**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 and subsequent regeneration, 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 alternative habitat for forest species. However, current understanding of the biodiversity value of secondary forest is poor. 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 (dietary preference) based metrics. Species richness relative to primary forest increased with secondary forest age and reached primary forest values after 43 years. The species richness of forest specialists relative to primary forest also increased with time since disturbance but was not predicted to reach equivalence with primary forest within 100 years. However, we found no difference between primary and secondary forest in terms of functional richness or functional divergence. Our results suggest that secondary tropical forests retain similar levels of avian dietary functional diversity to primary tropical forests and therefore, that levels of ecosystem functioning may be comparable in both forest types. Therefore, secondary tropical forest, particularly older regrowth, has high biodiversity value and can support important ecosystem functions. Secondary forest should be protected from further disturbance. However, preserving primary forest is vital to conserve 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 unique forest species. Traditionally, protected areas have been seen as the best way to protect ecosystems from conversion to human land use 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 tropical biodiversity (Gibson et al., 2011), as well as providing numerous ecosystem services such as carbon storage and non-timber forest products to local communities. However, we cannot rely solely on protected areas to conserve tropical forest biodiversity. Biodiversity declines continue in many protected areas established in tropical forests (Curran et al., 2004; Laurance et al., 2012). In addition, it is not always feasible to designate sufficient land to represent adequately the range of communities found in specific biomes (Cox and Underwood, 2011) or support viable populations of all species (Struhsaker et al., 2005). Possingham et al. (2015) showed through modelling that conservation actions should combine both protection and restoration to optimize benefits for biodiversity and ecosystem services

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. Forests that have been altered beyond the normal effects of natural processes, as a result of unsustainable use or natural disasters, are considered degraded; this includes secondary forests, which have undergone forest clearance (ITTO, 2002). Wright and Muller-Landau (2006) suggest 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 can be host to forest species, 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). Despite these suggestions, the potential role of secondary forest in conserving tropical forest species is poorly understood. Past quantitative syntheses have investigated only a limited number of biodiversity metrics, have not considered heterogeneity amongst sites or have failed to account for non-independence in data (Dent and Wright, 2009; Dunn, 2004a). Thus, there is a need for quantitative, global syntheses of the biodiversity value of secondary tropical forest.

Measures of conservation value 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 to ecosystems based on their functioning. Ecosystem functions are important in determining the persistence of interacting communities, and may also ultimately provide benefits to humans, including provision of food, which can be attributed an economic value (Gascon et al., 2015). Birds provide key functions, such as pollination, seed predation and dispersal, removal of carrion, and control of other animals, in tropical forests, and the roles of individual species are governed by 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 (V. Gagic et al., 2015). Therefore, to assess ecosystem functioning we need to consider the abundance and distribution of relevant traits in the community. It has been shown that disturbance to tropical forests causes declines in fruit and insect-eating birds while causing increases in seed-eating birds (Gray et al., 2007; Newbold et al., 2013), which suggest changes in functioning, and so the functional diversity of secondary forests, should be an informative measure of ecosystem recovery.

***Aim and objectives***

The aim of this study is to compare the functional diversity, based on dietary preferences defined by foraging strata, diet and body size, of avian communities in secondary tropical forest with that of primary tropical forest, and to investigate how this changes, and possibly recovers, with secondary forest age. In addition, changes in total avian species richness and the species richness of forest specialists are investigated as indicators of the recovery of biodiversity. To achieve these aims, we conducted a meta-analysis based on a systematic review. The analysis focused on birds as their distributions and ecological traits are well known and their populations are readily surveyed, with the result that they have been well studied across the tropics. Dietary preference was chosen as the functional trait for study to represent a particular and well-studied aspect of ecosystem functioning relating to trophic relationships, as dietary preference is directly linked to the processes of pollination, seed dispersal, carrion removal, and control of other animals.

