Predicting declines in avian species richness under nonrandom patterns of habitat loss in a Neotropical landscape

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Abstract. One of the key concerns in conservation is to document and predict the effects of habitat loss on species richness. To do this, the species–area relationship (SAR) is frequently used. That relationship assumes random patterns of habitat loss and species distributions. In nature, however, species distribution patterns are usually nonrandom, influenced by biotic and abiotic factors. Likewise, socioeconomic and environmental factors influence habitat loss and are not randomly distributed across landscapes. We used a recently developed SAR model that accounts for nonrandomness to predict rates of bird species loss in fragmented forests of the Panama Canal region, an area that was historically covered in forest but now has 53% forest cover. Predicted species loss was higher than that predicted by the standard SAR. Furthermore, a species loss threshold was evident when remaining forest cover declined by 25%. This level of forest cover corresponds to 40% of the historical forest cover, and our model predicts rapid species loss past that threshold. This study illustrates the importance of considering patterns of species distributions and realistic habitat loss scenarios to develop better estimates of losses in species richness. Forecasts of tropical biodiversity loss generated from simple species–area relationships may underestimate actual losses because nonrandom patterns of species distributions and habitat loss are probably not unique to the Panama Canal region.

Key words: bird species richness: fragmentation; habitat degradation; habitat loss scenarios; Neotropical rain forests; nonrandom patterns; Panama Canal corridor; species–area relationship; species loss threshold; tropical biodiversity.

INTRODUCTION

A central goal for applied ecology is to predict future changes in distributions of species, and therefore richness, as humans modify landscapes. The species–area relationship (SAR) has often been used to predict changes in richness as habitats change in size. The SAR allows predictions of how habitat loss is expected to erode biodiversity (Pimm and Askins 1995). Yet, simple application of the SAR has some key shortcomings (Lomolino 2001, Seabloom et al. 2002). It assumes that habitat loss and species distribution patterns are randomly distributed (Ewers and Didham 2005). It also does not allow opportunities to detect possible thresholds in species loss such as those that may be caused when habitat fragmentation occurs (Fahrig 2003, Lindenmayer et al. 2008). Fragmentation effects may be especially important in some environments, such as tropical forests, where species are often sensitive to habitat degradation (Laurance and Bierregaard 1997, Laurance et al. 2002b, Gaston et al. 2003, Stratford and Robinson 2005). In this study, we predict declines in richness of Neotropical bird species following habitat

degradation by using a newly developed SAR model that incorporates nonrandom spatial patterns of habitat loss and of species' geographic distributions.

The SAR, in which species number increases as a function of habitat area raised to a fixed exponent, z (≈ 0.25), is one of ecology's few general principles (Schoener 1976, Lomolino 2001):

$$S = cA^z \qquad (1)$$

where S represents species richness, A is area of habitat, c is the initial trajectory of the function, and z is a measure of the rate of change in the slope with increasing area (Arrhenius 1921, Rosenzweig 1995, He and Legendre 1996).The SAR constitutes one of the cornerstones of ecology and conservation (Rosenzweig 1995, Desmet and Cowling 2004, Ferrier et al. 2004). It forms the basis of important ecological and biogeographical theories (e.g., MacArthur and Wilson 1967, Rosenzweig 1995). As such, the species–area relationship has informed strategies for conservation as well. It has been used in designing nature reserves (Diamond 1975, Wilson and Willis 1975) and recently, in understanding the consequences of habitat loss for biodiversity (McDonald and Brown 1992, McKinney 1998). More importantly, the SAR may be used to make predictions of future losses of biodiversity as a function of habitat area reductions and of expected rates of

species loss after habitat fragmentation (Pimm and Askins 1995, Pimm et al. 1995, Brooks et al. 1997, 1999, 2002; for a review, see Lomolino 2001).

However, the predictive strength of SAR has been questioned recently (Lomolino 2001). One problem comes from the fact that SAR considers species richness, species loss, and habitat loss to be randomly distributed throughout the landscape (Ney-Nifle and Mangle 2000, Ewers and Didham 2005). Obviously, patterns of habitat loss are not random, as certain habitats are more likely to be converted than others, because of biophysical, socioeconomic, or other factors (Laurance et al. 2002a, Lambin et al. 2003). Neither are species richness and distribution random, because they reflect environmental and historical factors (Fattorini 2007). In response to the shortcomings of the standard SAR, a new SAR model was proposed by Seabloom et al. (2002). It addresses these issues by incorporating spatial variation explicitly to make more realistic predictions. Seabloom et al. (2002) showed that simple predictions ignoring nonrandom factors might underestimate species loss when species or habitat conversions are not distributed randomly. Their modified-SAR model more accurately and more realistically calculates the species loss rates following habitat conversion, via a series of habitat loss scenarios derived from species distribution and habitat loss patterns. Furthermore, unlike the traditional SAR approach, the model of Seabloom et al. (2002) might provide a potential tool to evaluate the presence of thresholds at which species loss is precipitated, a possibility often invoked in theoretical studies (e.g., Andrén et al. 1997).

Lomolino (2001) raised further concerns about simple applications of SAR, namely the manipulations of the power function itself. Often, the values of the constant and exponent in the SAR equation have been arbitrarily set, not estimated quantitatively. The exponent z is generally set to 0.25, even though it may vary according to the site, latitude, and area (Preston 1962, Rosenzweig 1995, Lomolino 2001, Drakare et al. 2006). Also, the constant c, by which habitat area is multiplied, is often not considered, even though it influences the expected rate of species loss with reduction in area (Gould 1979, Rosenzweig 1995, Lomolino 2001). Therefore, there should be more consideration of the influence of c and z parameters in attempts to predict species loss, either with the classic SAR or the SAR modified by Seabloom et al. (2002).

The method of Seabloom et al. (2002) has not yet been used in species-rich environments such as the tropics, where habitat loss and fragmentation are known to severely affect species richness (e.g., Pimm et al. 2006). Wright and Muller-Landau (2006) used the standard SAR to predict tropical deforestation rates and consequences for biodiversity. Their results were criticized (Brook et al. 2006, Laurance 2007) because not all known socioeconomic effects were included, habitat loss was considered to be random, and the influence of

nonrandom species distribution patterns, especially occurrence of endemics, was not included sufficiently. Nevertheless, the ensuing debate about their results (Laurance [2007] provides details on the controversy; see also Gardner et al. 2007, Sloan 2007) indicates great interest in the topic.

