

Meta-analysis

Recovery of amphibian, reptile, bird and mammal diversity during secondary forest succession in the tropics



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In tropical regions, many studies have focused on how vegetation and ecosystem processes recover following the abandonment of anthropogenic activities, but less attention has been given to the recovery patterns of vertebrates. Here we conduct a meta-analysis ($n = 147$ studies) of amphibian, reptile, bird and mammal recovery during tropical secondary forest succession (i.e. natural regeneration). For each taxonomic group, we compared changes in species richness and compositional similarity during natural secondary succession to reference forests (mature or old growth forest). In addition, we evaluated the response of forest specialists and the change in bird and mammal functional groups during natural secondary succession in the tropical moist forest biome. Overall, species richness of all groups reached levels of the reference forests during natural secondary succession, but this was not the case for species compositional similarity. The delay in recovery of forest specialists may be the reason for the delay in recovery of species compositional similarity. Overall, vertebrate recovery increased with successional stage, but other potential predictors of diversity recovery, such as, the geographical setting (amphibian and reptile species compositional similarity recovered more rapidly on islands), rainfall (mammal species richness and compositional similarity recovered faster in regions of low rainfall), and the landscape context (amphibian, reptile and mammal species compositional similarity recovered faster in regions with more forest patches) influenced vertebrate recovery. These results demonstrate the important role of secondary forests in providing habitat for many vertebrates, but the slow recovery of species compositional similarity, forest specialists and some functional groups (e.g. insectivorous birds) highlighted the challenge of secondary forest persistence, and strongly argues for the continued protection of old growth/mature forest as habitat for forest specialists and as sources for secondary forest sites.

Keywords: biodiversity recovery, natural regeneration, tropical secondary forest, vertebrates

Synthesis

Our study addresses the question of how faunal diversity changes during tropical secondary forest succession. We reviewed 147 studies of tropical amphibians, reptiles, birds and mammals and determined how species richness, species composition similarity, forest specialist richness, and functional groups richness changed during succession. Our results indicated that secondary forests provide habitat for many vertebrates, and in general species diversity could be similar to reference forest after approximately 40 years of succession. Species composition was very different, emphasizing the importance of long-term persistence of secondary forests and the conservation of intact old growth forests.



Introduction

Deforestation and reforestation are affecting biodiversity worldwide (Foley et al. 2005). The loss of forests is greatly modifying the distribution, abundance, function and composition of the biota (Ibarra and Martin 2015). In the extreme, deforestation results in species extinction (Pimm et al. 2014). In areas where human disturbed lands are abandoned (e.g. agriculture, pasture, slash and burn), the increase in natural regenerated secondary forest cover can provide habitat for many species and improve ecosystem services (Chazdon et al. 2009, Poorter et al. 2016, Rozendaal et al. 2019). Although ecologists and conservationists have focused on deforestation, extensive areas of the tropics are naturally regenerated forest and their importance for biodiversity has not been fully explored (Achard et al. 2002, Aide et al. 2013, Chazdon et al. 2016, Reid et al. 2018). While most secondary forest studies have focused on vegetation, recent studies have analysed the recovery patterns of vertebrates during secondary forest succession (Andrade and Rubio-Torgler 1994, Medellín and Equihua 1998, Blake and Loiselle 2001, Crouzeilles et al. 2017), or have evaluated the functional (Sayer et al. 2017) and phylogenetic diversity (Edwards et al. 2017) of vertebrates in tropical secondary forest. Understanding these dynamics is essential for generating management plans and conservation strategies.

During the last 20 years, extensive research on plant ecology of tropical secondary forests has shown that species richness and biomass often recover to levels similar to old growth forests in 40–60 years (Aide et al. 2000, Guariguata and Ostertag 2001, Poorter et al. 2016, Rozendaal et al. 2019). For the vertebrates, systematic reviews suggest that species richness can reach levels comparable to old growth forest in 20–40 years, but species composition recovers at a much slower rate (Dunn 2004, Dent and Wright 2009, Curran et al. 2014). Studies of amphibians and reptiles have shown species richness recovery in as little as 10–30 years following anthropogenic abandonment and secondary forest succession (Ríos-López and Aide 2007, Hilje and Aide 2012, Hernández-Ordóñez et al. 2015). In contrast, the recovery of some bird functional groups can be slower because they depend on a specific microhabitat (Şekercioğlu et al. 2002, Stratford and Stouffer 2015). For example, the rate of recovery of cavity nesting birds will be limited by the recovery time of large trees and tree related microhabitats (White et al. 2006, Larrieu et al. 2018). Thus, it is important to account for the variation in the recovery of different functional groups (Cadotte et al. 2011). In secondary forest, the recovery of bird forest specialists can take more than 100 years (Sayer et al. 2017), while bird phylogenetic recovery can occur in only 30 years (Edwards et al. 2017). The inconclusive and contrasting patterns of vertebrate diversity recovery is due to relatively few studies, grouping species with different natural histories such as forest specialists and habitat generalists, not controlling for different habitats, biomes or biotic and abiotic factors (e.g. past disturbance, forest cover), and highly variable

sampling techniques, which complicate comparisons among studies (Gardner et al. 2007a, Chazdon et al. 2009, Dent and Wright 2009, Sayer et al. 2017).

At least seventeen synthesis studies have included vertebrate recovery in the context of evaluating secondary forest value, evaluating forest restoration success, or comparing the effect of different human impacts, such as forest management strategies on biodiversity (Supplementary material Appendix 1 Table A1). These studies have included narrative reviews (Bowen et al. 2007, Gardner et al. 2007a, b, Chazdon et al. 2009, Karthik et al. 2009), vote counting analysis (Hudson et al. 2014, Jones and Schmitz 2009, Crouzeilles et al. 2016b), linear regression models (Dunn 2004), species composition and structure similarity (Dent and Wright 2009), and meta-analysis (Gibson et al. 2011, Curran et al. 2014, Chaudhary et al. 2016, Crouzeilles et al. 2016a, 2017, Meli et al. 2017, Sayer et al. 2017). Although these studies have helped to better understand the recovery process of vertebrates in tropical forest, they have combined the successional process into a single group (secondary forest), grouped a wide array of species (e.g. plants, animals), rarely separated specialists and generalists, combined studies from different biogeographic regions or settings (e.g. biomes, islands), or combined different ecological metrics (e.g. richness and composition). Furthermore, there have been only a few comprehensive analyses of vertebrate diversity recovery during naturally regenerated secondary forest succession (Crouzeilles et al. 2017, Meli et al. 2017).

Just as the rates of vegetation recovery vary among biomes (Poorter et al. 2016, Rozendaal et al. 2019), vertebrate recovery is likely to vary due to differences in natural history, physiology, behaviour and dispersal abilities of individual species. Furthermore, local, landscape and biogeographic setting will also influence the rate of recovery (Raman et al. 1998, Novosolov et al. 2016, Leal et al. 2017). Overall, the different measures of species recovery are expected to increase during secondary succession as forest structure, complexity and canopy height increase (Fig. 1). But, we expect species richness to recover faster than species compositional similarity, and the recovery of forest specialists and functional groups to be the slowest (Fig. 1).

