionally, it is not always feasible to designate sufficient land to adequately represent the range of communities found in specific biomes (Cox and Underwood, 2011) or support viable populations of all species (Struhsaker et al., 2005). Thus, it is clear that we cannot rely solely on protected areas of primary forest to conserve tropical forest biodiversity.

Forests that have been altered as a result of unsustainable use or natural disasters are considered degraded, and this includes secondary forests, which have undergone forest clearance (ITTO, 2002). While degraded tropical forests may be of lower biodiversity value than primary forests, given that over half of all tropical forests are now considered to be degraded (ITTO, 2002), they may provide a valuable opportunity for conservation. Wright and Muller-Landau (2006) suggested that expansion of secondary forests could play an important role in preventing extinctions by providing alternative habitat for forest species. Previous reviews suggest that secondary forests may provide habitat for forest specialists, but also that these forests differ in their conservation value depending on connectivity, disturbance history and, in particular, site age (Bowen et al., 2007; Chazdon et al., 2009; Gardner et al., 2007). Recently, the increasing recognition of the importance of degraded forests has led to ambitious restoration targets such as the Aichi Targets and the New York Declaration on Forests, which aim to restore more than 15% of degraded forests (Convention on Biological Diversity, 2010) and 200 million hectares of degraded forests (United Nations, 2014) worldwide, respectively. However, although there are numerous site and landscape level studies, there are a lack of syntheses on the benefits of secondary forests for biodiversity and ecosystem services, and those published are largely limited to impacts on plant communities and carbon storage (Derroire et al., 2016; Martin et al., 2013) or to a limited number of biodiversity metrics, such as species richness (Dent and Wright, 2009; Dunn, 2004a).

Measures of the conservation value of an ecosystem commonly use species-based metrics (Myers et al., 2000), with the value of an area measured by the community species richness or the presence of particular species of interest. A complementary approach to species-based metrics is to assess changes in functional diversity, which describes the range of functional roles played by species within a community (Petchey and Gaston, 2006). Ecosystem functioning in general tends to be correlated with both species richness and functional diversity, with indices based on traits (e.g. feeding behaviour) performing better than those based solely on species richness and abundance (Griffin et al., 2009; Petchey and Gaston, 2006). Both the identity and distribution of functional traits have been shown to be important in predicting function (Gagic et al., 2015).

In this study we focus on birds as they provide key functions, such as pollination, seed predation and dispersal, removal of carrion, and predation of other animals, in tropical forests, and as the roles of individual species can be characterized in terms of their feeding behaviour (Sekercioglu et al., 2004). We conducted a systematic review and analysis to assess: i) how avian species richness and species richness of forest specialists in secondary tropical forests compares with that of primary tropical forests; ii) the functional diversity of avian communities in secondary tropical forests compared with that of primary tropical forests; and iii) how both metrics change, and possibly recover, with secondary forest age.

Materials and Methods

Data collation

Using a standard methodology (Pullin and Stewart, 2006), a systematic review of the literature was conducted in May 2013 by searching Thomson Reuters Web of Knowledge with the terms bird* AND (secondary or disturb*) AND forest AND tropic*. Additional studies were found in the reviews by Barlow et al. (2007), Bowen et al. (2007), Gardner et al. (2007), Dent and Wright (2009) and Chazdon et al. (2009). Gilroy et al. (2014) and the PREDICTS database (Hudson et al., 2017), were searched for additional relevant data.

Studies were selected if they included details of avian community composition in at least one secondary forest site and a reference undisturbed primary forest site. A primary forest was defined as a naturally forested area where there was no evidence of previous deforestation or degradation. A secondary forest was defined as a previously forested area undergoing secondary succession following total or near-total removal of trees (Corlett, 1994). This definition allowed inclusion of forests that had previously been clear-cut or cleared for agriculture or villages, but not those undergoing succession after fires. Additionally, forests that had been selectively logged were excluded as these recover differently (Corlett, 1994; Dunn, 2004b). Only studies from the tropics and sub-tropics between the latitudes of 40°N and 40°S were included.

Data on the abundances of bird species present in forest sites were extracted from the articles. Additionally, for each secondary forest site, the age, land use history and whether the site was continuous or discontinuous with primary forest were noted. Article authors were contacted to request these data when articles suggested that they had been collected but were not presented. The median age of the secondary forest was recorded when a range of values was given. Methodologies used to sample bird communities, including sampling effort, were consistent within studies, but differed among studies. Methodologies used were recorded for use in statistical analyses to control for differences among studies. Data were recorded from only one study when multiple studies used the same dataset.

