



Review

The future of tropical species in secondary forests: A quantitative review

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ABSTRACT

Deforestation and degradation of tropical old-growth forests has the potential to cause catastrophic species extinctions. In this review, we assess whether regenerating secondary forests (SF) can support species typically found in old-growth forest (OG) and so prevent extinctions. We review 65 studies that compare faunal diversity in SF and corresponding OG, and compare the similarity of species composition both within and between these two forest types using the Sorensen, Morisita–Horn and Sorensen–Chao indices. Comparisons between traditional similarity indices and Sorensen–Chao, which minimizes sampling biases, indicated that limited sampling effort consistently reduced apparent similarity between SF and OG and that similarity between SF and OG is actually higher than previously appreciated. Similarity, which ranges from 0 to 1, varied from 0.49 to 0.92 between replicate OG sites and was correlated with similarity between SF and OG. This correlation might be an artefact of variation among studies in sampling effort, especially for vertebrates where small samples reduce apparent similarity across all comparisons, as well as a real effect of variation among studies in landscape heterogeneity and the presence of species with patchy distributions. Therefore, similarity between SF and OG cannot be interpreted without an understanding of background variation in OG. Similarity between different SF sites provided no evidence that disturbance specialists dominate SF. Similarity to OG increased rapidly with SF age; when SF was contiguous with OG; when SF was growing in small clearings; and after low intensity land uses including clearing only, shifting agriculture and tree plantations. This describes the most frequently observed tropical SF; isolated from roads and on hilly terrain unsuitable for mechanized agriculture. Thus, our analyses indicate that tropical SF can play an important role in biodiversity conservation particularly when OG forests are nearby. An important caveat remains, however. Abundance, geographic range and levels of habitat specialization are often related. Widespread, abundant, habitat generalists might dominate similarity analyses even when relatively rare OG specialists are present. Additional species-level analyses of habitat specialization will be needed before the conservation value of tropical SF is fully understood.

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1. Introduction

The two dominant types of land-use change occurring in the tropics today potentially have opposing effects on biodiversity conservation (Wright and Muller-Landau, 2006). The quantitatively most important change is deforestation and disturbance of old-growth forests (Achard et al., 2002; Hansen and DeFries, 2004; Wright, 2005; Asner et al., 2006). Habitat loss is the leading cause of modern extinctions and since the majority of all described species inhabit tropical forests, and an even larger proportion of undescribed species is believed to do so (Raven, 1988; Dirzo and Raven, 2003), the continued loss and degradation of tropical forests has the potential to cause a globally significant mass extinction. The second most important land-use change in the tropics is the regeneration of secondary vegetation on previously deforested and degraded lands (Achard et al., 2002; Hansen and DeFries, 2004; Asner et al., in press). Degraded and secondary forests comprise five of the 11 million km² of tropical forest that remains today (ITTO, 2002). In this review, we evaluate the species composition of secondary forests (SF) and nearby old-growth forests (OG) to determine whether the widespread regeneration of SF might mitigate the catastrophic species loss predicted from the loss of tropical OG.

Four recent reviews have addressed faunal recovery in secondary tropical forests (Dunn, 2004; Bowen et al., 2007; Gardner et al., 2007a; Chazdon et al., in press). Dunn (2004) found that species richness in SF resembled that of OG just 20–40 years after abandonment, but differences in species composition were more persistent. Dunn (2004) synthesized species richness data from 33 studies including a wide range of animal taxa; however, his analysis of species composition was restricted to three bird and four ant studies and therefore has limited generality. Bowen et al. (2007) include all animal taxa but their review is discursive and does not attempt a quantitative analysis, rather the authors identify gaps in current knowledge and highlight directions for further research. They conclude that species' utilisation of SF is highly variable and is strongly influenced by land-use history. Gardner et al. (2007a) summarize 37 studies that examine vertebrate species composition in secondary tropical forests. They draw attention to the paucity of studies with sufficient sampling effort and robust study design, particularly highlighting flaws in sampling and data analysis. Chazdon et al. (in press) review the proportion of OG species present in SF for 26 studies of animal and plant species. They suggest that the conservation value of SF increased with time since abandonment and was highest in regions where the ratio of SF to OG is relatively low, OG forests are close to regenerating SF, post-abandonment disturbance is low and seed dispersing fauna persist. All four reviews suggest that the results of many studies might be biased by limitations in sampling techniques and by the confounding effects of site characteristics, but none attempts to quantify how these factors affect similarity of species composition between SF and OG.

Insufficient sampling effort is the most frequent limitation encountered in these studies (Dunn, 2004; Bowen et al., 2007; Gardner et al., 2007a; Chazdon et al., in press). Local vertebrate faunas often include hundreds of species, and no one yet knows how many invertebrate species might coexist in tropical forests. Many of these species are truly rare (Terborgh et al., 1990; Robinson and Tuck, 1996; Novotny and Basset, 2000; Robinson

et al., 2000). Species-rich communities with many rare species are difficult to sample. Many studies of the similarity in species composition between tropical OG and SF have used presence–absence data and incidence based similarity indices to quantify similarity. These indices are highly sensitive to sample size especially when assemblages include many rare species and consistently underestimate similarity when sample size is small or sampling effort is unequally distributed across sites (Chao et al., 2005, 2006). Unequal sampling effort characterizes many tropical SF–OG comparisons, with greater effort expended in OG in 63% of the studies reviewed here. New abundance-based indices reduce bias by correcting for unseen, shared species (Chao et al., 2005). Chao et al. (2005) suggest that their new Sorensen and Jaccard estimators should be employed when similarity of relative abundance, and not just presence or absence, of species is important; samples differ in size; under sampling is suspected; or there are many rare species. These explicit recommendations suggest that these new abundance-based indices are ideally suited to estimate similarity in species composition among hyper-diverse tropical forests.

We use several diversity indices to evaluate hypotheses concerning the species composition of tropical forests with different histories of anthropogenic disturbance. Some biologists have suggested that widespread “trash” species or disturbance specialists proliferate in secondary tropical forests (Stotz et al., 1996), suggesting that similarity should be very high among replicate SF sites. Over time SF accumulates species and similarity to OG increases. However, site and landscape factors affect the rates of species colonization and accumulation in SF. Many studies of SF diversity and composition have underplayed the importance of these environmental variables (Chazdon, 2003). A range of conditions can slow species recovery. Intense disturbance such as fires, heavy grazing and agriculture, bulldozing or high-impact logging can reduce residual vegetation and seed sources and generate highly disturbed or compacted soils, which slow forest regeneration (Pinard et al., 1996; Guariguata and Ostertag, 2001; Chinea, 2002; Zarin et al., 2005). In contrast, forest patches and mature trees in the landscape can contribute seed sources and wildlife refugia that enhance forest regrowth and species colonization. Thus, landscape characteristics interact with local site factors to determine rates of species colonization and accumulation (Johnson et al., 2000; Moran et al., 2000; Zarin et al., 2001; Chazdon, 2003).

With the proliferation of SF across the tropics, a current quantitative review of the conservation value of these systems is essential. We analyze data from 62 published articles that record the recovery of vertebrate and invertebrate community composition in secondary tropical forests. We extend previous reviews (Dunn, 2004; Bowen et al., 2007; Gardner et al., 2007a) by using newly formulated indices to quantify similarity between SF and OG that minimize bias associated with low or unequal sampling effort. We also provide the first quantitative assessment of the effects of forest age, site history and landscape characteristics on community recovery across a broad range of taxa, and specifically address the following hypotheses:

1. Common, disturbance specialists dominate secondary forest and therefore similarity among replicate secondary forest sites is high.

2. Many species are restricted to old-growth forests and therefore similarity between secondary and nearby old-growth forests is low.
3. During succession old-growth specialists recruit into secondary forests and early successional species drop out, so species composition of secondary forest becomes more similar to that of old-growth forest with increasing time since abandonment.
4. Site characteristics influence the rate at which old-growth forest species accumulate in secondary forest, with greater isolation from old-growth forest and greater disturbance intensity prior to abandonment slowing succession and reducing similarity in species composition between secondary and old-growth forests.

2. Materials and methods

2.1. Forest and species definitions

We rely on descriptions in the original articles to identify SF and OG. We limited SF to natural regeneration of woody vegetation on abandoned lands following complete clearance of OG by humans. We excluded studies where the SF was the result of natural disturbances or partial forest clearance (e.g. selective logging) or where forest regrowth had been assisted by human activities such as planting seedlings or seeds. OG refers to natural forests that have no record of anthropogenic forest clearance. As the history of most of these forests is poorly recorded, we recognize that OG might include forests subjected to variable anthropogenic disturbances that are less intense than clear felling for pasture, agriculture or plantations, such as hunting or selective timber extraction.