In this analysis we describe the response of four vertebrate groups (amphibians, reptiles, birds and mammals) during four successional stages within secondary forest in three tropical biomes (moist forest, dry forest and savannahs, see Supplementary material Appendix 1 Fig. A1; Olson et al. 2001). For each taxonomic group, we estimated the recovery of species richness and species compositional similarity to reference forests (i.e. mature or control forest). Given that most studies occurred in tropical moist forest biome, we evaluated the recovery of forest specialist species and the distribution of bird and mammal functional groups during succession in this biome. Specifically, we addressed the following questions: 1) how does vertebrate species richness and species compositional similarity change during secondary forest succession? 2) how does vertebrate forest specialist

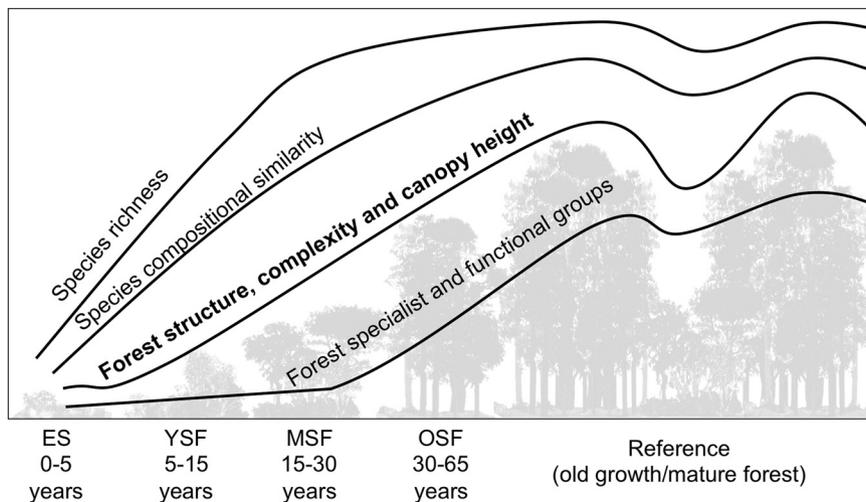


Figure 1. Conceptual trajectories of different measures of fauna recovery during secondary forest succession. We expect that forest stage (age) will be the best predictor of recovery, but the recovery trajectories will also be influenced by local, landscape and biogeographic variables. Stages: ES, early succession; YSF, young secondary forest; MSF, mid-successional secondary forest; OSF, old secondary forest. Age (years below each category) reflects time since abandonment.

richness change during secondary forest succession in the tropical moist forest biome? 3) how does the relative richness of functional groups change during secondary forest succession in the tropical moist forest biome? And 4) what variables could explain changes in the diversity metrics (species richness, compositional similarity, forest specialist richness, functional groups richness) of vertebrate recovery during secondary forest succession?

Material and methods

Data collection

We based our literature search on Dunn (2004), Bowen et al. (2007), Gardner et al. (2007a, b), Chazdon et al. (2009), Dent and Wright (2009), Jones and Schmitz (2009), Karthik et al. (2009), Gibson et al. (2011), Curran et al. (2014), Hudson et al. (2014), Chaudhary et al. (2016), Crouzeilles et al. (2016a, b) and Sayer et al. (2017); recent reviews that included information on vertebrates (amphibians, reptiles, birds or mammals) in tropical secondary forests. These reviews were related to secondary forests, restoration projects, changes in land-use, or different forest management strategies. Some of the reviews had a wide scope, including both temperate and tropical regions and responses to different impacts (e.g. slash and burn, selective logging, fragmentation), thus this first compilation comprised 398 studies. Additionally, we conducted a systematic review in April 2017 by searching Web of Knowledge using the terms: amphibian or bird or diversity recovery or mammal or reptile or tropics or secondary succession or land abandonment or secondary forest regeneration (Supplementary material Appendix 1 Table A1). We also identified two herpetological studies (Hernández-Ordóñez et al. 2015, Basham et al. 2016) that

provided 24 additional studies. We included 16 other studies cited elsewhere that were not detected in the previous datasets but addressed vertebrate succession in natural regenerated secondary forests. The studies included in our analysis were published prior to December 2016 (Basham et al. 2016). In total, we assessed 440 references, and for our analyses we included the studies that matched our inclusion criteria (Supplementary material Appendix 1 Table A2).

Our inclusion criteria included studies in the tropics (between the Tropic of Cancer at $\sim 23^{\circ}30'N$, and the Tropic of Capricorn at $\sim 23^{\circ}30'S$) that linked species richness or composition of amphibians, reptiles, birds or mammals, with at least one of four secondary forest successional stages (see below) and reference forests that were described in each study as mature, old growth, primary or 'undisturbed' (less-disturbed) forests. Our classification of the secondary forest successional stage and reference forest was based on the definition within each primary study. All studies included replicates for at least one of the four secondary forest successional stages (treatment groups) and for the reference forest stage (control group). The secondary forest successional stage often included forest age (i.e. time since abandonment). In many cases, the age of the reference forest was not provided, but this variable was not used in any analyses. All studies included natural forest regeneration after abandonment (i.e. we exclude data for plantations or active restoration). We excluded any sites that were selectively logged, as they can be ecologically similar to reference forests due to their lower cutting cycles in comparison with other secondary forests (Gibson et al. 2011, Crouzeilles et al. 2016a). In addition, studies that included more than one taxonomic group were analysed separately (e.g. a single herpetofaunal study was included as two different studies, an amphibian and a reptile study). We did not separate taxonomic groups into finer categories (e.g. non-volant and volant mammals) because our

major interest was to contrast the recovery patterns of the four main taxonomic groups.

Successional stages

In each study, all sites were assigned to one of four successional stages or reference forest (i.e. mature, old growth or less-disturbed forest) based on the original description, and similar to the stages used in a study of carbon sequestration in tropical secondary forests (Chazdon et al. 2016). The four successional stages were: early succession (pasture or open areas); young secondary forest (mainly shrublands, with dense understory); mid-successional secondary forest (intermediate successional forests, more open understory and taller canopy than young secondary forests); old secondary forest (advanced successional forest, with open understory and canopy height similar to reference forests); and the reference forests (Fig. 1). Although succession is a continuous process, these categories of forest structure and complexity are a useful way of comparing the responses of the vertebrate during succession (Pinotti et al. 2015, Chazdon et al. 2016). Furthermore, there were significant differences in the age (i.e. time since abandonment) among successional stages when reported (Supplementary material Appendix 1 Fig. A2, Kruskal–Wallis, $\chi^2 = 155.93$, $df = 3$, p -adjusted < 0.001 ; confirmed by post hoc multiple comparisons of medians with Bonferroni correction). These successional stages were used in the analysis of the secondary successional response of vertebrate species richness, species compositional similarity, richness of tropical moist forest specialist species and the bird and mammal functional groups. In addition, we used the mean ages of the successional stages, when reported, as local predictor variables in the generalized linear model selection.

Data extraction and potential predictors of diversity recovery during secondary succession

From each study, we extracted the following variables: study taxon (amphibian, reptile, bird or mammal); the mean value of rainfall and elevation; mean species richness of the reference forests; the species list if reported; and the geographic location (coordinates). In addition, we classified each study into: geographic setting (continent or island); zoogeographic realm (Supplementary material Appendix 1 Table A2–A8; Holt et al. 2013, Ficetola et al. 2017); and biome. We choose the zoogeographic realms classification (Holt et al. 2013) rather than other traditional biogeographic categorization (e.g. biogeographic realms in Olson et al. 2001) because it includes not only distributional, but phylogenetic relationships (Holt et al. 2013), and these realms have been shaped by multiple ecological and historical drivers (Ficetola et al. 2017). The biomes were: tropical and subtropical moist broadleaf forests (tropical moist forests); tropical and subtropical dry broadleaf forests (tropical dry forests); and tropical, subtropical and montane grassland, savannas and shrublands (tropical savannas) following Olson et al. (2001). Although

the tropical savannas biome is dominated by open grasslands, in this study we only included studies that focused on woody vegetation succession (e.g. gallery forests in the Orinoco and the Cerrado regions in South America). For the sites within each study, we extracted the age if reported (25 studies did not reported year since recovery began); habitat description (see Successional stages above); previous land use (e.g. secondary forest following abandoned croplands, pasture – mainly for cattle ranching, or slash and burn agriculture – fire-fallow cultivation); and the mean species richness of each successional stage.

