**Secondary tropical forests retain avian functional diversity but not species richness: a meta-analysis**

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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 a meta-analysis of avian responses to secondary forest succession, comparing data from 45 tropical secondary forest sites with nearby primary forest sites and investigating both species and functional diversity based metrics. Total species richness relative to primary forest increased with secondary forest age and reached primary forest values after about 40 years. Forest specialist species richness also increased with time since disturbance but was not predicted to reach equivalence with primary forest within 100 years. However, differences between secondary and primary forest in terms of functional diversity were less marked. Although functional richness (FRic) was lower in secondary forests than in primary forests, overall our results suggest that secondary tropical forests retain similar levels of functional diversity to primary tropical forests indicating that levels of ecosystem functioning may be comparable in both types. Therefore, secondary tropical forest, particularly older regrowth, has biodiversity value and can support important ecosystem functions. These secondary forests should be protected from further disturbance but preserving primary forest is vital for forest specialists, which recover relatively slowly in secondary forests.

**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 et al., 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. In 2006, Wright and Muller-Landau 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, Bonn Challenge and New York Declaration on Forests, which aim to restore more than 15% of degraded forests. However, our knowledge about the benefits of the resulting secondary forests for biodiversity and ecosystem services is 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 et al., 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. 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 the roles of individual species can be characterized in terms of their feeding behaviour (Sekercioglu et al., 2004). 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 use systematic review and meta-analysis to assess: 1) how avian species richness and species richness of forest specialists in secondary tropical forest compares with that of primary tropical forest; 2) the functional diversity of avian communities in secondary tropical forest compared with that of primary tropical forest; and 3) how both metrics change, and possibly recover, with secondary forest age.

**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 Barlow et al. (2007), Bowen et al. (Jos Barlow et al., 2007), Gardner et al. (Gardner et al., 2007), Dent and Wright (Dent and Wright, 2009) and Chazdon et al. (Chazdon et al., 2009).

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 discontinuity in forest cover or modification by human activities. A secondary forest was defined as a naturally forested area where there had been discontinuity in forest cover over time (Corlett, 1994). We focused on forests that had previously been converted for agriculture and so excluded those that had been selectively logged as these types of site 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 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 on the traits of bird species were obtained from Wilman *et al.* (2014). 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); and (iii) body mass in grams. 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 the remaining species were classed as forest generalists. The species richness for specialist species was calculated for each site.

We then calculated total species richness and five functional diversity metrics: functional diversity (FD), 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 in at each site. Using the R package fundiv we calculated FD (Petchey and Gaston, 2002). We calculated the remaining functional diversity metrics (FRic, FEve, FDiv and FDis; Table 1) using the R package FD (Laliberte et al., 2010).

***Statistical analyses***

Prior to analysis the log response ratio (Hedges et al., 1999) for species richness and all functional diversity metrics in secondary forest relative to primary forest was calculated for all paired sites. The log response ratio is similar to proportional difference, but conforms to statistical assumptions as it is centred at zero and can take any value (Hedges et al., 1999). Before analysis, data exploration was carried out following the protocol of Zuur *et al.* (2010). As a result forest age was log-transformed as data exploration indicated only 3 forests over 50 years old, which would otherwise exert a large influence on coefficient values. For all response variables, linear mixed-effects models, using the package lme4 (Bates et al., 2014), were used along with the package MuMIn (Barton, 2014) to test the parsimony of models including secondary forest age, as well as null, intercept only models. 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), with the models with lowest AICc considered to be the best. The goodness of fit of the most parsimonious models was estimated by calculating *R*2GLMM using the package MuMIn (Barton, 2014) following Nakagawa and Schielzeth (2013). Prior to model selection the impact of different 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 study 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 3.1.1 (R Core Team, 2014).

**Results**

A total of 28 studies that aimed to sample the entire avian community with data on 45 paired secondary and primary forest sites were found through the systematic review (Table 1). These studies documented 5065 observations of 1785 bird species. Sites were widely distributed across the tropics but most were found in the Americas (46% of sites) or Asia (25%) (Table 1, Fig. 1). Secondary forest sites had regenerated for between 1 and 100 years but half of the sites had been disturbed within 10 years prior to the studies taking place (Table 1). Only five sites were older than 40 years since disturbance.

***Total and forest specialist species richness***

The best model describing difference in species richness in secondary and primary forests contained only age as a predictor (Table 3). Species richness relative to primary forest increased with secondary forest age (slope=0.08, SE=0.04, P=0.06), and was predicted to reach equivalence with primary forest 43 years after disturbance (Figure 2a). After 1 year secondary forests were predicted to have a species richness 22% lower than primary forest, and after 100 years this had risen to 7% higher than primary forest. However, this model had relatively low explanatory power (*R*2GLMM=0.07, Table 3).