We define habitat generalists as species that inhabit both OG and SF. We define disturbance specialists as species restricted to highly disturbed and early successional forest and OG specialists as species that have behavioural or dietary requirements that can only be met by old forest, for example, cavity-nesting species of birds that require large, dead trees (Cornelius et al., 2008).

2.2. Literature search

We located most of the articles reviewed here using ISI Web of Science® database searches (<http://www.isiwebknowledge.com>). We used the following search terms: Secondary and Forest* and Tropic*, Disturb* and Forest* and Tropic*, Forest* and Disturb* and (Bird* or Mammal* or Amphibian* or Reptile* or Invertebrate* or Butterfly*). Searches were limited to the years 1975–2008. Additional articles were found in the literature cited by these articles and by recent reviews (Bowen et al., 2007; Gardner et al., 2007a). We only included the 62 articles that provided species-level incidence or abundance data for SF and OG. Two articles presented data for multiple taxa, we analysed the taxa separately, so we examined 65 separate studies.

We recorded the following site characteristics: location, SF age, distance from SF to OG, and previous land use of the SF. SF age was recorded as years since abandonment, or, if an age range was provided, as the midpoint of that range. The four previous land use categories were plantation, cleared and not cultivated, shifting or slash and burn agriculture, and intensive agriculture or pasture. The distance from SF to OG was dichotomized as either contiguous with OG or not contiguous with OG. This classification is an over simplification of landscape context but for this measure we were highly constrained by data presented in the original articles. We recorded as many of these site characteristics as possible from each study. Finally, we recorded the taxonomic group studied and the incidence or abundance of each species in SF and OG. If data from more than one SF or OG site was presented, we recorded these data

separately. In each of the original articles replicate SF and OG sites were placed to reduce altitudinal and edaphic variation.

We held census methods constant for all similarity estimates. For example, where mist-net and point-count data were presented separately for birds we compared data from the two methods separately. We used the census method that provided the more complete assessment of species diversity in subsequent analyses; for example, we used point-count data in preference to mist-net data for birds. We excluded one article that confounded forest age and sampling methodology (Appendix A).

2.3. Data analysis

We distinguished secondary–secondary (SF–SF), secondary–old-growth (SF–OG) and old-growth–old-growth (OG–OG) comparisons and calculated the incidence based Sorensen index (S_{Classic}) and the abundance-based Morisita–Horn index and Sorensen Chao estimator (S_{Chao}) for every comparison of replicate sites within each of the 65 studies. Additionally, we calculated the proportion of OG species present in SF for all SF–OG comparisons. The S_{Classic} index is calculated as

$$S_{\text{Classic}} = \frac{2A}{2A + B + C}$$

where A is the number of shared species between two sites and B and C are the number species unique to each site, thus the S_{Classic} index is the proportion of species shared between two sites adjusted for the number present at both sites. Insufficient and uneven sampling bias the S_{Classic} index downwards (Chao et al., 2006). However, by using this index we were able to use all studies, even unreplicated incidence data, to generate the largest possible set of comparisons. We calculated Morisita–Horn similarity indices for all 38 studies that included abundance data. We chose the Morisita–Horn index because, of all the traditional abundance-based similarity indices, Morisita–Horn is the most robust to uneven and insufficient sampling (Chao et al., 2006). To further remove biases associated with under sampling, we applied the jackknife method recommended by Schechtman and Wang (2004) to the Morisita–Horn index (henceforth, Jackknife Morisita–Horn index). To calculate the S_{Chao} index, two sites must have at least 10 shared species and one or more shared species that occurs twice at one site (Chao et al., 2006). To evaluate possible bias in the S_{Classic} and Jackknife Morisita–Horn indices, we calculated all three similarity indices for the 21 studies that met these final criteria. The S_{Classic} and S_{Chao} indices were calculated using EstimateS software (v. 8.0; Colwell, 2004). The Jackknife Morisita–Horn index was calculated using the vegan library (v. 1.13-8; Oksanen et al., 2008) in R (v. 2.7.2; R Core Team 8 Development, 2008). For further details about the calculation of the S_{Classic} , S_{Chao} and Morisita–Horn indices refer to Chao et al. (2006). To identify how sampling effort affects similarity between two sites, we used the 38 studies that presented abundance data to calculate the mean number of individuals sampled per species for each comparison as a surrogate for sampling effort. We then used regression analysis to investigate the relationship between this metric and the S_{Classic} index.

To investigate similarity within and between forest types, we calculated the S_{Classic} index for all possible site comparisons for studies with replicate sites in both SF and OG. We then calculated mean values for SF–SF, SF–OG and OG–OG comparisons within each study and used standardised major axis regression (SMA) to estimate slopes, intercepts and their 95% confidence intervals for relationships between SF–OG similarity vs. OG–OG similarity and between SF–OG similarity vs. SF–SF similarity. SMA analysis is used to estimate the line best describing the bivariate scatter of X and Y , where there is variance in both the X and Y variables (Warton et al., 2006). Too few studies presented abundance data

for multiple SF and OG sites to permit this analysis for the Jackknife Morisita–Horn or S_{Chao} indices. We used the program SMATR to conduct the standardised major axis regression (Warton et al., 2006).

To evaluate the effect of SF age, we calculated the S_{Classic} index and, if abundance data were presented the Jackknife Morisita–Horn index between OG and each SF for every study with two or more SF ages. We then plotted SF–OG similarity against SF age using mean values when there were replicate sites at a particular SF age. We also plotted the mean similarity for OG–OG comparisons on the same graph for studies that included two or more OG surveys. We used Sign Tests to assess whether similarity (S_{Classic}) to OG increased significantly with SF age. Each within-study comparison of a SF with the next older SF contributed once to the Sign Test. Thus, a study with n SF ages contributed $n-1$ comparisons to the sample size for the Sign Test.

We used analysis of covariance (ANCOVA) to evaluate the hypotheses that SF age, SF isolation and land-use history influenced similarity. The dependent variable was the S_{Classic} index for all studies, with a second analysis performed for the Jackknife Morisita–Horn index for studies with abundance data. The two grouping factors – SF isolation and land-use history – are dependent. The clearest example of this dependence is provided by shifting agriculture, which was virtually always contiguous with old-growth forest. For this reason, we performed two ANCOVAs with SF age as the covariate and SF isolation or land-use history as the single grouping factor using R (v. 2.7.2; R Core Team & Development, 2008). Preliminary analyses evaluated the homogeneity of slopes assumption of ANCOVA (i.e., SF age by site characteristic interactions). All SF age by site characteristic interactions were insignificant, and only the main effects of SF age and site characteristic are presented.

3. Results

3.1. Literature summary

The 65 studies were located in 23 countries distributed broadly across the tropics with 20 studies in South America, 14 in Central America and the Caribbean, 8 in Africa, 20 in South and Southeast Asia and 3 in Australasia (Appendix A). The 65 studies included 44 locations (on the scale of a research station or national park).

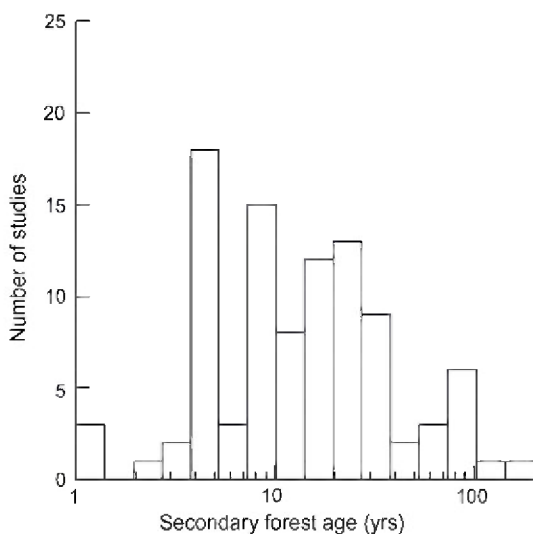


Fig. 1. The age of 97 secondary forests surveyed for species composition of an animal taxa, from 46 published articles that provide secondary forest age (Appendix A).