Comparisons based on species richness are incomplete because they ignore the importance of species composition. Thus, we also evaluated successional response of vertebrate species compositional similarity (Anderson et al. 2011), calculated as the proportion of similarity in species composition between each successional stage and the reference forests using Sørensen similarity index (SS). Few studies reported abundance for all species; therefore, we could not use a more robust ecological metric such as the Chao–Sorensen index (Dent and Wright 2009). For this analysis, we only used studies that provided species lists (Supplementary material Appendix 1 Table A2) and the analysis was based on incidence data, regardless if abundance data were reported. Sørensen index is a pairwise measure, which provides a multiplicative point of view of species turnover in a community (Anderson et al. 2011). It is defined as $SS = 2c_{ik} / (2c_{ik} + a_i + a_k)$, where c_{ik} is the number of species shared between two sites (e.g. successional stage versus reference forest, ik), a_i is the number of unique species in a site (e.g. the successional stage i), and a_k is the number of unique species in another site (e.g. the reference forest k). Similarity indices were calculated using the package ‘vegan’ in R (Oksanen et al. 2016).

We used the geographic location of each study to estimate landscape variables (Fahrig 2013). Specifically, we estimated the percent forest cover, the number of forest patches, the mean area of all patches, and the mean patch perimeter–area ratio in six buffer radii following Crouzeilles and Curran (2016). The median distance between sites (secondary versus reference forests) for most studies included in this review were ~ 5 km; therefore, the 5 km radius included the potential effect of primary forest as source of biodiversity. Each of the variables were extracted for the year of the corresponding study, and the radii were: 5, 10, 25, 50, 75 and 100 km. Our analysis was based on MODIS land cover data provided by Channan et al. (2014), which allowed for the extraction of specific data for each year during the period 2001–2012. Ninety-five (65%) of the studies occurred during this period. Studies conducted five years before this period (1996–2000) were matched with data from the first year (2001; $n = 16$), while studies conducted 5 years after this period were matched with data from the last year (2012; $n = 17$). The landscape context variables in older studies (1969–1995) ($n = 19$) were labelled as not available.

In studies from the tropical moist forest biome that included species lists, we classified each species as a forest

specialist (i.e. forest interior specialist, see Fahrig 2013) or generalist based on the original studies or from animal life-history databases (AmphibiaWeb 2013, IUCN 2019, Parr et al. 2014, del Hoyo et al. 2017). In addition, for each bird and mammal species in the tropical moist forest biome, we assigned one of seven functional groups based on their diet (Wilman et al. 2014). These groups were used because there is more detailed diet information for birds and mammals (Wilman et al. 2014), which facilitated assigning species to a functional group (Şekercioğlu 2006). The functional groups were: 1) grazers (no-reproductive plant parts), 2) granivores (seeds, nuts, dry-fruits), 3) seed dispersers (fruits, drupes), 4) pollinators (nectar), 5) insectivores sensu lato (invertebrates, arthropods), 6) predators (terrestrial and aquatic vertebrates) and 7) scavengers (carrion). These functional groups are similar to those used to link ecosystem functioning with genetic and trophic process (Şekercioğlu 2006, Cumming and Child 2009).

Potential predictor variables of diversity recovery included local (3), landscape (24) and biogeographic (5) variables (Supplementary material Appendix 1 Table A9). The local context variables included: 1) successional stage, 2) age (i.e. time since abandonment) and 3) the previous land use. The landscape context variables included: 1) percent forest cover, 2) the number of forest patches, 3) the mean area of all patches and 4) the mean patch perimeter–area ratio within the 5, 10, 25, 50, 75 and 100 km radii, as described above. The biogeographic context variables included: 1) geographical setting (continent versus island), 2) zoogeographical realm, 3) biome, 4) mean elevation and 5) mean rainfall.

Response ratio calculation and meta-analysis

For the four vertebrate groups, the changes in species richness, species compositional similarity, and forest specialist species richness in tropical moist forests during each successional stage were analysed using a response ratio for each response variable. Similarly, the change in each bird and mammal functional group in the tropical moist forest biome were also analysed using an independent response ratio for each functional group. Response ratios are commonly used in this type of ecological meta-analysis (Hedges et al. 1999), because an effect size does not require an estimate of the standard deviation (Adams et al. 1997). In addition, the ln-transformation of the response ratio can improve the statistical properties of the response ratio effect size in small samples (Hedges et al. 1999, Koricheva et al. 2013). Each response ratio was calculated as the mean value within each successional stage (mean of treatment group – X_i) in relation to the mean value in the reference forests (mean of control group – X_k), or $\ln(RR_Y) = \ln(X_i/X_k) = \ln(X_i) - \ln(X_k)$ within each study. This calculation was made independently for each response variable as follow: RR_R for species richness; RR_S for species compositional similarity, RR_{FSp} for forest specialist species richness in the tropical moist forest, RR_{In} for bird and mammal insectivores, RR_{SD} for seed dispersers, RR_{Gr} for granivores, RR_{Pr} for predators, RR_{Po}

for pollinators, RR_{Sc} for scavengers and RR_{Gz} for grazers. An effect size ($\ln[RR_Y]$) of zero indicates no differences between the response variable of the secondary forest successional stage and the reference forests. A positive effect size (>0) indicates that the response variable was greater in a given successional stage in comparison to the reference forests, and a negative effect size (<0) indicates lower value of the response variable in comparison to the reference forests (Koricheva et al. 2013). Comparisons that reported mean values of zero (i.e. no species or no similarity) were excluded because the response ratio could not be calculated. Overall, we calculate 872 response ratios, 240 for species richness ($\ln[RR_R]$), 186 for species compositional similarity ($\ln[RR_S]$), 136 for tropical moist forest specialist species ($\ln[RR_{FSp}]$), 70 for bird and mammal insectivores ($\ln[RR_{In}]$), 74 for seed dispersers ($\ln[RR_{SD}]$), 57 for granivores ($\ln[RR_{Gr}]$), 42 for predators ($\ln[RR_{Pr}]$), 32 for pollinators ($\ln[RR_{Po}]$), 14 for scavengers ($\ln[RR_{Sc}]$) and 21 for grazers ($\ln[RR_{Gz}]$).