**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). Forests that had previously been selectively logged were excluded as such sites recover differently to those converted for agriculture (Corlett, 1994; Dunn, 2004b). 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. Article authors were contacted to request these data when articles suggested that they had been collected but were not presented. Additionally, for each secondary forest site, the age, and whether the site was continuous or discontinuous with primary forest, were noted. Where age and disturbance history were not presented, article authors were contacted to request the information. The median age of secondary forest was recorded when a range of possible values was given. Methodologies used to sample bird communities 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 linked to (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. 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. Species richness was calculated by summing the number of species found in at each site. In all studies sampling effort was the same in secondary and primary sites. Using the R package fundiv we calculated FD (Petchey and Gaston, 2002) a distance based metric of functional diversity that is not influenced by species abundances. FD is calculated by summing all the branch lengths of a functional dendrogram for all occurring species (Petchey and Gaston, 2002). We calculated the remaining functional diversity metrics (FRic, FEve, FDiv and FDis) using the R package FD (Laliberte et al., 2010). These metrics are calculated in multidimentional trait space, with each axis representing a different trait, from which a convex hull containing all species is created (Villéger, 2008). FRic represents the volume of the convex hull and thus the volume of trait space occupied by a community. High FRic indicates that many traits are present within a community, while low FRic indicates that some traits may be missing from the community. FEve represents 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). FDiv represents how species abundance is distributed along 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). FDis represents the distance from the centroid of trait space, weighted by species abundances (Laliberte et al., 2010). This metric is influenced by both the range of trait values in a community and the uniformity of species abundances within multidimensional trait space and it has thus been suggested that this metric can be used as a unified metric for functional diversity (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 over 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 in the systematic review. These studies documented 5065 observations of 1785 bird species. Details of studies used can be found in Table 1. 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 showed relatively low explanatory power (*R*2GLMM=0.07, Table 3). The species richness of forest specialist species was best described by a model including 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 though bird species richness in young secondary forests is lower than adjacent primary forest, this recovers within 50 years. However, species richness of forest specialists shows a slower recovery and is likely to require more than 100 years for recovery. This reemphasizes the importance of primary forest for specialist species. Regarding functional diversity, differences between secondary and primary forest were less marked. Functional divergence (FDiv) was slightly higher in young secondary forests than in primary forests, reaching equivalence after approximately 100 years. Functional richness (FRic), which is closely correlated with species richness, was lower in secondary forests, but functional dispersal (FDis), functional evenness (FEve) and functional diversity (FD) were similar in secondary and primary forest.

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

Our results show that total bird species richness increases with age in secondary tropical forests, reaching levels equivalent to primary forest within 50 years. In contrast to our findings Dunn (2004a) found that bird 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 off Dunn (2004a). Our results are similar to those of Martin et al. (2013) who found that tree species richness in secondary forests recovering from agricultural clearance recovers within approximately 50 years. This trend of increasing species richness 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 indicated that species richness of forest specialist bird species 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 >100 and between 60-150 years (Philip A Martin et al., 2013; Poorter et al., 2016) to recover in tropical secondary forests respectively it is perhaps unsurprising that bird forest specialists require similar amount of time to recolonize 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.

Previous qualitative reviews have suggested that land use history and landscape factors influence the recovery of faunal communities (Bowen et al., 2007; Chazdon et al., 2009), but our results did not support such relationships. The floristic and structural recovery of vegetation has been found to differ depending on land use history in terms of disturbance duration, intensity and type, which particularly impacts the state of the seed bank and soil fertility (Guariguata and Ostertag, 2001; Kammesheidt, 2002). For example, Borges and Stouffer (1999) found that a small change in disturbance regime resulted in distinct floral and avian communities. Details of disturbance history beyond broad classifications were largely absent from the publications we accessed, which could explain the disparity and highlights the need for improved metadata collection. Forest specialists refrain from travelling through open or intensively used areas (Laurance and Gomez, 2005; Stouffer et al., 2006) to avoid risks posed by open and edge habitats where abiotic and biotic conditions differ (Aben et al., 2012; Laurance et al., 2004), suggesting these species might be absent from isolated secondary forest patches. We found that whether secondary forest was continuous or discontinuous with primary forest had no influence on species richness. A better measure of isolation might have been the distance to primary forest as some bird species are vagile and can disperse over gaps (Lees and Peres, 2009), but the relevant data were not available.

***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 general 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. This result mirrors that of previous work that has found similar levels of functional diversity in degraded forests (Edwards et al., 2013). mayFDiv 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, in our study 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 potential conservation value of secondary forests. Functional diversity has been shown to explain changes in ecosystem function more effectively than metrics based on species identity (Vesna Gagic et al., 2015). As a result, the functions 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. 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). Reductions in large bodied frugivores can dramatically affect seed dispersal, 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 (Diaz and Cabido). Therefore, our results also suggest that communities in secondary forest may be less stable through time potentially resulting in changes in ecosystem functions.

***Caveats***

Any synthesis is affected by quality and representativeness of data used (Gonzalez et al., 2016; P. A. Martin et al., 2013). Data in our study 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 varied in quality as statistical controls since definitions of primary forest 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 tropical secondary forest. Relatively few sites were previously intensively farmed, as is broadly the case with secondary forest (Asner et al., 2009). In addition, the majority of sites were younger than 40 years old, as is the case with secondary forests more generally which may be reconverted to agriculture after 20 years in slash-and-burn systems (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 services, including pollination and seed dispersal. However, secondary tropical forests are at high risk of conversion to other land uses. In South America, mid-age stands are often converted to agriculture (Smith et al., 2003) and in Southeast Asia, degraded forests are regularly converted to oil palm or runner plantations (Koh and Wilcove, 2008). This conversion to agricultural or agroforestry land use reduces species and functional diversity (Edwards et al., 2013; Tscharntke et al., 2008). Young secondary forest retains high species richness, but regrowth cannot support as many forest specialists as primary forest. It is vital to preserve primary forest for protection of these species. Although species richness is high in new secondary forest, this increases with forest age and so the conservation value of secondary forest will never be maximised if regrowth is deforested or disturbed.