We used the SAR model of Seabloom et al. (2002), including recently described distribution patterns of forest-dwelling bird species and habitat loss scenarios derived from biophysical and socioeconomic variables (Rompré et al. 2007, 2008), to predict local bird species loss near the Panama Canal. Additionally, we compared different realistic habitat loss scenarios, among themselves and with the SAR as a null hypothesis. We also tested for the existence of a threshold in species loss following deforestation. Like most species-rich tropical landscapes, the region experiences high rates of species extirpation as forest is being converted to other land uses (Condit et al. 2001, Ibañez et al. 2002, Robinson et al. 2004). Several environmental factors influence bird species distribution patterns within the fragments still existing in Panama Canal region (Robinson et al. 2004, Rompré et al. 2007), showing nonrandom patterns in distribution of species richness. Similarly, environmental and socioeconomic factors strongly influence patterns of habitat loss in the Panama Canal region (Condit et al. 2004, Rompré et al. 2008). In this study, we used the term extirpation to express local or regional extinction or species loss from the study region, as opposed to global extinction.

METHODS

Study area

The Panama Canal region extends 65 km north from the Pacific Ocean to the Caribbean Sea and 10–30 km east and west of the Canal (Fig. 1). The continental divide, which reaches a maximum altitude in the study region of 300 m, separates Pacific from Caribbean slopes. Annual rainfall declines rapidly toward the Pacific slope, especially south of the continental divide. Seasonally dry forests on the Pacific slope receive mean annual precipitation as low as 1500 mm/yr, whereas wet evergreen lowland and pre-montane forests on the Caribbean slope experience >4000 mm/yr (Rand and Rand 1982, Windsor et al. 1990, Pyke et al. 2001). Higher altitudes (≥500 m) occur just outside the western and, especially, eastern peripheries of the Canal region in foothills.

Most forests in the study area are considered to be mature secondary (80–125 years old), although a few patches are >500 years old (Denslow and Guzman 2000, ANAM 2003, DeWalt et al. 2003). All forests are fragmented, with patch sizes varying from <15 ha to 15 020 ha. Because of deforestation, the entire region is now isolated from the forest corridor that used to exist between Central American and South American forests. Human impact is important in this region, especially because two major cities (Panama City on the Pacific
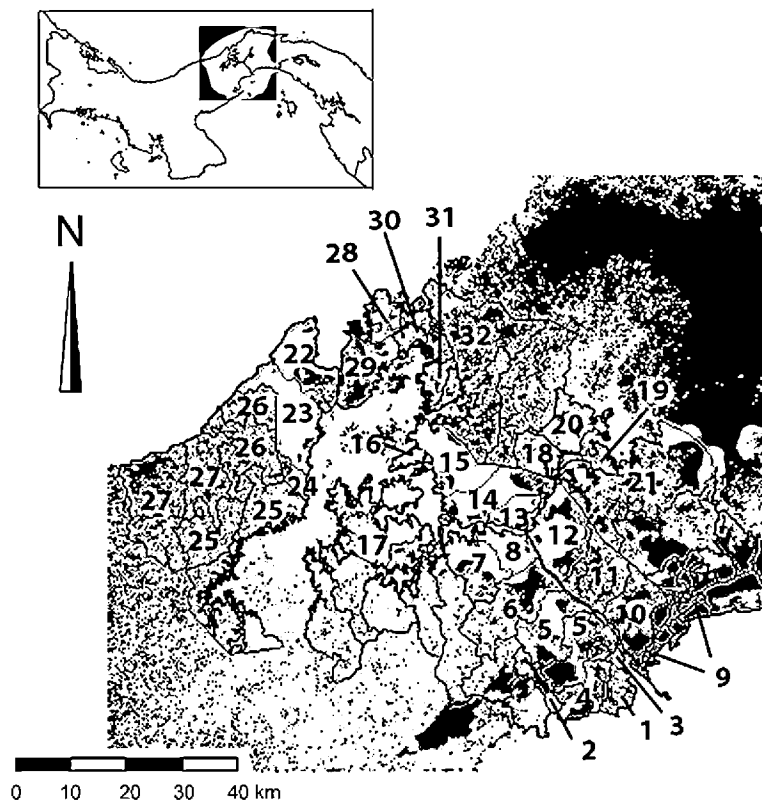
Fig. 1. Subregions in the Panama Canal corridor. Black lines and numbers indicate the subregions used for the study. Dark gray represents the forests; lighter shades of gray represent the shrubs and pastures, and black represents the urban areas. Water from the canal is indicated in white, as was the case for the sea. This digitized map from 1999 was provided by the ACP (Panama Canal Authority).

coast and Colon on the Caribbean coast) are present and are home to most of the region's 1.3 million inhabitants (Anonymous 2003). Humans first occupied the region 11 000 years ago (Piperno et al. 1990). Potential vegetation in the region is forest, so prior to human settlement the entire region was forested. Today, 53% of the original pre-Colombian forests remain. There is a high percentage of forest cover close to the major cities; almost half of the current forest cover of the area is contained in national parks and other protected areas (ANAM 2004, Robinson et al. 2004). The remainder of the forest is not protected, and mostly consists of a mosaic of fragments interspersed with regenerating second growth (matorales), pastures (portreros), and urban areas (ANAM 2003). Loss of forest cover relative to its presettlement extent varies across the region. In the area concerned here (Fig. 1), forest loss varied from less than 10% to 100% according to the different subregions, with most land cover converted to urban and/or agricultural uses.

Subregion selection

To use a species–area relationship (SAR) model that incorporates nonrandom bird species' distributions and nonrandom habitat loss scenarios, we divided the study area into 32 physiographic subregions. Each subregion included forest fragments as well as other types of land cover surrounding the fragments. Subregions were first defined based on existing political boundaries of counties (corregimientos). Some counties were then divided by us to create additional subregions when underlying geology or topography was highly variable. For additional details and descriptions of subregions, see Rompré et al. (2007). Subregion characteristics are given in Appendix A.

Species richness distribution patterns

The canal region of Panama harbors nearly 500 terrestrial bird species, and up to 194 of them are considered forest specialists (Angehr 2003, 2006, Robinson et al. 2004). We gathered more than 50 000 bird observations from 55 different sites included in the 32 subregions (Rompré et al. 2007) and compared species' distributions with biophysical characteristics of each subregion and modeled bird distribution patterns. Generally, forest bird species richness was not distributed randomly across the study area. Instead, richness increased strongly from the dry Pacific coast to the wet Caribbean coast (Robinson et al. 2004). According to structural equation modeling, bird species richness is

TABLE 1. Habitat loss scenarios used in this study to calculate species extinction rates in the Panama Canal region.

