



# Species–fragmented area relationship

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**The species–area relationship (SAR) gives a quantitative description of the increasing number of species in a community with increasing area of habitat. In conservation, SARs have been used to predict the number of extinctions when the area of habitat is reduced. Such predictions are most needed for landscapes rather than for individual habitat fragments, but SAR-based predictions of extinctions for landscapes with highly fragmented habitat are likely to be biased because SAR assumes contiguous habitat. In reality, habitat loss is typically accompanied by habitat fragmentation. To quantify the effect of fragmentation in addition to the effect of habitat loss on the number of species, we extend the power-law SAR to the species–fragmented area relationship. This model unites the single-species metapopulation theory with the multispecies SAR for communities. We demonstrate with a realistic simulation model and with empirical data for forest-inhabiting subtropical birds that the species–fragmented area relationship gives a far superior prediction than SAR of the number of species in fragmented landscapes. The results demonstrate that for communities of species that are not well adapted to live in fragmented landscapes, the conventional SAR underestimates the number of extinctions for landscapes in which little habitat remains and it is highly fragmented.**

extinction threshold | habitat conversion | metapopulation capacity | Atlantic forest | Nagoya biodiversity agreement

**T**he species–area relationship (SAR) describes a very general pattern in the occurrence of species, which is fundamental to community ecology (1), biogeography (2), and macroecology (3). Since the 1920s (4, 5), SARs have been applied to describe the occurrence of a wide range of organisms on true islands (6–8), in fragments of distinct habitat (9, 10), and in parts of more arbitrarily delimited contiguous landscapes (1, 3). In the past decades, SAR has become an important concept and a tool also in conservation biology, where it has been used to make broad assessments of species extinctions from habitat loss (11–18). These calculations have been criticized for various reasons (17, 19–21), but minimally SAR provides a valuable point of reference for the threat that habitat loss poses to biodiversity.

SARs are typically applied to a set of habitat fragments within a single landscape, but in conservation, in contrast, the essential question is how many species will persist in different landscapes (regions) with dissimilar amounts of habitat rather than in different fragments within a single landscape. This creates a problem: Habitat loss is virtually always accompanied by fragmentation (22–24), and hence the remaining habitat is not contiguous, unlike assumed by SAR, at the landscape level. In other words, SAR does not account for any adverse effects of fragmentation on the occurrence of species (25, 26). Fragmentation matters whenever individual habitat fragments are small enough to reduce the viability of the respective local populations (27, 28). Apart from conservation applications, it would be helpful to have a version of SAR that could be applied to multiple fragmented landscapes with dissimilar total amounts of habitat regardless of whether the landscape is naturally fragmented or fragmented by human land use.

Biologically, the effect of habitat fragmentation on species number is due to decreasing viability of individual species in increasingly fragmented landscapes. Mathematical models (29–32) and a suite of empirical studies (22, 33–35) have demonstrated an extinction threshold in the occurrence of species living in fragmented landscapes. Below the extinction threshold, the value of which depends on the traits of the species, the rate of establishment of new populations is insufficient to compensate for local extinctions, and hence the entire metapopulation declines to network-level extinction. The extinction threshold is analogous to the eradication threshold in the dynamics of infectious diseases (36), which describes the critical density of a host population below which the disease agent declines to extinction. Here, we measure habitat fragmentation with the metapopulation capacity, denoted by  $\lambda$ , which stems from single-species metapopulation theory and defines the extinction threshold in combination with species parameters (30, 37). The metapopulation capacity  $\lambda$  of a landscape increases with the pooled area of habitat, but it decreases with increasing fragmentation owing to, for example, declining connectivity among habitat fragments (*Materials and Methods*). The value of metapopulation capacity at the extinction threshold typically varies among the species in a community, because of interspecific variation in the parameters of population dynamics, but we verify here our previous conjecture (26) that a highly predictive “species–fragmented area relationship” (SFAR) can nonetheless be derived for a community of species.

