Rates of species loss from Amazonian forest fragments

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In the face of worldwide habitat fragmentation, managers need to devise a time frame for action. We ask how fast do understory bird species disappear from experimentally isolated plots in the Biological Dynamics of Forest Fragments Project, central Amazon, Brazil. Our data consist of mist-net records obtained over a period of 13 years in 11 sites of 1, 10, and 100 hectares. The numbers of captures per species per unit time, analyzed under different simplifying assumptions, reveal a set of species-loss curves. From those declining numbers, we derive a scaling rule for the time it takes to lose half the species in a fragment as a function of its area. A 10-fold decrease in the rate of species loss requires a 1,000-fold increase in area. Fragments of 100 hectares lose one half of their species in <15 years, too short a time for implementing conservation measures.

Humid tropical forests, harboring at least half of all species (1, 2), are disappearing rapidly because of fire, selective logging, and clear-cutting (3). Only approximately half their pre-industrial area remains (1, 2), divided into fragments that are often very small (4, 5). Twenty years ago, one of us (T.E.L.) engineered an experiment to follow species numbers before and after fragment isolations (6). When this experiment began, there was controversy over whether the equilibrium theory of island biogeography would extend to forest fragments. The theory explained the widespread pattern that islands surrounded by water hold fewer species the smaller they are and the more distant they are from mainland sources of immigrants (7, 8). That forest fragments, habitat "islands" surrounded by a "sea" of cattle pastures (9), also hold few species is no longer controversial (10–12), but another question is pressing (13) and unanswered: How fast do fragments lose their species?

The Brazilian Government's Medida Provisória MP2.166-67 (a presidential decree pending approval into law) requires that forest clearing in the Amazon leave 80% (originally 50%) of the forest intact. A collaborative effort between Brazil and the US, the Biological Dynamics of Forest Fragments Project (6, 14) ensured that clearing for cattle ranching in the Manaus free-trade zone would leave predetermined forest islands in a sea of pasture. Between 1980 and 1990, the project established 11 fragments 80 km north of Manaus, two of ≈100 hectares (ha), four of 10 ha, and five of 1 ha (Table 1). At isolation time, fragments were separated from continuous forest by at least 100 m of cleared land. Here we analyze the understory mist-net captures of birds up to 13 years postisolation.

Fragmentation in the central Amazon takes place against a background of very extensive, continuous forest. Any cleared surface larger than a forest gap is a radically contrasting landscape feature likely to limit the movement of animals (15). This often results in well isolated forest fragments, where recolonization is too slow to compensate for local extinction on a management time scale. The Biological Dynamics of Forest Fragments Project sites result from such a drastic process of isolation, making them good sources of information on local species loss.

The Data

Sampling lasted from 1979 to 1993. We captured birds in mist nets extending for 100 m in 1-ha fragments and 200 m in 10- and 100-ha fragments. Nets touched the ground and were placed in the interior of the fragments in approximately the same locations throughout the duration of the study. Mist-netting days (1,087) distributed among the sites produced >21,600 captures. Each newly captured bird was given an individually numbered band. Our analysis ignores all the same-day recaptures but does not discriminate between first captures and recaptures on subsequent days. The data include captures of each species in each site from 1979 to 1992, containing information on 164 bird species: mostly flycatchers, antbirds, tanagers, woodcreepers, and foliage-gleaners. More than one half (95) of the species belongs to one of the four families: *Tyrannidae* (32), *Thamnophilidae* (21), *Furnariidae* (22), and *Emberizidae* (20). The remaining species are distributed among 24 different families. Our sample includes 40% of the regional bird species list (16). Species from open fields, inundated areas, and the high canopy are the most consistent absences. The families *Icteridae*, *Hirundinidae*, *Apodidae*, *Psittacidae*, and *Cracidae* are regionally well represented but do not appear in our data set. We also have no data on any *Charadriiformes* or *Ciconiiformes* and only a few captures of *Falconiformes*.