Scenario	Description
Precipitation	As precipitation increases, habitat loss decreases.
Topography	As topography complexity increases, habitat loss decreases.
Distance to main city	Habitat loss increases the closer a subregion is to a city.
Distance to main highway	Habitat loss increases the closer a subregion is to a main highway.
Urban population size	Habitat loss increases with human urban population size.
Habitat loss, urban	Habitat loss increases with area converted to urban land use.
Rural population density	Habitat loss increases with human rural population density.
Habitat loss, agriculture	Habitat loss increases with area converted to agriculture.

Note: The scenarios are not mutually exclusive. See *Methods* for details.

influenced mostly by precipitation (indirectly through plant community richness), and by topographic complexity, forest age, area, and configuration (Rompré et al. 2007). The latter metric, a continuum between few large and several small forest fragments, has a stronger negative effect on diversity than habitat loss alone. Subregions with high richness also harbor higher proportions of forest-specialist species. In other words, subregions with more precipitation, more complex topography, and mature forests (mostly on the Atlantic side of the Canal region) contain not only more forest bird species, but also more "sensitive" ones. Drier subregions with flatter terrain and younger forests (mostly on the Pacific side) contain few forest species, most of which are common and widely distributed. Finally, larger continuous forest tracts contain the highest proportion of forest bird species, and the highest proportion of sensitive species. In Rompré et al. (2007), the authors calculated sensitivity to a habitat change score for all forest bird species in the study area. The score was calculated according to their life-history characteristics and conservation status. Species deemed most sensitive and present in five subregions or fewer are listed in Appendix B.

Causes of habitat loss in the region

To provide our models with realistic habitat loss scenarios, we examined potential causes of habitat loss in the Canal region. Each of the 32 subregions was characterized by biophysical (e.g., rainfall, topography) and socioeconomic variables (e.g., human population density, level of poverty), all of which may potentially help in understanding patterns and causes of habitat loss. Based on canonical correlation analyses (CCA), we identified the strongest associations between those characteristics and the likelihood of forested habitat conversion to agriculture (including pastures) and urbanization (for full details, see Rompré et al. 2008). Annual rainfall and topography were negatively associated with habitat loss, whereas human population density (rural and urban) and the number of roads (density per subregion), proximity to a main highway or main city, and population wealth were highly associated with loss of forests (Rompré 2007, Rompré et al. 2008). From these results, we established eight habitat loss

scenarios that are likely to occur and to cause eventual forested habitat loss to urban areas or agriculture. Table 1 describes the eight scenarios used in our species loss predictions following habitat conversion. For each scenario, the 32 subregions are ordered in decreasing order of susceptibility to habitat loss, thus yielding eight different sequences of subregions for species–area models.

Species–area model used for the study

The method used is fully explained by Seabloom et al. (2002) and summarized here. It builds from the relationship between species richness and area (SAR, Eq. 1), which presents species richness in a habitat patch (S) as a nonlinear function of its area (A) (Rosenzweig 1995, Ovadia 2003). The method of Seabloom et al. (2002) allows the incorporation of habitat loss scenarios. For example, in our study, each of the 32 subregions was classified according to biophysical or socioeconomic variables of interest, allowing us to compare scenarios with habitat loss proceeding in a specific sequence of subregions (from the first to the nth region). To illustrate this, ranking the 32 subregions by mean precipitation results in a different sequence of subregions than ranking them by topography (see Table 1). Thus, for any given region j, the proportion of habitat remaining, a, can be calculated:

$$a(j,k) = 1 - \frac{1}{1 + \left(\frac{j}{k}\right)^b}. \quad (2)$$

A relative index, k runs from no habitat loss (or current state; $k = 0$) until all habitat is lost (e.g., $k = 100$). The maximum value of k is arbitrary and does not affect the final results. The exponent b is described by Seabloom et al. (2002) as the shape of the loss function. It allows calibration of Eq. 2 depending on the rate of habitat loss among regions. For example, if $b \in [1, 2]$, habitat loss is concurrent in all regions and nearly randomly distributed. However, if $b > 2.0$, habitat loss rates are highly variable among regions and may ultimately lead to sequential loss of habitat, region after region (where one region may lose all its habitat while another remain intact). We tested several b values (range 2–200) to determine a realistic subset of values for the

regions under study. Merging Eqs. 1 and 2 yields

$$S_{jk} = c(j)a(j,k)^z. \quad (3)$$

Here the value $c(j)$ represents the number of species currently in the jth region before any habitat loss ($k=0$). Finally, the proportion of habitat remaining across the whole canal corridor (Ak), for each k, for each habitat loss scenario analyzed in this study, will be current area summed across all regions divided by the total area in the system when $k = 0$:

$$A_k = \frac{\sum_{j=1}^{N} a(j,k)}{\sum_{j=1}^{N} a(j,0)}. \quad (4)$$

The proportion of species remaining across all regions for any given k (Sk) is

$$S_k = \frac{\sum_{j=1}^{N} c(j)a(j,k)^z}{\sum_{j=1}^{N} c(j)}. \quad (5)$$

In order to validate the model, we compared the results obtained from the eight habitat loss scenarios described in Table 1 with the results of 100 simulations of the model. For each simulation, we randomly selected one of the existing 32 subregions as a starting point for a scenario. From this point, we ordered the other 31 subregions from the closest to the farthest, based on distances to centroids. This means that habitat loss would start from the randomly selected subregion until it reaches the most distant subregion. For example, if subregion 28 is randomly selected, then the second subregion would be the closest (subregion 30), the third (subregion 29) would be the next closest, and so on until reaching subregion 1, which is the farthest. We repeated the simulations for two values of habitat loss function ($b = 2$ and 16), producing 100 simulations each. All simulations were done using $z = 0.29$ (a value selection that we will justify later).

Detection of a threshold

To examine the existence of a species loss threshold resulting from our predictions, we used piecewise regressions, which include straight-line segments joined by breakpoints whose locations are estimated by a least-squares method (Toms and Lesperance 2003, Légaré et al. 2004, Robbins et al. 2006). Using the piecewise regression models described by Robbins et al. (2006), we were able to estimate the exact value of area (or proportion of habitat remaining) for which the level of forest bird species richness experienced a rapid decline. The following equations were used to fit the data, including the two breakpoints in the curves:

$$y = b_1 + b_2 x \qquad \text{if } x < \tau_1 \quad (6)$$

$$y = (b_1 + b_2\tau_1) + b_3(x - \tau_1) \qquad \text{if } \tau_1 < x < \tau_2 \quad (7)$$

$$y = (b_1 + b_2\tau_1) + b_3(\tau_2 - \tau_1) + b_4(x - \tau_2) \qquad \text{if } x > \tau_2 \quad (8)$$

where y is the number of forest bird species at x total forested area remaining (km^2), τ_1 represents the first (lower) breakpoint, τ_2 the second (higher) breakpoint, and b_1 to b_4 represent the slopes of the different line segments (Robbins et al. 2006). The goal of using these equations was to confirm and estimate the location of the two breakpoints. Therefore, to run our regressions, we used the linear segments directly before and after the two breakpoints (x values from ~98 to 919 km^2). The very initial section of each curve (from the intercept to 98 km^2) was not used because it varied little among the different scenarios and, by excluding that segment, we avoided the use of additional terms in the equation, unnecessary to estimation of the breakpoint locations.