Data on the traits of bird species were obtained from Wilman *et al.* (2014), the Handbook of the Birds of the World (del Hoyo et al., 2016) and BirdLife International (BirdLife International, 2013). For this study we selected traits with importance for ecological functions: (i) foraging strata (ground, understory, mid-high levels in trees, canopy, or well above vegetation); (ii) diet (invertebrates, mammals/birds, reptiles/amphibians, fish, scavenger, fruit, nectar, seeds, or other plant material); (iii) body mass in grams; (iv) body length in cm; and (v) movement pattern (migrant/not migrant). We selected these traits because they can be directly linked to ecosystem processes such as seed dispersal and pollination. Where no match was found for the Latin binomial name of a species in the trait database of Wilman *et al.* (2014) a web search was carried out to find synonymous names and the correct trait values assigned using these (10 species). Forest dependency data for all bird species were provided by BirdLife International, with each species categorised as having high, medium or low forest dependency, or being a non-forest species (BirdLife International, 2013). Species with high forest dependency were then classed as forest specialists and forest specialist species richness was calculated for each site.

We then calculated total species richness and six functional diversity metrics: functional diversity (FD), the standardized effect size of FD (sesFD), functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) for each of our secondary and primary forest sites (see Table 1 for a description of the functional diversity metrics used). Species richness was calculated by summing the number of species found at each site. Using the R package fundiv we calculated FD (Petchey and Gaston, 2006). Since FD is known to be correlated with species richness, following this we calculated sesFD, a metric which adjusts FD for species richness. To calculate sesFD we used the r package picante (Kembel et al., 2010) to compare observed FD to 999 iterations in which the number of species is constant but the identity of species is randomly drawn from the community, following previous studies (Edwards et al., 2013; Prescott et al., 2016). We calculated the remaining functional diversity metrics (FRic, FEve, FDiv and FDis; Table 1) using the R package FD (Laliberté and Legendre, 2010).

Statistical analyses

This work aimed to compare changes in different metrics of species and functional diversity in avian communities in secondary tropical forests. However, functional diversity metrics are often highly correlated with species richness. Prior to analysis the log response ratio (Hedges et al., 1999) for species richness and all functional diversity metrics, apart from sesFD, in secondary forests relative to primary forests was calculated for all paired sites. The log response ratio represents a standardized effect size which can range from $-\infty$ to ∞, where negative values indicate lower values in secondary forests, positive values represent higher values in secondary forests, and 0 indicates no difference. The log response ratio is commonly used in ecological syntheses because it conforms to statistical assumptions and is intuitive (Hedges et al., 1999). Since values of sesFD can be negative or positive, calculation of the log response ratio for this metric would be problematic. As a result, we calculated the raw difference between secondary and primary forests sesFD. Before analysis, data exploration was carried out following the protocol of Zuur *et al.* (2010). As a result we identified that a small number of older sites strongly influenced coefficient values. To reduce the effect of these outliers we log transformed the variable forest age as recommended by Zuur *et al.* (2010).

Linear mixed-effects models were constructed for all response variables using the R package lme4 (Bates et al., 2015). Models tested included additive models containing all combinations of variables describing secondary forest age and land-use history, as well as a null intercept only model. Models including a variable describing proximity of forests to undisturbed forests were not possible as not all studies contained data on this. Study identity was included as a random effect to avoid pseudoreplication as some studies compared multiple secondary forest sites with a single primary forest site. Models were run using maximum likelihood methods and model selection was based on Akaike information criterion adjusted for small sample size (AICc). The models with lowest AICc were considered to be the most well supported. The goodness of fit of the most parsimonious models was estimated by calculating R^2_{GLMM} using the package MuMIn (Barton, 2015) following Nakagawa and Schielzeth (2013).

Prior to model selection the impact of different sampling methods on results was tested by fitting models with methods (point count, transect, mist-netting) included as random effects with the model with lowest AICc selected. On no occasion did a model including sampling methods outperform one which solely contained a random effect for each individual study (Table S1). Phylogenetic correction was not used as we assessed functional trait changes in terms of their putative impact on ecosystem function and not to explain changes in the avian community. All statistical analyses were performed using R version 3.3.0 (R Core Team, 2016).