We produce one data matrix per site by listing species in rows and time intervals in columns and filling in each cell with the corresponding number of captures. Each row is the time series vector of the number of captures of one species over time. Time is divided into years or into netting days depending on the method. When using years, because the number of netting days varies, we complement each site's data matrix with a vector containing the number of net hours or "effort" in each year. When using days, there is only a negligible variation in effort, which we therefore ignore.

The Problem of Missing Species

The number of species and individuals recorded in each fragment (especially before fragmentation) measures not only those occurring exclusively therein but also those using the area for varying amounts of time. Some individuals are residents, whereas others are transients. In determining species loss we must interpret the changing captures of each species both before, and after, a fragment's isolation. Some variation may stem from unequal trapping effort, but we know the effort, so we can

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Abbreviation: ha, hectare(s).

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Table 1. Fragment characterization and t_{50} values

Fragment/location	Area	Start	Isolation	S_0	t_{50}, minimum	t_{50}, μ uniform	t_{50}, $\mu = 0.1$	t_{50}, runs test	t_{50}, jackknife (all)	t_{50}, jackknife (initial)
1104/Colosso	2.8	1979	1980	90	3	3.3 ± 0.9	5.0 ± 1.4	5	4.4	2.0
1112/Cidade Powell	1.6	1981	1983	73	2	3.0 ± 0.8	5.0 ± 1.8	7	15.7	1.0
2107/Dimona	1.8	1980	1984	86	2	2.5 ± 1.0	4.6 ± 1.3	6	5.5	1.1
2108/Dimona	1.1	1980	1984	84	2	2.4 ± 0.9	4.2 ± 1.2	6	7.3	1.1
3114/Porto Alegre	1.6	1982	1983	82	5	5.8 ± 0.8	6.3 ± 1.0	7	6.4	1.8
1202/Colosso	13.0	1979	1980	85	5	3.9 ± 1.0	5.8 ± 1.2	10	10.5	2.3
1207/Cidade Powell	11.2	1981	1983	101	7	8.4 ± 1.3	10.4 ± 1.4	>9	5.3	2.0
2206/Dimona	10.7	1980	1984	92	3	4.0 ± 0.9	5.7 ± 1.2	8	8.1	1.9
3209/Porto Alegre	11.0	1982	1983	89	8	8.8 ± 0.8	9.0 ± 0.7	10	14.2	2.0
2303/Dimona	98.1	1980	1990	115	—	—	—	—	—	—
3304/Porto Alegre	101.2	1982	1983	111	10	11.7 ± 1.4	12.2 ± 1.4	>10	14.9	5.3

The actual fragment areas in hectares, as measured from an aerial image, differ slightly from the target areas. S_0, initial number of species.

correct for it. In addition, if we assume perfectly isolated fragments, an absence followed by a presence is taken to mean the species was present but not detected. But how do we interpret the absences that follow the final capture? Is the species truly missing, or are we failing to detect it? If fragment isolation is not perfect, some species may disappear from a fragment but return later. Should all temporary absences be regarded as detection failures? First, we ask what would be the minimum number of species present through time if isolation were perfect and there was no possibility of recolonization. Then, we maintain the assumption of perfect isolation and use two methods for estimating the number of species through time. The first is a Bayesian approach developed by one of us (G.J.R.) specifically for this study. It has the special feature of predicting the number of species in each fragment for some time after the sampling period. The second is a variant of a runs test, obtained from the literature. Finally, knowing there was secondary growth of varying extent around fragments (17), we withdraw the assumption of perfect isolation and explore the consequences with a jackknife estimation of the number of species in each year. Excluding the minimum, all estimates account for heterogeneity of detection probability across species (for a formal explanation see *Supporting Methods*, which is published as supporting information on the PNAS web site). After using these different methods involving a variety of assumptions, we ask whether this variety alters our basic conclusions.