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 birds 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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**References**

Aben, J., Adriaensen, F., Thijs, K.W., Pellikka, P., Siljander, M., Lens, L., Matthysen, E., 2012. Effects of matrix composition and configuration on forest bird movements in a fragmented Afromontane biodiversity hot spot: Forest bird movements across an Afrotropical matrix. Anim. Conserv. 15, 658–668. doi:10.1111/j.1469-1795.2012.00562.x

Asner, G.P., Rudel, T.K., Aide, T.M., Defries, R., Emerson, R., Evaluaci, U., 2009. A Contemporary Assessment of Change in Humid Tropical Forests. Conserv. Biol. 23, 1386–1395. doi:10.1111/j.1523-1739.2009.01333.x

Banks-Leite, C., Ewers, R.M., Metzger, J.-P., 2010. Edge effects as the principal cause of area effects on birds in fragmented secondary forest. Oikos 119, 918–926. doi:10.1111/j.1600-0706.2009.18061.x

Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L. V, Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro-Junior, M.A., da Silva, M.N.F., da Silva Motta, C., Peres, C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. 104, 18555–18560. doi:10.1073/pnas.0703333104

Barlow, J., Mestre, L.A.M., Gardner, T.A., Peres, C.A., 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

Barton, K., 2014. MuMIn: Multi-model inference.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. ArXiv.

BirdLife International, 2013. IUCN Red List for birds [WWW Document].

Borges, S.H., Stouffer, P.C., 1999. Bird Communities in Two Types of Anthropogenic Successional Vegetation in Central Amazonia. Condor 101, 529–536. doi:10.2307/1370182

Bowen, M.E., McAlpine, C. a., House, A.P.N., Smith, G.C., 2007. Regrowth forests on abandoned agricultural land: A review of their habitat values for recovering forest fauna. Biol. Conserv. 140, 273–296. doi:10.1016/j.biocon.2007.08.012

Chazdon, R.L., Peres, C.A., Dent, D., Sheil, D., Lugo, A.E., Lamb, D., Stork, N.E., Miller, S.E., 2009. The potential for species conservation in tropical secondary forests. Conserv. Biol. 23, 1406–17. doi:10.1111/j.1523-1739.2009.01338.x

Corlett, R.T., 1994. What is secondary forest? J. Trop. Ecol. 10, 445–447.

Costantini, D., Edwards, D.P., Simons, M.J.P., 2016. Life after logging in tropical forests of Borneo : A meta-analysis. BIOC 196, 182–188. doi:10.1016/j.biocon.2016.02.020

Cox, R.L., Underwood, E.C., 2011. The Importance of Conserving Biodiversity Outside of Protected Areas in Mediterranean Ecosystems. PLoS One 6, e14508. doi:10.1371/journal.pone.0014508

Curran, L.M., Trigg, S.N., McDonald, A.K., Astiani, D., Hardiono, Y.M., Siregar, P., Caniago, I., Kasischke, E., 2004. Lowland Forest Loss in Protected Areas of Indonesian Borneo. Science (80-. ). 303, 1000–1003. doi:10.1126/science.1091714

Dent, D.H., Wright, S.J., 2009. The future of tropical species in secondary forests: A quantitative review. Biol. Conserv. 142, 2833 – 2843. doi:http://dx.doi.org/10.1016/j.biocon.2009.05.035

Dudley, N., 2008. Guidelines for Applying Protected Area Management Categories. IUCN, Gland, Switzerland.

Dunn, R.R., 2004a. Recovery of faunal communities during tropical forest regeneration. Conserv. Biol. 18, 302–309. doi:10.1111/j.1523-1739.2004.00151.x

Dunn, R.R., 2004b. Managing the tropical landscape: a comparison of the effects of logging and forest conversion to agriculture on ants, birds, and lepidoptera. For. Ecol. Manage. 191, 215–224. doi:10.1016/j.foreco.2003.12.008

Edwards, F.A., Edwards, D.P., Hamer, K.C., Davies, R.G., 2013. Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland 313–326.

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-Dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W., Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. Proc. R. Soc. B Biol. Sci. 282, 20142620–20142620. doi:10.1098/rspb.2014.2620

Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., Slade, E.M., Steffan-dewenter, I., Emmerson, M., Potts, S.G., Tscharntke, T., Weisser, W., Bommarco, R., 2015. Functional identity and diversity of animals predict ecosystem functioning better than species-based indices.