Several taxa were studied in the Rio Jari watershed (4 studies) and the Biological Diversity of Forest Fragments Project (4), Brazil; the La Selva Biological Station, Costa Rica (4); and Lore Lindu National Park, Sulawesi, Indonesia (5). There were 23, 13, 14 and 15 studies for invertebrates, amphibians and reptiles, birds and mammals, respectively. The 23 invertebrate studies include 2 for arachnids and 21 for insects, with 9, 6, 5 and 1 studies for butterflies, ants, beetles and termites, respectively.

The 65 studies included 114 SF sites (here we treat replicate plots within a single even aged stand as one site). Secondary forests

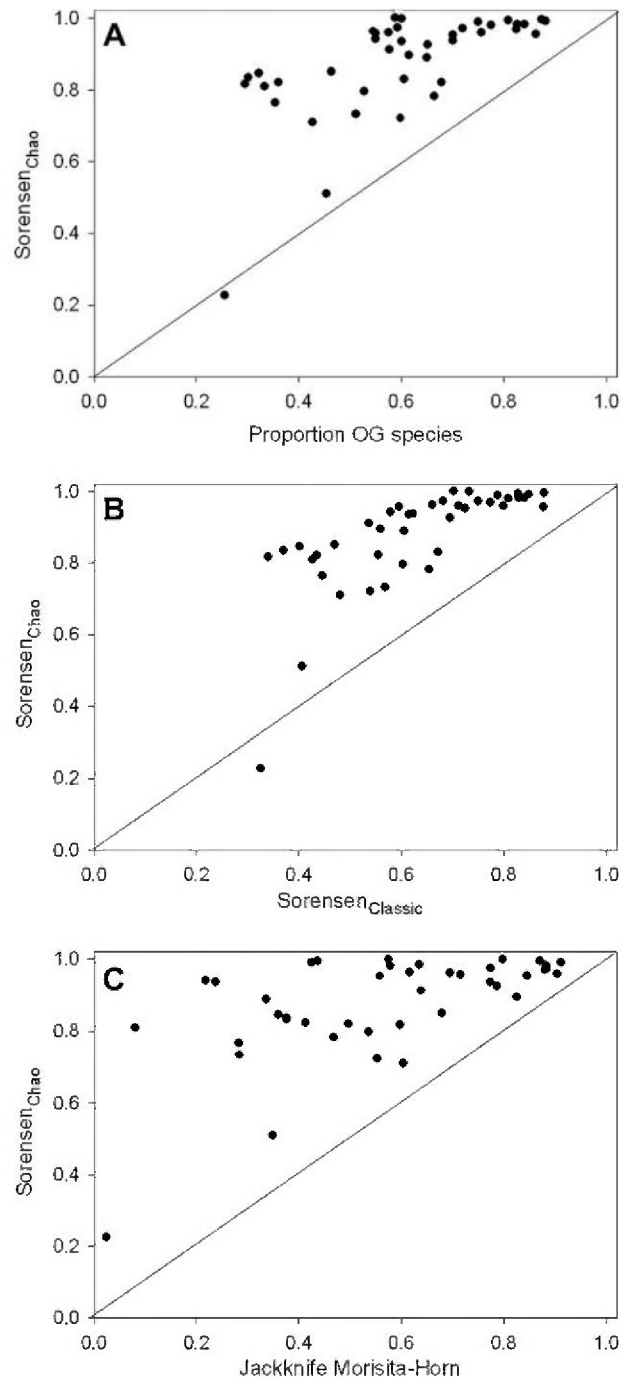


Fig. 2. The relationship between the S_{Chao} similarity index and (A) the proportion of old-growth species present in secondary forest, (B) S_{Classic} and (C) Jackknife Morisita–Horn similarity indices. Data points represent old-growth and secondary forest comparisons from 21 study that meet the criteria required for robust calculation of S_{Chao} .

of known age were mostly young, with 65 less than 21 years old and only 11 more than 40 years old (Fig. 1). Secondary forests with known land-use history grew on land abandoned from intensive, large-scale agriculture or pasture ($N = 35$), shifting agriculture ($N = 44$), or plantations ($N = 10$) or on land that had been cleared but not farmed ($N = 20$). Secondary forests from described landscapes were contiguous with old-growth ($N = 76$), contiguous with other disturbed forests ($N = 29$) or isolated from any other forest ($N = 4$). The original articles did not give SF age, land-use history and SF isolation for 17, 5 and 5 sites, respectively.

3.2. Similarity in species composition among different forest types

Across all OG–SF comparisons, the mean proportion of OG species present in SF was $0.58 (\pm 0.006)$. Similarity in species composition between SF and OG was consistently higher when calculated using S_{Chao} than the traditional incidence based S_{Classic} or the abundance-based Jackknife Morisita–Horn indices (Fig. 2B and C, respectively). The single exception was a 1-year old SF that had low species overlap with nearby OG (Raman et al., 1998). The S_{Classic} index was significantly positively correlated with the mean number of individuals sampled per species for vertebrates ($r = 0.499$, $P = 0.0132$), but not for invertebrates ($r < 0.001$, $P = 0.981$).

Replication is essential to evaluate similarity in species composition yet just 11 studies provided data for replicate SF and OG

sites. Too few studies presented abundance data for multiple SF and OG sites to evaluate similarity for replicate sites with the Jackknife Morisita–Horn or S_{Chao} indices. Mean values of the S_{Classic} index were $0.708 (\pm 0.035)$, $0.577 (\pm 0.035)$ and $0.614 (\pm 0.037)$ for OG–OG, SF–OG and SF–SF comparisons, respectively. There were significant positive relationships between OG–OG and SF–OG S_{Classic} similarity (Fig. 3A, $r^2 = 0.542$, $P = 0.010$) and also between SF–SF and SF–OG S_{Classic} similarity (Fig. 3B; $r^2 = 0.717$, $P < 0.001$) for the 11 studies that provided replicate SF and OG sites. For both relationships the major axis slopes and intercepts were indistinguishable from one and zero, respectively [Slope (95% CI) = $0.957 (0.586\text{--}1.562)$, intercept = $-0.101 (-0.454 \text{ to } 0.252)$ for the OG–OG vs. SF–OG relationship and Slope = $0.891 (0.603\text{--}1.318)$, intercept = $0.039 (-0.183 \text{ to } 0.262)$ for the SF–SF vs. SF–OG relationship]. Thus, this first analysis suggests that there are very large differences among studies in similarity regardless of forest type. This has important implications for the interpretation of subsequent analyses that include sites from multiple studies (see Section 4).

3.3. Effects of forest age and site and landscape characteristics

We calculated the S_{Classic} index for each SF–OG comparison for the 22 studies that included multiple SF ages (Fig. 4). We then compared SF–OG similarity for each temporally contiguous SF pair within each study, summed over studies, and found a significant