Results

A total of 24 studies that aimed to sample the entire avian community with data on 44 paired secondary and primary forest sites were found through the systematic review (Table 2). These studies documented 29,023 observations of 1,673 bird species. Sites were widely distributed across the tropics but most were found in the Americas or Asia (Table 2, Figure 1). Secondary forest sites had regenerated for between one and 100 years but nearly half of the sites had been disturbed within 10 years prior to the studies taking place (Table 2). Only five sites had been recovering for at least 40 years since disturbance.

Total and forest specialist species richness

The most well supported model describing differences in species richness in secondary and primary forests was a null model (Table S2). Species richness in secondary forests was on average 12% lower than in primary forests (intercept=-0.13, SE=0.06, p=0.03, Figure 3).

The species richness of forest specialists was best described by a model including only secondary forest age as a predictor (Table S2). Forest specialist species richness increased with time since disturbance (slope=0.21, SE=0.07, p=0.01), but was not predicted to reach equivalence with primary forests within 100 years (Figure 2a). After one year since disturbance forest specialist species richness in secondary forests was predicted to be 63% lower than primary forests, and after 100 years this had risen to 1% lower than primary forests. This model showed a reasonable explanatory power (R^2_{GLMM}=0.14, Table S2).

Functional diversity metrics

FD and FRic were found to be highly correlated both with each other (correlation coefficient of 0.9) and with species richness (correlation coefficient of 0.9 with FD and 0.8 with FRic). As a result, these two metrics were removed from this analysis. A null, intercept only model was the most well supported for FDis, FDiv and FEve (Table S2, Figure 3). FDis and FDiv did not differ significantly between primary and secondary forests. However, FEve was 5% higher in secondary forests than in primary forests (intercept=0.06, SE=0.03, p=0.03).

sesFD declined with time since last disturbance (slope=-1.17, SE=0.24, Figure 2b) and was higher in younger forests than in primary forests (Table S2). sesFD was predicted to reach equivalence with primary forest values after approximately 22 years (Figure 2b). This model showed relatively high explanatory power (R^2_{GLMM}=0.35, Table S2).

Discussion

Our study represents the largest quantitative synthesis of avian responses to secondary tropical forest succession to date. Our results indicate that avian species richness is lower in secondary forests than in primary forests. Forest specialist species richness increases with secondary forest age and is likely to take over 100 years to recover. Regarding functional diversity, two metrics (FDis and FDiv) were similar in secondary and primary forests, whereas FEve was higher in secondary forests. Once differences in species richness were accounted for, sesFD showed a marked decline with increasing age of secondary forests, suggesting increasing functional redundancy in avian communities during succession.

Species Richness

Our results show that avian species richness is lower in secondary forests than in primary forests, in agreement with previous reviews (Barlow et al., 2007; Bowen et al., 2007), and also that species richness does not respond to secondary forest age. The latter result is in contrast to Dunn (2004a) who found that avian species richness in secondary forests increased with time since disturbance and reached equivalence with primary forests after 20 years. However, Dunn (2004a) considered a more limited number of sites than our analysis and only one of these sites had been recovering for more than 40 years. It is possible that in younger secondary forests time since disturbance has an important role in determining avian community composition, but for older secondary forests other factors, such as patch size, have a greater influence on the successional state.

Although our analysis found species richness of forest specialists failed to recover within 100 years, this metric was predicted to be only 1% lower in secondary forests after 100 years of recovery than in primary forests. This mirrors the observation that avian community composition of secondary forests approaches equivalence with that of primary forests after around 100 years (Dent and Wright, 2009). The rate of change in forest specialist species richness is perhaps unsurprising given that although secondary forests attain much of the structure and plant diversity of primary forests within 50 years, tree community composition, and therefore the structural complexity of forests, is likely to take much longer (Derroire et al., 2016; Martin et al., 2013; Poorter et al., 2016). Thus, the results of our study reinforce the view that, although conservation value is accumulated relatively rapidly in secondary forests, primary forests (and potentially mature secondary forests) are vital to prevent extinctions of forest specialists (Gibson et al., 2011).

Although some guilds are particularly sensitive to disturbance (e.g. understory insectivores; see Powell et al., 2016, 2015), our results indicate that some forest specialist species are found in young secondary forests. After one year of succession forest specialist species richness in secondary forests was 63% lower than in primary forests. This raises the question of why are there any forest specialist species at all in such young secondary forests. Part of the answer to this relates to how forests are cleared prior to agricultural use. Many secondary forests in the tropics are the result of abandonment of subsistence agriculture during which some large trees are often retained during forest clearance (Guevara et al., 1986; Harvey and Haber, 1998). Harvey and Haber (1998) found that agricultural fields in Costa Rica contained an average of 25 trees per hectare, and that a third of these trees were primary forest specialist species. As a result, large trees located in the agricultural matrix may be used by forest species to feed or roost (Harvey and Haber, 1998), increasing the species richness of avian forest specialists in young secondary forests.