We used SAS PROC NLIN procedure (SAS institute 2004) to perform the regressions and compare all habitat loss scenarios. Finally, we ran the piecewise regressions according to the aforementioned section of the curves and compared the explained variance (R^2) with log-fitting curves ($y = \log x$; for the same section of the curves, but excluding breakpoints). Because the piecewise regressions had more parameters than the log-fitting models (increasing the value of R^2), we used the adjusted R^2, which corrects for the added parameters alone and allows direct comparison with lower parameter models such as the log-fitting curves (Robbins et al. 2006). Even though the differences between the R^2 and adjusted R^2 values were not statistically meaningful, we preferred using the adjusted measures as a more conservative approach.

Estimation of parameters z and c in the model

Most studies using species–area relationship for predictions of species loss employ an arbitrary value of z, which is often 0.25 or near (average 0.27 for 794 SAR; Drakare et al. 2006). This value appears to apply to a wide selection of taxa and sites, mainland as well as islands (Rosenzweig 1995, May and Stumpf 2000). Nevertheless, because we gathered data on bird species richness all over the study region and measured all surface area of forest habitat, we were able to obtain estimates of c and z that best fit our data, using PROC NLIN in SAS (SAS Institute 2004). Bird species richness differed in the different subregions of the Panama Canal corridor, especially in forests on the wetter Atlantic side of the continental divide vs. those on the drier Pacific side. Therefore, we estimated z for groups of subregions to evaluate the influence of variation in z on model predictions.

RESULTS

Species loss patterns were highly dependent on the habitat loss function (uniform vs. heterogeneous) and, to a
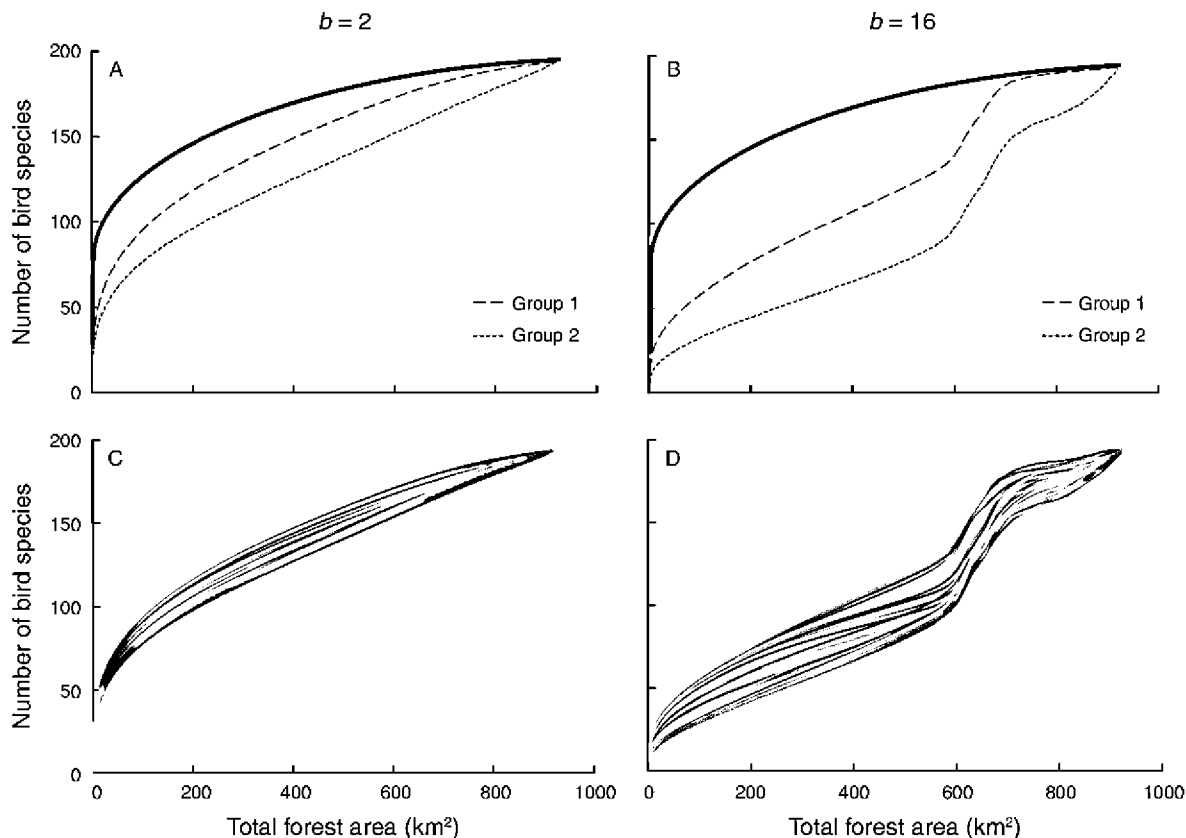
FIG. 2.   Effects of nonrandom forested habitat loss on predicted species extinction rates of forest birds in the canal corridor, central Panama, with different values of b, the shape of the habitat loss function: (A) predicted richness when habitat loss scenarios are similar among regions ($b = 2$); (B) predicted richness when habitat loss rates are different among regions ($b = 16$); (C) predicted richness using $b = 2$ based on 100 random simulations of the model; (D) predicted richness using $b = 16$ based on 100 random simulations of the model. In (A) and (B), the heavy solid black line shows the species–area relationship under random habitat loss ($S = cA^{z}$). We show the predicted richness as a function of area under the habitat loss scenarios presented in Table 1. Groups 1 and 2 represent gradual and accelerated species loss, respectively, following habitat loss scenarios with similar responses (see Table 2 for details). The total forest cover presently in the study area is ~920 km^2, representing 53% of the original historical cover (see *Methods*). The second (higher) threshold is located at around the 700 km^2 mark, representing ~40% of the historical forest cover.

lesser extent, on habitat loss scenarios (Fig. 2). For each habitat loss function, we divided the scenarios into two groups, based on the relative performance of gradual (log) vs. piecewise regression models (Table 2) of species vs. area. Group 1 included precipitation, topography, distance to main city, and distance to main highway, whereas Group 2 included human population factors (urban and rural population) and land use (urban and rural). Group 2 produced a substantially accelerated rate of species loss compared to Group 1 (Fig. 2). As predicted, the shape of the habitat loss function (b) varied among models. When b = 2 (Fig. 2A), the predicted proportion of habitat lost was relatively even across the landscape. In contrast, when b = 16 (Fig. 2B), the proportion of habitat lost occurred in steps, reflecting the documented scenario that most forested habitat may be lost in a given subregion before habitat loss starts in another. Fig. 2 also shows the results of the predicted species richness based on the 100 simulations; this was done using both $b = 2$ and $b = 16$. All simulations confirmed the model: they show the same

patterns within a similar range of values. Fig. 3 illustrates the combined effects of b and k parameters (see Eq. 2) on the proportion of habitat remaining for all subregions. Results were robust to variation of b well above 16 (Fig. 4).