Inferring Decays Under Perfect Isolation

The Minimum. Many species in our data set show signs of having gone extinct. For example, in one fragment, we caught 7, 6, 4, 3, 5, 2, 1, 0, 0, 0, 0, 0, and 0 *Formicarius colma* from 1980 to 1992. This pattern of consistent presence followed by consistent absence suggests that the bird was extinct by 1987, the year it first went missing. Method 1 assumes that all species go extinct immediately after the last sighting. This assumption provides an absolute lower bound on times to extinction and hence a baseline against which to compare other methods.

Method 1 makes the extreme assumption that species are extinct immediately after their final capture and never return. The opposite extreme would be to assume that no species ever really disappears from any fragment. In this case, the apparent absence of many species after fragmentation might be explained by individuals becoming extremely trap-shy once their habitat is fragmented or as their numbers decline. This seems very unlikely. Most often, nets were opened at a given site <7 days/year and never opened for 2 consecutive days in the same site. There were always at least 2 weeks between consecutive nettings at one site; often the interval was 1 or 2 months. During 1990, netting

was interrupted for 7 months. There was no increase in captures per unit effort during the subsequent period.

Instead, abundant evidence shows that small fragments retain few species (18, 19). Between the extremes of immediate extinction and eternal hiding, there is a plethora of models of how long a species persists after its last observation. They invoke different assumptions about detection and isolation. The following two methods assume perfect isolation. Both estimate the number of species present each year by using capture information for all years.

The Bayesian Method. For each species, we want to know the year t_e, at which it went extinct. A Bayesian approach will give us not one value with confidence intervals but the probability associated with each possible value of t_e. This key result is the 'posterior' probability distribution for t_e. We obtain it from the combination of a likelihood function and a "prior" probability distribution for t_e. The likelihood function incorporates a specified model of how the data are generated, returning the probability of the observed data given each t_e value. The prior is a formulation of what we know or assume about t_e before looking at the data.

For method 2 we assume that each species has a constant but unknown annual probability of extinction μ in each fragment. From various studies we know that species differ in how prone they are to extinction (20–25). On the other hand, studies of small bird populations on islands roughly the same size as these fragments (26) find that annual turnover, and hence mean yearly extinction probability, is clustered around $\mu = 0.1$. We therefore use three alternative assumptions about the distribution of μ to generate prior probability functions for the year of extinction, t_e: a "fixed μ" prior ($\mu = 0.1$; Fig. 1 and Table 1), a "uniform μ" prior (μ uniform on [0,1]; Table 1), and a "beta μ" prior (see *Supporting Methods* and Figs. 3–8, which are published as supporting information on the PNAS web site). For the likelihood, we use two alternative models of population decay toward extinction: linear decay, assuming a gradual loss of individuals, and step decay, assuming an abrupt population collapse. Both models treat capture as a Poisson process. Intuitively, the step decay is not the most appealing, but it fits our data better than the linear decay (Fig. 3). The three priors and two decay models generate six variants of method 2, but because the results did not vary substantially, we focus only on two variants here: those involving a fixed μ and a uniform μ prior (μ uniform on [0,1]; Table 1) under the step-decay model.

Once we have a posterior probability distribution of t_e for each species, we sample t_e values from those distributions (one per species) and obtain a curve of the number of species extant in

Fig. 1. Plots of species loss for all fragments according to four different methods: minimum under perfect isolation, Bayesian with $\mu = 0.1$ and step-decay, runs-test, and jackknife estimates. The gray bars indicate the timing of isolation.

each year. We repeat this process 1,000 times per fragment to obtain the mean curves and 95% bounds shown in Fig. 1.