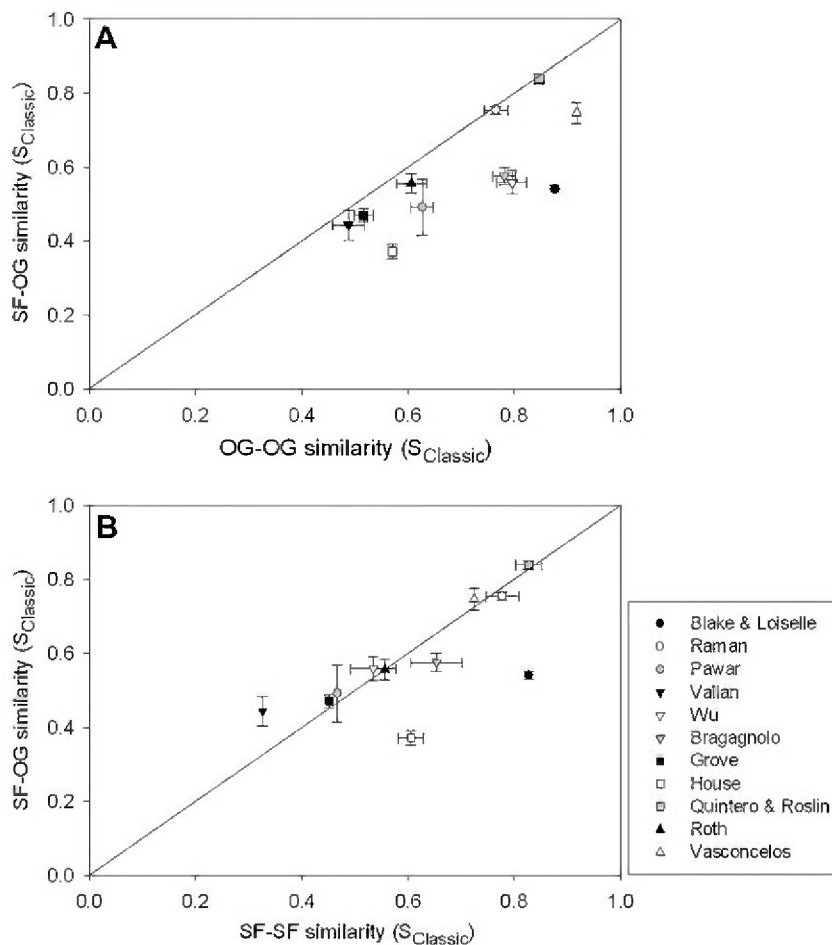


Fig. 3. The relationship between Sorensen's Classic (S_{Classic}) indices of similarity for old-growth and secondary forest comparisons (SF–OG) and comparisons within (A) old-growth (OG–OG) and (B) secondary forest (SF–SF). Symbols present means (± 1 SE). Data are from bird studies in 8.5 (Blake and Loiselle, 2001) and 5–15 year old SF (Raman et al., 1998), herpetofauna studies in 10–35 (Pawar et al., 2004) and 2–25 year old SF (Vallan, 2002), a mammal study in 13 year old SF (Wu et al., 1996) and invertebrate studies in 65 (Bragagnolo et al., 2007), 90 (Grove, 2002), 15–20 (House et al., 2006), 5–17 (Quintero and Roslin, 2005), 24 (Roth et al., 1994) and 10–13 (Vasconcelos, 1999) year old SF.

tendency for SF–OG similarity to increase with SF age (29 increases vs. 10 decreases, Sign Test, $P = 0.0017$), with more increases than decreases for each major taxon (10 vs. 1, 7 vs. 4, 5 vs. 1, and 7 vs. 4 for birds, herpetofauna, mammals and invertebrates, respectively). Twelve of these 22 studies included abundance data, and the Jackknife Morisita–Horn index behaved similarly (Fig. 5, 16 increases vs. 5 decreases, Sign Test, $P = 0.027$). Seven of the chronosequence studies also included replicate OG sites, and OG–OG similarity was always within 17% of SF–OG similarity for the oldest SF for these seven studies (Figs. 4 and 5).

The mean proportion of OG species in SF increased with SF age from 0.35 (± 0.05) in SF < 5 years old to 0.80 (± 0.06) in SF > 50 years old. Site and landscape conditions both affected the colonization of SF by OG species. The proportion of OG species present in SF was 0.686 (± 0.026), 0.629 (± 0.015), 0.611 (± 0.039) and 0.458 (± 0.026) for SF regenerating after forest clearance with no cultivation, shifting agriculture, plantation and intensive agriculture or pasture, respectively. SF contiguous to old-growth had a slightly higher proportion of OG species (0.587, ± 0.007) compared to SF not contiguous with OG (0.552, ± 0.020)

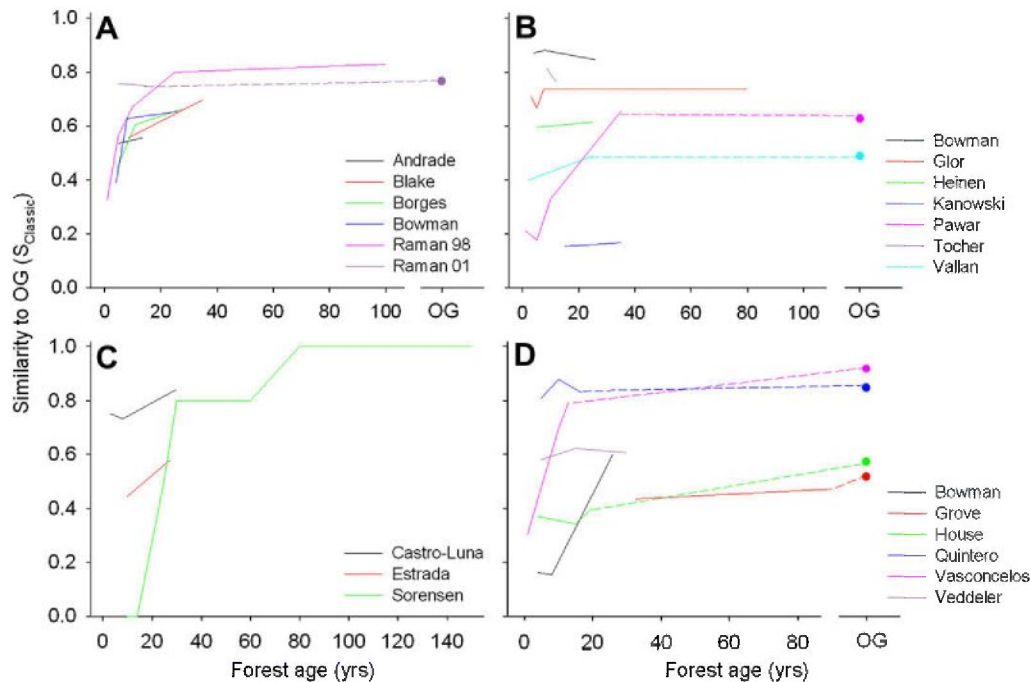


Fig. 4. Sorensen_{Classic} similarity indices ($S_{Classic}$) for comparisons of secondary (SF) and old-growth (OG) forests for (A) birds, (B) herpetofauna, (C) mammals and (D) invertebrates. Solid lines represent mean SF–OG similarity for a chronosequence of secondary forests. Closed circles represent mean OG–OG similarity when available, and dashed lines connect OG–OG similarity with SF–OG similarity for the oldest SF included in the study. Colours represent 22 studies (Andrade and Rubio-Torgler, 1994; Blake and Loiselle, 2001; Borges, 2007; Bowman et al., 1990; Raman et al., 1998; Raman, 2001 for birds; Bowman et al., 1990; Glor et al., 2001; Heinen, 1992; Kanowski et al., 2006; Pawar et al., 2004; Tocher et al., 2002; Vallan, 2002 for herpetofauna; Castro-Luna et al., 2007; Estrada et al., 1994; Sorensen and Fedigan, 2000 for mammals; and Bowman et al., 1990; Grove, 2002; House et al., 2006; Quintero and Roslin, 2005; Vasconcelos, 1999; Veddeler et al., 2005 for invertebrates). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

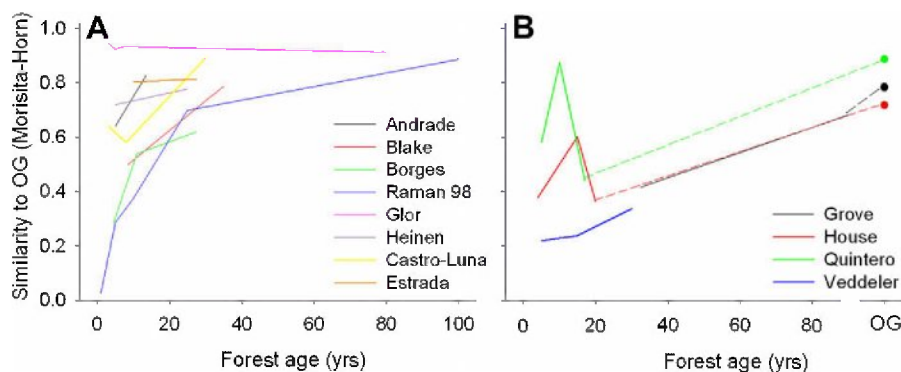


Fig. 5. Jackknife Morisita–Horn similarity indices for comparisons of secondary (SF) and old-growth (OG) forests for (A) vertebrates and (B) invertebrates. Solid lines represent mean SF–OG similarity for chronosequences of secondary forests. Closed circles represent mean OG–OG similarity when available, and dashed lines connect OG–OG similarity with SF–OG similarity for the oldest SF included in the study. Colours represent 12 studies (Andrade and Rubio-Torgler, 1994; Blake and Loiselle, 2001; Borges, 2007; Raman et al., 1998 for birds; Glor et al., 2001; Heinen, 1992 for herpetofauna; Castro-Luna et al., 2007; Estrada et al., 1994 for mammals; Grove, 2002; House et al., 2006; Quintero and Roslin, 2005; Veddeler et al., 2005 for invertebrates). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Analyses of covariance to evaluate the effect of secondary forest age, land-use history and isolation on the similarity in species composition between secondary forest and nearby old-growth forest. Analyses were performed for incidence based (Sorensen_{Classic}) and abundance-based (Jackknife Morisita–Horn) similarity indices. Degrees of freedom (df), mean squared error (MS), *F*-statistics and significance values are reported.