The species richness of forest specialists was also best described by a model including only age as a predictor (Table 3). Forest specialist species richness increased over time since disturbance (slope=0.19, SE=0.07, P=0.01), but was not predicted to reach equivalence with primary forests within 100 years (Figure 2b). After 1 year since disturbance forest species richness in secondary forests was predicted to be 55% lower than primary forest, and after 100 years this had risen to 8% lower than primary forest. This model showed a higher explanatory power than that for total species richness (*R*2GLMM=0.12, Table 3).

***Functional diversity metrics***

Of the functional diversity metrics we investigated FDiv was the only one for which the most parsimonious model included the time since last disturbance (Table 3). FDiv was negatively related to time since disturbance (slope=-0.015, SE=0.007), and tended to be higher in young secondary forests than in primary forests (Fig. 2c). After 1 year since disturbance FDiv in secondary forests was predicted to be 7% higher than in primary forest, and after 100 years this reached approximate equivalence. However, this model showed low explanatory power (*R*2GLMM=0.06, Table 3). A null, intercept only model was the best supported for FD, FRic, FDis and FEve (Table 3, Fig. 3). FRic was approximately 65% lower in secondary forests (intercept=-1.04, SE=0.51, P=0.042), though confidence intervals for the estimate were very large (Fig. 3). FD, FDis and FEve did not differ between secondary and primary tropical forests (Table 2, Fig. 3).

**Discussion**

This study represents the largest meta-analysis of avian responses to secondary tropical forest succession to date. Our results indicate that although avian species richness in young secondary forest is lower than primary forest, this recovers within 50 years. However, forest specialist species richness increases more slowly and is likely to take over 100 years to recover. This reemphasises the importance of primary forest for specialist species. Regarding functional diversity, differences between secondary and primary forest were less marked. FDiv was slightly higher in young secondary forests than in primary forests, reaching equivalence after approximately 100 years. FRic, which is closely correlated with species richness, was lower in secondary forests, but FDis, FEve and FD were similar in secondary and primary forest.

***Changes in total and forest specialist species richness***

Our results show that total avian species richness increases with age in secondary tropical forests, reaching equivalence to primary forest within 50 years. In contrast to our findings, Dunn (2004a) found that avian species richness recovered within 20 years. The wider range of site conditions and greater sample size of our study (45 compared to 22 secondary forest sites) mean it is likely to give a more robust representation of this relationship than that of Dunn (2004a). Our results are similar to those of Martin et al. (2013) who found that tree species richness in secondary forests resulting from agricultural clearance recovers within approximately 50 years. This trend of increasing species richness over time since disturbance appears to be general, with Newbold et al. (2015) demonstrating species richness increases from early- through mid-stage communities to peak in late-stage and primary vegetation.

Our study indicates that species richness of forest specialists recovered more slowly than total richness, failing to recover within 100 years. This is probably reflective of changes in vegetation structure, composition and complexity leading to increased suitability for forest species (MacArthur and MacArthur, 1961; Sodhi et al., 2005; Terborgh, 1985). Given that tree community composition and forest structure can take over 100 and between 60-150 years, respectively, to recover in tropical secondary forests (Martin et al., 2013; Poorter et al., 2016) it is likely that avian forest specialists require similar amount of time to recolonise secondary forests. Our finding is similar to that of previous narrative reviews (J Barlow et al., 2007; Bowen et al., 2007) suggesting that preservation of primary forest is important for the conservation of forest specialists.

Interestingly, our results also suggests that after one year of succession specialist species richness was 55% lower than in primary forests. Why are there any forest specialist species at all in such young secondary forests? The answer to this is likely to relate to how forests are cleared prior to agricultural use and subsequent abandonment and succession. Most secondary forests in the tropics are the result of abandonment subsistence agriculture. Subsistence farmers often choose to retain some large trees during forest clearance since they may provide edible fruits, shade for workers or simply as a result of tradition (Guevara et al., 1986; Harvey and Haber, 1998). Indeed, Harvey and Haber (1998) found that fields in Costa Rica contained an average of 25 trees per hectare, a third of which were primary forest specialists. As a result, large trees located in the agricultural matrix may be used as forest species to feed or roost (Harvey and Haber, 1998), increasing the species richness of forest specialists in young secondary forests. As such, although secondary forests are likely to represent similar conditions when they are abandoned, this is not equivalent to a total lack of tree cover.

***Functional diversity***

FEve, FD and FDis were found to be equivalent in primary and secondary tropical forests. Taken together these results suggest that the evenness of species in trait space and overall functional diversity was similar in secondary and primary forests. This implies a relatively similar efficiency of resource use in secondary forests when compared to primary forest mirroring previous work that has found similar levels of functional diversity in degraded and primary forests (Edwards et al., 2013).