Functional diversity

FDis, a unified metric for functional diversity (Laliberté and Legendre, 2010), was found to be equivalent between primary and secondary forests. FDiv in secondary forests was also similar to primary forest levels, suggesting that the degree to which abundant species had the most extreme trait values was similar in secondary and primary forests. These results both suggest similar levels of ecosystem functioning between the two forest types. Only one other study has investigated the effects of forest degradation or conversion on FDis, finding that it was higher in pastures and oil palm plantations than in forest remnants (Prescott et al., 2016). Together with our results, this study hints that degradation through conversion of forests to other habitat types may lead to increased FDis and a reduction in ecosystem function (Prescott et al., 2016), although more work is needed to relate FDis to specific ecosystem functions.

FEve was 5% higher in secondary forests than primary forests, suggesting a more equal abundance of species in trait space in secondary forests. Assuming that resources are evenly distributed, this means in theory that resources within secondary forests are being used more efficiently than in primary forests (Mason et al., 2005), which would be an unexpected result. However alternatively, a high FEve value could also suggest that the habitat is not very structurally complex, meaning that there are a smaller number of evenly occupied niches with few interactions between species (García-Morales et al., 2016; Schleuter et al., 2010). As primary forests have greater structural complexity than secondary forests (Derroire et al., 2016), this could explain the difference in FEve between these two forest types in our analysis.

At present, there is no clear picture on the relationship between FEve of avian communities and forest degradation in the literature. Prescott et al. (2016) found FEve to be lower in pasture than in forest remnants but equivalent in forest remnants and oil palm plantations. In contrast, Edwards et al. (2013) found that FEve was lower in oil palm plantations (and in twice-logged forests) than in unlogged (and once-logged) forests. Thirdly, Ibarra and Martin (2015) found no relationship between the degree of deforestation and FEve. Given these conflicting results, we suggest this is an area requiring further research.

The most pronounced relationship with forest age was seen in the standardized effect size of FD (sesFD). As secondary forest age increased sesFD declined, reaching equivalence with primary forests after approximately 22 years. This metric adjusts FD by accounting for species richness at sites, with negative values indicating lower FD than expected given site level richness. Thus, the reduction in relative sesFD with forest age that we observed suggests increasing functional redundancy in older secondary forests (Pavoine and Bonsall, 2011). Previous studies have found that sesFD for bird communities can increase (Edwards et al., 2013) or decrease across a gradient of degradation (Prescott et al., 2016). However, our observation of an increase in functional redundancy suggests that the resilience of ecosystem processes may increase with secondary forest age due to buffering of the negative impacts of species extinction. Equally this suggests that even where functional diversity in young secondary tropical forests is similar to that found in primary forests, these communities and the ecosystem services they supply may be less stable over time.

Caveats

Our study represents the most comprehensive synthesis of avian functional diversity in secondary forests to date but, like all syntheses, it was affected by the quality and representativeness of the data we used (Gonzalez et al., 2016). As a result there are two important caveats that relate to our analysis. Firstly, our study highlights the importance of the age of secondary forests as a determinant of the biodiversity it plays host to, but there are many other important variables that we could not account for in this study. For example, the duration and intensity of previous land use affect the initial conditions of secondary forests following abandonment (Jakovac et al., 2015). Following abandonment, the connectivity, proximity to primary forest, and patch size can all play important roles in determining the rate at which forest species colonise degraded forests (Banks-Leite et al., 2010; Maldonado-Coelho and Marini, 2000; Prugh et al., 2008). Secondly, the primary forest sites used in our study may have varied in quality as statistical controls since definitions of primary forest probably differed between studies. In both of these cases it was not possible to account for this potential variation amongst studies and addressing how these factors interact with age of secondary forests is a key research gap.

Regarding representativeness, the sites used in our study are likely to be broadly representative of secondary forests throughout the tropics. Few sites had been intensively farmed and the majority of sites were under 40 years old, reflecting secondary tropical forests generally (Asner et al., 2009; Smith et al., 2003).