Gardner, T.A., Barlow, J., Parry, L.W., Peres, C.A., 2007. Predicting the Uncertain Future of Tropical Forest Species in a Data Vacuum. Biotropica 39, 25–30. doi:10.1111/j.1744-7429.2006.00228.x

Gascon, C., Brooks, T.M., Contreras-MacBeath, T., Heard, N., Konstant, W., Lamoreux, J., Launay, F., Maunder, M., Mittermeier, R.A., Molur, S., Al Mubarak, R.K., Parr, M.J., Rhodin, A.G.J., Rylands, A.B., Soorae, P., Sanderson, J.G., Vié, J.-C., 2015. The Importance and Benefits of Species. Curr. Biol. 25, R431–R438. doi:10.1016/j.cub.2015.03.041

Gibbs, H.K., Ruesch, A.S., Achard, F., Clayton, M.K., Holmgren, P., Ramankutty, N., Foley, J.A., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc. Natl. Acad. Sci. 107, 16732–16737.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J. a, Laurance, W.F., Lovejoy, T.E., Sodhi, N.S., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. Nature 478, 378–81. doi:10.1038/nature10425

Gonzalez, A., Cardinale, B.J., Allington, G.R.H., Byrnes, J., Endsley, K.A., Brown, D.G., Hooper, D.U., Isbell, F., Loreau, M., Arbor, A., Paul, S., Station, E.E., 2016. Estimating local biodiversity change: a critique of papers claiming no net loss of local diversity. Ecology.

Gray, M.A., Baldauf, S.L., Mayhew, P.J., Hill, J.K., 2007. The Response of Avian Feeding Guilds to Tropical Forest Disturbance. Conserv. Biol. 21, 133–141. doi:10.1111/j.1523-1739.2006.00557.x

Griffin, J.N., Méndez, V., Johnson, A.F., Jenkins, S.R., Foggo, A., 2009. Functional diversity predicts overyielding effect of species combination on primary productivity. Oikos 118, 37–44. doi:10.1111/j.1600-0706.2008.16960.x

Griscom, H.P., Ashton, M.S., 2011. Restoration of dry tropical forests in Central America: A review of pattern and process. For. Ecol. Manage. 261, 1564–1579. doi:10.1016/j.foreco.2010.08.027

Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. For. Ecol. Manage. 148, 185–206. doi:10.1016/S0378-1127(00)00535-1

Hedges, L.V.L.V. V, Gurevitch, J., Curtis, P.S.S.P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150–1156. doi:10.1890/0012-9658(1999)080[1150:TMAORR]2.0.CO;2

ITTO, 2002. ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests.

Kammesheidt, L., 2002. Perspectives on secondary forest management in tropical humid lowland America. Ambio 31, 243–250.

Koh, L.P., Wilcove, D.S., 2008. Is oil palm agriculture really destroying tropical biodiversity?: Oil palm agriculture and tropical biodiversity. Conserv. Lett. 1, 60–64. doi:10.1111/j.1755-263X.2008.00011.x

Laliberte, E., Legendre, P., Ecology, S., January, N., 2010. A distance-based framework for measuring functional diversity from multiple traits A distance-based framework for measuring from multiple traits functional diversity. Ecology 91, 299–305. doi:10.1890/08-2244.1

Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical forest landscapes. Science 310, 1628–32. doi:10.1126/science.1111773

Laurance, S.G.W., Gomez, M.S., 2005. Clearing Width and Movements of Understory Rainforest Birds. Biotropica 37, 149–152. doi:10.1111/j.1744-7429.2005.04099.x

Laurance, S.G.W., Stouffer, P.C., Laurance, W.F., 2004. Effects of Road Clearings on Movement Patterns of Understory Rainforest Birds in Central Amazonia. Conserv. Biol. 18, 1099–1109. doi:10.1111/j.1523-1739.2004.00268.x