However, FRic was significantly lower in secondary forest than in primary forest, indicating that some of the traits investigated may be missing in secondary forest communities. FDiv was found to be highest in young secondary forest and declined with time since disturbance, suggesting higher niche differentiation and potentially lower competition for resources in young secondary forest. However, at its greatest, the difference between secondary and primary forest FDiv was only 7%. This response is in contrast with that found in other types of degraded forest; in selectively logged forests and those converted to oil palm plantations and pastures FDiv has been found to be equivalent to primary forest (Edwards et al. 2013b, Prescott et al. 2016).

Our results, apart from those for FRic, suggest similar levels of functional diversity in secondary and primary tropical forest. Along with other studies that have shown that degraded forest can retain functional diversity (Edwards et al., 2013) but that conversion to agricultural land use can result in a decline (Prescott et al., 2016), our results emphasise the conservation value of secondary forests. Functional diversity has been shown to explain changes in ecosystem function more effectively than metrics based on species identity (Gagic et al., 2015) and thus, our results suggest that functions provided by birds may be similar in recovering secondary and primary tropical forests.

However, our study also indicated that FRic was lower in secondary than primary forests. Prescott et al. (2016) also found that FRic of birds was reduced in oil palm plantations and pastures with forest remnants in Colombia. This lower FRic may be the result of a decline in functional roles available in the more structurally simple degraded habitats. In particular, the reduction may result from lower abundance of larger bodied bird species, which may be absent in degraded tropical forests (Costantini et al., 2016; Newbold et al., 2013). This may have serious consequences for seed dispersal, with losses in large bodied frugivores resulting in declines in the abundance of tree species that depend on them and potential declines in forest carbon stocks (Osuri et al., 2016). Functionally rich communities may also be able to maintain functions in the face of environmental change (Díaz and Cabido, 2001). Therefore, our results also suggest that communities in secondary forests may be less stable through time, particularly in the face of increasing disturbance, potentially resulting in fluctuations in ecosystem functions and services.

***Quality and representativeness of empirical studies***

Any synthesis is affected by quality and representativeness of data used (Gonzalez et al., 2016; Martin et al., 2013). The studies used for the meta-analyses may have been affected by two sources of error in particular. Firstly, secondary forests may have been more greatly affected by fragmentation than primary sites, given that they occur in areas that have previously been deforested, resulting in loss of disturbance sensitive species (Banks-Leite et al., 2010). 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 variation in study methodology. Regarding representativeness, the sites used in our study are likely to be broadly representative of secondary forest throughout the tropics. Few sites had been intensively farmed, and the majority of sites were under 40 years old - reflecting secondary forests generally (Asner et al., 2009; Smith et al., 2003). However, median forest cover was 78% within 1 km of the secondary forest sites used (data not presented) and while it is unclear whether this is representative of the landscapes in which secondary forests are found, this relatively high forest cover may partly explain the relatively modest biodiversity differences between secondary and primary forests.

***Implications for conservation***

Our results suggest that secondary tropical forests retain similar levels of functional diversity to primary tropical forests and therefore, that levels of ecosystem functioning are similar in both forest types. This supports the argument that secondary tropical forests have conservation value and can support provision of ecosystem functions, including pollination and seed dispersal. 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 South East 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). Although species richness is relatively high in young secondary forest, this increases with forest age and so the conservation value of secondary forest will never be maximised if regrowth is deforested.

Therefore, to maximise the biodiversity value of tropical landscapes, secondary forest should be protected, particularly in landscapes where little pristine habitat remains. Protecting older secondary forest 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 forest has a role to play in the conservation of forest species and this should be recognised in tropical conservation strategies.