We used an unweighted meta-analysis to remove the effect of unequal sample size in the different successional stages (Gruner et al. 2017). To estimate confidence limits within each successional stage, we used a conservative nonparametric approach, resampling randomization and bootstrapping technique (Adams et al. 1997, Hedges et al. 1999). If a vertebrate/successional stage group had a $n \geq 5$ it was resampled 10 000 times with replacement for each response variable. If a vertebrate/successional stage had a $n < 5$ the raw mean value was reported, but not used in any analyses. For species richness and species compositional similarity, we resampled the response ratio of each group of vertebrate/successional stage for zoogeographic realms, biomes and continents/island categories. To avoid potential spatial pseudo-replication, we randomly selected only one comparison per study in each bootstrapping iteration (Gibson et al. 2011, Crouzeilles et al. 2016a). Resampling provides an estimation of the mean effect size and the 2.5 and 97.5 bootstrapped percentiles (i.e. 95% confidence limits). Bootstrapped confidence limits that include the zero response ratio indicate no significant differences for the response variable within the successional stage in relation to the reference forests (Adams et al. 1997). Differences between bootstrapped confidence limits are interpreted as differences between the response variable among the successional stages for a taxonomic group, or differences between the response ratio in the same successional stage among taxonomic groups.

Generalized linear model selection

We conducted an information–theoretical approach of a candidate set of generalized linear models (GLM) to identify predictor variables related with each response variable during secondary succession (Burnham and Anderson 2002). We used absolute response ratios as the response variables to compare raw differences between successional stages and reference forests (Crouzeilles et al. 2016a). The absolute response ratios ranged from zero to infinity, and thus we modelled them

assuming a Gamma distribution with an identity link function, and outliers were removed to achieve a normal distribution of residuals following methods described in Bolker (2008) and Crouzeilles et al. (2016a). For each of the four taxonomic groups, we compared each response variable separately, and they were related with the local, landscape and biogeographic variables. To compare across the predictor variables, each numeric variable was scaled by centering around the mean and dividing by two standard deviations (Gelman 2008). Furthermore, if numeric variables had a Spearman's R^2 correlation >0.7 only a single variable was used in the model selection (Supplementary material Appendix 1 Fig. A3–A26, Table A9). In addition, all categorical predictors had to have at least two factors.

To examine the candidate models, first we conducted an automated model selection using the *glmulti* package in R (Calcagno 2015) with all variables except those that were excluded due to high correlation (Supplementary material Appendix 1 Fig. A3–A26, Table A9). This model selection procedure ranked models based on the small-sample-size corrected Akaike information criterion (AICc) and the Akaike weight (w_i), which is the probability that a model_{*i*} was the best explanatory model within the set of models. We select the top-ranked models (sometimes up to 100 models) as candidate set of models in the information-theoretical approach. Top-ranked models were those with the $\Delta AICc < 7$, which means that several models could be equally plausible (Burnham and Anderson 2002). Then, we used these subset candidate models to resample with 10 000 bootstraps, to identify the most frequent top-ranked model (Gibson et al. 2011, Crouzeilles et al. 2016a). We also included a null model in both steps of model selection. In each bootstrapping iteration, we randomly selected only one comparison per study, to avoid potential spatial pseudo-replication. For the most frequent model in the bootstrap, we calculated the percent of variation explained by the predictor variables included in the model, dividing the regression sum of squares for each variable by the total sum of squares (Marín-Spiotta et al. 2013). All statistics and figures, except the maps, were produced using R, ver. 3.2.4 (<www.r-project.org>). The maps were produced using QGIS.

Data statement

Data, R code, and the detailed species list provided by the studies are accessible in figshare <<https://doi.org/10.6084/m9.figshare.7717640.v1>> (Acevedo-Charry and Aide 2019). All figures have been tested for color-blind individuals using the color blindness simulator 'Sim Daltonism' ver. 1.0.1 for Mac.

Results

Our systematic review of vertebrate recovery during secondary forest succession was based on 147 studies (birds – 58, mammals – 33, amphibians – 32, reptiles – 24) from 115 articles (Supplementary material Appendix 1 Table A2–A8). These studies were conducted in tropical moist forest ($n=130$), tropical dry forest ($n=10$) and tropical savannah ($n=7$) biomes, and the geographical setting included continental ($n=117$) and island ($n=30$). Most the studies occurred in the Panamanian zoogeographical realm ($n=46$), followed by the Neotropical ($n=42$), Oriental ($n=27$), Afrotropical ($n=13$), Oceanian ($n=7$), Australian ($n=5$), Nearctic ($n=5$), and Madagascan ($n=2$) realms (Fig. 2, Supplementary material Appendix 1 Fig. A1). The general pattern of vertebrate species richness, compositional similarity, forest specialist richness and some functional groups during secondary forest succession (treatment group) is to increase gradually toward the reference forests (control group), but there were minor differences among metrics.

Vertebrate species richness during secondary forest succession

Overall the mean response ratio of the four vertebrate groups increased toward the zero effect size during succession, but the patterns varied among groups (Fig. 3a). Confidence intervals of the early succession stage did not overlap with the other successional stages for birds and mammals. There were not enough studies ($n < 5$) in the old secondary forest stage for amphibians, reptiles and mammals to estimate confidence intervals.

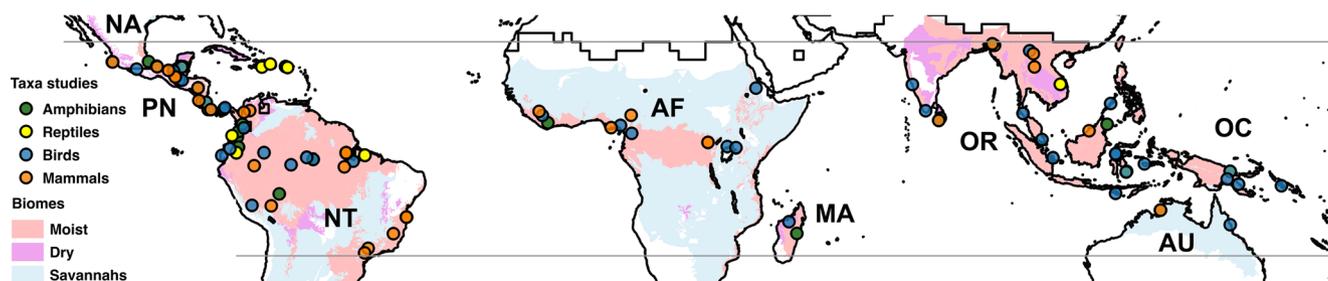


Figure 2. The locations of the 147 studies of amphibians, reptiles, birds and mammals during secondary forest succession. Biomes are defined by Olson et al. (2001), and the zoogeographic realms correspond to Holt et al. (2013). The grey lines indicate the Tropics of Cancer and Capricorn. See Supplementary material Appendix 1 Fig. A1 for the locations of each vertebrate group separately. Biogeographic realms are: NA, Nearctic; PN, Panamanian; NT, Neotropical; AF, Afrotropical; MA, Madagascan; OR, Oriental; AU, Australian; OC, Oceanian.