The Runs-Test Method. The application of Bayesian methods in ecology elicits statistical controversies that we do not intend to resolve here (27). Method 3, one frequentist alternative to method 2, is a computationally simple version of a runs test. If we assume that captures per species follow one particular distribution, then it is possible to calculate the probability of obtaining a run of a certain number of captures along a series of consecutive capture occasions. This is true in the same way as, when rolling a die, we can calculate the probability of obtaining, say, five "ones" in a row. In the species-extinction context, the interesting question is: If one species is present at one site throughout a whole series of capture occasions, and if we know the probability of detecting 0, 1, 2, ... , n individuals at any occasion, what is the probability of getting a run of t occasions with zero captures? More precisely, what is the probability of observing a run of zeros of a certain length at the end of a series? If there is a high probability associated with one terminal run of zeros, then we will not be surprised to not see the species. We will believe that it is still there, but we failed to detect it. If the observed run has a low probability, we will suspect that the species was actually not present throughout the whole series and interpret the run of zeros as evidence of extinction.

Solow (28) used this approach in inferring extinction from presence/absence data, and Burgman *et al*. (29) adapted it for use with frequency data. Both cases treat capture success as a stationary Poisson process, implying constant density until the

moment of extinction, just as in the step-decay model above. Solow and Helser (30) did formulate a variant for testing extinction with declining populations, but we have seen that a model of gradual population decline does not fit the data on most species. We therefore feel justified in applying Burgman's approach to our frequency data (see *Supporting Methods* for details).

Forest Recovery Allows Recolonization: Jackknife Estimates

Finally, we withdraw the assumption of perfect isolation and estimate the number of species in any given year based exclusively on data from that year. In this approach, because it allows extinctions and recolonizations to occur from year to year, the knowledge of how many species were seen over the sampling period does not help us define a lower bound for their numbers. Increased realism comes at a price. We must assume community closure, i.e., that the number of extinctions and colonizations over 1 year is negligible with respect to the changes taking place between years. To the best of our knowledge, there is no satisfying goodness-of-fit test for closed capture models. We also assume that species-specific capture probabilities are constant (each species keeps its particular capture probability throughout the year) and that captures are independent events.

Method 4 gives a jackknife estimate of the number of species present in each year (31). It was developed originally for estimating the size of closed single-species populations based on mark-recapture data. Our use of the method treats species as marked individuals with heterogeneous capture probabilities. At each site in each year there are a total of I species captured over

Fig. 2. Time to lose 50% of the species from forest fragments in Manaus (circles and triangles) and Kakamega (diamonds). The graph shows three different results from Manaus: Bayesian decay with 95% bounds (triangles), jackknife estimates with exponential fit to all years (empty circles), and jackknife estimates with exponential fit to initial decay (filled circles).

t days. Not all species are captured in all days; therefore, if community closure applies, we must be missing species in some of the visits. It follows that I is necessarily a negatively biased estimate of the true number of species, S. The higher the difference between the species lists from individual days, the higher the bias. We apply the jackknife as a means of reducing this bias.

We use the software package CAPTURE (32) to obtain one estimate of the number of species per year whenever there are a sufficient number of netting days. *Supporting Methods* provides more details of the method.

Rates of Species Loss

Methods 1–3 produce curves (Fig. 1) that yield t_{50} values, the time it takes to lose half the initial number of species (Table 1 and Fig. 2). Methods 2 and 3 yield such similar results that we omit the latter in Fig. 2. The jackknife estimates, however, produce only a set of points with confidence intervals. In this case, we obtain the t_{50} values by fitting an exponential curve to the set of points from each fragment. We fit curves in two ways. First, we use all points from the year before isolation to the end of sampling, which returns a t_{50} that neglects the possible historical effects of relaxing isolation. A second, generally better fit uses fewer data points. It starts the year before isolation and ends the year before the number of species begins to recover. The resulting t_{50} illustrates how fast species would disappear had the isolation held constant throughout the study period. The aggregate result of the four methods allows some general conclusions.