	Sorensen _{Classic}				Jackknife Morisita–Horn			
	df	MS	<i>F</i>	<i>P</i>	df	MS	<i>F</i>	<i>P</i>
Age	1	0.376	8.75	0.004	1	0.292	4.81	0.033
History	3	0.178		0.008	3	0.008	0.13	0.939
Error	91	0.043			50	0.061		
Age	1	0.886	18.91	<0.001	1	0.425	8.21	0.006
Isolation	1	0.211	4.50	0.037	1	0.163	3.17	0.082
Error	89	0.047			48	0.052		

For the S_{Classic} index, SF forest age, land-use history and isolation affected SF–OG similarity significantly (Table 1; Fig. 6). SF–OG similarity was significantly smaller for SF recovering from intensive agriculture or pasture than for SF recovering from slash and burn agriculture or after clearing without cultivation (Tukey's HSD). SF–OG similarity was significantly greater for SF that was contiguous to OG than for SF contiguous to other disturbed forests or entirely isolated from other forests (Tukey's HSD). For the abundance-based Jackknife Morisita–Horn index, SF–OG similarity increased significantly with SF age (Table 1); however, none of the site characteristics had a significant effect perhaps because sample size was much smaller for the Jackknife Morisita–Horn than for the S_{Classic} index (Table 1).

4. Discussion

4.1. Problems estimating faunal similarity for species-rich tropical forests

Sensitivity to sample size varies widely among the indices used to quantify similarity in species composition (Chao et al., 2005, 2006). Previously, the traditional Sorensen, Jaccard and Morisita–Horn indices have been used to quantify similarity between secondary (SF) and old-growth (OG) tropical forests. Small, unequal sample sizes bias all three indices downwards (Chao et al., 2005, 2006). This downward bias was evident here for vertebrates and the traditional Sorensen similarity index, which increased with the number of individuals sampled per species ($r = 0.499$, $P = 0.0132$). Tropical forest animals are likely to be under sampled because there are hundreds (vertebrates) to thousands (insects) of sympatric species, which are frequently elusive and/or truly rare (Terborgh et al., 1990; Robinson and Tuck, 1996; Novotny and Basset, 2000; Robinson et al., 2000). To gain insight into the potential for inadequate sample representation to bias apparent similarity downwards, we compared the traditional S_{Classic} and Jackknife Morisita–Horn indices with a new S_{Chao} index, which provides an unbiased estimate of similarity over a very wide range of sample sizes (Chao et al., 2005, 2006). Estimated similarity was consistently greater for the S_{Chao} index than for the two traditional indices (Fig. 2), suggesting that similarity in faunal species composition between tropical SF and OG is greater than has been appreciated previously.

To evaluate SF–OG similarity, it is also important to understand baseline variation among OG sites. Many of the studies we reviewed implicitly assume that OG sites have identical species composition. However, OG–OG similarity ranged across 43% of its possible range ($0.49 < S_{\text{Classic}} < 0.92$) for the 11 studies that presented data from replicate OG sites. Furthermore, where background levels of OG–OG similarity were low SF–OG similarity

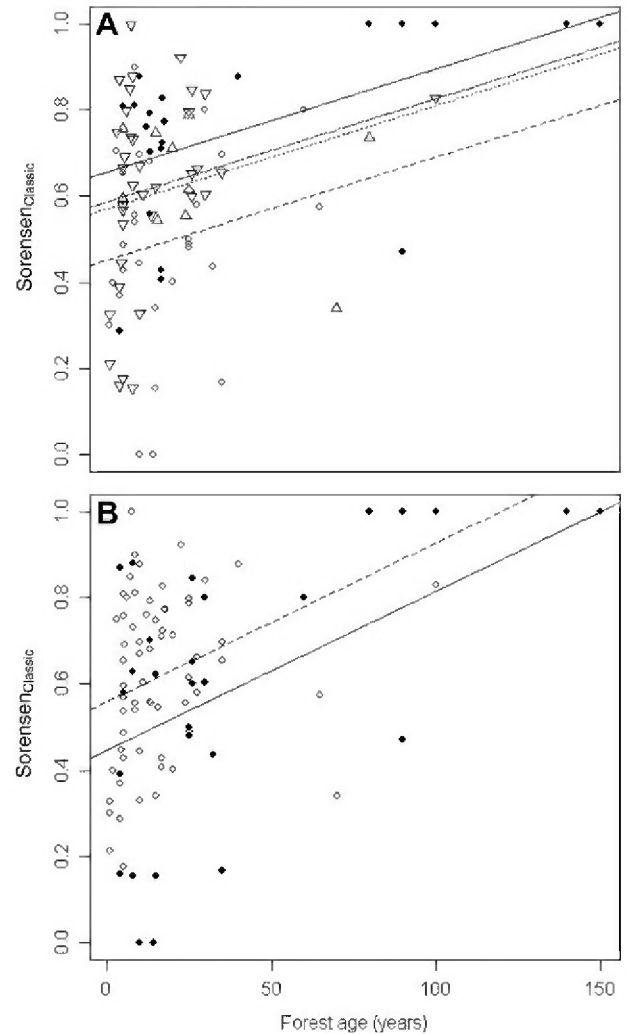


Fig. 6. Mean effects from analyses of covariance illustrate the effect of secondary forest age, land-use history (A) and isolation (B) on the similarity in species composition between secondary forest and nearby old-growth forest. Analyses were performed for the Sorensen_{Classic} similarity index. For panel A, open circles and the short dashed line represent areas abandoned after intensive agriculture or pasture, filled circles and the solid line represent areas cleared but not cultivated, open triangles and the long dashed line represent shifting agriculture and inverted triangles and the dotted line represent abandoned plantations. For panel B, open circles and the short dashed line represent secondary forests contiguous with old-growth and filled circles and the solid line represent forests not contiguous with old-growth forest.

was also low (Fig. 3A). This may be an artefact of variation among studies in sampling effort, especially for vertebrates where small samples reduce apparent similarity across all comparisons, as well as a real effect of variation among studies in landscape heterogeneity and the presence of species with patchy distributions. Many studies of SF–OG similarity have overlooked variation in species composition within OG. Species composition of OG varies locally in relation to edaphic variation, topography and historic disturbance events (Chazdon et al., 2007). Therefore, sufficient replication within OG is essential and caution must be used when interpreting SF–OG similarity in the absence of OG–OG comparisons.

4.2. Predictions concerning faunal similarity

We evaluated four predictions concerning similarity in species composition among tropical forests with different histories of

anthropogenic disturbance (see Section 1). The first concerned the impact of widespread disturbance specialists on SF species composition. Stotz et al. (1996) referred to these as “trash” species. If a limited number of “trash” species dominate tropical SF, then species composition should be very similar among secondary forests. The studies reviewed here provide no evidence for this prediction. Instead, SF–SF similarity tends to be very similar to SF–OG similarity (Fig. 3B). This is consistent with Dunn’s (2004) conclusion that SF diversity resembles that of undisturbed forest just 20–40 years after abandonment and suggests that, like OG, SF contains relatively diverse assemblages of species able to tolerate a wide range of forest conditions (Chazdon, 2003; Petit and Petit, 2003; Barlow et al., 2007). The second prediction was that SF–OG similarity should be consistently low if large numbers of species are restricted to OG. However, even in very young SF (<10 years) the proportion of OG species present averaged 0.51 (± 0.02) and SF–OG and OG–OG similarity were surprisingly similar (Fig. 3A). Tropical faunas undoubtedly include many species specialized to OG and many others specialized to disturbed habitats. However, the broad similarity in species composition between SF and OG evident in Fig. 3A suggests that SF could still play an important role in tropical conservation.

The final two predictions concern changes in SF–OG similarity with SF age and other site (previous land use) and landscape (distance to OG) characteristics. In every analysis we conducted SF–OG similarity increased significantly with SF age (Figs. 4–6, Table 1). The conservation value of SF increases over time. As SF vegetation matures, species specialized to open, disturbed habitats drop out and species specialized to older, closed vegetation colonise from remnant old-growth forest (Chazdon, 2003). Some species typical of OG may be missing from young SF but the increase in the proportion of OG species present in SF with time since abandonment suggests a gradual accumulation of OG species over time or “successional influx” (Chazdon et al., *in press*).