All scenarios under nonrandom habitat loss showed two clear breakpoints. First, bird species richness decreased substantially around 700 km^2 or ~25% forest loss from the current situation. Another breakpoint was present at around 580 km^2 or ~36% habitat loss just before the rate of species loss slowed again. With habitat loss assumed to be regionally variable ($b = 16$), the explanatory power of piecewise regression models was consistently high, irrespective of habitat loss scenario (Table 2). Log-fitting curves (which did not include any breakpoints) generally yielded substantially lower R^2 than piecewise regressions, confirming the strength of the latter method (Table 2). Table 2 presents the adjusted R^2 for the piecewise regressions, which allows direct comparison of models with lower numbers of

TABLE 2. Species loss thresholds based on piecewise regressions between forest bird species richness and forest area lost in the Panama Canal region.

	Higher breakpoint		Lower breakpoint		Regression R^2	
Scenario	Area lost (km²)	Forest loss (%)	Area lost (km²)	Forest loss (%)	Piecewise model†	Log model
Group 1: gradual species loss						
Precipitation	696.8 ± 2.9	76%	585.9 ± 3.4	64%	0.98	0.88
Topography	682.3 ± 4.7	74%	578.1 ± 5.8	63%	0.98	0.89
Distance from main city	692.7 ± 2.7	75%	584.2 ± 3.0	64%	0.98	0.88
Distance from main highway	701.5 ± 4.8	76%	597.8 ± 4.9	65%	0.98	0.90
Group 2: accelerated species loss						
Urban population size	705.9 ± 2.5	77%	577.8 ± 1.9	63%	0.98	0.76
Habitat loss, urban	699.0 ± 6.3	76%	577.3 ± 4.1	63%	0.98	0.77
Rural population density	700.2 ± 3.1	76%	579.0 ± 2.1	63%	0.98	0.75
Habitat loss, agriculture	690.5 ± 3.1	75%	579.9 ± 2.3	63%	0.98	0.75

Notes: Breakpoints represent areas of forest lost (mean ± SE) at which the model of Seabloom et al. (2002) predicts precipitous changes in species loss rates. The higher breakpoint marks the start of accelerated species loss when habitat starts to decrease, whereas the lower marks the end of accelerated species loss. Model values for exponents z (rate of change in the slope relating species to increasing area) and b (shape of the habitat loss function) were set at 0.29 and 16, respectively. If $b \in [1, 2]$, habitat loss is concurrent in all regions and nearly randomly distributed; if $b > 2.0$, habitat loss rates are highly variable among regions and may lead to sequential loss of habitat, region after region.

† Adjusted R^2 is shown for piecewise regression models.

parameters such as the log-fitting curves (see *Methods*). Appendix C shows the piecewise regression equation sets for two prediction curves (one each for Groups 1 and 2 of habitat loss scenario). Overall, the regressions indicate that the higher threshold will occur when an average of 25% of the current habitat will be lost, which is also equivalent to a loss of all but 40% of the forests historically present in the Canal study area.
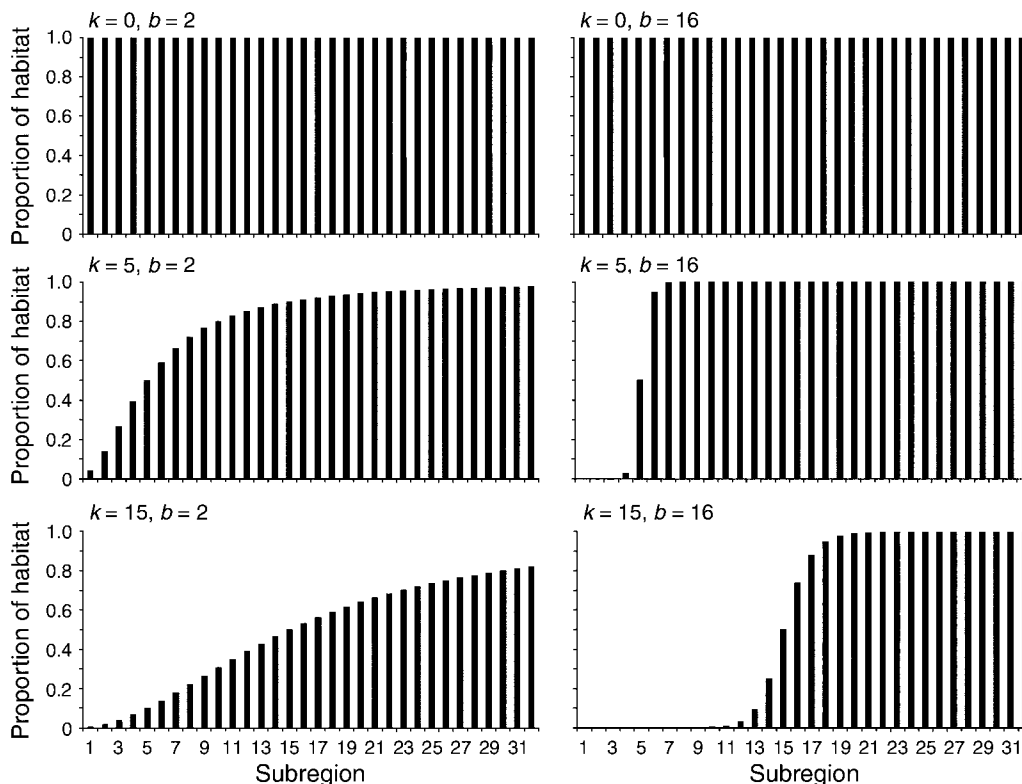

