RESEARCH PAPER

Mean latitudinal range sizes of bird assemblages in six Neotropical forest chronosequences

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ABSTRACT

Aim The geographical range size frequency distributions of animal and plant assemblages are among the most important factors affecting large-scale patterns of diversity. Nonetheless, the relationship between habitat type and the range size distributions of species forming assemblages remains poorly understood. We examined how the mean latitudinal range sizes of species in Neotropical bird species assemblages shift during forest clearance and subsequent regeneration. We tested the hypothesis that bird species assemblages in early successional habitats tend to have larger latitudinal ranges than those in more mature forests.

Location We considered breeding bird chronosequence data from six Neotropical forests.

Results Breeding bird assemblages were found to have the species with the largest average latitudinal range sizes in cleared areas, intermediate in young secondary forests and smallest in old secondary and mature forests. Similar differences were also found when we compared congeners differing in their successional preferences. Sizes of regional ranges (within the Neotropics) did not, however, differ consistently among successional stages. The larger latitudinal (but not regional) ranges of early successional species was as a result in part of the tendency of early successional species to have ranges that extend beyond the Neotropical forest biome.

Conclusions Our analysis of chronosequences suggests that as early successional habitats mature, a consistent shift from large-ranged species towards more small ranged species occurs. Even relatively old secondary forests have bird species with larger average ranges than mature forests. As a consequence, conservation of secondary forests alone will miss many of the species most at risk of extinction and most unlikely to be conserved in other locations or biomes.

Keywords

Beta diversity, birds, disturbance, range size frequency distribution, secondary forest, tropical forest.

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INTRODUCTION

Distributions of the sizes of the geographical ranges of species in any assemblage or taxon can be studied in the same way one might study frequency distributions of abundance or other ecological characteristics. Such geographical range size frequency distributions (RSFD) of species are one of the most important factors affecting large-scale patterns of species turnover and regional diversity (Colwell & Lees, 2000; Koleff & Gaston, 2001; Arita & Rodriguez, 2002; Colwell *et al.*, 2004). Together, the distributions of geographical range sizes and of geographical range midpoints determine the pattern of species richness within a region. In general, for a given regional diversity, where geographical ranges are smaller, local diversity is lower and beta diversity is higher. When geographical ranges are small, fewer species' ranges overlap in any given point sampled (e.g. Arita & Rodriguez, 2002). If we understood the causes of differences among taxa or assemblages in their range size frequency distributions, and in particular in mean range size, we could better understand the determinants of regional patterns of biological diversity.

At the scale of entire geographical domains, there remains little consensus, with regard to the relationship between geographical range size and latitude (Stevens, 1989; Colwell & Hurtt, 1994; Gaston *et al.*, 1998), bathymetry (Stevens, 1996; Smith & Brown, 2002), or elevation (Stevens, 1992; Grytnes & Vetaas, 2002; Sanders, 2002; Vetaas & Grytnes, 2002). Even within a given region, RSFDs of assemblages in different habitats can differ dramatically, for reasons that remain poorly understood. One of the habitat variables shown to affect geographical range size of the species assemblages present in a given habitat is the degree of habitat disturbance (Duncan *et al.*, 1999; Fjeldså, 1999).

Ecologists have long been interested in the relationship between an organism's geographical range size and its response to disturbance. Bates in *On the Amazon* (1863) states that: 'The species observed in the weedy and open places, as already remarked, were generally different from those that dwell in the shades of the forest … Those species which have the widest distribution in America, […] are such that occur in open sunny places near town.' Wilson (1961) later argued along similar lines to Bates, suggesting that species in marginal habitats have wider, more rapidly expanding ranges. More recently, Fjeldså (1999) reported that for Tanzanian birds, the mean two-dimensional geographical range size of bird species in assemblages is greater in more disturbed areas. Similarly, Duncan *et al.* (1999) found habitat preference to be an important predictor of geographical range size for bird species introduced to New Zealand, with agricultural specialists having larger ranges than other species. Support is growing for the hypothesis that the geographical range size of bird assemblages may generally be greatest for those species occurring in disturbed areas, as a consequence of the replacement of small-ranged species by large-ranged species. One of the most common forest disturbances in many tropical regions is small-scale agriculture. When forests are disturbed by agriculture, the mean geographical range size of bird and other assemblages can be hypothesized to increase through changes in species composition. Average geographical range sizes may then slowly decrease as abandoned fields begin succession and mature forest specialists begin to return (Dunn, 2004a, 2004b).