The rate at which secondary forests accumulate species is strongly affected by initial site conditions and the surrounding landscape (Chazdon, 2003; Chazdon et al., *in press*). Previous land use and distance to OG had significant effects on SF–OG similarity. Similarity to OG was greatest for SF contiguous with OG and where the previous land use was limited to shifting agriculture or clearing without agriculture (Table 1). A wide range of environmental conditions are likely to be responsible for these effects. Examples include the presence of residual trees and vegetation, the presence of pollinators and seed dispersers, and the extent of forest clearance and habitat composition at the landscape scale (Thomlinson et al., 1996; Blake and Loiselle, 2001; Chazdon, 2003; Arroyo-Mora et al., 2005; Muscarella and Fleming, 2007). Shifting agriculture typically occurs in small areas (<10 ha) contiguous with old-growth forest, where previous cultivation times were brief, soil disturbance was relatively low, and availability of seed dispersing animals is high (Finegan and Nasi, 2004). Thus, shifting agriculture provides a suite of conditions that favours rapid forest succession and the colonization and accumulation of old-growth species (Raman, 2001; Finegan and Nasi, 2004; Vulinac et al., 2006). It has even been suggested that traditional shifting agricultural practices favour species that encourage forest succession (Diemont et al., 2006). In contrast, intensive agriculture tends to have the opposite characteristics and, hence, slower forest succession. Industrialised agriculture tends to extend over large areas within a matrix of agriculture and disturbed forest, often isolated from OG. In these habitats succession is slowed by a scarcity of seed sources and an absence of seed dispersing animals (Chazdon, 2003).

Dependence among landscape characteristics and land-use history limits causal inferences that might be drawn from our analyses (Table 1). We agree with other studies that call for experiments

designed to disentangle landscape characteristics and land-use history to determine which of these factors has the largest impact on SF–OG faunal similarity (Barlow et al., 2007; Gardner et al., 2007b, 2009). We recommend, however, that any such experiments be informed by environmental conditions that describe real SF. More specifically, we suggest that the most relevant approach would be to determine the conditions that describe the majority of SF in the study region and design experiments for representative SF sites.

4.3. Caveats

Spatial scale can confound comparisons of faunal similarity if the spatial scale that influences species distributions differs among the sites being compared (Hill and Hamer, 2004; Dumbrell et al., 2008). In a study in Borneo, Dumbrell et al. (2008) found that species turnover and beta-diversity increased more rapidly with spatial scale in OG than in SF, presumably because large-scale anthropogenic disturbances tend to reduce habitat heterogeneity and increase spatial autocorrelation of species distributions. The 65 studies reviewed here uniformly sampled spatially constrained sites and the strong similarity evident between OG and SF at this spatial scale (Figs. 2–6) might not persist at landscape and regional scales. A second, related line of reasoning suggests that SF–OG similarity is likely to vary with spatial scale. Abundance, geographic range and levels of habitat specialization are often related, with habitat generalists tending to be widespread and abundant and habitat specialists tending to the opposite traits (Brown, 1995; Gaston and Kunin, 1997). Widespread, abundant, habitat generalists might dominate similarity analyses even when relatively rare OG specialists are present. A new meta-analysis of species-level studies of habitat specialization and new field studies of faunal similarity at larger spatial scales are needed to complete an evaluation of the conservation value of tropical SF.

4.4. Conservation implications

The 65 studies reviewed here clearly demonstrate that many tropical forest species tolerate secondary tropical forest (Figs. 3–5). This is perhaps not surprising given the rapid rates of secondary forest succession in the tropics. Short-lived, rapidly growing pioneer tree species accumulate up to 100 Mg/ha in above-ground biomass within 20 years of land abandonment (Brown and Lugo, 1990; Guariguata and Ostertag, 2001). The closure of the forest canopy and high rates of litterfall create environmental conditions that encourage recruitment of slow-growing, shade-tolerant tree species within 20 years (Guariguata and Ostertag, 2001) and woody plant species richness is often equivalent to old-growth within 80 years (Brown and Lugo, 1990). However, the generation times of most tropical tree species are measured in centuries and, even though, old-growth trees colonize the seedling layer relatively quickly (Norden et al., 2009), estimates of the time for species composition in the canopy layer to resemble old-growth range from 80 to 500 years (Richards, 1952; Riswan et al., 1985; Brown and Lugo, 1990; Whitmore, 1991; Kartawinata, 1994; Guariguata and Ostertag, 2001). Thus, secondary tropical forests rapidly attain many aspects of the structure, environment and diversity of old-growth forests while plant species composition lags behind (Raman et al., 1998; Dewalt et al., 2003; Lamb et al., 2005; Liebsch et al., 2008). Estimates of the time for species composition in the canopy layer to resemble old-growth range from 80 to 500 years (Richards, 1952; Riswan et al., 1985; Brown and Lugo, 1990; Whitmore, 1991; Kartawinata, 1994; Guariguata and Ostertag, 2001).

The recovery of forest structure and plant diversity sets the stage for faunal recovery. Recovery can be rapid for animals dependent on structural traits that recover rapidly. For example, in Amazonian SF contiguous with OG, understory insectivorous birds increase approximately 10 years after abandonment as the understory micro-climate starts to resemble old-growth (Andrade and Rubio-Torgler, 1994). Recovery is slower for animals dependent on structural traits or plant species that recover slowly. For example, saproxylic beetles only become abundant as large woody debris and dead trees increase in tropical Australia (Grove, 2002), and folivorous primates whose diet includes mature shade-tolerant tree species are absent from West African secondary forests (Fimbel, 1994). Thus, animal species that inhabit old-growth forests will colonize secondary forests at different species-specific times during succession, and the potential of a secondary tropical forest to conserve old-growth species increases with its age (Figs. 4 and 5, Table 1). If secondary forests are allowed to develop structural complexity and species diversity then they can play an important supplementary role in efforts to boost forest species populations in landscapes that have been heavily modified by human-use.

Across the studies we review the proportion of old-growth species present in old SF was high (0.80 ± 0.06 for forest >50 years old). However, regional endemics are often highly susceptible to land-use change (Scales and Marsden, 2008). A number of the studies reviewed here that report high representation of OG species in SF (>70% of OG species) also report a SF fauna depauperate in endemic species and species with highly specialized dietary or habitat requirements (Spitzer et al., 1993; Fermon et al., 2005; Veddeler et al., 2005; Renner et al., 2006). The possibility that species that are consistently absent from SF tend to be the most threatened species should be explored.

Site selection biases might influence our perception of the potential conservation value of tropical SF. The SF sites studied to date tend to be young (Fig. 1), contiguous with OG (70% of SF sites), and abandoned immediately after clearing or after shifting agriculture (59%). Young SF constrains SF–OG similarity while proximity to OG and benign prior land uses increase SF–OG similarity (Figs. 4 and 5, Table 1). Thus, the potential for SF site selection to bias perceptions of the conservation value of tropical SF is real. It would clearly be inappropriate to extrapolate to a site abandoned after intensive agriculture in isolation from any other forest. This does not necessarily mean, however, that the 65 studies reviewed here are not representative of tropical SF. Tropical SF are concentrated in areas of high topographic relief that are inappropriate for intensive agriculture (Asner et al., in press). Tropical SF also tends to be located far from roads and close to OG where land is frequently abandoned first (Chazdon, 2003; Chazdon et al., in press). Proximity to OG and benign prior land uses are likely to characterize many tropical SF, perhaps particularly those most likely to escape future conversion to other land uses because they are far from roads and on topographically difficult terrain.

Gardner et al. (2007a) conclude that “whilst speculation about the potential biodiversity value of secondary forest is intellectually stimulating, it detracts from the most pragmatic conservation recommendation that is to assist countries with tropical forest to protect primary forest”. We do not contest the importance of primary old-growth forests and the imperative to conserve and protect them. However, degraded and secondary forests now comprise as much as 60 percent of the world’s remaining tropical forests and 42 tropical countries report a greater area of degraded forest than primary forest (FAO, 2006). Disturbed and secondary forests will be critical if these countries are to conserve their biodiversity. The luxury of concentrating conservation efforts solely on old-growth forests is no longer a viable conservation strategy in many tropical countries, and it is essential that we have a better understanding of

the potential of secondary and degraded forests to help conserve tropical forest species.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2009.05.035](https://doi.org/10.1016/j.biocon.2009.05.035).