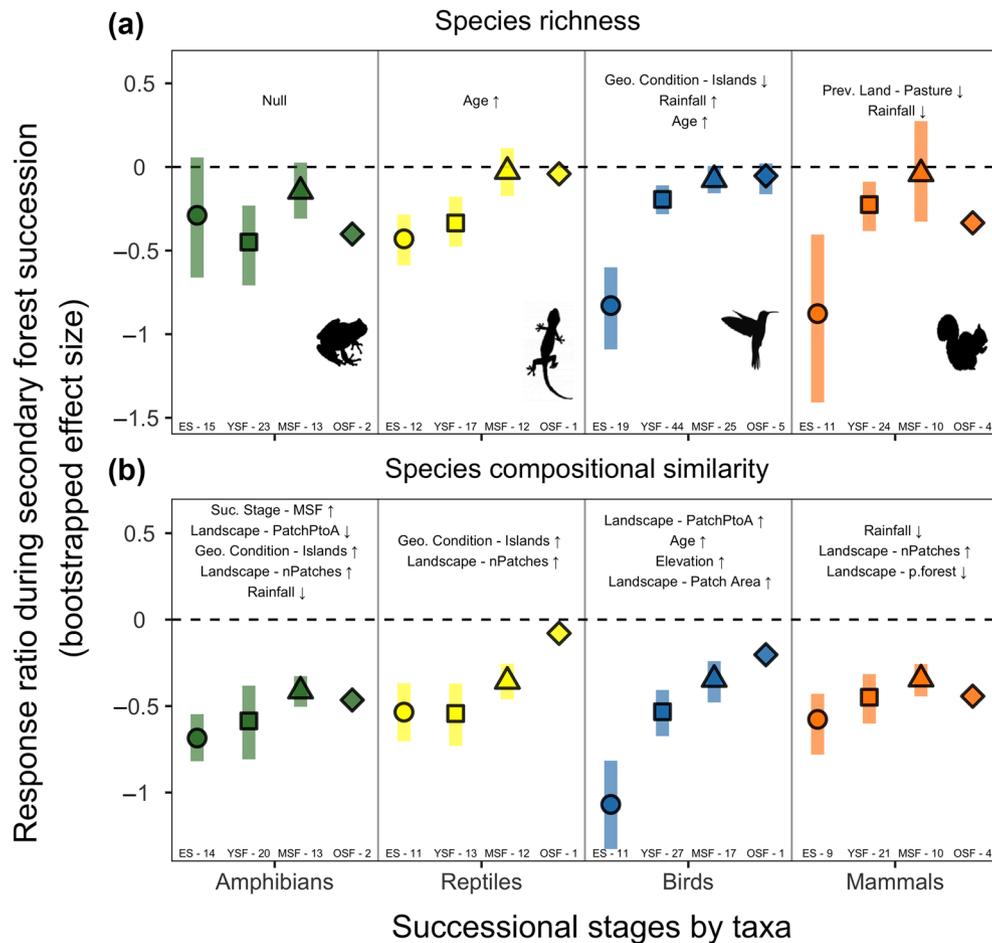


Figure 3. Bootstrapped response ratio (effect size) for species richness (a) and species compositional similarity (b) of tropical vertebrates during four secondary successional stages (circles – early succession, ES; squares – young secondary forest, YSF; triangles – mid-successional secondary forest, MSF; diamonds – old secondary forest, OSF), in relationship with the reference sites (dashed horizontal line). Points and horizontal lines represent the bootstrapped mean effect size and the bootstrapped 95% (percentile) confidence limits based on 10 000 bootstraps (for groups with $n \geq 5$). Sample sizes are indicated along with the successional stage. The raw mean is shown for small sample sizes ($n < 5$). An overlap of the confidence limits indicates no differences between groups. An overlap of confidence limits with the response ratio zero (dashed horizontal line) indicates no differences with the reference sites. Positive and negative response ratios indicate higher or lower values of species richness or compositional similarity in comparison with the reference sites. The predictors included in the best-fitted model for the absolute response ratio and the relationships (arrows up – positive; arrow down – negative), are presented along with each taxonomic group.

Amphibians were an exception to the general pattern because the effect sizes in the early succession (–0.289) and the mid-successional secondary forest (–0.146) stages were higher than in the young secondary forest stage (–0.449). The confidence intervals of these three stages overlapped (Fig. 3a, Supplementary material Appendix 1 Table A10–A13). The confidence intervals in the early succession (–0.661 to 0.057) and the mid-successional secondary forest (–0.309 to 0.026) stages also overlapped with the zero effect size (Supplementary material Appendix 1 Table A10–A13). This variation was not explained by any of the models (w_i , Akaike weight=0.17; π_i , percentage of times the model was top-ranked=46.25; Supplementary material Appendix 1 Table A20).

In contrast, the effect size for reptiles increased from low values in the early succession (–0.430) and the young

secondary forest (–0.335) stages to a higher value (–0.027) with confidence intervals (–0.173 to 0.113) overlapping with the zero effect size in the mid-successional secondary forest stage. The confidence intervals between the early succession (–0.588 to –0.285) and the young secondary forest (–0.476 to –0.178) stages overlapped but were different from the mid-successional secondary forest stage (–0.173 to 0.113). Age explained ~15% of the variation in species richness recovery ($w_i = 0.44$; $\pi_i = 33.81$).

The response ratio for birds also increased through succession, from a low value (–0.829) in the early succession stage to a higher value in the young secondary forest (–0.194), and then to levels close to the zero effect size in the mid-successional secondary forest (–0.076) and the old secondary forest (–0.053) stages. The confidence intervals of the

mid-successional secondary forest (−0.157 to 0.006) and the old secondary forest stages (−0.163 to 0.021) overlapped with the zero effect size (Fig. 3a). Although the confidence intervals overlapped among the young secondary forest (−0.282 to −0.110), the mid-successional secondary forest and the old secondary forest stages, they were different from the early succession stage (−1.091 to −0.600). The best-fit model ($w_i=0.17$; $\pi_i=23.46$) suggested faster species richness recovery on continental sites (11% of the variation explained), regions with higher rainfall (~9%) and in older sites (~6%).

Similarly, the response ratio for mammals increased from the lowest value of all vertebrate/successional group (−0.877) in the early succession stage to a higher value in the young secondary forest stage (−0.225), and then to levels close to the zero effect size in the mid-successional secondary forest stage (−0.041). The confidence intervals of the mid-successional secondary forest stage (−0.327 to 0.274) overlapped with the zero effect size and with the young secondary forest stage (−0.383 to −0.088). The confidence intervals of the early succession stage (−1.408 to −0.404) did not overlap with any other successional stage. The best-fit model ($w_i=0.26$; $\pi_i=20.49$) suggested slower species richness recovery where both the previous land use was pastures (~31% of the variation explained) and in areas of low rainfall (~9%).

Vertebrate species compositional similarity during secondary forest succession

The meta-analysis of species compositional similarity showed lower values (Fig. 3b) in comparison with the values of species richness (Fig. 3a), but the mean response ratio increased from the early succession stage to the older secondary forest stages in all vertebrate groups (Fig. 3b, Supplementary material Appendix 1 Table A14). None of the confidence intervals of the four taxonomic groups overlapped with the zero effect size. Although there were not enough studies to estimate confidence intervals of old secondary forest in any vertebrate group, the raw values of reptiles (−0.079) and birds (−0.203) were the most similar to the zero effect size (Fig. 3b, Supplementary material Appendix 1 Table A14–A17). The confidence intervals of the mid-successional secondary forest stage were the closest to reference forests.

The mean response ratio of amphibian species compositional similarity increased from the early succession stage (−0.685) to the young secondary forest stage (−0.586), to the mid-successional secondary forest stage (−0.413) and there was no overlap between the confidence intervals of the early succession (−0.819 to −0.547) and the mid-successional secondary forest stages (−0.504 to −0.327; see Fig. 3b, Supplementary material Appendix 1 Table A14–A17). However, confidence intervals of the early succession (−0.819 to −0.547) and the young secondary forest (−0.808 to −0.382) stages overlapped. The best-fit model ($w_i=0.78$; $\pi_i=13.36$) suggested faster recovery in species compositional similarity during mid-successional secondary forest stage

(~39% of the variation explained), lower perimeter–area ratio at 5, 10 and 25 km radii (~17%) and better recovery on island in comparison with continental sites (~16%).