Birds present a good subject for the study of geographical range sizes because their alpha taxonomy is fairly complete, distributions are well documented, and the basic natural history of most bird species is at least somewhat known. We focus on Neotropical birds in six sites, spanning the area between northern Mexico and central Peru. Using databases of continent-wide distributions of bird species found in these sites, we compare the mean latitudinal range size, one metric of RSFD, of all bird species found in cleared areas, in young secondary forests, and in old secondary forests to that of bird species found in mature forests, within each site and overall. For a subset of bird taxa, we also compare the latitudinal range sizes of congeneric species differing in their successional preferences. We also examine the relationship between successional stage and the average regional ranges of species in those assemblages, where regional ranges are the latitudinal extent of species' ranges within the Neotropics.

METHODS

Our study compared the bird communities across four successional stages – mature forest, young and old secondary forest, and cleared areas – using data from published studies on successional chronosequences. We restricted our analysis to those studies that have reported species-by-site matrices of occurrence in at least a secondary and mature forest or agricultural land and mature forest. We did not include secondary forests that resulted from logging, as previous work has shown that logged sites undergo a much different recovery process than do abandoned agricultural fields (Dunn, 2004b).

Six sites were found ranging throughout the Neotropics (Terborgh & Weske, 1969; Hutto, 1989; Johns, 1991; Andrade & Rubiotorgler, 1994; Estrada & Coates-Estrada, 1997; Blake & Loiselle, 2001) (Table 1). Four studies (Andrade & Rubiotorgler, 1994; Terborgh & Weske, 1969; Hutto, 1989; Blake & Loiselle, 2001) compared species found in secondary forests to those found in mature forests. Two studies (Johns, 1991; Estrada & Coates-Estrada, 1997) compared only cleared areas and mature forests. Mature forests included in this study varied in mean annual rainfall from 1200 to 4946 mm per year. All study sites were below 1000 m in elevation. The secondary forests included in the study varied both in age and sample size. Secondary forests had regenerated from 1 to 35 years since abandonment. Sample size within successional stages ranged from one to three forests. Two of the secondary forests considered were recovering from being old fields and two were recovering from being old pastures (Table 1). Cleared areas were all active fields or pastures. Both cleared areas and secondary forests tended to be relatively small in scale. Sampled forest stands varied from 1 to 7 ha in size (Table 1). We have included six sites and 14 samples in this study, where samples are successional stages within the six study sites. In studies where data from multiple transects were reported for each sample, the cumulative species occurrence data were used for that sample and the data were included only once. Secondary forests were divided into old secondary forests (old SF) and young secondary forests (young SF), where old SF are 17 to 35 years old and young SF 3 to16 years old. Sampling procedures used within the six study sites varied among study sites but were consistent within study sites. See original studies for full descriptions of sampling methodologies.

All bird species included in original data sets were included in the analysis, except those that were identified only to genus. We used the Sibley and Monroe list as a basis for combining data from different studies (Sibley & Monroe, 1990, 1993). We calculated latitudinal ranges to the nearest degree for all species based on published sources. Latitudinal ranges were calculated as the N-S distance between the northernmost and southernmost occurrence of each species. Regional ranges were calculated as the N-S distance between the northernmost and southernmost occurrence of a species within the Neotropics, defined here broadly as the area between 25° N and 25° S. The disadvantage of focusing on latitudinal ranges is the limitation in examining the relationship between disturbance and range shape, but one-dimensional analyses proved to be more practical than two-dimensional analyses.

Table 1 Site data for studies included in the analyses. Stand age for the secondary forest in the Terborgh study is estimated based on the description of the site. Here and throughout this paper, names correspond to the last names of the first authors. Region indicates the place where each study was conducted. Sample size (*N*) indicates the number of independent samples of each successional stage. Cl; cleared area, YSF; young secondary forest, OSF; old secondary forest, MF; mature forest, SF; secondary forest. ND = no data means that a given successional stage was not sampled by a study's authors. Ag; agriculture, and Pa; pasture.?; information not available