Laurance, W.F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C.J.A., Sloan, S.P., Laurance, S.G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K.S., Cannon, C.H., Cao, M., Carroll, R., Chapman, C., Coates, R., Cords, M., Danielsen, F., De Dijn, B., Dinerstein, E., Donnelly, M.A., Edwards, D., Edwards, F., Farwig, N., Fashing, P., Forget, P.-M., Foster, M., Gale, G., Harris, D., Harrison, R., Hart, J., Karpanty, S., John Kress, W., Krishnaswamy, J., Logsdon, W., Lovett, J., Magnusson, W., Maisels, F., Marshall, A.R., McClearn, D., Mudappa, D., Nielsen, M.R., Pearson, R., Pitman, N., van der Ploeg, J., Plumptre, A., Poulsen, J., Quesada, M., Rainey, H., Robinson, D., Roetgers, C., Rovero, F., Scatena, F., Schulze, C., Sheil, D., Struhsaker, T., Terborgh, J., Thomas, D., Timm, R., Nicolas Urbina-Cardona, J., Vasudevan, K., Joseph Wright, S., Carlos Arias-G., J., Arroyo, L., Ashton, M., Auzel, P., Babaasa, D., Babweteera, F., Baker, P., Banki, O., Bass, M., Bila-Isia, I., Blake, S., Brockelman, W., Brokaw, N., Brühl, C.A., Bunyavejchewin, S., Chao, J.-T., Chave, J., Chellam, R., Clark, C.J., Clavijo, J., Congdon, R., Corlett, R., Dattaraja, H.S., Dave, C., Davies, G., de Mello Beisiegel, B., de Nazaré Paes da Silva, R., Di Fiore, A., Diesmos, A., Dirzo, R., Doran-Sheehy, D., Eaton, M., Emmons, L., Estrada, A., Ewango, C., Fedigan, L., Feer, F., Fruth, B., Giacalone Willis, J., Goodale, U., Goodman, S., Guix, J.C., Guthiga, P., Haber, W., Hamer, K., Herbinger, I., Hill, J., Huang, Z., Fang Sun, I., Ickes, K., Itoh, A., Ivanauskas, N., Jackes, B., Janovec, J., Janzen, D., Jiangming, M., Jin, C., Jones, T., Justiniano, H., Kalko, E., Kasangaki, A., Killeen, T., King, H., Klop, E., Knott, C., Koné, I., Kudavidanage, E., Lahoz da Silva Ribeiro, J., Lattke, J., Laval, R., Lawton, R., Leal, M., Leighton, M., Lentino, M., Leonel, C., Lindsell, J., Ling-Ling, L., Eduard Linsenmair, K., Losos, E., Lugo, A., Lwanga, J., Mack, A.L., Martins, M., Scott McGraw, W., McNab, R., Montag, L., Myers Thompson, J., Nabe-Nielsen, J., Nakagawa, M., Nepal, S., Norconk, M., Novotny, V., O’Donnell, S., Opiang, M., Ouboter, P., Parker, K., Parthasarathy, N., Pisciotta, K., Prawiradilaga, D., Pringle, C., Rajathurai, S., Reichard, U., Reinartz, G., Renton, K., Reynolds, G., Reynolds, V., Riley, E., Rödel, M.-O., Rothman, J., Round, P., Sakai, S., Sanaiotti, T., Savini, T., Schaab, G., Seidensticker, J., Siaka, A., Silman, M.R., Smith, T.B., de Almeida, S.S., Sodhi, N., Stanford, C., Stewart, K., Stokes, E., Stoner, K.E., Sukumar, R., Surbeck, M., Tobler, M., Tscharntke, T., Turkalo, A., Umapathy, G., van Weerd, M., Vega Rivera, J., Venkataraman, M., Venn, L., Verea, C., Volkmer de Castilho, C., Waltert, M., Wang, B., Watts, D., Weber, W., West, P., Whitacre, D., Whitney, K., Wilkie, D., Williams, S., Wright, D.D., Wright, P., Xiankai, L., Yonzon, P., Zamzani, F., 2012. Averting biodiversity collapse in tropical forest protected areas. Nature 489, 290–294. doi:10.1038/nature11318

Lees, A.C., Peres, C. a., 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. Oikos 118, 280–290. doi:10.1111/j.1600-0706.2008.16842.x

MacArthur, R.H., MacArthur, J.W., 1961. On Bird Species Diversity. Ecology 42, 594–598. doi:10.2307/1932254

Martin, P.A., Newton, A.C., Bullock, J.M., 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proc. R. Soc. B Biol. Sci. 280. doi:10.1098/rspb.2013.2236

Martin, P.A., Newton, A.C., Bullock, J.M., 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. Proc. R. Soc. B Biol. Sci. 280, 20132236–20132236. doi:10.1098/rspb.2013.2236

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858. doi:10.1038/35002501

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R 2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. doi:10.1111/j.2041-210x.2012.00261.x

Newbold, T., Hudson, L.N.L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Dıáz, S., Echeverria-Londoño, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Laginha Pinto Correia, D., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.J.P.W., Purvis, A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.J.P.W., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520, 45–. doi:10.1038/nature14324

Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Şekercioğlu, Ç.H., Alkemade, R., Booth, H., Purves, D.W., 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. Proc. R. Soc. B Biol. Sci. 280.