Below, we first demonstrate with a realistic, spatially explicit, lattice-based simulation model that SAR severely overestimates the number of species persisting in a community when there is little habitat at the landscape level and the habitat is highly fragmented. This is an increasingly common situation for many habitats in many parts of the world owing to habitat conversion by humans. Second, we show that SFAR, which includes the effect of habitat fragmentation, fits much better than SAR to data generated by the simulation model. Third, we examine the effect of species parameters in the simulation model on the strength of the fragmentation effect as described by SFAR. Fourth, we show that SFAR fits better than SAR to extensive datasets on subtropical forest birds in landscapes with dissimilar forest cover and degree of fragmentation.

## Results

**Effect of Fragmentation on Species Number.** Fig. 1 shows the results of spatially explicit simulations of a large number of ecologically dissimilar species inhabiting a heterogeneous landscape (ref. 26 and *SI Text*). In the example in Fig. 1A, the model was simulated

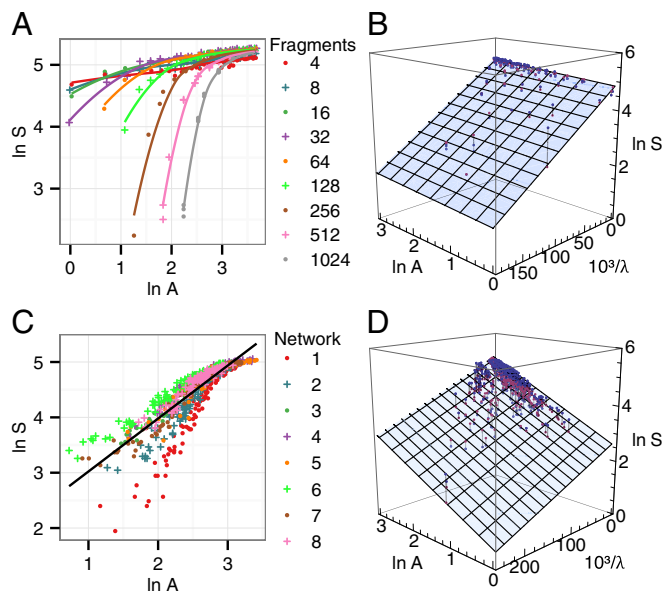
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**Fig. 1.** The SAR and the SFAR in simulated data. (A and B) Results for patch networks in which the total area of habitat is divided into 4, 8, ..., 1,024 equally large and randomly located fragments. (A) The logarithm of species number against the logarithm of total habitat area (SAR), with separate lines fitted to networks with the same number of habitat fragments (4, 8, ..., 1,024). (B) The SFAR, with the logarithm of species number plotted against the logarithm of total habitat area and the inverse of the metapopulation capacity ( $1/\lambda$ ). Note the orientation of the horizontal axes in B, where the blue points give the actual values and the red points the projected values on the regression plane. (C and D) Similar results for sets of patch networks in which the total habitat area and the degree of fragmentation vary (SI Text and Table S1). In C, a single straight line (power-law SAR) has been fitted to the data. The statistics are given in Table 1.

on landscapes in which a given amount of habitat was divided into a varying number of equally large and randomly located habitat fragments. When the amount of remaining habitat  $A$  is large, more than 20% of the total landscape area in this example, the number of species  $S$  persisting at the landscape level is roughly linearly related to the amount of habitat in log-log space, as predicted by the power-law SAR,  $\log S = c + z \log A$ , where  $c$  and  $z$  are two parameters. Similarly, when the total amount of habitat is smaller but it occurs in one or a few fragments only, SAR gives a good prediction of the number of species. In contrast, when the total amount of habitat is relatively small and the habitat is highly fragmented, SAR severely overestimates the number of species (Fig. 1A). Fig. 1C shows the results for several sets of dissimilarly fragmented landscapes with variation in fragment areas (SI Text and Table S1). It is apparent that SAR does not describe well the number of species persisting in this assembly of dissimilarly fragmented landscapes.