The confidence intervals of reptiles in the early succession (−0.703 to −0.368) and the young secondary forest (−0.730 to −0.370) were very similar and overlapped with the mid-successional secondary forest (−0.461 to −0.256). The best-fit model ($w_i=0.31$; $\pi_i=28.12$) suggested an increase in recovery on island (~28% of the variation explained) and in landscape with more patches at 5 and 25 km radii (~12%).

Similar to amphibians, bird species compositional similarity increased from the early succession stage (−1.069) to the young secondary forest stage (−0.533), to the mid-successional secondary forest stage (−0.346), and there was no overlap between the confidence intervals of the early succession (−1.327 to −0.816) and the mid-successional secondary forest stages (−0.479 to −0.240; see Fig. 3b, Supplementary material Appendix 1 Table A4–A17). Birds showed a rapid change from low similarity with the reference forest sites in the early succession stage (−1.069), and no overlap with the other successional stages, to the highest value of confidence intervals of all vertebrate/successional stage groups in the mid-successional secondary forest (−0.479 to −0.240). The best-fit model ($w_i=0.10$; $\pi_i=29.20$) suggested an increase in recovery in older (~15% of the variation explained) and higher sites (~8%), in landscapes with greater perimeter–area at 75 km radius (~20%) and larger mean patch area at 50 km radius (~7%).

Similar to reptiles, the mammal confidence intervals of all successional stages overlapped. The largest difference was between the early succession (−0.781 to −0.429) and mid-successional secondary forest (−0.444 to −0.257) stages. The best-fit model ($w_i=0.54$; $\pi_i=74.92$) suggested an increase in recovery in areas with low rainfall (~36% of the variation explained), in landscape with more number of patches at 25 and 10 km radii (~9%), and lower percentage of forest at 5 and 50 km radii (~3%).

Vertebrate tropical moist forest specialist species during secondary forest succession

Although there was a gradual increase in response ratios of forest specialist species richness, only mammals recovered to reference forest values (Fig. 4, Supplementary material Appendix 1 Table A18). The mammal confidence interval of the mid-successional secondary forest stage overlapped with the zero effect size (−0.577 to 0.225). As in the previous analyses, mammal recovery was negatively related with rainfall ($w_i=0.41$; $\pi_i=92.52$; ~48% of the variation explained). Although amphibian and reptile forest specialist richness increased through the successional stages, the null model was the best-fit model (amphibians $w_i=0.70$; $\pi_i=71.58$; reptiles $w_i=0.79$; $\pi_i=70.42$). In contrast, bird specialist recovery was best explained by forest age ($w_i=0.13$; $\pi_i=55.30$; ~18% of the variation explained).

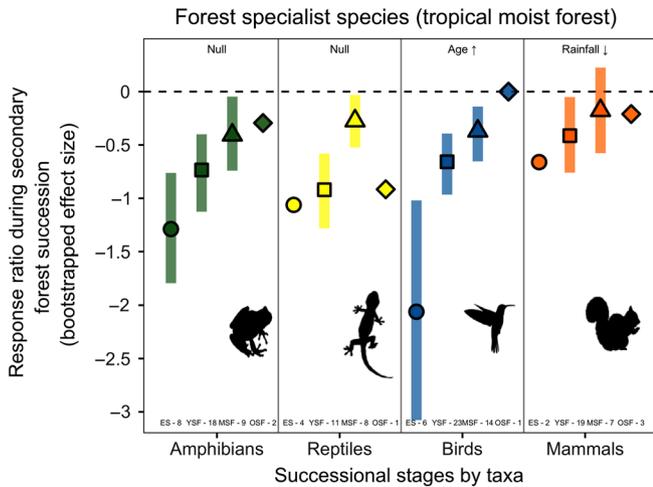


Figure 4. Bootstrapped response ratio (effect size) of the forest specialist species richness of tropical moist forest vertebrates during four secondary successional stages (shapes and colours as in Fig. 3), in relationship with the reference sites (dashed horizontal line). Points and vertical lines represent the bootstrapped mean effect size and the bootstrapped 95% (percentile) confidence limits after 10 000 bootstraps (for groups with $n \geq 5$). Sample sizes are indicated along with the successional stage. The raw mean is shown for small sample sizes ($n < 5$). An overlap of the confidence limits indicates no differences between groups. An overlap of confidence limits with response ratio zero (dashed horizontal line) indicates no differences with the reference site. Positive and negative response ratios indicate higher or lower values of species richness in comparison with the reference sites. The predictors included in the best-fitted model for the absolute response ratio and the relationships (arrows up – positive; arrow down – negative), are presented along with each taxonomic group.

Tropical moist forest bird and mammal functional groups during secondary forest succession

The confidence intervals of the response ratio overlapped among the successional stages for all functional groups. This suggests that the relative richness of each functional group did not vary much through the successional stages for tropical moist forest birds and mammals (Fig. 5). However, some functional groups did not overlap with the reference forests (Fig. 5, Supplementary material Appendix 1 Table A19). For example, the number of insectivorous birds were lower than the reference forests during all the successional stages, suggesting incomplete recovery (Fig. 5a). This incomplete recovery was also identified in bird seed dispersers during the early succession stage, where the best-fit model ($w_i = 0.14$; $\pi_i = 30.46$) suggested a strong relationship with sites with lower patch area at 50 and 10 km radii (~29% of the variation explained), older (~14%) and higher in elevation (~10%). Similarly, insectivorous and mammal seed dispersers during the early successional and the young secondary forest stages were lower than the reference forest, but the mid-successional secondary forest overlapped with effect size zero (Fig. 5b). The best-fit model for mammal seed dispersers ($w_i = 0.78$; $\pi_i = 36.19$) suggested better recovery in sites with lower rainfall (~46%

of the variation explained), lower perimeter–area at 50 and 100 km radii (~20%) and lower percentage of forest at 10 km radius (~6%). The young secondary forest stage was the only stage with sufficient data to estimate a confidence interval for granivore, predator, pollinator and grazers mammals, reflecting lower values of predators, greater values of pollinators, and similar values of grazers in comparison with the reference stage (Fig. 5b, Supplementary material Appendix 1 Table A19).

Discussion

Understanding the recovery patterns of vertebrates during secondary forest succession is essential for management plans and conservation strategies. In particular, how and why traditional metrics (e.g. species richness) differ with other kind of metrics (e.g. forest specialist or functional groups). Although our meta-analysis showed a general pattern of a gradual decline in the difference between secondary forest and reference forests during succession, it is clear that species richness overestimates the recovery of vertebrate diversity during secondary forest succession. The general pattern of convergence toward reference forests supports the argument that secondary forests, if maintained, can play an important role in providing habitat for many vertebrate species. However, even though some groups recovered to similar levels as reference forests, in the tropical moist forest biome many forest specialist species and functional groups (e.g. insectivorous birds) did not. These results confirm the urgent need to conserve old growth (i.e. reference) forests (Gibson et al. 2011) for habitat for many species and as sources of diversity for secondary forest colonization (Blake and Loiselle 2001, Chazdon et al. 2009, Hernández-Ordóñez et al. 2015). Below we explain the implications of the recovery dynamics of the four vertebrate groups in more detail.