FIG. 3. Proportion of habitat remaining in the Panama Canal area, composed of the 32 subregions. In this example, habitat loss begins at subregion 1, proceeding toward subregion 32. The index k is arbitrary and represents the state of habitat lost; it runs from 0 (no loss has occurred) until all habitat is lost (for example, 100). This value uses arbitrary units and does not affect the final analysis. The diagrams show three values of k (0 = no habitat loss has occurred, 5 = early stage of habitat loss, and 15 = advanced stage of habitat loss), varying according to two different values of loss function ($b = 2$ and $b = 16$). See *Methods* for details.
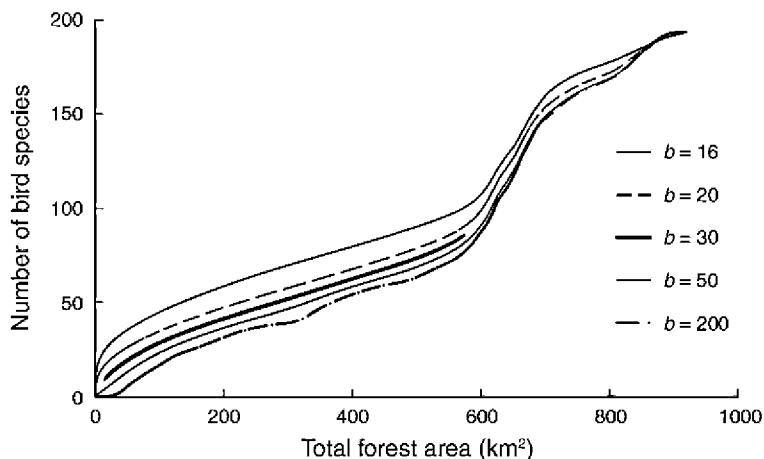
Fig. 4. Forest bird species richness related to forested habitat area according to different values of b (from Eq. 2 in *Methods*). Species richness data represent the value following the habitat loss scenario "habitat loss increasing with area converted to urban"; curves result from the method using a value of $z = 0.29$ (where z is a constant that measures the slope of the line relating species to area that best fit the species richness in our study area).

Based on the 32 subregions of our study, nonlinear regression yielded $z = 0.29$ (SE $= 0.068$). When we divided the 32 subregions into two different groups, Pacific and Atlantic (with a separation near Gamboa, subregion 13 in Fig. 1), we obtained $z = 0.31$ (SE $= 0.11$) and $z = 0.25$ (SE $= 0.08$), respectively (Table 3). If we further divided the 32 subregions into three groups (Pacific, middle, and Atlantic), z was much greater for the Pacific (Table 3). Fig. 5 shows that lower values of z provide steeper slopes; however, z values in the observed range of variation had almost no discernible effect on expected species loss. As with z, the constant c varied substantially among subregions. Notwithstanding the subdivision, forests north of the continental divide up to the Atlantic coast showed less variation in c (between 44 and 49). The subregions on the Pacific side of the continental divide harbor an extremely low c value (Table 3). As with z, c had almost no effect on expected species loss.

DISCUSSION

All of the eight habitat loss scenarios based on the method of Seabloom et al. (2002) contrasted strongly with predictions derived from the standard species–area

relationship. All scenarios suggested patterns of species loss similar to those obtained by Seabloom et al. (2002) for plants in California. However, our results differ in that all our scenarios revealed a strong species loss threshold originating from the combination of two breakpoints in species loss curves. This might be due to the high species richness of forest birds in our study area, and the sensitivity shown by several species to habitat degradation (Stotz et al. 1996, Andrén et al. 1997, Robinson et al. 2000, Radford et al. 2005, Rompré et al. 2007). Forest specialists, which constitute a high proportion of the forest bird community in the study area, may be more prone to extirpation than habitat generalists (Andrén et al. 1997), and thus may contribute to the observed threshold.

The entire region of central Panama was forested before first disturbance by humans some 11 000 years ago (Piperno et al. 1990; see also Robinson et al. 2000). It is noteworthy that the loss of ~25% of forest from the current situation would leave ~40% of forest relative to the total area of land, a value at the high end of predicted fragmentation thresholds calculated for single species or populations in the northern hemisphere (Andrén 1994, Fahrig 1998, 2001, 2003, Flather and

TABLE 3. Estimates for parameters z and c in the species–area relationship according to bird species richness collected in the 32 subregions of the Panama Canal area.

Subregion group	Subregion numbers	z estimate (SE)	c estimate (SE)
All subregions	1–32	0.29 (0.07)	34.5 (8.3)
Pacific	1–12, 19, 21	0.31 (0.11)	26.4 (9.78)
Atlantic	13–18, 20, 22–32	0.25 (0.07)	44.6 (12.3)
South of Continental Divide	1–5, 9–11	0.41 (0.11)	18.8 (6.85)
Continental Divide	6–8, 12–14, 16–21	0.18 (0.11)	49.8 (18.5)
North of Continental Divide	15, 22–32	0.21 (0.12)	49.9 (21.6)

Notes: Values are shown representing the different grouping in the subregions. Subregion numbers appear in Fig. 1. Estimates are z (rate of change in the slope) and c (a constant measuring the number of species per unit area).
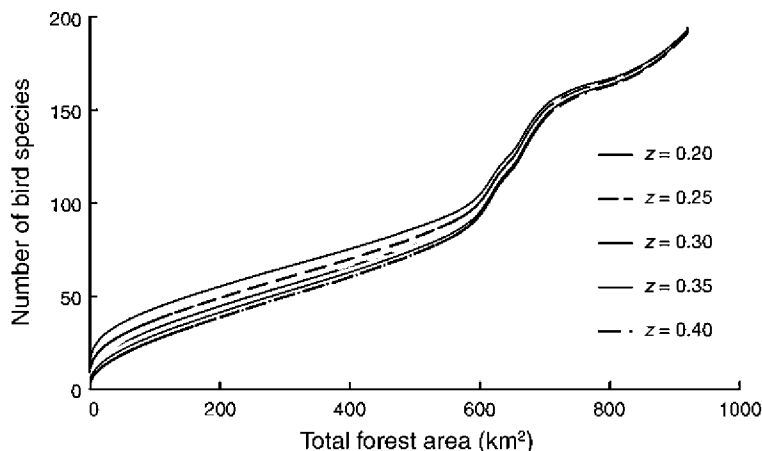
FIG. 5. Forest bird species richness related to forested habitat area according to different values of z (from Eq. 5 in *Methods*). Species richness data represent the value following the habitat loss scenario "habitat loss increasing with area converted to urban"; curves result from the method using a value of $b = 16$ (habitat loss rates are distinct among subregions).