Conclusion

The conservation value of secondary tropical forests will vary depending upon the aims of conservation strategies. If the aims are to support overall or forest specialist species richness at primary forest levels then our results suggest that preservation of primary forests is vital, in agreement with previous reviews (Barlow et al., 2007; Bowen et al., 2007), although the richness of forest specialist species, and hence the conservation value of regrowth, does increase with secondary forest age. If strategies are related to the levels of ecosystem functioning of the forests then, although there were some differences between secondary and primary tropical forests for functional diversity metrics, our results suggest that secondary forests can support provision of ecosystem functions, including pollination and seed dispersal (but see Markl et al., 2012). Our results also suggest that secondary forest age influences conservation value in terms of ecosystem functioning, with older secondary forests having increased functional redundancy.

The conservation value of secondary forests will never be maximised if regrowth is deforested. However, mid-age stands are often converted to agriculture in South America (Smith et al., 2003) and degraded forests are regularly converted to oil palm or rubber plantations in Southeast Asia (Abood et al., 2015; Koh and Wilcove, 2008), resulting in loss of avian species and functional diversity (Edwards et al., 2013; Prescott et al., 2016; Tscharntke et al., 2008). Therefore, to maximise the biodiversity value of tropical landscapes, secondary forests should be protected, particularly in landscapes where little pristine habitat remains. Protecting older secondary forests provides high conservation value now, whereas protecting young regrowth promises future returns. Restoration of young secondary forests could also play a role. Enrichment planting can be used to enhance biodiversity by adding tree species that are unlikely to colonise unassisted, for example late-successional species or those lacking dispersers (Griscom and Ashton, 2011; Lamb et al., 2005). Assisting vegetative recovery to a late-successional species composition could improve habitat suitability for forest specialists and hence, accelerate their recovery. Secondary forests have a role to play in the conservation of forest species and provision of ecosystem services and this should be recognised in tropical conservation strategies.

Conflict of Interest: The authors declare that they have no conflict of interest.

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Figures

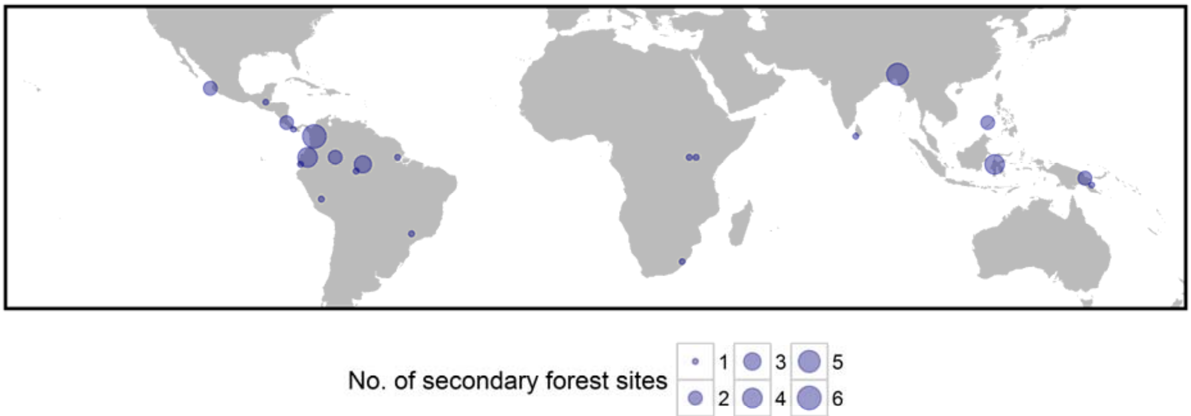

Figure 1 Geographic distribution of the study sites used in this analysis.