We denote by  $SAR(A)$  the number of species that is predicted to occur by the power-law SAR within area  $A$  of contiguous habitat, thus  $SAR(A) = cA^z$ . Let us further denote by  $P(\lambda)$  the fraction of these species that are expected to persist when the degree of fragmentation of  $A$  is given by  $\lambda$ . A convenient, simple functional form for a community of species with moderate interspecific variation in extinction and colonization rates and other species traits is given by  $P(\lambda) = \exp(-b/\lambda)$  (Fig. 2B). Note that the function fits less well if there are no interspecific differences at all (Fig. 2A) or if interspecific differences in species parameters are very large (Fig. 2C; details in Materials and Methods). With this assumption for  $P(\lambda)$ , we extend the power-law SAR to the SFAR, which takes into account the effect of habitat fragmentation on the number of species persisting in

a landscape with total habitat area  $A$  and degree of fragmentation given by  $\lambda$ . The SFAR is given by

$$S = SAR(A)P(\lambda) = cA^z \exp(-b/\lambda). \quad [1]$$

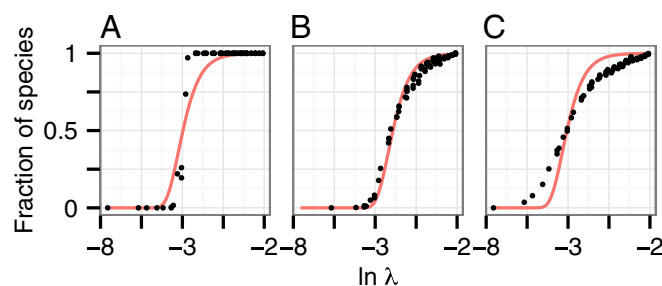
In log-log space, the model is linear:

$$\log S = \log c + z \log A - b\lambda^{-1}. \quad [2]$$

This model fits the simulated data in Fig. 1 very well. Whereas the power-law SAR explains 24% and 75% of the variation in log species number in the examples in Fig. 1A and C, respectively, SFAR explains 94% and 92% of the variation in the same data (Fig. 1B and D and Table 1). We calculated the corrected Akaike's information criterion (AICc) for the two models, confirming that SFAR with the extra parameter  $b$  clearly outperforms SAR (Fig. 1A and B, SAR 263.3, SFAR -552.3; Fig. 1C and D, SAR 34.5, SFAR -831.5). Materials and Methods gives the parameters involved in the calculation of metapopulation capacity  $\lambda$ .

**Effect of Species Traits.** Parameter  $b$  in Eq. 2 depends on the traits of the species, and especially on the value of  $\delta$ , defined as the ratio of the extinction and colonization rate parameters (Fig. 3). When  $\delta$  is small, local populations have a low rate of extinction and/or the species have good colonization capacity, and consequently the species occupy most of the habitat fragments most of the time; in other words, the occurrence of the species in the landscape is little affected by fragmentation. For a community of such species, exemplified by species that have evolved to live in naturally fragmented habitats, the value of  $b$  is small. In contrast, if  $\delta$  is large, the occurrence of species is sensitive to habitat fragmentation and the value of  $b$  is large (Fig. 3). The spatial range of dispersal and colonization also influence the value of  $b$ , as shown by the examples in Fig. 3 (SI Text and Fig. S1). We emphasize that the examples in Fig. 1 involve communities with substantial interspecific variation in  $\delta$  and other species parameters (SI Text), yet SFAR gives a good fit when  $\lambda$  is calculated using the average dispersal distance of the species.

**Application to Forest Birds.** We fitted SAR and SFAR to data on the occurrence of specialist subtropical forest bird species in 48 landscapes of 100 km<sup>2</sup> each in Argentina, Paraguay, and Brazil (35). The cover of native forest ranged from 5% to 100% and the number of specialist forest bird species from 1 to 38 species per



**Fig. 2.** The fraction of species persisting in the simulation (points) and the value of  $P(\lambda) = \exp(-b/\lambda)$  (continuous line) against the logarithm of metapopulation capacity. In (A), there is no variation among the species in any parameter (details in SI Text). In (B), parameter values were drawn from the same distributions as in Fig. 1A, including roughly twofold variation in colonization and extinction rate parameters. In (C), the same parameter values as in B except that now there is 10-fold variation in colonization and extinction rates. The fraction of species persisting in the simulation is the number of species persisting divided by 188 (200 in A), which is the maximum number of species surviving in landscapes with very high habitat cover.