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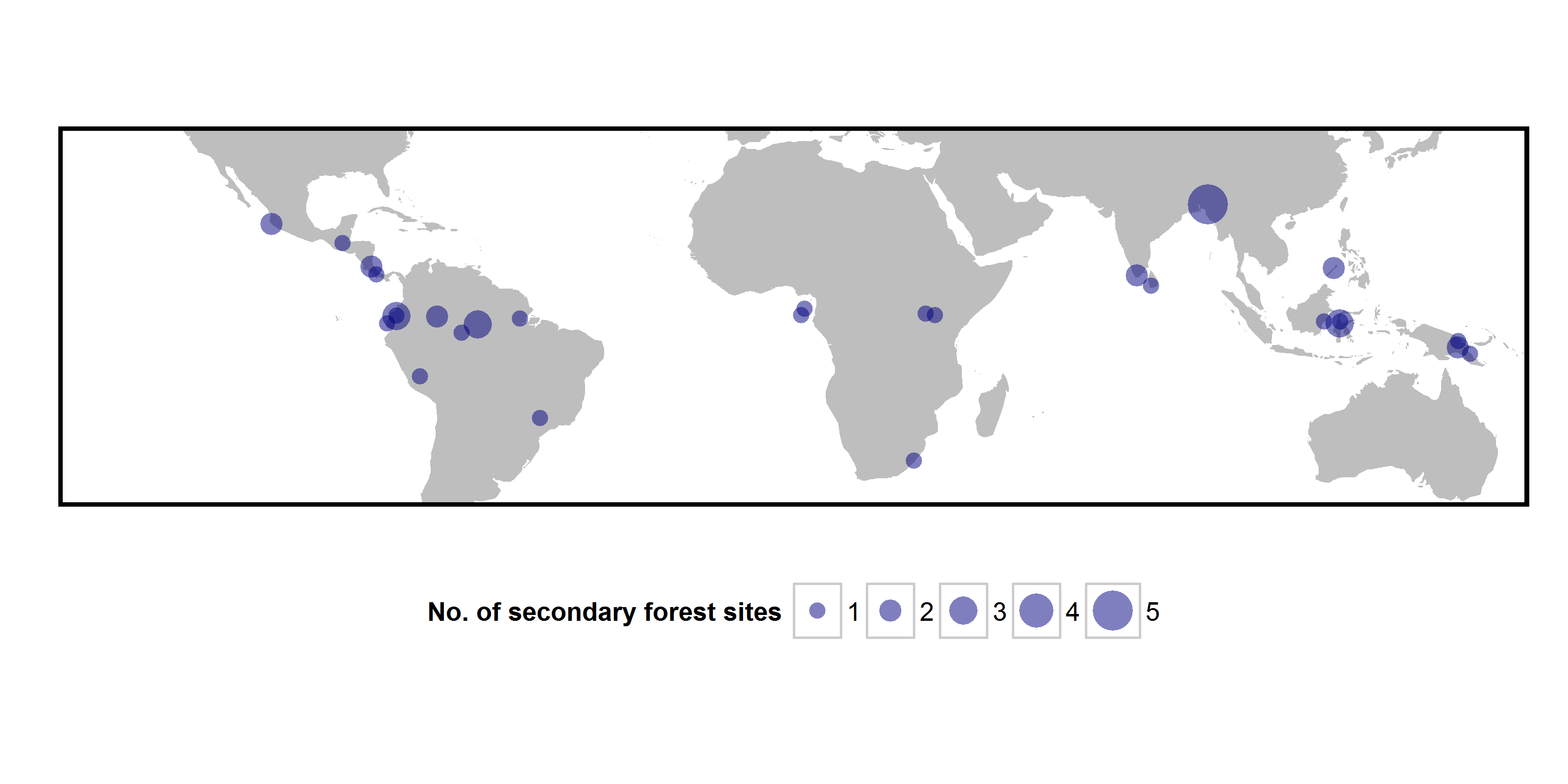
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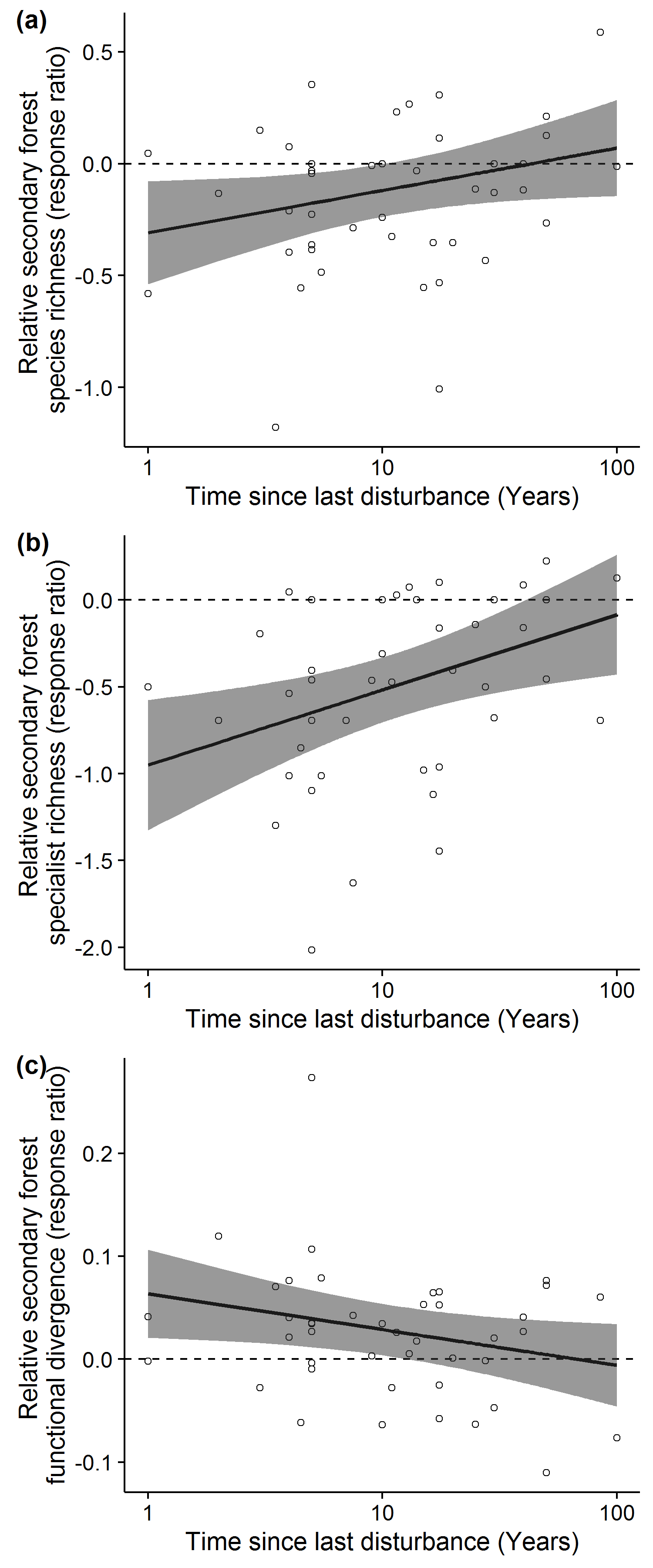
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**Figures**