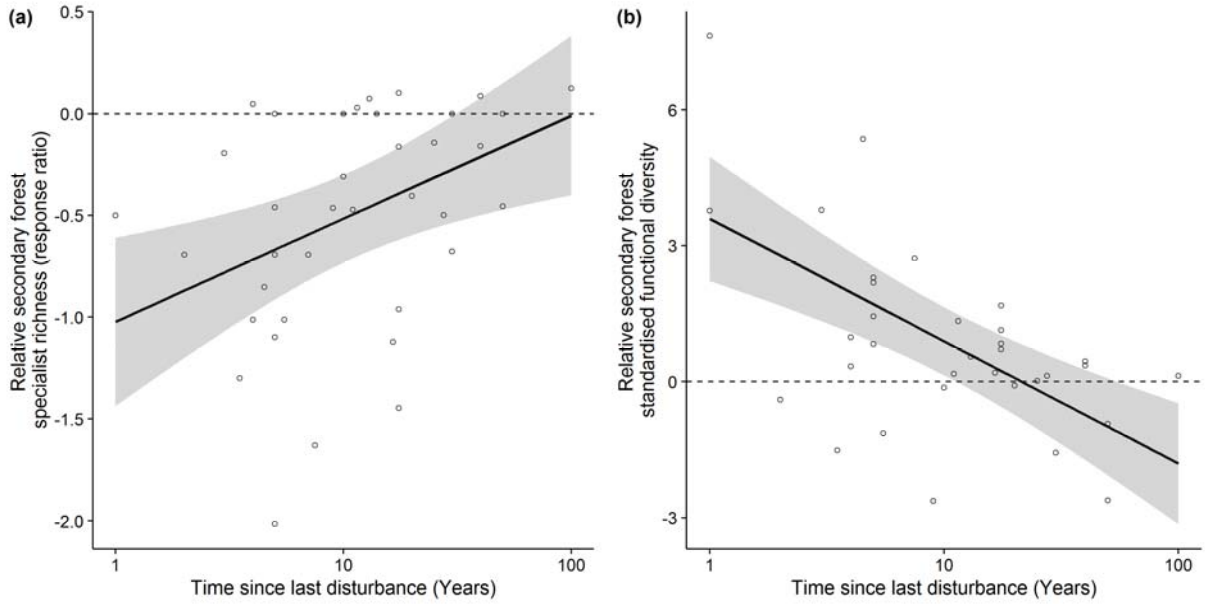

Figure 2 The relationship between secondary forest age and (a) forest specialist species richness and (b) standardized functional diversity (sesFD) in secondary tropical forests relative to primary tropical forests. The dotted black line represents the point at which metrics are equal in secondary and primary forest sites. Solid lines represent predictions from models with the lowest AICc and grey shaded areas represent the 95% confidence intervals for these predictions.