**Table 1. SAR and SFAR fitted to simulated (Fig. 1) and empirical (Fig. 4) data in log-log space**

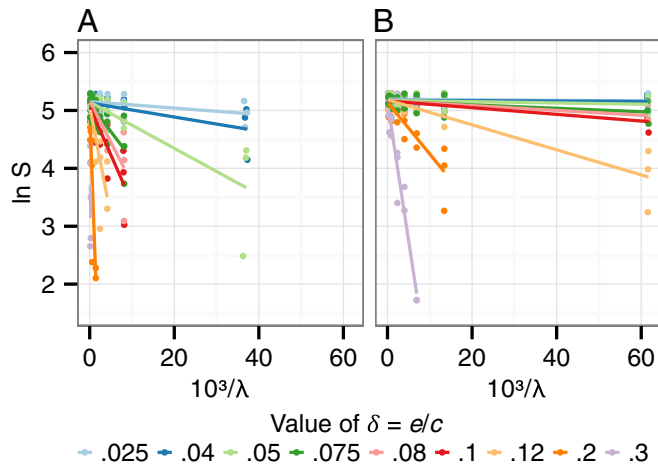
Data	Model	$z$	$b \times 10^5$	$R^2$
Fig. 1A	SAR	0.27 (0.22, 0.32)	—	0.24
Fig. 1B	SFAR	0.10 (0.08, 0.11)	1.8 (1.7, 1.9)	0.94
Fig. 1C	SAR	0.95 (0.92, 1.00)	—	0.75
Fig. 1D	SFAR	0.79 (0.77, 0.82)	0.86 (0.81, 0.90)	0.92
Fig. 4A	SAR	1.38 (0.78, 1.97)	—	0.65
Fig. 4B	SFAR	-0.10 (-1.17, 0.98)	$1.77 (0.60, 2.95) \times 10^5$	0.81

The table gives the least-squares parameter estimates and their 95% confidence intervals (in parentheses).

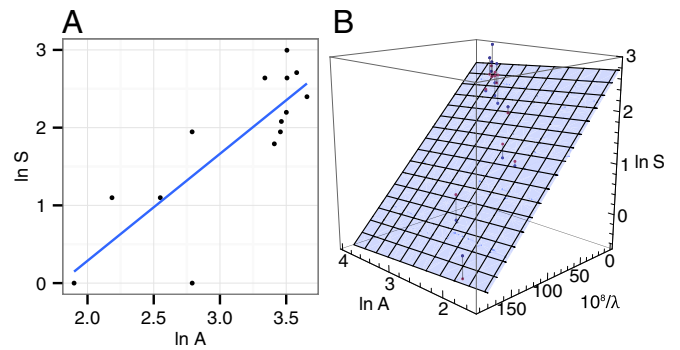
landscape. SAR and SFAR were fitted to the 14 landscapes in which native forest cover was less than 40%; in the remaining landscapes, forest cover is so high that any fragmentation effect is necessarily negligible and the delimitation of discrete forest fragments to calculate  $\lambda$  is difficult (SI Text). While calculating the metapopulation capacity, we assumed the average dispersal distance of 300 m based on independent empirical data (38).

The power-law SAR explains 65% of variation in species number among the 14 landscapes, but the slope is suspiciously large,  $z = 1.38$  (Table 1 and Fig. 4A), in comparison with values reported in the literature, typically ranging from 0.1 to 0.5 (1, 7). A plausible explanation is that species number is much reduced by fragmentation in landscapes with little forest cover, which then leads to an elevated value of  $z$ . In this perspective, the relatively good relationship between species number and area is due to correlation between the amount and fragmentation of habitat. SFAR fits the data better, explaining 81% of variation in species number, and now the  $z$  value is very small, not significantly different from 0 (Table 1 and Fig. 4B). According to the AICc, SFAR outperforms SAR (AICc scores: SAR 28.45, SFAR 26.01).