Bevers 2002, Betts et al. 2006, 2007). Consequently, this means that little habitat loss from that currently present may have a strong effect on forest bird communities. Most studies on thresholds are theoretical models examining a rapid decline located across a wide range of habitat loss values (20–80%; Jansson and Angelstam 1999, Parker and Mac Nally 2002, Fahrig 2003, Ewers and Didham 2005) or studies looking at single-species' populations (Betts et al. 2006, 2007), but our study is among the few to describe a threshold obtained for species richness through predictions from empirical data. A recent study by Radford et al. (2005) describes thresholds obtained through empirical data. In their comparison of forest cover and species richness, they were able to calculate the breakpoint for bird species communities in forest remnants in Australia (located close to 10% of remaining forests). Our results, being at 40% of remaining forests, are more alarming. Nevertheless, we obtained from our data, contrary to what was presented by Andrén et al. (1997) and Radford et al. (2005), not one, but two breakpoints in species loss. A possible explanation for our prediction curves with two breakpoints might come from the degree of sensitivity of the species present in our system. Species with high sensitivity to habitat change respond more rapidly to habitat loss, and then the curve relaxes to a slower species loss rate as generalist and more resilient species disappear gradually. As the lower threshold is reached, even generalist forest species begin to decline and disappear. Tropical forests are known to have many specialist bird species, which react strongly and negatively to habitat conversion (Stotz et al. 1996). Even some generalist species may persist well in fragmented landscapes, but decline rapidly if fragments are reduced too much in area or isolated too much, as has been found in the Brazilian forest fragmentation project (Stouffer and Bierregaard 1995).

The significance of model parameters

May and Stumpf (2000) argued that researchers should assure that their sampling effort invested in estimating richness is sufficient before estimating z. We used nonparametric richness estimators for 55 sites included in the 32 subregions and found that our empirical measures of richness fell outside the 95% confidence interval of predicted richness in four of the 32 subregions (for details, see Rompré et al. 2007). Although that constitutes about twice the expected number of values outside the 95% confidence interval, it is sufficiently low to warrant the assumption that underestimation of species richness was minimal (Williams 1964, Gould 1979).

The drier and flatter Pacific subregions hosted very few forest bird species (Rompré et al. 2007), primarily species that are common throughout the study area, and included proportionally fewer rare and sensitive species than more complex, wetter regions (on the Atlantic side). For example, the very small forest fragments on the Atlantic slope included a high number of persistent humid-forest specialists, whereas forest fragments of similar size on the drier Pacific side harbored lower species richness and a tiny fraction of the humid-forest specialists (Robinson et al. 2004; G. Rompré and W. D. Robinson, *unpublished data*). Therefore, the variation in z that we documented might be due partly to this high variation in the proportion of rare species in the communities across subregions (Robinson et al. 2004). In the literature (reviewed by Lomolino 2001), there is little consideration for the variation in c to be significant, because it is considered to be characteristic of a taxonomic group (May and Stumpf 2000). Even though standard errors were relatively high (see Table 3), there remained a difference between Pacific and Atlantic regions in the c value. In fact, our results for the subregions that harbor lower forest bird richness (and proportionally more common species) also generate a

substantially lower value of c. This could be due to the presence of more species on the Atlantic side, but we also need to look at species composition (e.g., sensitive vs. common widespread species). As Gould (1979) reasoned in his study of c, a lower value may indicate more isolated habitat or fragments. We suggest that subregions with richer diversity and a higher proportion of sensitive species, independently of forested habitat area, help to drive c higher, and, consequently, z decreases (providing a steeper slope); subregions with lower diversity and proportionally more common species, again independently of forest area, yield lower c but higher z values. According to Willig and Lyons (2000) and Lomolino (2001), higher values of z are usually accompanied by a corresponding decrease in c values, and vice versa (Rosenzweig 1995). These observations indicate the need for careful evaluation of the two constants in the species–area relationship, even within a fairly small study area in the tropics (Lee and Peres 2006).

An important concern that may be raised in the model developed by Seabloom et al. (2002) is the shape of the loss function (b). Considering that habitat loss rates are similar among subregions ($b = 2$) may mean just as well that habitat loss is completely random, which brings similar results as when using standard SAR (see Fig. 2). In our evaluation of the causes of habitat loss in the same study area (Rompré et al. 2008), we showed that some subregions were more affected by habitat loss than others, by being closer to a main city, a main highway, and with higher urban population size. Therefore, subregions did not have similar habitat loss rates, independently of conversion type, urbanization or agriculture. Even though we used a wide range of values in the preliminary analysis, we found that the results were robust to substantial variation in b (between 16 and 200; Fig. 4). Like Seabloom et al. (2002), we consider that using $b = 16$ closely mimics a spatial aggregation of habitat loss, and that it only affects species loss rates when habitat loss rates are distinct among subregions. Our empirical results show that this is true with forest bird species in central Panama (Robinson et al. 2004, Rompré et al. 2007).

Habitat loss scenarios and species loss threshold

Comparing habitat loss scenarios based on environmental or socioeconomic factors may help us to understand mechanisms by which heterogeneity in habitat loss may produce complex species loss patterns. In this study we investigated eight habitat loss scenarios, not mutually exclusive. All of these scenarios were derived from strong correlations between biophysical and socioeconomic factors (Rompré et al. 2008). For example, precipitation is positively related to richer plant diversity, which is related to degree of resistance (steeper terrain with more impenetrable "jungle") encountered by colonizing humans over history (see

also Suarez 1981, Steininger et al. 2001, Veldkamp and Lambin 2001, Laurance et al. 2002a).

A possible shortcoming of analyzing one scenario at a time is that no one scenario adequately reflects real patterns of habitat loss (Lambin et al. 2003). Indeed, our comparison of scenarios, when habitat loss rates are distinct among regions, resulted in two groups, one with environmental or physical components and the other with components of human population and changes in forest area. The latter group (Group 2) yielded the most precipitous rates of species loss. This is consistent with the argument that socioeconomic factors are vital in understanding habitat patterns of conversion (Brooks et al. 2002, Laurance et al. 2002a, Lambin et al. 2003) and in making predictions of how species richness patterns will change (Seabloom et al. 2002).