First author	Region	Elevation (m)	Clearance type	Successional stages (*N*)	Age of SF (years)	Size of SF or Cl	Latitude, longitude	Rainfall (mm)
Andrade & Rubiotorgler (1994)	Mirití-paraná, Columbia	< 1000 m	Ag.	MF(4), OSF(3), YSF(3)	1–5, 7–17	~1 ha	0°6′ S, 70°8′ W	> 3500
Blake & Loiselle (2001)	Sarapiqui, Costa Rica	< 500 m	Pa.	MF(1), OSF(1), YSF(1)	20–35	?	10°25′ N, 84°01′ W	4000
Estrada & Coates-Estrada (1997)	Las Tuxtlas, Mexico	0–800 m	Ag.	MF(1), Cl (4)	ND	?	18°25′ N, 95°00′ W	4964
Hutto (1989)	Jalisco, Mexico	< 500 m	Pa.	MF(1), YSF(2)	~2, ~5	< 5 ha	19°30′ N, 105°03′ W	~1200
Johns (1991)	Amazonas, Brazil	< 1000 m	Ag.	MF(1), Cl (1)	ND	~7 ha	3°32′ S, 64°38′ W	3200
Terborgh & Weske (1969)	Ayacucho, Peru	650 m	Ag.	MF(1), YSF(1)	~5–10	~4 acres	12°39′ S, 73°44′ W	3000

For the North American extensions of species' ranges, we used the volumes of *The Birds of North America* (Poole & Gill, 2000) as our primary source, supplemented with ranges used in Monroe and Sibley (1993) for species not yet covered. Most of Central America is accounted for by Howell and Webb (1995), and for Costa Rica and Panama we used Stiles and Skutch (1989) and Ridgely and Gwynne (1992). Nicaragua is not covered by an authoritative work, but Howell and Webb (1995) and Ridgely and Gwynne (1992) provide the information necessary for recognizing boundaries within that country. Data for South American birds are from Fjeldså, Rahbek and collaborators (based on confirmed records) and the consensus of taxonomic specialists (Fjeldså & Rahbek, 1998; Rahbek & Graves, 2001).

We compared the latitudinal range size and regional range size of all bird species found in cleared areas to those in secondary forests and mature forests within each study site. The bird species in different successional stages cannot be compared using standard analysis of variance (ANOVA), as the data from the different successional stages are non-independent. For example, the same bird species may occur in secondary forests and mature forests. Consequently, it was necessary to compare the bird ranges in different successional stages using resampling-based analyses. We used randomization-based ANOVAs for all comparisons of bird range size and northern and southernmost occurrence across successional stages. Randomization-based ANOVAs are conceptually similar to traditional ANOVAs, but differ in that they do not assume that data points are independent (Manly, 1997). Randomization-based ANOVAs randomize the identity of the dependent variable relative to the independent categorical variable. We randomized range sizes and northernmost and southernmost point relative to species using the program EcoSim (Gotelli & Entsminger, 2001). Species identities and the successional stages in which they occurred were held constant. We then compared the distribution of ranges in the simulated communities to the observed range size distributions. We tested whether bird assemblages in early successional stages were more likely to have ranges that extend beyond the Neotropics by conducting a chi-square test on the ratios of bird species with ranges extending outside of the Neotropics in different successional stages.

Congener comparisons

We pooled data from the multiple sites in order to understand the relationship between a species' successional preferences and its range size. Within this pooled data set, we identified bird species found in all of the successional stages considered, those that were unique to mature forest, and those unique to either secondary forest or to cleared areas, depending on the study (successional generalists, mature forest uniques, secondary forest uniques and cleared area uniques, respectively). We identified those genera that contained species of more than one successional preference. We then compared the range size of congeneric species differing in successional preference. Comparing congeneric species allowed us to examine whether successional preference is associated with range size, while at the same time

Mean range size of bird assemblages

Table 2 Bird species counts per study. Numbers can be slightly different from those in the original papers because of species excluded due to missing species names (e.g. names were recorded as *Genus sp*? only)[a] = total number of species found in corn fields, Jalepeño fields and pasture. ND = no data means that the given successional stage was not sampled by the authors of the study. NA indicates that data were not available in the original study

First author	No. of mist net collections/ No. of point obs.	No. of species obs. + captured (No. of individuals)			
		Young secondary forest	Old secondary forest	Mature forest	Total
Comparison between secondary forest and mature forest					
Andrade & Rubiotorgler (1994)	878/0	57 (300)	61 (240)	50 (338)	83 (878)
Blake & Loiselle (2001)	10,019/15,577	206 (11 299)	95 (1463)	157 (12 834)	249 (25 596)
Hutto (1989)	0/1706	72 (860)	ND	59 (846)	92 (1706)
Terborgh & Weske (1969)	551/NA	55 (NA)	ND	132 (NA)	158 (551 +)
Comparison between cleared areas and mature forest					
Cleared areas	Mature forest	Total			
Estrada & Coates-Estrada (1997)	0/8557	ND	38[a] (1633)	164 (4932)	180 (8557)
Johns (1991)	0/3433	ND	76 (1250)	131 (2183)	169 (3433)