The number of specialist bird species in the landscapes that are mostly forested (forest cover >70%) was 28.3 on average ( $n = 15$ , SD = 7.0), which we use as an estimate of the number of species living in intact forest landscapes. Assuming the usual  $z$  values from 0.25 to 0.1, SAR predicts that 16–22 species would remain in landscapes with 10% forest cover. Using the observed  $z = 0.63$  in these data, the number of surviving species is seven. In



**Fig. 3.** The effect of  $\delta = e/c$ , the ratio of the extinction rate and colonization rate parameters, on the value of  $b$ , the slope of the logarithm of species number against  $1/\lambda$ . Small  $b$  indicates small effect of habitat fragmentation on the occurrence of species. (A and B) The results for two values of  $1/\alpha$ , the average dispersal distance, 10 and 3 lattice cells, respectively (Fig. S1).



**Fig. 4.** The SAR and the SFAR in subtropical bird species in large (100-km<sup>2</sup>) forest landscapes with less than 40% native forest cover ( $n = 14$ ). (A) The logarithm of species number against the logarithm of habitat area and (B) the logarithm of species number plotted against the logarithm of total habitat area and the inverse of the metapopulation capacity ( $1/\lambda$ ). Note the orientation of the horizontal axes in B, where the blue points give the actual values and the red points the projected values on the regression plane. Table 1 gives the statistics.

contrast, the observed value is only *ca.* two species (Fig. 4A), which shows that, in this case, the conventional SAR greatly underestimates extinctions. We reiterate that although SAR fits the data quite well in this example (Fig. 4A) it would be misleading to conclude that species number is primarily determined by the pooled area of habitat rather than by fragmentation.

### Discussion

The fragmentation effect on species number at the landscape level that we have described in this paper is due to local extinctions in individual habitat fragments and to nonviable metapopulations in highly fragmented landscapes. In contrast, fragmentation at very large spatial scales would not lead to the same conclusions, because very large habitat fragments can harbor individually viable populations, and hence SAR-based predictions about extinctions at continental scale (16) may not be much affected by fragmentation. At large spatial scales, species number may even increase with “fragmentation” if several large fragments located far apart have dissimilar environmental conditions and hence satisfy the ecological requirements of different sets of species (see figure 4b in ref. 26). This effect of spatial variation in environmental conditions is one reason for the original species-area relationship at large spatial scales.

So, when do we expect fragmentation to matter? Fragmentation matters when the local populations inhabiting individual habitat fragments have a substantial risk of extinction. In general, extinction risk increases with decreasing fragment size (22). Ferraz et al. (39) and Brooks et al. (40) studied bird extinctions in forest fragments in Manaus, Brazil and in Kenya, respectively. In the former case, half of the original species were inferred to have gone extinct in 1–16 y from forest fragments ranging in size from 1 to 100 ha. Brooks et al. (40) studied larger fragments, from 100 to 1,500 ha, and concluded that the relaxation time to half of the original species number was from 23 to 55 y. Halley and Iwasa (41) fitted an empirical power law to these and other data on birds, obtaining  $T_{50} = 4.34 \times A^{0.65}$ , which gives a half-life to extinction of  $T_{50} = 87$  y for a fragment of 100 ha. There is inevitably much variation in the rate of local extinction, which is affected by landscape-specific and species-specific factors, but a conservative conclusion is that whenever forest fragments are of the order of 100 ha or less the fragmentation effects for birds are so large, and the extinctions occur so quickly, that fragmentation should not be ignored.

Canale et al. (42) have examined the presence of 18 species of forest-inhabiting mammals in forest fragments in four