Amphibians

The meta-analysis showed similar species richness values of the early succession and the mid-successional secondary forest stages with the reference forests. This may reflect the formation of ephemeral habitats during early successional stages, which increases microhabitat availability for generalist amphibian species. For instance, the early successional stages (e.g. pastures and open areas) often have temporary ponds that can be used by generalist amphibians (e.g. *Rhinella marina* or *Hypsiboas punctatus*; de Souza et al. 2008). The highly variable environmental conditions during the early successional stages can also favour generalist species (e.g. *Incilius marmoratus* or *Leptodactylus melanonotus*; Suazo-Ortuno et al. 2008). The decline of amphibian species richness in the young secondary forest stage is possibly due to the loss of these types of microhabitats, and a turnover from generalist species to forest specialist species during the mid-successional secondary forest stage (Gardner et al. 2007c, Hilje and Aide 2012), which is reflected in our analysis in

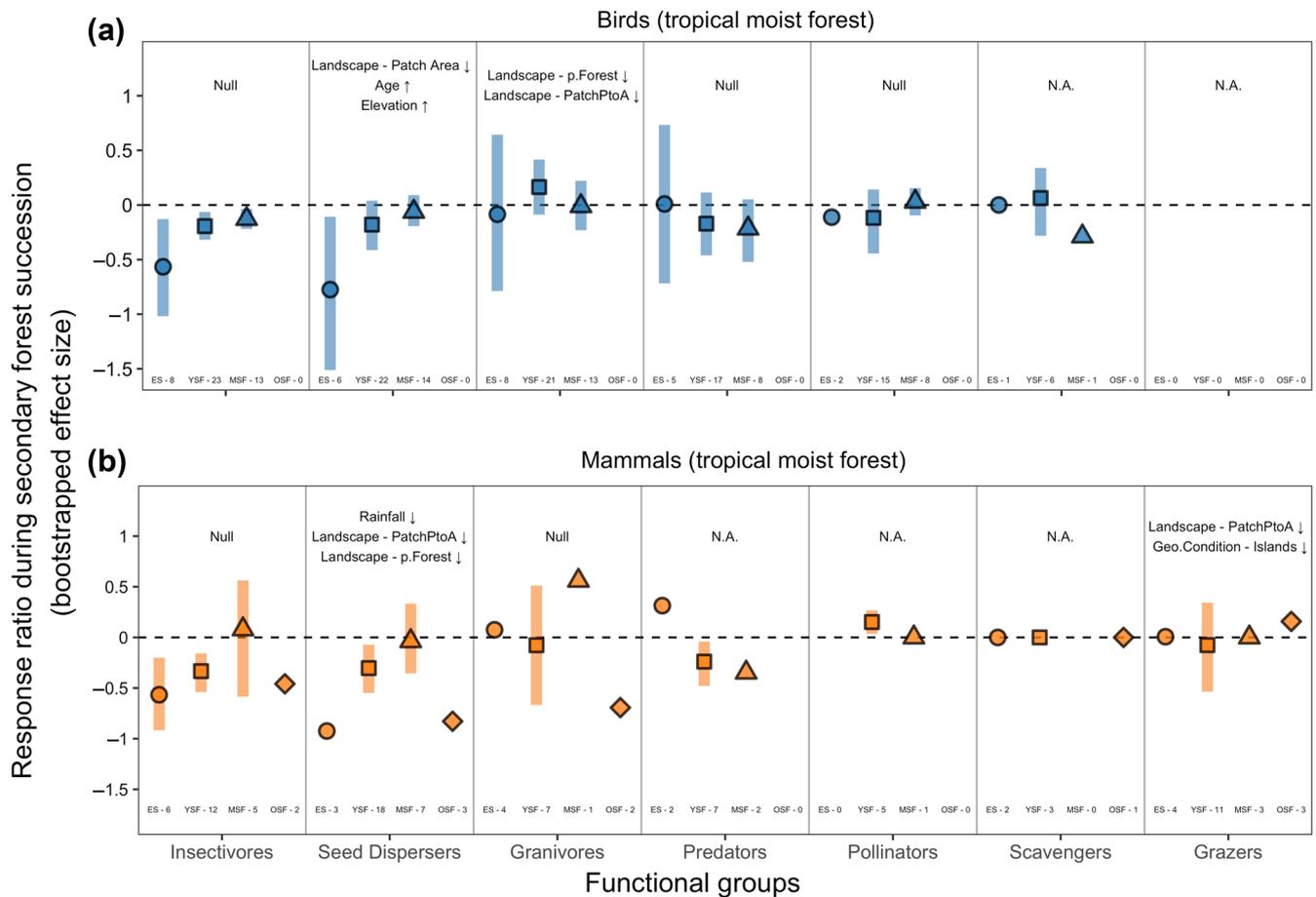


Figure 5. Bootstrapped response ratio (effect size) of seven functional groups of birds (a) and mammals (b) in the tropical moist forest biome (shapes and colours as in Fig. 3), in relationship with the reference sites (dashed horizontal line). Points and vertical lines represent the bootstrapped mean effect size and the bootstrapped 95% (percentile) confidence limits after 10 000 resamples (for groups with $n \geq 5$). Sample sizes are indicated along with the successional stage. Raw mean is shown for small sample sizes ($n < 5$). An overlap of the confidence limits indicates no differences between groups. An overlap of confidence limits with response ratio zero (dashed horizontal line) indicates no differences with the reference site. Positive and negative response ratios indicate higher or lower values of species richness in comparison with the reference. The predictors included in the best-fitted model for the absolute response ratio and the relationships (arrows up – positive; arrow down – negative), are presented along with each functional group.

the gradual increase of species compositional similarity and species forest specialists (Fig. 3a, 4).

In contrast to species richness, amphibian forest specialist species colonize secondary forests gradually. It seems that many species do not need mature forest as long as there is a closed canopy, leaf litter and relatively humid conditions (e.g. mid-successional secondary forest), which can increase food availability such as leaf litter arthropods (Hilje and Aide 2012), and aquatic habitats (e.g. small streams; Ernst et al. 2006, 2011). In fact, change in species compositional similarity was better explained by successional stages, reflecting the contrasting amphibian composition among successional stages (Gardner et al. 2007c, Hilje and Aide 2012). The largest difference in species compositional similarity between secondary forest stages and reference forest was also related to landscape

variables (patch perimeter–area ratio and number of patches), which supports the habitat amount hypothesis (Fahrig 2013). Similarly, Gibson et al. (2011) suggested that landscape modifications, such as extensive deforestation and the expansion of oil palm plantations will greatly reduce source populations, which will be very detrimental for amphibians given their limited dispersal abilities (Dobrovolski et al. 2012). In addition, biogeographic variables such as geographical setting (island versus continent) and rainfall were also related to difference in species compositional similarity, unfortunately the lack of studies in other biomes (dry forests and savannahs) did not allow for quantitative comparisons with tropical moist forest biome (Supplementary material Appendix 1 Table A16), but Ernst et al. (2006, 2011) showed strong difference in trait assemblages between tropical moist and dry forests.