Table 3 Mean latitudinal range of Neotropical birds by successional stage. Mean values indicate mean latitudinal breeding range size of all bird species in a given forest stage at a site. Sample size is in parentheses. ND = no data because a given successional stage was not sampled by the authors of the study. In pairwise comparisons in the Andrade study, both the MF vs. young SF and MF vs. old SF comparisons were significant ($P = 0.04$, $P = 0.05$)

First author	Stages included	Range size in degrees				*P*-value overall
		Cl	Young SF	Old SF	MF	
Andrade & Rubiotorgler (1994)	MF, Sec.	ND	33.2 (57)	26.7 (61)	27.5 (50)	0.03
Blake & Loiselle (2001)	MF, Sec.	ND	30.2 (206)	27.6 (95)	26.7 (157)	0.12
Hutto (1989)	MF, Sec.	ND	35.7 (72)	ND	25.2 (59)	0.009
Terborgh & Weske (1969)	MF, Sec.	ND	43.4 (55)	ND	35.2 (132)	0.002
Estrada & Coates-Estrada (1997)	MF, Cl.	43.7 (38)	ND	ND	36.4 (164)	0.003
Johns (1991)	MF, Cl.	41.3 (76)	ND	ND	31.6 (131)	< 0.001

minimizing the effects of phylogeny on the analysis. There were 42 pairs of congeners for which one species was a mature forest unique and the other a secondary forest unique, and 20 pairs of congeners for which one species was a cleared area unique and one species a mature forest unique. For each mature forest/ secondary forest contrast, we measured the difference between the range size of the secondary forest unique and mature forest unique. Range sizes of secondary forest uniques were arbitrarily subtracted from those of mature forest uniques, instead of vice versa. The same procedure was repeated for the cleared area/mature forest contrasts. The null hypothesis is that mean difference between the range sizes of secondary forest uniques and mature forest uniques, or cleared area uniques and mature forest uniques, will be zero and that there will be the same number of positive and negative results. We used the nonparametric Wilcoxon signed rank test to test for significant departure from the null.

RESULTS

The six data sets combined included 631 species of birds, not including 12 species identified only to genus. Latitudinal range

data were available for all species. Sampling efforts varied almost two orders of magnitude among studies when measured as number of individuals captured or observed (Table 2).

Differences among bird assemblages

Latitudinal range size was lowest in cleared areas and increased with forest age. When all species were considered, latitudinal range size of bird assemblages was greater in mature forests than in secondary forest in the Andrade and Rubiotorgler (1994), Hutto (1989) and Terborgh and Weske (1969) data sets. Latitudinal range size was greater in cleared areas than in mature forests in the studies of Estrada and Coates-Estrada (1997) and Johns (1991) data sets. Latitudinal range size did not differ significantly overall among successional stages in the Blake and Loiselle (2001) data set, although the pairwise comparison between young secondary and mature forests was significant ($P = 0.04$; Table 3; Fig. 1).

Average regional range size did not vary consistently among successional stages. When regional ranges were compared among successional stages, comparisons were significant only in Terborgh and Weske (1969; $P = 0.032$) and Estrada and Coates-Estrada (1997; $P = 0.029$). All other comparisons were non-significant
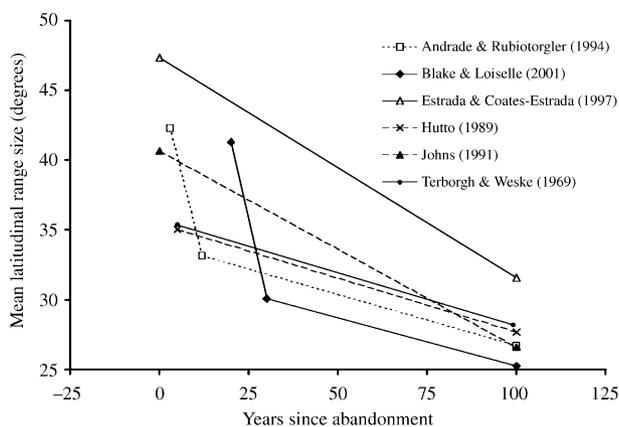
Figure 1 Mean latitudinal range sizes of all bird species in cleared areas, young secondary, old secondary and mature forests in each study by years since abandonment. Mature forests are labelled as 100 years old, though some are older. Some points were slightly jittered to aid in presentation. Names in the legend correspond to the studies from which each data set came. Lines indicate only which pairs of points are from the same site, not necessarily a slope.