biogeographic subregions of the Atlantic forest biome of north-eastern Brazil. The original area of 25 million ha has been fragmented into 738,000 fragments, the vast majority of which are <10 ha in size. In a sample of 196 fragments ranging from 0.2 to 194,000 ha (median 82 ha), only 22% of the presumed original populations (196 fragments  $\times$  18 species) remained. Even forest fragments greater than 5,000 ha had only 7.2 species on average out of the original 18 species. Another study comparing the occurrence of 27 forest specialist small mammal species in three landscapes of 100 km<sup>2</sup> in the Atlantic forest in Brazil found that about half of the species persisted in the landscape with 30% forest cover, but only one species persisted in the landscape with 10% forest cover (43, 44). This result is consistent with data for forest-inhabiting birds in Fig. 4 as well as with other data for forest birds and mammals (34), suggesting that landscapes with 10% forest cover are below the extinction threshold of most forest specialist bird and mammal species. In general, much of the Atlantic forest region in Brazil, one of the major biodiversity hotspots on Earth, is already so highly fragmented (45) that using the conventional SAR at the landscape level would almost certainly severely underestimate extinctions (see ref. 42). Given the rates of habitat conversion in many biomes (46, 47), the Atlantic forest biome may represent a model system of what will happen in many other biomes as well as highlight the importance of taking fragmentation effects into account in our analyses.

The fraction of the original species that is expected to survive when the area of habitat is reduced from  $A$  to  $A_{new}$  with metapopulation capacity  $\lambda_{new}$  is given by

$$S_{new}/S = (A_{new}/A)^z \exp(-b/\lambda_{new}). \quad [3]$$

To calculate  $S_{new}/S$  for a change in the amount and configuration of habitat in a landscape, one needs to know the values of  $z$  and  $b$ . There is a large literature on the  $z$  values, and the value of 0.1 is often used for various organisms in contiguous landscapes (1). In contrast, the effect of fragmentation varies so greatly between different kinds of species (Fig. 3) that there is no generic value of  $b$  that would apply even approximately to all communities (note that the value of  $b$  also depends on the unit of landscape size). For instance, the simulation results in Fig. 1A assumed parameter values with which the fragmentation effect became apparent only when less than 20% of the landscape was covered by habitat, whereas the subtropical bird community in Fig. 4 is much more sensitive to fragmentation, and only roughly 10% of the species persisted in landscapes with <20% native forest cover. However, SFAR fits the data in Figs. 1B and D and 4B so well that even a single data point consisting of estimates of  $A$ ,  $\lambda$ , and  $S$  for a highly fragmented landscape would yield a reasonable estimate of  $b$  for the focal community. However, one should apply Eq. 3 with caution, because it involves assumptions that may often be violated. For instance, the values of parameters  $z$  and  $b$  may change with habitat loss and fragmentation. Nonetheless, for broad assessments of extinctions from habitat loss, the fragmentation effect in Eq. 3 is well justified for many communities and landscapes.

The SFAR model has three other "hidden" parameters apart from  $z$  and  $b$ . These parameters, which are needed for the calculation of the metapopulation capacity, are the average dispersal distance of species and the two parameters that scale the migration and extinction rates with patch area (*Materials and Methods*). The average dispersal distance can often be estimated with independent data, as we have done here for the forest birds, whereas the scaling factors are more difficult to estimate empirically. Previous studies (referred to in *Materials and Methods*) suggest that the values  $x = 1.5$  and  $y = 1$ , used in our analysis in Fig. 4, are realistic for birds and mammals. Finally, we point out that the effects of fragmentation on species number will occur with some delay, just as the effects of habitat loss in general

(48, 49). However, the greater the degree of habitat fragmentation and the faster the rate of population turnover, the shorter the transient time following perturbations (such as reduction in habitat area) and hence the faster the community will approach the new stochastic equilibrium (50).

Participating nations in the United Nations biodiversity summit in Nagoya in 2010 agreed on the target of protecting 17% of terrestrial habitats by 2020 to stop the decline of biodiversity. Our results demonstrate that, in the case of highly fragmented landscapes, it is not sufficient to consider only the total area of habitat, because fragmentation may cause a severe reduction of biodiversity for a given total habitat area. The fragmentation effects include high risk of extinction of small populations and reduced dispersal to isolated habitat fragments, but also factors such as hunting, wildfires, and various other anthropogenic impacts that may become elevated in fragmented landscapes (42). The SFAR model allows one to incorporate the fragmentation effects into a quantitative assessment of the threat that habitat loss and fragmentation pose to biodiversity. The model also leads to a simple management recommendation for reducing the adverse effect of fragmentation: increase the metapopulation capacity  $\lambda$ .