Osuri, A.M., Ratnam, J., Varma, V., Alvarez-Loayza, P., Astaiza, J.H., Bradford, M., Fletcher, C., Ndoundou-Hockemba, M., Jansen, P.A., Kenfack, D., Marshall, A.R., Ramesh, B.R., Rovero, F., Sankaran, M., 2016. Contrasting effects of defaunation on aboveground carbon storage across the global tropics. Nat. Commun. doi:10.1038/ncomms11351

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758. doi:10.1111/j.1461-0248.2006.00924.x

Petchey, O.L., Gaston, K.J., 2002. Functional diversity (FD), species richness and community composition. Ecol. Lett. 5, 402–411. doi:10.1046/j.1461-0248.2002.00339.x

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., de Almeida-Cortez, J.S., Cabral, G.A.L., de Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.-C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Muñoz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., de Oliveira, A.A., Orihuela-Belmonte, E., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., van Breugel, M., van der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. Nature 1–15. doi:10.1038/nature16512

Possingham, H.P., Bode, M., Klein, C.J., 2015. Optimal Conservation Outcomes Require Both Restoration and Protection. PLOS Biol. 13, e1002052. doi:10.1371/journal.pbio.1002052

Prescott, G.W., Gilroy, J.J., Haugaasen, T., Medina, C.A., Foster, W.A., Edwards, D.P., 2016. Reducing the impacts of Neotropical oil palm development on functional diversity. Biol. Conserv. 197, 139–145. doi:10.1016/j.biocon.2016.02.013

Pullin, A.S., Stewart, G.B., 2006. Guidelines for Systematic Review in Conservation and Environmental Management. Conserv. Biol. 20, 1647–1656. doi:10.1111/j.1523-1739.2006.00485.x

R Core Team, 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Sekercioglu, C.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystem consequences of bird declines. Proc. Natl. Acad. Sci. 101, 18042–18047. doi:10.1073/pnas.0408049101

Smith, J., Ferreira, S., van de Kop, P., Palheta Ferreira, C., Sabogal, C., 2003. The persistence of secondary forests on colonist farms in the Brazilian Amazon. Agrofor. Syst. 58, 125–135. doi:10.1023/A:1026049507421

Sodhi, N.S., Koh, L.P., Prawiradilaga, D.M., Darjono, Tinulele, I., Putra, D.D., Tong Tan, T.H., 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

Stouffer, P.C., Bierregaard, R.O., Strong, C., Lovejoy, T.E., 2006. Long-Term Landscape Change and Bird Abundance in Amazonian Rainforest Fragments: Birds in Amazonian Forest Fragments. Conserv. Biol. 20, 1212–1223. doi:10.1111/j.1523-1739.2006.00427.x

Struhsaker, T.T., Struhsaker, P.J., Siex, K.S., 2005. Conserving Africa’s rain forests: problems in protected areas and possible solutions. Biol. Conserv. 123, 45 – 54. doi:http://dx.doi.org/10.1016/j.biocon.2004.10.007

Terborgh, J., 1985. Habitat selection in Amazonian birds. Academic Press, Inc., Orlando, Florida & London.

Tscharntke, T., Sekercioglu, C.H., Dietsch, T. V., Sodhi, N.S., Hoehn, P., Tylianakis, J.M., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosytems. Ecology 89, 944–951. doi:10.1890/07-0455.1

Villéger, S., 2008. New multidimensional functional diversity indices for a multifaceted framwork in functional ecology. Ecology 89, 2290–2301. doi:10.1890/07-1206.1