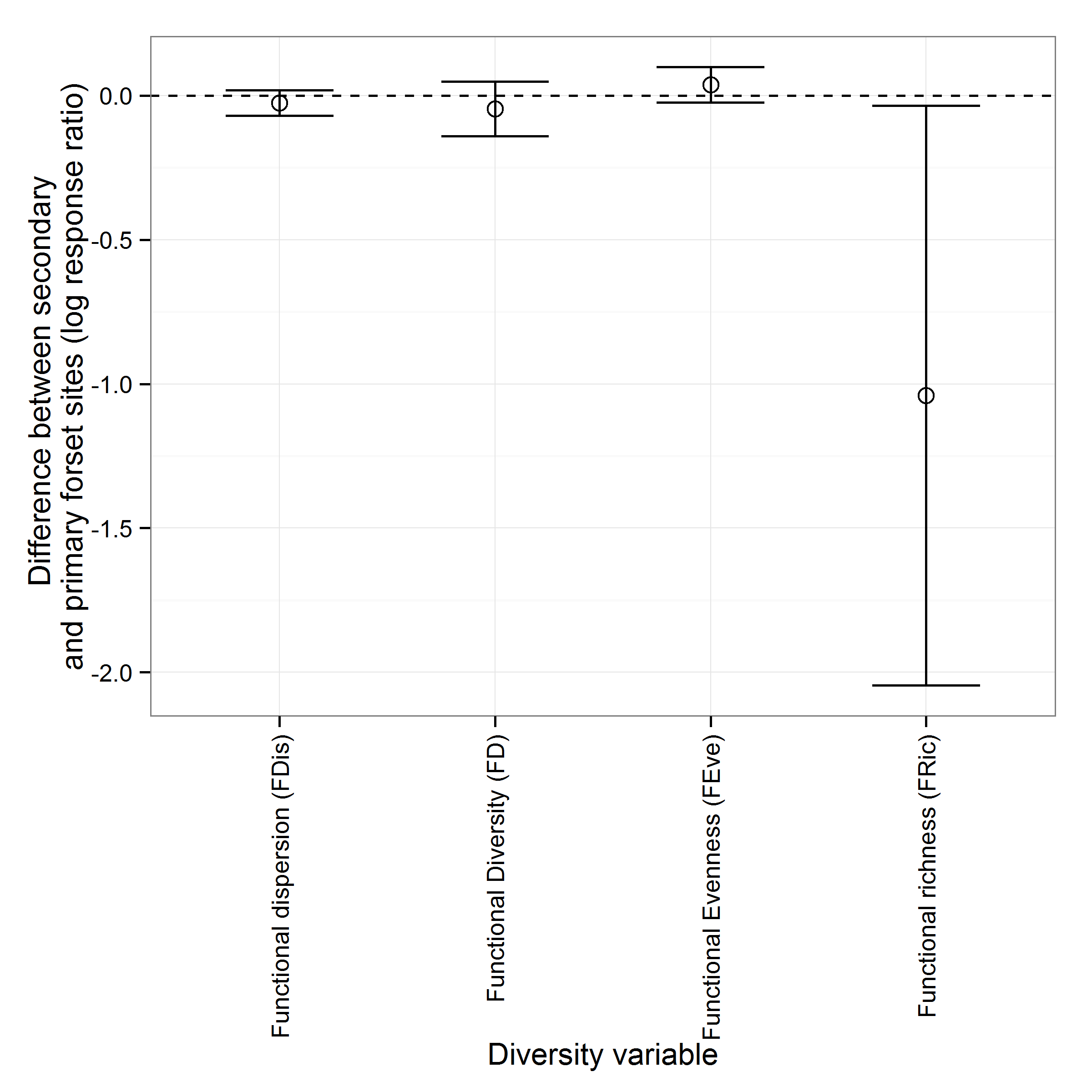
**Fig. 1** Geographic distribution of the study sites used in this analysis