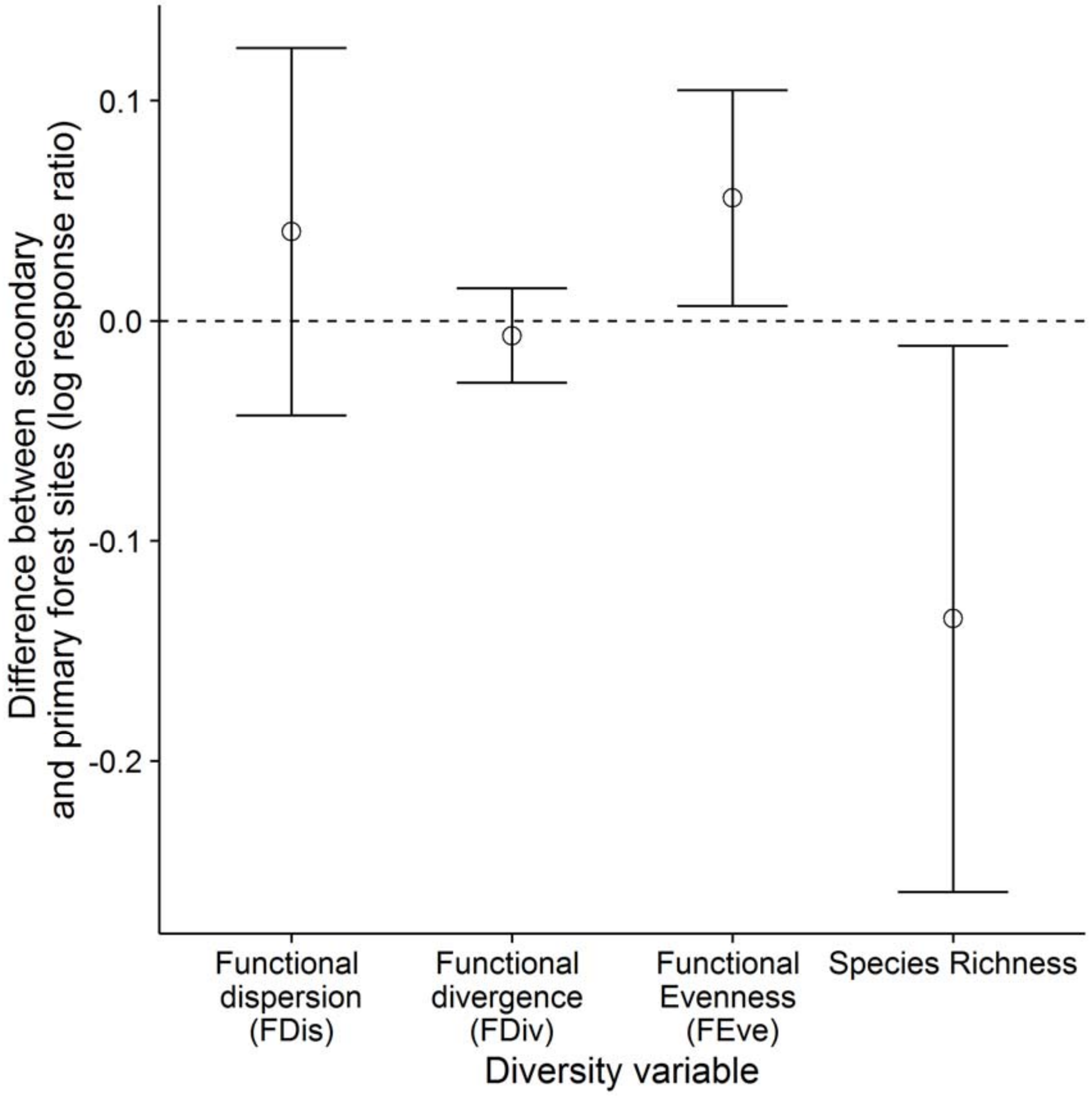

Figure 3 Difference between secondary and primary tropical forest site diversity for variables where the null model was considered most parsimonious. Dots represent mean differences between secondary and primary sites and error bars represent 95% confidence intervals. The dotted black line represents the point at which metrics are equal in secondary and primary forest sites.

Tables

Table 1 Descriptions of functional diversity metrics used in this study

Metric name	Abbreviation used in this study	Metric description	Relevant references
Functional Diversity	FD	A distance based metric of functional diversity that is not influenced by species abundances.	Petchey and Gaston, 2006
Functional Richness	FRic	The volume multidimensional trait space occupied by a community. High FRic indicates that many traits are present within a community.	Laliberté and Legendre, 2010; Villéger et al., 2008
Functional Evenness	FEve	The evenness of species abundances in multidimensional trait space. High FEve values suggest a relatively equal abundance of species in trait space, and in theory this means that resources within an ecosystem are being used in an efficient manner (Prescott et al., 2016)	Laliberté and Legendre, 2010; Villéger et al., 2008
Functional Divergence	FDiv	The distribution of species abundance along multidimensional trait axes. FDiv is low when abundant species have trait values that are close to the centre of functional trait space, but high when abundant species have extreme trait values (Villéger et al., 2008). This can be seen as a measure of the niche differentiation within a community, such that if FDiv is high, then there are high levels of niche differentiation (Prescott et al., 2016).	Laliberté and Legendre, 2010; Villéger et al., 2008
Functional Dispersion	FDis	The distance from the centroid of multidimensional trait space, weighted by species abundances. This metric has been suggested as a unified metric for functional diversity (Laliberté and Legendre, 2010).	Laliberté and Legendre, 2010; Villéger et al., 2008

Table 2 Studies from which avian community composition data were extracted, with location recorded at a country level and the age of secondary forest sites (measured as the number of years since disturbance) in each study

Reference	Location of forest sites	Age of secondary forest site(s) (years)
Andrade and Rubio-Torgler, 1994	Colombia	3, 11.5
Banks-Leite et al., 2012	Brazil	50
Barlow et al., 2007	Brazil	16.5
Becker and Agreda, 2005	Ecuador	17.5
Becker et al., 2008	Ecuador	17.5, 17.5, 40
Blake and Loiselle, 2001	Costa Rica	5, 27.5
Borges, 2007	Brazil	4.5, 11, 27.5
Dawson et al., 2011	Papua New Guinea	20
Gilroy et al., 2014	Colombia	3, 8, 8, 20, 20, 35
Hutto, 1989	Mexico	2, 5
Johns, 1991	Brazil	1
Maas et al., 2009	Indonesia	3.5, 4, 5.5
Mallari et al., 2011	Philippines	10, 30
Marsden et al., 2006	Papua New Guinea	5, 14
Mulwa et al., 2012	Kenya	50
Naidoo, 2004	Uganda	13
O'Dea and Whittaker, 2007	Ecuador	17.5
Raman et al., 1998	India	1, 5, 10, 25, 100
Reid et al., 2012	Costa Rica	9
Renner et al., 2006	Guatemala	4
Sodhi et al., 2005	Indonesia	40
Terborgh and Weske, 1969	Peru	7.5
Tvardikova, 2010	Papua New Guinea	7

Wijesinghe and Brooke, 2005	Sri Lanka	5

Supplementary materials

Table S1 Model selection table showing test of different random effects structures for different variables investigated.