## Materials and Methods

**Description of Simulations.** We used a lattice-based stochastic patch occupancy model (26) to simulate spatially explicit dynamics of large numbers of species with dissimilar ecological traits. The model assumes that different lattice cells may represent different habitat type, and that habitat type across the lattice may be spatially correlated (26). In the present simulations, we assumed a high degree of spatial correlation in habitat type (parameter  $\omega = 2$  in ref. 26). Interspecific interactions are not modeled, but each species has distinct ecological traits defined by five parameters: colonization rate ( $c$ ), extinction rate ( $e$ ), average dispersal distance ( $1/\alpha$ ), mean phenotype ( $\mu$ ), and niche width ( $\gamma$ ). Colonization rate and extinction rate control the probability of a species populating an unoccupied lattice cell and the probability of extinction in an occupied cell in unit time, respectively. These probabilities are affected by the habitat type of the cell in relation to the mean phenotype and niche width of the species (26). Cells with habitat type close to the species mean phenotype support populations best, whereas niche width controls the sensitivity of the species to habitat type. In the present simulations, a species typically reaches the stochastic stationary state from a few dozen to a few hundred time steps (26). We run the simulations for at least 500 steps to ensure that most species had reached the quasi-stationary state. Increasing the simulation time did not qualitatively alter the results, although it resulted in a few additional extinctions as expected due to stochasticity. Further details of the simulations are given in *SI Text*.

**Metapopulation Capacity.** We describe the degree of habitat fragmentation on the occurrence of species by metapopulation capacity  $\lambda$ , which is a measure of landscape structure in single-species metapopulation theory (30). The landscape is described as a network of  $n$  discrete habitat fragments (patches), which are here defined as contiguous groups of lattice cells in the simulation model. Biologically, the metapopulation capacity together with species parameters defines the deterministic threshold condition for persistence in a fragmented landscape. Formally in the single-species metapopulation theory, the metapopulation capacity is given by the leading eigenvalue of a  $n \times n$  matrix with elements  $m_{ii} = 0$  and  $m_{ij} = A_i^x A_j^y f(d_{ij})$ , where  $A_i$  and  $A_j$  are the areas of fragments  $i$  and  $j$ ,  $d_{ij}$  is the Euclidean distance between the centroids of fragments  $i$  and  $j$ , and  $f(d_{ij})$  is the dispersal kernel. We assume the exponential dispersal kernel with a cutoff at 0.01,  $f(d_{ij}) = \max\{\exp(-\alpha d_{ij}), 0.01\}$ , where  $1/\alpha$  gives the average dispersal distance. The exponent  $x$  is a sum of two scaling factors,  $x_{ex}$  scaling the effect of fragment area on extinction rate and  $x_{im}$  scaling the effect of area on immigration rate, whereas  $y$  scales the effect of fragment area on emigration rate (51). To start with the latter,  $y = 1$  assumes that emigration rate is proportional to fragment area, which is the case if per capita emigration rate is constant and population size is proportional to fragment area. A study on the American pika yielded the estimate 0.74 (52). The scaling of extinction rate with fragment area depends on the relative strengths of demographic and environmental stochasticities in increasing extinction rate (53). Five values for small mammals and birds averaged  $x_{ex} = 1.15$  (54). Finally, if immigration is proportional to the length of patch boundary,

$x_{im} = 0.5$  for round patches and somewhat greater for elongated patches. In the simulation model, there was no environmental stochasticity, hence we assumed  $x = 2$ , a somewhat larger value than measured for the natural populations. For  $y$  we used the value of  $y = 1$ . We conducted a sensitivity analysis of the modeling results in Fig. 1 A and B for different values of  $x$  and  $y$ . The results are not sensitive across a range of values around  $x = 2$  and  $y = 1$  (SI Text and Table S2). The size of the landscape (lattice) was scaled to  $10 \times 10$  cells to make the values of the metapopulation capacity comparable.