**Fig. 2** The relationship between secondary forest age and (a) species richness (b) forest specialist species richness and (c) functional divergence (FDiv) in secondary tropical forest relative to primary tropical forest. 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.

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**Fig. 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. Only functional richness (FRic) was significantly different (P<0.05).



**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, 2002) |
| Functional richness | FRic | The volume multidimensional trait space occupied by a community. High FRic indicates that many traits are present within a community. | (Laliberte et al., 2010; Villéger, 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). | (Laliberte et al., 2010; Villéger, 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, 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). | (Laliberte et al., 2010; Villéger, 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 (Laliberte et al., 2010). | (Laliberte et al., 2010; Villéger, 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 GI, Rubio-Torgler H (1994) Sustainable Use of the Tropical Rain Forest: Evidence from the Avifauna in a Shifting-Cultivation Habitat Mosaic in the Colombian Amazon. Conserv Biol 8:545–554. doi: 10.1046/j.1523-1739.1994.08020545.x | Colombia | 3, 11.5 |
| Banks-Leite C, Ewers RM, Metzger JP (2012) Unraveling the drivers of community dissimilarity and species extinction in fragmented landscapes. Ecology 93:2560–2569. | Brazil | 50 |
| Barlow J, Mestre LAM, Gardner TA, Peres CA (2007) The value of primary, secondary and plantation forests for Amazonian birds. Biol Conserv 136:212 – 231. doi: http://dx.doi.org/10.1016/j.biocon.2006.11.021 | Brazil | 16.5 |
| Becker CD, Agreda A Bird community differences in mature and second growth Garua forest in Machalilla National Park, Ecuador. Ornitol Neotropical 16:297–319. | Ecuador | 17.5 |
| Becker CD, Loughin TM, Santander T (2008) Identifying forest-obligate birds in tropical moist cloud forest of Andean Ecuador. J Field Ornithol 79:229–244. doi: 10.1111/j.1557-9263.2008.00184.x | Ecuador | 17.5, 17.5, 40 |
| Blake JG, Loiselle BA (2001) Bird assemblages in second-growth and old-growth forests, Costa Rica: Perspectives from mist nets and point counts. The Auk 118:304–326. doi: 10.1642/0004-8038(2001)118[0304:BAISGA]2.0.CO;2 | Costa Rica | 5, 27.5 |
| Borges SH (2007) Bird assemblages in secondary forests developing after slash-and-burn agriculture in the Brazilian Amazon. J Trop Ecol 23:469–477. doi: 10.1017/S0266467407004105 | Brazil | 4.5, 11, 27.5 |
| Dallimer M, Parnell M, Bicknell JE, Melo M (2012) The importance of novel and agricultural habitats for the avifauna of an oceanic island. J Nat Conserv 20:191–199. doi: 10.1016/j.jnc.2012.04.001 | São Tomé and Príncipe | 5 |
| Dawson J, Turner C, Pileng O, et al Bird communities of the lower Waria Valley, Morobe Province, Papua New Guinea: a comparison between habitat types. Trop Conserv Sci 4:317–348. | Papua New Guinea | 20 |
| De Lima RF, Dallimer M, Atkinson PW, Barlow J (2013) Biodiversity and land-use change: understanding the complex responses of an endemic-rich bird assemblage. Divers Distrib 19:411–422. doi: 10.1111/ddi.12015 | São Tomé and Príncipe | 50 |
| Hutto RL (1989) The Effect of Habitat Alteration on Migratory Land Birds in a West Mexican Tropical Deciduous Forest: A Conservation Perspective. Conserv Biol 3:138–148. doi: 10.1111/j.1523-1739.1989.tb00066.x | Mexico | 2, 5 |
| Johns AD (1991) Responses of Amazonian rain forest birds to habitat modification. J Trop Ecol 7:417–437. doi: 10.1017/S0266467400005812 | Brazil | 1 |
| Maas B, Putra DD, Waltert M, et al (2009) Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species. Biol Conserv 142:2665–2671. doi: 10.1016/j.biocon.2009.06.018 | Indonesia | 3.5, 4, 5.5 |
| Mallari NAD, Collar NJ, Lee DC, et al (2011) Population densities of understorey birds across a habitat gradient in Palawan, Philippines: implications for conservation. Oryx 45:234–242. doi: 10.1017/S0030605310001031 | Philippines | 10, 30 |