($P > 0.05$). Where the frequency of ranges extending beyond the Neotropics varied among successional stages, the trend was always for a higher proportion of ranges extending outside the Neotropics in earlier successional stages. For those sites north of the equator, latitudinal ranges were more likely to extend north of the tropics in the studies of Estrada and Coates-Estrada (1991, $P = 0.014$) and Blake and Loiselle (2001; $P = 0.024$), but not in that of Hutto (1989; $P = 0.9$). For those sites south of the equator, latitudinal ranges were more likely to extend south of the tropics in Terborgh and Weske (1969; $P = 0.008$) but not in Andrade and Rubiotorgler (1994; $P = 0.56$) or Johns (1991; 0.6). In no study north of the equator did the proportion of species with ranges beyond the southern boundary of the Neotropics vary among successional stage ($P > 0.05$). In no study south of the equator did the proportion of species with ranges beyond the northern boundary of the Neotropics vary among successional stages ($P > 0.05$).

Congeneric comparison with pooled data

There were 42 independent contrasts between congeneric mature forest unique/secondary forest unique pairs. There were significantly more cases where secondary forest uniques had a larger range than the mature forest uniques than vice versa ($P = 0.003$, Wilcoxon signed rank test). There were 20 possible comparisons among cleared areas and mature forests. There were more cases where cleared area uniques had larger ranges than their mature forest unique congeners, however, the difference was non-significant (12, 6, $P = 0.085$).

DISCUSSION

Most studies of geographical range size have focused on the relatively large-scale patterns among continents or on elevational

gradients (Colwell & Hurtt, 1994; Blackburn & Gaston, 1996; Gaston *et al.*, 1998; Colwell & Lees, 2000; Koleff & Gaston, 2001; Colwell *et al.*, 2004). While such large-scale patterns in range size are certainly interesting, they are just one part of the story. Relatively few studies have examined range size as an attribute of species in local communities within elevational or latitudinal bands (Thomas, 1991; Fjeldså, 1999; Gillespie, 2002; Kessler, 2002). Disturbance appears to be one of several important factors related to the range size distribution of bird assemblages at a local scale (Kessler, 2002).

Our study demonstrates that in a variety of Neotropical regions, assemblages of birds found in secondary forests and cleared areas have larger mean latitudinal ranges than those in mature forests. When pairs of congeneric bird species differing in successional preference were compared, a similar pattern emerged, in which species that preferred earlier successional stages had larger ranges. The differences we observed in range size distribution along chronosequences appear to be due primarily to differences in the latitudinal ranges of species restricted to early and late successional stages. When secondary forests regenerate on abandoned agricultural lands, opportunistic species with relatively larger ranges are slowly replaced by forest bird species, which on average have smaller ranges. As secondary forests age and the percentage of mature forest species increases, the mean size of the latitudinal ranges of bird species in secondary forest continues to decline to mature forest levels. The fact that the study with the oldest secondary forest (20–30 years; Blake & Loiselle, 2001) was the only one for which no significant difference in mean range size (albeit a trend) was found when compared with mature forest supports our suggestion that the mean range size of assemblages in old secondary forests ultimately resembles that of mature forests.

We suspect that our results are likely to reflect a general pattern of increasing range size in more disturbed habitats. While we focused on latitudinal range, it seems likely that the same patterns in range size will be found when two-dimensional ranges are considered. The only circumstance in which this would not be the case would be if, in addition to latitudinal range, the shape of ranges also varies consistently with the successional preference of species. One potential bias in our analysis is that few of the individual studies we used in our analyses were likely to have sampled all bird species found in each successional stage. Species may have been missed, particularly in the mature forests which tended to have the most species. Missed species are most likely to have been small-ranged and rare, which would suggest that actual mean range sizes in mature forests may have been even smaller than we observed.