References

- Achard, F., Eva, H.D., Stibig, H.-J., Mayaux, P., Gallego, J., Richards, T., Malingreau, J.-P., 2002. Determination of deforestation rates of the world’s humid tropical forests. *Science* 297, 999–1002.
- Andrade, G.I., 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. *Conservation Biology* 8, 545–554.
- Arroyo-Mora, J.P., Sánchez-Azofeifa, A., Rivard, B., Calvo, J.C., Janzen, D.H., 2005. Dynamics in landscape structure and composition for the Chorotega region, Costa Rica, from 1960 to 2000. *Agriculture, Ecosystems and Environment* 106, 27–39.
- Asner, G.P., Broadbent, E., Oliveira, P., Keller, M., Knapp, D., Silva, J., 2006. Condition and fate of logged forests in the Brazilian Amazon. *Proceedings of the National Academy of Sciences* 103, 12947–12950.
- Asner, G.P., Rudel, T.K., Aide, T.M., DeFries, R., Emerson, R., in press. Forest tsunami: global humid tropical forest change in the 21st century. *Conservation Biology*.
- Barlow, J., Gardner, T.A., Araujo, I.S., Avila-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. *Proceedings of the National Academy of Sciences* 104, 18555–18560.
- Blake, J.G., Loiselle, B.A., 2001. Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. *Auk* 118, 304–326.
- Borges, S.H., 2007. Bird assemblages in secondary forests developing after slash-and-burn agriculture in the Brazilian Amazon. *Journal of Tropical Ecology* 23, 469–477.
- 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. *Biological Conservation* 140, 273–296.
- Bowman, D., Woinarski, J.C.Z., Sands, D.P.A., Wells, A., McShane, V.J., 1990. Slash-and-burn agriculture in the wet coastal lowlands of Papua New Guinea – response of birds, butterflies and reptiles. *Journal of Biogeography* 17, 227–239.
- Bragagnolo, C., Nogueira, A.A., Pinto-da-Rocha, R., Pardini, R., 2007. Harvestmen in an Atlantic forest fragmented landscape: evaluating assemblage response to habitat quality and quantity. *Biological Conservation* 139, 389–400.
- Brown, J.H., 1995. *Macroecology*. University of Chicago Press, Chicago, USA.
- Brown, S., Lugo, A.E., 1990. Tropical secondary forests. *Journal of Tropical Ecology* 6, 1–32.
- Castro-Luna, A.A., Sosa, V.J., Castillo-Campos, G., 2007. Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. *Animal Conservation* 10, 219–228.
- Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.-J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters* 8, 148–159.
- Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.-J., 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62, 361–371.
- Chazdon, R.L., 2003. Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics* 6, 51–71.
- Chazdon, R.L., Letcher, S.G., van Breugel, M., Martinez-Ramos, M., Bongers, F., Finegan, B., 2007. Rates of change in tree communities of secondary Neotropical forests following major disturbances. *Philosophical Transactions of the Royal Society B – Biological Sciences* 362, 273–289.
- Chazdon, R., Peres, C.A., Dent, D.H., Shiel, D., Lugo, A.E., Lamb, D., Stork, N., in press. Where are the wild things? Assessing the potential for species conservation in tropical secondary forests. *Conservation Biology*.
- China, J.D., 2002. Tropical forest succession on abandoned farms in the Humacao municipality of eastern Puerto Rico. *Forest Ecology and Management* 167, 195–207.