| Marsden SJ, Symes CT, Mack AL (2006) The response of a New Guinean avifauna to conversion of forest to small-scale agriculture. Ibis 148:629–640. doi: 10.1111/j.1474-919X.2006.00577.x | Papua New Guinea | 5, 14 |
| Mulwa RK, Böhning-Gaese K, Schleuning M (2012) High Bird Species Diversity in Structurally Heterogeneous Farmland in Western Kenya. Biotropica 44:801–809. doi: 10.1111/j.1744-7429.2012.00877.x | Kenya | 50 |
| Naidoo R (2004) Species richness and community composition of songbirds in a tropical forest-agricultural landscape. Anim Conserv 7:93–105. doi: 10.1017/S1367943003001185 | Uganda | 13 |
| Neuschulz EL, Botzat A, Farwig N (2011) Effects of forest modification on bird community composition and seed removal in a heterogeneous landscape in South Africa. Oikos 120:1371–1379. doi: 10.1111/j.1600-0706.2011.19097.x | South Africa | 85 |
| O’Dea N, Whittaker R (2007) How resilient are Andean montane forest bird communities to habitat degradation? Biodivers Conserv 16:1131–1159. doi: 10.1007/s10531-006-9095-9 | Ecuador | 17.5 |
| Raman TRS, Rawat GS, Johnsingh AJT (1998) Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. J Appl Ecol 35:214–231. doi: 10.1046/j.1365-2664.1998.00297.x | India | 1, 5, 10, 25, 100 |
| Raman TRS, Sukumar R (2002) Responses of tropical rainforest birds to abandoned plantations, edges and logged forest in the Western Ghats, India. Anim Conserv 5:201–216. doi: 10.1017/S1367943002002251 | India | 5, 15 |
| Reid JL, Harris JBC, Zahawi RA (2012) Avian Habitat Preference in Tropical Forest Restoration in Southern Costa Rica. Biotropica 44:350–359. doi: 10.1111/j.1744-7429.2011.00814.x | Costa Rica | 9 |
| Renner S, Waltert M, Mühlenberg M (2006) Comparison of Bird Communities in Primary vs. Young Secondary Tropical Montane Cloud Forest in Guatemala. Biodivers Conserv 15:1545–1575. doi: 10.1007/s10531-005-2930-6 | Guatemala | 4 |
| Slik JWF, Van Balen S (2006) Bird Community Changes in Response to Single and Repeated Fires in a Lowland Tropical Rainforest of Eastern Borneo. Biodivers Conserv 15:4425–4451. doi: 10.1007/s10531-005-4385-1 | Indonesia | 4 |
| Sodhi NS, Koh LP, Prawiradilaga DM, et al (2005) Land use and conservation value for forest birds in Central Sulawesi (Indonesia). Biol Conserv 122:547–558. doi: 10.1016/j.biocon.2004.07.023 | Indonesia | 40 |
| Terborgh J, Weske JS (1969) Colonization of Secondary Habitats by Peruvian Birds. Ecology 50:765–782. doi: 10.2307/1933691 | Peru | 7.5 |
| Tvardikova K Bird abundances in primary and secondary growths in Papua New Guinea: a preliminary assessment. Trop Conserv Sci 3:373–388. | Papua New Guinea | 7 |
| Wijesinghe MR, Brooke M de L (2005) Impact of habitat disturbance on the distribution of endemic species of small mammals and birds in a tropical rain forest in Sri Lanka. J Trop Ecol 21:661–668. doi: 10.1017/S0266467405002695 | Sri Lanka | 5 |

**Table 2** Parameter estimates for fixed effects in all best models (selected based on AICc). Where data were transformed prior to analysis estimates are based on the transformed data used for model fitting

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Variable** | **Parameter** | **Estimate** | **SE** | **t-value** | **P value** |
| Species Richness | Intercept | -0.30838 | 0.115256 | -2.67563 | 0.011 |
| log(Age) | 0.082037 | 0.041059 | 1.998044 | 0.060 |
| Forest Specialist Species Richness | Intercept | -0.95031 | 0.18766 | -5.064 | <0.001 |
| log(Age) | 0.18780 | 0.06691 | 2.807 | 0.01 |
| Functional Diversity (FD) | Intercept | -0.04689 | 0.048301 | -0.97083 | 0.332 |
| Functional Richness (FRic) | Intercept | -1.04061 | 0.512686 | -2.02971 | 0.042 |
| Functional Evenness (FEve) | Intercept | 0.037418 | 0.031058 | 1.204752 | 0.228 |
| Functional Divergence (FDiv) | Intercept | 0.063619 | 0.021463 | 2.964176 | 0.006 |
| log(Age) | -0.01512 | 0.00719 | -2.1033 | 0.051 |
| Functional Dispersion (FDis) | Intercept | -0.02556 | 0.022802 | -1.12099 | 0.262 |