**Approximation for the Fraction of Species Persisting Despite Fragmentation.** In the deterministic, spatially realistic metapopulation theory, the weighted average of patch-specific occupancy probabilities, which is the appropriate measure of metapopulation size, is given by ref. 30:

$$p_i = 1 - \delta/\lambda, \quad [4]$$

where  $\delta$  is the ratio of the extinction rate parameter over the colonization rate parameter,  $\delta = e/c$ , and  $\lambda$  is the metapopulation capacity. The entire metapopulation is predicted to go extinct if  $\delta > \lambda$ , whereas the metapopulation survives if  $\delta < \lambda$ . In the corresponding stochastic model, and in reality, the probability  $p_i$  of species  $i$  persisting in the landscape in the quasi-stationary state increases more gradually with increasing  $\lambda$ , because there is substantial risk of stochastic metapopulation extinction when  $\delta$  is only slightly smaller than  $\lambda$ .

In a community of species, we denote by  $P(\lambda)$  the expected fraction of species out of the  $S$  species in the species pool that persist in the quasi-stationary state. Thus,  $P(\lambda)$  is given by  $\sum p_i(\lambda)/S$ . Apart from stochasticity, the rate at which  $P(\lambda)$  increases with  $\lambda$  is affected by interspecific differences in parameter values, and in particular by differences in  $\delta$ . Fig. 2 gives three examples, with no interspecific variation in any of the species parameters (Fig. 2A), using the parameter values in Fig. 1A (SI Text) with roughly two-fold variation in extinction and colonization rate parameters (Fig. 2B), and assuming 10-fold variation in extinction and colonization rate parameters (Fig. 2C). We compare the simulated results with the following simple choice for  $P(\lambda)$ :

$$P(\lambda) = \exp(-b/\lambda). \quad [5]$$

It is apparent from Fig. 2 that this formula gives a very good description of the increase in  $P(\lambda)$  with increasing metapopulation capacity  $\lambda$  when there is moderate interspecific variation in parameter values (Fig. 2B). Thus, Eq. 5 for  $P(\lambda)$ , and hence the SFAR model given by Eq. 1, is best applicable to communities with moderate variation in species' ecological traits, such as many taxonomically defined communities, for instance the community of forest specialist bird species in Fig. 4. If necessary, one could assume a more elaborate functional form for  $P(\lambda)$ .

**Application to Forest Birds.** A grid of  $10 \times 10$ -km Universal Transverse Mercator Landsat cells was overlaid on the 18,000-km<sup>2</sup> study area in Argentina, Paraguay, and Brazil (35). We selected 48 grid cells (landscapes) to represent a range of native forest cover, which varied from 5% to 100% among the landscapes. For each  $10 \times 10$ -km landscape, we performed a non-supervised land use classification. The land use classes were grouped into native forest versus human-converted habitats based on field data and IKONOS images. Human-converted habitats include annual crop fields (mainly soybean and tobacco), perennial crop fields (mainly yerba mate), tree plantations from young sapling stage to mature plantations, and cattle pastures. The accuracy of the classification was assessed with independent ground-visited control points. For more details on the landscape setting see ref. 35.

We established 20 bird point counts in each landscape, for a total of 960 point counts in the 48 landscapes. The proportion of point counts located in native forest was similar to the proportion of area covered by native forest in each landscape; the remaining point counts were located randomly in human-created habitats. In each point count, we recorded all birds heard or seen within a 50-m radius during a 5-min period between sunrise and 9:00 AM during the breeding season (September–January) in 2004–2010. To increase the accuracy of bird detection, the same highly trained observer performed all point counts. Additionally, bird songs were recorded with a directional microphone Sennheiser ME66 and identifications were confirmed with song databases. We used an independent dataset of 800 bird point counts (55) to classify bird species as native forest specialists versus habitat generalists, based on the presence/absence of each species in native forests and human-converted habitats. A species was considered native forest specialist if more than 90% of the records were from native forest. A total of 5,255 individual birds representing 209 species were recorded during the survey. Of these species, 97 were classified as native-forest specialists and 112 as habitat generalists. The calculation of metapopulation capacity for the forest landscapes is described in SI Text and illustrated in Fig. S2. For the scaling parameters  $x$  and  $y$  we used the values  $x = 1.5$  and  $y = 1$ , which are biologically realistic values for birds (Materials and Methods, Metapopulation Capacity).

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