Species loss and forest fragmentation

Rompré et al. (2007) provide clues that may help to explain the species loss threshold. The threshold might be caused not only by habitat loss differences among regions, but also by the degree of fragmentation, i.e., the degree to which forested habitats in a subregion are composed of several small fragments instead of a few large ones. According to Flather and Bevers (2002), species persistence varies according to the degree of habitat fragmentation or fragment aggregation (species disappearance is higher if fragments are less aggregated). This brings us back to the influence of b in the model of Seabloom et al. (2002). If habitat loss rates are similar among regions ($b = 2$) and habitat loss is also random, as in standard SAR, there is no local extinction threshold for forest bird species. If habitat loss rates are different among regions (spatially aggregated, $b = 16$), a possible effect of habitat configuration is better represented, providing a stronger effect of spatial aggregation on species loss (see Fig. 2B). Nevertheless, fragmentation may not be the only reason behind the threshold. Low values of b would correspond to "fine-grained" fragmentation throughout the area under study. By contrast, high values of b would correspond to much coarser fragmentation, in which entire regions may be deforested while others would remain intact. The species loss threshold that we found with high values of b may not necessarily indicate a fragmentation effect, but simply the simultaneous, near-complete loss of habitat in key areas, e.g., the Achiote region (#23 in Fig. 1), which harbors almost 80% of the forest bird specialists species of the entire study area. In the latter case, complete extirpation of a rich subregion may provoke a rapid loss in species richness, explaining the threshold.

Because most species in the study area are well known and their sensitivity to habitat change has been documented (Rompré et al. 2007), we can suggest a list of species most likely to go locally extinct first following habitat loss (see Appendix B). We notice that most sensitive and distribution-limited species are present in two main subregions, which represent the two most

diversity-rich subregions of our study area (Achiote region and Soberania National Park; subregions 23–24 and 13–15, respectively; see Fig. 1). Because all forests in the Panama Canal region are already fragments (Robinson et al. 2004), few species unrecorded since the mid-1980s may have represented the ones most sensitive to habitat conversion. Rich tropical forests harbor a very high proportion of rare and sensitive species (Robinson et al. 1990, Terborgh et al. 1990, Thiollay 1994, Robinson et al. 2000, Ferraz et al. 2007), therefore possibly increasing the threshold to a higher level of habitat remaining in the system, relative to temperate regions (Andrén et al. 1997).

Because, as we already noticed, using $z = 0.29$ means that species loss rates for Pacific drier subregions are possibly overestimated, the species loss threshold might also be lower, which means greater persistence of drier-forest bird species below the level of suitable habitat. Rompré et al. (2007) suggested that bird species in drier subregions are more common, with a lower proportion of species sensitive to habitat loss. Similarly, if we evaluate the species loss threshold only for subregions rich in sensitive species, we encounter a threshold at a level higher than 75%. More studies are needed to evaluate on a local level how the value of z influences the species loss threshold. The results may determine the exact location of the breakpoint for different habitat types in the tropics; drier forests could eventually obtain a level of suitable habitat similar to temperate regions, whereas humid, rich forest would obtain a fragmentation threshold at a higher level of available habitat.

One aspect that is not clearly answered by the model concerns the short- vs. long-term levels of species richness predicted by the model. Habitat loss happens at a point in time, but few data on how long it takes for richness to decline are available. This would help to determine when the "regime shift" described by Folke et al. (2004) may actually happen, a critical point still difficult to identify (Lindenmayer et al. 2008). In our study area, the example of Barro Colorado Island (BCI) shows that local extinctions are still happening some 90 years after isolation (Willis 1974, Karr 1982, Robinson 1999). Brooks and Balmford (1996) and Brooks et al. (1997, 1999, 2002) showed mathematically how the standard SAR model can be used to calculate the time lag between deforestation and the relaxation time (within 120 years in tropical forest fragments). Time lags could occur for even more than a century (Tilman et al. 1994, Lomolino 2001, Hanski and Ovaskainen 2002, Helm et al. 2006). Because some species persist long after their habitat amount has been reduced and not all species respond in the same manners following habitat degradation, the SAR may underestimate predicted numbers of species that are actually lost. Hence, there is a need to better understand the relaxation time at a specific period and apply this dynamic to our understanding of species loss in the tropics. Ferraz et al. (2007), in their recent use of patch occupancy models in

the Amazonian fragments, were able to calculate extinctions and colonization a few years after isolation. Further studies are needed to fully understand species loss immediately and long after isolation in tropical systems (Ewers and Didham 2005).

Conclusions

Our application of the modified SAR model shows that a small increment in tropical forest loss may take forest bird richness beyond a threshold of rapid decline. The model confirms the importance of the spatial aggregation of habitat loss, itself dependent on socio-economic forces. Our results further emphasize the sensitivity of biodiversity to alterations in tropical forests and should increase our concerns for conservation. Similar results were obtained by Radford et al. (2005) using standard SAR, although they obtained generally lower species loss thresholds (closer to 10% according to their best model). Our results indicate that species loss thresholds may attain much higher values and emphasize the urgency of establishing priorities for protected areas in our study area. Although superior to the standard SAR, the modified form requires several parameters for each subregion under study, in addition to documentation of species richness and area of habitat. Our analysis of the parameters c and z shows how much variation in species richness and the proportion of rare, sensitive species can affect the parameters' values. Our study also shows the importance of including multiple variables relevant to predictions of species loss patterns if predictions are to be more realistic than those generated by simple SAR models. Only by incorporating several aspects of species distribution patterns, sensitivity analysis, landscape configuration, and local or regional socioeconomic factors, can modified SAR models attain accurate predictive power and, thus, high conservation relevance (Lee and Peres 2006). According to Zhang et al. (2003), we could not only lose species more dramatically, but also may produce irreversible changes in ecological processes if we go beyond the threshold (Lindenmayer et al. 2008, Tabarelli et al. 2008). If appropriate data can be gathered, these models could be applied to much larger areas than the one we studied, and effects of habitat loss could be better quantified, even for areas as large as the Amazon basin. Using detailed habitat loss scenarios, we may even be able to substantially improve our understanding of how habitat degradation will affect biodiversity worldwide.

thank Elena de Lombardo, Maria Leone, Oris Ovecedo, Benjamen Ordoñez (STRI), Charlotte Elton (CEASPA), Sayda de Grimaldo (ARI), Anjel Muela (FPP), Pascual Fiengo, José and Gladys Isturain, and Jeovanna Lowe for making things easier in the field by giving access and helping to coordinate and organize the fieldwork. Eric Seabloom, Marc-André Villard, Mathieu Bouchard, and Louis Bélanger brought helpful comments to the discussion and statistical analysis.

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APPENDIX A

Characteristics for the 32 subregions covering the lowland rain forest of the canal corridor, Panama (*Ecological Archives* A019-065-A1).

APPENDIX B

Extant forest bird species in the Panama Canal region showing strong sensitivity to habitat conversion, and having a very limited distribution among subregions (present in five subregions or less) (*Ecological Archives* A019-065-A2).

APPENDIX C

Example of two of the piecewise regression equation sets obtained from the modified species–area relationship prediction curves (*Ecological Archives* A019-065-A3).