Reptiles

Species richness of reptiles and forest specialist species increased through succession, possibly due to increasing habitat complexity with forest age (Fig. 3a; Ríos-López and Aide 2007, Hernández-Ordóñez et al. 2015). On the other hand, species compositional similarity of reptiles was associated with the geographical setting (island versus continent) and the number of patches in the landscape (Fig. 3b). In particular, species compositional similarity recovery occurred more rapidly in island in comparison with continental sites (Fig. 3b; Glor et al. 2001, Ríos-López and Aide 2007, Herrera-Montes and Brokaw 2010), possible due to a greater presence of generalist species, which often have high population densities on islands (Ríos-López and Aide 2007, Novosolov et al. 2016). In addition, land use change often occurs at smaller spatial scales on islands, and this could reduce the distance to source populations, again supporting the importance of the amount of habitat in the surrounding landscape (Fahrig 2013).

Birds

Species richness of birds increased rapidly between the early succession and young secondary forest stages where it seems to reach a plateau with values close to the reference forests, reflecting a large difference in the bird communities in the early successional stage (open areas) and all secondary forest stages (Fig. 3). This variation in species richness was associated with the geographical setting, with better recovery in continents than in islands, age and rainfall (Fig. 3a, Supplementary material Appendix 1 Table A20). Although species richness change little among the young, mid-successional and old secondary forest stages, there was a continuous increase in species compositional similarity during succession (Robinson and Terborgh 1997, Raman et al. 1998). The recovery of species compositional similarity in birds was the fastest of the four vertebrate groups, and was related with local (age), landscape (patch perimeter–area ratio) and biogeographic (elevation) scales. This rapid change in bird species compositional similarity resembles a directional turnover during secondary forest succession (Blake and Loiselle 2001, Robinson and Terborgh 1997, Raman et al. 1998); early successional bird species that tolerate degraded and open area sites were replaced by species that use edges or young forest stages, and then gradually by forest specialists in later forest successional stages. This directional turnover was associated mainly with the perimeter–area ratio at a radius of 75 km, which reflect the size and shape of the surrounding patches or the habitat amount (Helzer and Jelinski 1999, Fahrig 2013), and the age of the secondary forest. Furthermore, the recovery of forest specialist species was also associated with secondary forest age. The rapid recovery in species compositional similarity and forest specialists among the successional stages may have been related to their greater

dispersal ability (Dobrovolski et al. 2012), but this was not quantified in our study.

The relative richness of functional groups of tropical moist forest birds did not change during secondary succession. The overall lack of change in functional groups contrasts with the high turnover of species compositional similarity. This result suggests that different species could fulfil the functional roles in different successional stages (Blake and Loiselle 2001, Sayer et al. 2017). For example, the species richness of insectivorous birds did not change during succession, but in early successional sites generalist insectivores may dominate and sensitive groups such as understory insectivores may be absent (Şekercioğlu et al. 2002). In later successional stages, as microhabitat changes, reference forest specialist species (e.g. understory insectivores) are more common (Stratford and Robinson 2005, Stratford and Stouffer 2015). However, species richness of insectivorous birds did not overlap with the zero effect size, suggesting that this functional group may partially fulfil this function during succession, but it was short of a complete recovery. Furthermore, even if a functional group during an early successional stage has the same species richness as a later stage, this does not necessarily result in the same functionality. Finer categorization of functional groups, and longer studies including more observations in the old secondary forest successional stage could help to better understand the dynamics of turnover of generalist and specialist species during succession (Raman et al. 1998).

Mammals

The overall pattern of mammal recovery during secondary forest succession showed a gradual increase in species richness, compositional similarity and forest specialists' richness through succession (Fig. 3, 4). Furthermore, all analyses showed an increase in recovery with decreasing rainfall. The strongest relationship was between forest specialist species richness and rainfall (47% of variation explained), with the drier sites recovering species levels similar to reference forest more rapidly than wetter sites. One possible explanation for this pattern is that within the context of tropical forests, drier habitats may have lower overall mammal species richness permitting more rapid recover and a relative increase in the proportion of mammals (Kay and Madden 1997), which can disperse over long distances and open areas (Dobrovolski et al. 2012). Mammal species compositional similarity recovered faster also in regions with more forest patches, as documented in other studies (Fahrig 2013, Leal et al. 2017). Nevertheless, in the tropical moist forest biome, the relative richness of functional groups did not change during secondary succession, suggesting that different species may be fulfilling these functional roles in these secondary forests. Further functional analysis of mammals should include not just trophic information but habit mode (volant, arboreal, terrestrial fossorial), body size (body mass) and even finer taxonomic categories (orders level).

Conclusions and recommendations

This meta-analysis of tropical forest vertebrate recovery differs from previous analyses because we separated the taxa into four terrestrial vertebrate groups, we included different biogeographic components, and we separated secondary forests into four different age/structure stages. By separating the vertebrates in taxonomic classes (e.g. amphibians and reptiles), we showed that the groups responded to different predictors during succession, but a finer taxonomic scale (e.g. orders) could help to understand how variation in body size or dispersal ability (e.g. in mammals) are related with diversity recovery. By including different biogeographic components, we identified large study gaps for islands (Supplementary material Appendix 1 Table A11, A15), tropical dry forest and savannahs biomes (Supplementary material Appendix 1 Table A12, A16), and several zoogeographical realms (e.g. Madagascan, Australasian, Oceanian, Nearctic, Afrotropical or Oriental; Supplementary material Appendix 1 Table A13, A17). Finally, by separating the studies into different successional stages, we provide a more detailed description of the vertebrate successional process. These allow us to identify some mechanistic predictors at local, landscape or biogeographic scale related with the recovery of diversity through secondary forest succession. Unfortunately, there were very few studies that included data from the late successional stage (e.g. old secondary forests), but hopefully many of the studies reviewed here will continue monitoring these sites into the future, thus increasing the number of sites in the older stages (Bradfer-Lawrence et al. 2018). In conclusion, tropical secondary forests provide habitat for a diversity of vertebrates, but the slow recovery of species compositional similarity, forest specialists and some functional groups (e.g. insectivorous birds) highlighted the challenge of secondary forest persistence (Reid et al. 2018), and strongly argues for the continued protection of old growth/mature forest (Gibson et al. 2011) as habitat for forest specialists and as sources for secondary forest sites.

Our review of the secondary forest literature highlights both important opportunities and challenges. Clearly, secondary forests can provide habitat for many vertebrate species, in particular the functionality that different vertebrate offer during secondary forest succession. If the extent of secondary forest increases either through natural regeneration (Aide et al. 2013) or active restoration (e.g. Bonn Challenge), this could begin to counterbalance the long history of deforestation in the tropics, and provide more habitat for many species. But, the recovery of forest on abandoned lands or through active restoration projects are not sufficient; these new forests need to persist if they will have a long-term positive impact for the vertebrates. Furthermore, we showed that the vertebrate conservation value increased with succession, yet there were very few studies that included sites > 40 years. The lack of older secondary forest sites could be related with many socioeconomic factors (e.g. land tenure, fluctuation in commodity prices) and highlights the challenge of secondary forest persistence (Schwartz et al. 2017, Reid et al. 2018).

Alternatively, if local stakeholders are provided with economic alternatives, such as payment for ecosystem services (e.g. REDD++) this could help avoid further deforestation and increase the probability of secondary forest persistence (Gilroy et al. 2014). Clearly, a large proportion of the tropical vertebrates have the capacity to colonize and survive in secondary forests, but for many species this is a long process (>100 years). If these new habitats are going to contribute to the long-term persistence of these species, these areas need to persist, i.e. they need to be protected and regeneration needs to occur across large areas.

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Author contribution – OAC and TMA conceived the study. OAC performed all analyses with the advice from TMA. OAC wrote the manuscript, with contributions from TMA.

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