Several authors have highlighted the possibility that mature forest specialists may be especially at risk of extinction, because they are both habitat-restricted and have small range sizes. Goerk *et al.* (1997), for example, found that in the Atlantic rain forest in Brazil, bird species that are sensitive to disturbance have smaller ranges on average than do wider spread species. Conversely, Marsden (1998) found that bird species that were sensitive to logging in the forests of Seram, Indonesia, had no more restricted ranges than other bird species. Our results strongly support the

hypothesis that mature forest specialists tend to have smaller latitudinal ranges and highlight the importance of the conservation of mature forests for those species. While secondary forests may conserve many species (Dunn, 2004a), there is a subset of species that is missing in secondary forests. That subset of species is of particular concern, both because they are absent from secondary forests and because they have small ranges.

At the opposite successional extreme, little work has examined the range sizes of disturbance specialists or secondary forest specialists. Wilson (1961) in his seminal papers on the taxon cycle hypothesized that species in 'marginal' habitats have large rapidly expanding ranges. While other aspects of the taxon cycle have received substantial attention since Wilson's original paper (Ricklefs & Bermingham, 2002), the range size predictions have not. Studies that have compared range size among successional stages or disturbance levels have found that species in disturbed habitats, whether they be Bolivian bromeliads (Kessler, 2002), Costa Rican butterflies (Thomas, 1991), Nicaraguan birds (Gillespie, 2002) or Tanzanian bird species (Fjeldså, 1999), have larger ranges than those in mature forests.

When we compared the regional range sizes of the bird species in our data sets by excluding those portions of the ranges that extend beyond the Neotropics, we found no consistent relationship between successional stage and range size. The larger ranges of species in early successional habitats appear to be the result of the tendency of the species in those habitats to extend their ranges outside of the Neotropics. Assemblages in early successional habitats were in fact more likely to have species with ranges that extended outside the Neotropics. Why might species in early successional habitats be more likely to have ranges that extend outside the Neotropics? One possibility is that early successional habitat has a greater latitudinal extent than does Neotropical forest. Duncan *et al.* found support for a similar hypothesis in New Zealand, where they found that disturbed habitat was more extensive than was undisturbed habitat, and hence disturbance specialists had a greater potential area into which they can expand (Duncan *et al.*, 1999). Alternatively, species found in early successional habitats may be more likely to have traits that predispose them to reproducing and expanding their ranges across a greater range of environmental conditions.

Many of the species in disturbed habitats are *r*-selected species that reproduce quickly, disperse well, and are able to persist in relatively patchy habitats, and in doing so, spread their ranges. Studies examining the evolution of disturbance specialization and life history traits associated with disturbance specialization could help us greatly understand the patterns of range sizes along successional gradients and the evolution of habitat specialization more generally.

The difference in mean latitudinal range sizes of birds and other assemblages during succession may have direct, but poorly appreciated consequences for patterns of diversity at larger scales. The regional range size distribution of species in a region is one of just two factors influencing species turnover, the other being habitat heterogeneity (e.g. Arita & Rodriguez, 2002). Species turnover couples point and regional diversity. Within a region, differences in the mean regional range sizes of assemblages are analogous to differences in beta diversity. Where mean range sizes are lower, beta diversity is higher or vice versa. Thus for two assemblages that are similar in alpha diversity, the assemblage with a smaller mean regional range size will have a greater beta diversity, and hence regional diversity (e.g. Arita & Rodriguez, 2002). We did not find consistent differences in the regional range size of assemblages among successional stages, suggesting that within the Neotropics no clear differences in species turnover are expected among successional stages. However, we did find clear differences in the latitudinal range sizes of assemblages among successional stages. This suggests that at continental scales, early successional habitats may host assemblages with lower species turnover. As one travels north or south beyond the extent of the Neotropics and samples habitats in different successional stages, the likelihood of encountering bird species also found in mature tropical forests is lower than that of finding bird species also found in early successional tropical habitats.

Because bird species from early successional stages are more likely to extend outside of the Neotropics than species from mature forests, they are more likely to be conserved by conservation programs directed at other biomes. Many small-ranged mature forest species, on the other hand, are likely to be missed by conservation programs targeted at anything other than mature tropical forest. Put another way, while conserving early and mid-successional habitats may often conserve as many species locally as conserving mature forest (e.g. Dunn, 2004a), many of those species in early successional habitats have the potential to be conserved in other regions, whereas the same is not true of mature forests.

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