Variable	**Random_effects**	**AICc**	**Model Rank**
Species Richness	Study	33.76	1
	Mist_nets+Transect+Study	36.45	2
	Mist_nets+Study	36.45	3
	Mist nets+ Transect+Vocal+Study	39.31	4
	Mist nets+Transect+Vocal+Study	42.38	5
	Point obs+Mist nets+Transect+Vocal+Study	45.66	6
Forest Specialist Species Richness	Study	70.59	1
	Mist_nets+Transect+Study	73.15	2
	Mist_nets+Study	73.15	3
	Mist nets+ Transect+Vocal+Study	75.87	4
	Mist nets+Transect+Vocal+Study	78.73	5
	Point observation+Mist nets+Transect+Vocal+Study	81.77	6
Functional Diversity (FD)	Study	20.16	1
	Mist_nets+Study	22.81	2
	Mist_nets+Transect+Study	22.84	3
	Mist nets+ Transect+Vocal+Study	25.71	4
	Mist nets+Transect+Vocal+Study	28.77	5
	Point obs+Mist nets+Transect+Vocal+Study	32.05	6
Functional Richness (FRic)	Study	171.03	1
	Mist_nets+Transect+Study	173.72	2
	Mist_nets+Study	173.72	3
	Mist nets+ Transect+Vocal+Study	176.58	4
	Mist nets+Transect+Vocal+Study	179.64	5
	Point obs+Mist nets+Transect+Vocal+Study	182.92	6
Functional Evenness (FEve)	Study	-44.77	1
	Mist_nets+Study	-42.09	2
	Mist_nets+Transect+Study	-42.09	3
	Mist nets+ Transect+Vocal+Study	-40.07	4
	Mist nets+Transect+Vocal+Study	-37.01	5
	Point obs+Mist nets+Transect+Vocal+Study	-33.73	6
Functional Divergence (FDiv)	Study	-77.38	1
	Mist_nets+Transect+Study	-74.69	2
	Mist_nets+Study	-74.69	3
	Mist nets+ Transect+Vocal+Study	-73.27	4

	Mist nets+Transect+Vocal+Study	-70.22	5
	Point obs+Mist nets+Transect+Vocal+Study	-66.93	6
Functional Dispersion (FDis)	Study	-9.47	1
	Mist_nets+Transect+Study	-6.82	2
	Mist_nets+Study	-6.80	3
	Mist nets+ Transect+Vocal+Study	-4.42	4
	Mist nets+Transect+Vocal+Study	-1.36	5
	Point obs+Mist nets+Transect+Vocal+Study	1.92	6

Table S2 Model selection table for all models considered in this study.

Variable	Model	AICc	ΔAICc	Conditional R^2
Species Richness	Null model	24.93	0.00	0.00
	Age	25.68	0.76	0.04
	Disturbance type	28.83	3.90	0.22
Forest Specialist Species Richness	Null model	65.41	1.78	0
	Age	63.63	0	0.14
	Disturbance type	70.50	6.87	0.25
Functional Diversity (FD)	Null model	8.78	0.00	0.00
	Age	11.29	2.51	0.00
	Disturbance type	14.80	6.02	0.17
Functional Richness (FRic)	Null model	168.37	0.00	0.00
	Age	170.74	2.36	0.00
	Disturbance type	174.16	5.79	0.16
Functional Evenness (FEve)	Null model	-58.52	0.00	0.00
	Age	-57.24	1.28	0.02
	Disturbance type	-50.65	7.87	0.12
Functional Divergence (FDiv)	Null model	-93.68	0.00	0.00
	Age	-92.15	1.54	0.03
	Disturbance type	-84.39	9.30	0.05
Functional Dispersion (FDis)	Null model	-21.34	0.00	0.00
	Age	-19.92	1.42	0.01
	Disturbance type	-16.47	4.87	0.24
Standardised Effect Size of FD (sesFD)	Null model	148.74	12.59	0
	Age	136.15	0	0.35
	Disturbance type	145.09	8.94	0.19