**Table 3** Model selection table for all models considered in this study

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Variable** | **Model** | **AICc** | **ΔAICc** | **Conditional R2** |
| Species richness | Null model | 30.02455 | 1.514925 | 0 |
| log(Age) | 28.50963 | 0 | 0.07 |
| Forest Specialist Species Richness | Null model | 71.67288 | 1.514925 | 0 |
| log(Age) | 70.58519 | 0 | 0.12 |
| Functional Diversity (FD) | Null model | 6.584348 | 0 | 0 |
| log(Age) | 8.845862 | 2.261514 | <0.01 |
| Functional Richness (FRic) | Null model | 213.029 | 0 | 0 |
| log(Age) | 214.3756 | 1.346595 | 0.02 |
| Functional Evenness (FEve) | Null model | -57.9035 | 0 | 0 |
| log(Age) | -55.9112 | 1.992294 | <0.01 |
| Functional Divergence (FDiv) | Null model | -112.745 | 1.784054 | 0 |
| log(Age) | -114.529 | 0 | 0.06 |
| Functional Dispersion (FDis) | Null model | -56.2951 | 0 | 0 |
| log(Age) | -55.6519 | 0.643162 | 0.03 |

**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 | 36.93706 | 1 |
| Mist\_nets+Transect+Study | 39.50605 | 2 |
| Mist\_nets+Study | 39.50605 | 3 |
| Mist nets+ Transect+Vocal+Study | 42.19209 | 4 |
| Mist nets+Transect+Vocal+Study | 45.05876 | 5 |
| Point observation+Mist nets+Transect+Vocal+Study | 48.09405 | 6 |
| Specialist Species Richness | Study | 70.58519 | 1 |
| Mist\_nets+Transect+Study | 73.15418 | 2 |
| Mist\_nets+Study | 73.15418 | 3 |
| Mist nets+ Transect+Vocal+Study | 75.86589 | 4 |
| Mist nets+Transect+Vocal+Study | 78.73255 | 5 |
| Point observation+Mist nets+Transect+Vocal+Study | 81.76785 | 6 |
| Functional Diversity (FD) | Study | 18.15588 | 1 |
| Mist\_nets+Transect+Study | 20.72487 | 2 |
| Mist\_nets+Study | 20.72487 | 3 |
| Mist nets+ Transect+Vocal+Study | 23.41996 | 4 |
| Mist nets+Transect+Vocal+Study | 26.28663 | 5 |
| Point obs+Mist nets+Transect+Vocal+Study | 29.32192 | 6 |
| Functional Richness (FRic) | Study | 214.1521 | 1 |
| Mist\_nets+Transect+Study | 216.721 | 2 |
| Mist\_nets+Study | 216.721 | 3 |
| Mist nets+ Transect+Vocal+Study | 219.4328 | 4 |
| Mist nets+Transect+Vocal+Study | 222.2994 | 5 |
| Point obs+Mist nets+Transect+Vocal+Study | 225.3347 | 6 |
| Functional Evenness (FEve) | Study | -43.5699 | 1 |
| Mist\_nets+Study | -41.0009 | 2 |
| Mist\_nets+Transect+Study | -41.0009 | 3 |
| Mist nets+ Transect+Vocal+Study | -38.2892 | 4 |
| Mist nets+Transect+Vocal+Study | -36.2568 | 5 |
| Point obs+Mist nets+Transect+Vocal+Study | -33.2215 | 6 |
| Functional Divergence (FDiv) | Study | -99.5184 | 1 |
| Mist\_nets+Transect+Study | -96.9494 | 2 |
| Mist\_nets+Study | -96.9494 | 3 |
| Mist nets+ Transect+Vocal+Study | -94.2384 | 4 |
| Mist nets+Transect+Vocal+Study | -91.3717 | 5 |
| Point obs+Mist nets+Transect+Vocal+Study | -88.3364 | 6 |
| Functional Dispersion (FDis) | Study | -43.32 | 1 |
| Mist\_nets+Study | -40.9265 | 2 |
| Mist\_nets+Transect+Study | -40.8142 | 3 |
| Mist nets+ Transect+Vocal+Study | -38.7318 | 4 |
| Mist nets+Transect+Vocal+Study | -35.8651 | 5 |
| Point obs+Mist nets+Transect+Vocal+Study | -32.8298 | 6 |