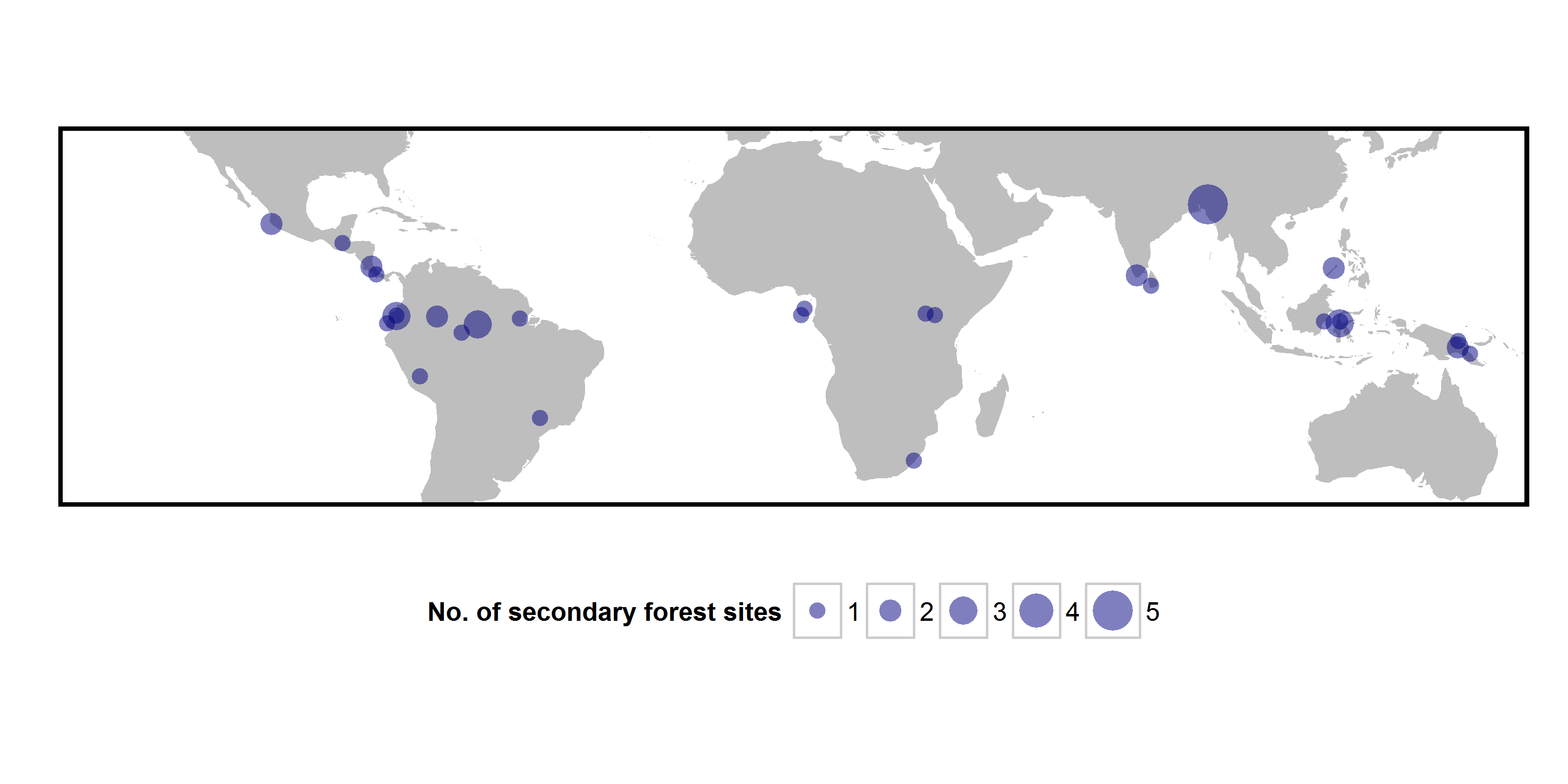
Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., Jetz, W., 2014. EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals. Ecology 95, 2027–2027. doi:10.1890/13-1917.1

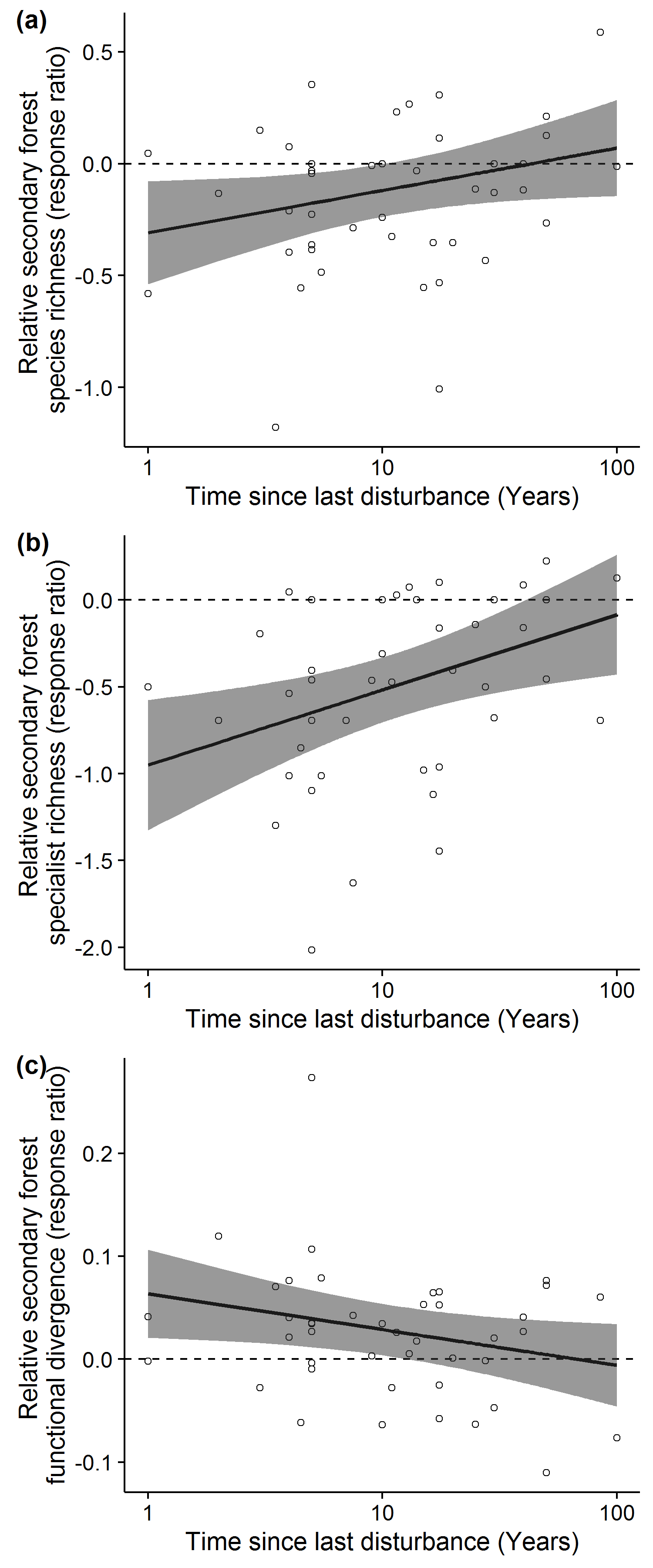
Wright, S.J., Muller-Landau, H.C., 2006. The Future of Tropical Forest Species. Biotropica 38, 287–301. doi:10.1111/j.1744-7429.2006.00154.x