- Colwell, R.K. 2004. Estimates: Statistical estimation of species richness and shared species from samples. v. 8.0 Available from: <<http://purl.oclc.org/estimates>>.
- Cornelius, C., Cockle, K., Politi, N., Berkunsky, I., Sandoval, L., Ojeda, V., Rivera, L., Hunter, M., Martin, K., 2008. Cavity-nesting birds in neotropical forests: cavities as a potentially limiting resource. *Ornitologia Neotropical* 19 (8), 253–268.
- DeWalt, S.J., Maliakal, S.K., Denslow, J.S., 2003. Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. *Forest Ecology and Management* 182, 139–151.
- Diemont, S.A.W., Martin, J.F., Levy-Tacher, S.L., Nigh, R.B., Lopez, P.R., Golicher, J.D., 2006. Lacandon Maya forest management: restoration of soil fertility using native tree species. *Ecological Engineering* 28, 205–212.
- Dirzo, R., Raven, P.H., 2003. Global state of biodiversity and loss. *Annual Review of Environment and Resources* 28, 137–167.
- Dumbrell, A.J., Clark, E.J., Frost, G.A., Randell, T.E., Pitchford, J.W., Hill, J.K., 2008. Changes in species diversity following habitat disturbance are dependent on spatial scale: theoretical and empirical evidence. *Journal of Applied Ecology* 45, 1531–1539.
- Dunn, R.R., 2004. Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18, 302–309.
- Estrada, A., Coates-Estrada, R., Meritt, D.J., 1994. Non flying mammals and landscape changes in the tropical rain forest region of Los Tuxtlas, Mexico. *Ecography* 17, 229–241.
- FAO, 2006. Global Forest Resources Assessment 2005: Progress Toward Sustainable Forest Management. FAO Forestry Paper, vol. 147, pp. 1–348.
- Fermon, H., Waltert, M., Vane-Wright, R.L., Muhlenberg, M., 2005. Forest use and vertical stratification in fruit-feeding butterflies of Sulawesi, Indonesia: impacts for conservation. *Biodiversity and Conservation* 14, 333–350.
- Fimbel, C., 1994. The relative use of abandoned farm clearings and old forest habitats by primates and a forest antelope at Tiwai, Sierra-Leone, West-Africa. *Biological Conservation* 70, 277–286.
- Finegan, B., Nasi, R., 2004. The biodiversity and conservation potential of shifting cultivation landscapes. In: Schroth, G., da Fonseca, G.A.B., Harvey, C.A., Gascon, C., Vasconcelos, H.L., Izac, A.M.N. (Eds.), *Agroforestry and Biodiversity Conservation in Tropical Landscapes*. Island Press, Washington, DC, USA, pp. 153–197.
- Gardner, T.A., Barlow, J., Parry, L.W., Peres, C.A., 2007a. Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica* 39, 25–30.
- Gardner, T.A., Ribeiro-Junior, M.A., Barlow, J., Avila-Pires, T.C., Hoogmoed, M.S., Peres, C.A., 2007b. The value of primary, secondary, and plantation forests for a neotropical herpetofauna. *Conservation Biology* 21, 775–787.
- Gardner, T.A., Barlow, J., Chazdon, R.L., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N.S., 2009. Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters* 12, 561–582.
- Gaston, K.J., Kunin, W.E., 1997. Rare–common differences: an over-view. In: Kunin, W.E., Gaston, K.J. (Eds.), *The Biology of Rarity: Causes and Consequences of Rare–Common Differences*. Chapman and Hall, UK.
- Glor, R.E., Flecker, A.S., Benard, M.F., Power, A.G., 2001. Lizard diversity and agricultural disturbance in a Caribbean forest landscape. *Biodiversity and Conservation* 10, 711–723.
- Grove, S.J., 2002. The influence of forest management history on the integrity of the saproxylic beetle fauna in an Australian lowland tropical rainforest. *Biological Conservation* 104, 149–171.
- Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management* 148, 185–206.
- Hansen, M.C., DeFries, R.S., 2004. Detecting long-term global forest change using continuous fields of tree-cover maps from 8-km advanced very high resolution radiometer (AVHRR) data for the years 1982–99. *Ecosystems* 7, 695–716.
- Heinen, J.T., 1992. Comparisons of the leaf litter herpetofauna in abandoned cacao plantations and primary rain-forest in Costa-Rica – some implications for faunal restoration. *Biotropica* 24, 431–439.
- Hill, J.K., Hamer, K.C., 2004. Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology* 41, 744–754.
- House, A., Burwell, C., Brown, S., 2006. Ant assemblages in Brigalow regrowth vegetation. *Ecological Management and Restoration* 7, 136–140.
- ITTO, 2002. International Tropical Timber Organisation Guidelines for the Restoration, Management and Rehabilitation of Degraded and Secondary Tropical Forests. Policy Development Series 13.
- Johnson, C.M., Zarin, D.J., Johnson, A.H., 2000. Post-disturbance aboveground biomass accumulation in global secondary forests. *Ecology* 81, 1395–1401.
- Kanowski, J.J., Reis, T.M., Catterall, C.P., Piper, S.D., 2006. Factors affecting the use of reforested sites by reptiles in cleared rainforest landscapes in tropical and subtropical Australia. *Restoration Ecology* 14, 67–76.
- Kartawinata, K., 1994. The use of secondary forest species in rehabilitation of degraded forest lands. *Journal of Tropical Forest Science* 7, 76–86.
- Lamb, D., Erskine, P.D., Parrotta, J.A., 2005. Restoration of degraded tropical landscapes. *Science* 310, 1628–1632.
- Liebsch, D., Marques, M.C.M., Goldenberg, R., 2008. How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession. *Biological Conservation* 141, 1717–1725.
- Moran, E.F., Brondizio, E.S., Tucker, J.M., da Silva Forsberg, M.C., McCracken, S., Falesi, I., 2000. Effects of soil fertility and land-use on forest succession in Amazonia. *Forest Ecology and Management* 139, 93–108.
- Muscarella, R., Fleming, T.H., 2007. The role of frugivorous bats in tropical forest succession. *Biological Reviews* 82, 573–590.
- Norden, N., Chazdon, R.L., Chao, A., Jiang, Y.-H., Vilchez Alvarado, B., 2009. Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecology Letters* 12, 384–394.
- Novotny, V., Basset, Y., 2000. Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos* 89, 564–572.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G.L., Stevens, M.H.H., Wagner H., 2008. *Vegan: Community Ecology Package*, vol. 1, pp. 13–8. <<http://vegan.r-forge.r-project.org/>>.
- Pawar, S.S., Rawat, G.S., Choudhury, B.C., 2004. Recovery of frog and lizard communities alteration in Mizoram, Northeast India. *BMC Ecology* 4.
- Petit, L.J., Petit, D.R., 2003. Evaluating the importance of human-modified lands for Neotropical bird conservation. *Conservation Biology* 17, 687–694.
- Pinard, M., Howlett, B., Davidson, D., 1996. Site conditions limit pioneer tree recruitment after logging of Dipterocarp forests in Sabah, Malaysia. *Biotropica* 28, 2–12.
- Quintero, I., Roslin, T., 2005. Rapid recovery of dung beetle communities following habitat fragmentation in central Amazonia. *Ecology* 86, 3303–3311.
- R Core Team Development, 2008. *R: A language and environment for statistical computing*, v. 2.7.2. R Foundation for Statistical Computing, Vienna, Austria. <<http://www.R-project.org/>>.
- Raman, T.R.S., 2001. Effect of slash-and-burn shifting cultivation on rainforest birds in Mizoram, northeast India. *Conservation Biology* 15, 685–698.
- Raman, T.R.S., Rawat, G.S., Johnsingh, A.J.T., 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology* 35, 214–231.
- Raven, P.H., 1988. Our diminishing tropical forests. In: Wilson, E.O., Peter, F.M. (Eds.), *Biodiversity*. National Academy Press, Washington, DC, USA, pp. 119–122.
- Renner, S.C., Waltert, M., Muhlenberg, M., 2006. Comparison of bird communities in primary vs. Young secondary tropical montane cloud forest in Guatemala. *Biodiversity and Conservation* 15, 1545–1575.
- Richards, P.W., 1952. *The Tropical Rain Forest: An Ecological Study*. Cambridge University Press, Cambridge, UK.
- Riswan, S., Kenworthy, J.B., Kartawinata, K., 1985. The estimation of temporal processes in tropical rain forest: a study of primary mixed dipterocarp forest in Indonesia. *Journal of Tropical Ecology* 1, 171–182.
- Robinson, G.S., Tuck, K.R., 1996. Describing and comparing high invertebrate diversity in tropical forest – a case study of small moths in Borneo. In: Edwards, D.S., Booth, W.E., Choy, S.C. (Eds.), *Tropical Rainforest Research – Current Issues*. Kluwer, pp. 29–42.
- Robinson, W.D., Brawn, J.D., Robinson, S.K., 2000. Forest bird community structure in central Panama: Influence of spatial scale and biogeography. *Ecological Monographs* 70, 209–235.
- Roth, D.S., Perfecto, I., Rathcke, B., 1994. The effects of management systems on ground-foraging ant diversity in Costa Rica. *Ecological Applications* 4, 423–436.
- Scales, B.R., Marsden, S.J., 2008. Biodiversity in small-scale tropical agroforests: a review of species richness and abundance shifts and the factors influencing them. *Environmental Conservation* 35, 160–172.
- Schechtman, E., Wang, S., 2004. Jackknifing two-sample statistics. *Journal of Statistical Planning and Inference* 119, 329–340.
- Sorensen, T.C., Fedigan, L.M., 2000. Distribution of three monkey species along a gradient of regenerating tropical dry forest. *Biological Conservation* 92, 227–240.
- Spitzer, K., Novotny, V., Tonner, M., Leps, J., 1993. Habitat preferences, distribution and seasonality of the butterflies (Lepidoptera: Papilionoidea) in a montane tropical rain forest, Vietnam. *Journal of Biogeography* 20, 109–121.
- Stotz, D.F., Fitzpatrick, J.W., Parker III, T.A., Moskovits, D.K., 1996. *Neotropical birds: ecology and conservation*. University of Chicago Press, Chicago.
- Terborgh, J., Robinson, S.K., Parker, T.A., Munn, C.A., Pierpont, N., 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* 60, 213–238.
- Thomlinson, J.R., Serrano, M.I., Lopez, T.M., Aide, T.M., Zimmerman, J.K., 1996. Land-use dynamics in a post-agricultural Puerto Rican landscape (1936–1988). *Biotropica* 28, 525–536.
- Tocher, M., Gascon, C., Meyer, J.R., 2002. Community composition and breeding success of Amazonian frogs in continuous forest and matrix aquatic sites. In: Bierregaard, R.O., Gascon, C., Lovejoy, T.E., Mesquita, R. (Eds.), *Lessons from Amazonia: the ecology and conservation of a fragmented forest*. Yale University Press, New Haven, USA, pp. 235–247.
- Vallan, D., 2002. Effects of anthropogenic environmental changes on amphibian diversity in the rain forests of eastern Madagascar. *Journal of Tropical Ecology* 18, 725–742.
- Vasconcelos, H.L., 1999. Effects of forest disturbance on the structure of ground-foraging ant communities in central Amazonia. *Biodiversity and Conservation* 8, 409–420.
- Veddeler, D., Schulze, C.H., Steffan-Dewenter, I., Buchori, D., Tschantke, T., 2005. The contribution of tropical secondary forest fragments to the conservation of fruit-feeding butterflies: effects of isolation and age. *Biodiversity and Conservation* 14, 3577–3592.
- Vulinec, K., Lambert, J.E., Mellow, D.J., 2006. Primate and dung beetle communities in secondary growth rain forests: implications for conservation of seed dispersal systems. *International Journal of Primatology* 27, 855–879.
- Warton, D.I., Wright, I.J., Falster, D.S., Westoby, M., 2006. Bivariate line-fitting methods for allometry. *Biological Reviews* 81, 259–291.

- Whitmore, T.C., 1991. Tropical forest dynamics and its implications for management. In: Gomez-Pompa, A., Whitmore, T.C., Hadley, M. (Eds.), *Rain Forest Regeneration and Management*, UNESCO, Paris, France. The Parthenon Publishing Group, NJ, USA, pp. 67–89.
- Wright, S.J., 2005. Tropical forests in a changing environment. *Trends in Ecology and Evolution* 20, 553–560.
- Wright, S.J., Muller-Landau, H.C., 2006. The future of tropical forest species. *Biotropica* 38, 287–301.
- Wu, D.L., Luo, J., Fox, B.J., 1996. A comparison of ground-dwelling small mammal communities in primary and secondary tropical rainforests in China. *Journal of Tropical Ecology* 12, 215–230.
- Zarin, D.J., Ducey, M.J., Tucker, J.M., Salas, W.A., 2001. Potential biomass accumulation in Amazonian regrowth forests. *Ecosystems* 4, 658–668.
- Zarin, D.J., Davidson, E.A., Brondizio, E., Vieira, I.C.G., Sá, T., Feldpausch, T., Schuur, E.A.G., Mesquita, R., Moran, E., Delamonica, P., Ducey, M.J., Hurtt, G.C., Salimon, C., Denich, M., 2005. Legacy of fire slows carbon accumulation in Amazonian forest regrowth. *Frontiers in Ecology and the Environment* 3, 365–369.