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. doi:10.1111/j.2041-210X.2009.00001.x

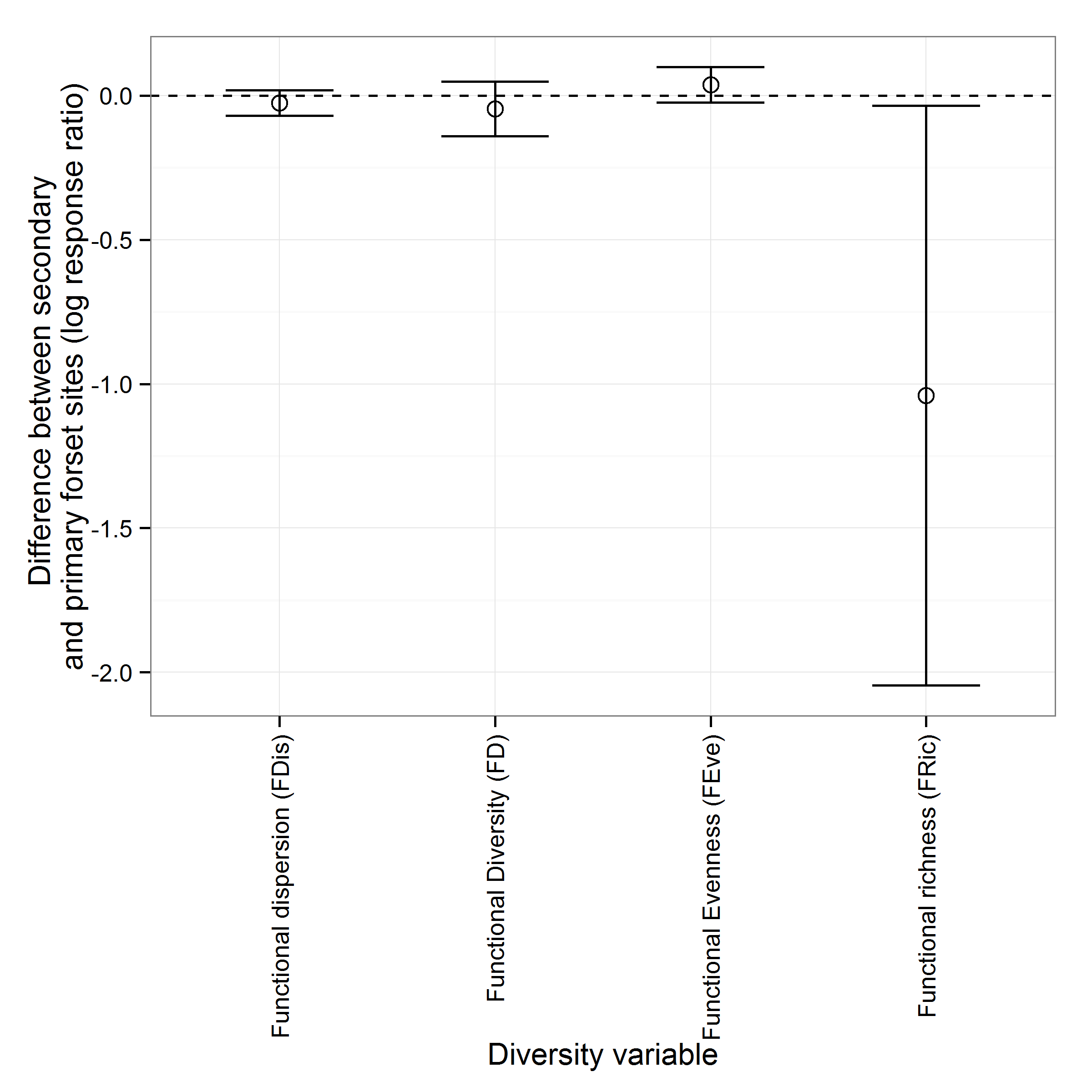
**Figures**

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



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



**Fig. 3** Difference between secondary and primary 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** 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 |
| 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 |
| 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 |
| 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 |