1. On average, smaller fragments start with fewer species than larger ones, as expected by the species–area relationship. This tendency is perceivable ($z \approx 0.07$) but not very pronounced, as expected from different-sized samples of a continuous biota (10).
2. The number of species drops quickly. A slightly higher than expected number of species in the first year after isolation is likely because of the temporary presence of refugee birds from the recently destroyed adjacent forest (33). An occa-

sionally steeper drop in some methods at the end of the survey is caused by species not captured in the very last survey year; the most recent capture will be deemed "final" and the species therefore extinct. Our sample of fragment interior locations does not detect species that regularly use deforested areas, a small proportion of the regional avifauna (16). The quickly dropping initial number of species reflects a fast loss of forest-dependent birds. Fragments in areas that have been patchy for a long time, at the confluence of different biota, lose species more slowly than the fragments in our sample (23).

3. Species differ greatly in their probabilities of extinction. For example, *Cyphorhinus arada*, *Sclerurus caudacutus*, and *Myrmornis torquata* consistently disappear early from all fragments, whereas *Phaethornis superciliosus*, *Glyphorhynchus spirurus*, and *Mionectes macconnelli* remain present until the end of the sampling period. On a log graph, this heterogeneity of extinction probabilities results in a concave species-loss curve, with interesting implications for conservation. An initial, transient, high rate of vulnerable species loss means that infrequent surveys taken long after fragmentation may only record occasional extinctions of long-lasting species. From this one might infer a spuriously long time for species losses (7). Conversely, surveys soon after fragmentation may mistake the slowing rate of extinction for its cessation and thus underestimate the continuing but slow decline in species numbers. Drawing inferences about the exact shape of the curves in Fig. 1 is complicated when, with the Bayesian method, we assume a priori probability distributions. There is also the problem of forest regrowth around fragments: The jackknife estimates suggest that species numbers may not just be declining more slowly toward the end of the sampling period, but they may actually be increasing. We will address species differences in the probability of extinction and the role of regrowth on recolonization elsewhere.

4. Despite different assumptions, the t_{50} estimates are broadly similar. Smaller fragments lose a given proportion of species more quickly than larger ones (Table 1 and Fig. 2). The t_{50} estimates are shortest when we estimate them from the initial decay of the jackknife estimates, which suggests that fragmentation would have had more drastic effects if there had not been some forest regrowth (24).

Fig. 2 also shows rates of species loss for generally larger forest fragments at Kakamega, Kenya (34). This study has significant differences in methods, species, and history. It assumed exponential decay from an initial to a final, equilibrium number of species, both estimated from species–area relationships. The initial estimate used parameters typical of areas within continuous forest, and the final used parameters typical of long-isolated forest fragments (10). The empirical datum is the number of species observed a known time after forest isolation. In calculating a half-life for the numbers of species lost, the Manaus study assumes that fragments will eventually lose all their species. This cannot be far from wrong given the rapid loss and extreme disparity between pre- and postfragmentation areas. (If the fragments retained some species, then t_{50} estimates would be smaller than those shown.) The Kakamega study, in contrast, assumes nonzero equilibrium numbers of species, a better assumption for larger fragments.

Given these differences, there are interesting similarities. Fig. 2 suggests a rough scaling: a 1,000-fold increase in area leads to a 10-fold increase in the time it takes fragments to lose half the species they will eventually lose. Fragments of ≈ 100 ha (1 km^2) lose many species within one or two decades. Fragments with >100 ha still lose some species but do so over a time scale of a few decades to perhaps a century.

This experiment originated in the search for a minimum forest fragment area that would be sensible for conservation. Much work in the intervening two decades has shown that smaller areas simply retain fewer species than do larger ones. However, area itself does not set a clear enough constraint on conservation measures. The results we present connect area to time, and time does impose such a constraint. Only the largest fragments retain species long enough to offer hope of remedial actions such as the regeneration of cleared forests. It may take a couple of decades for secondary forest to achieve any structural development (35) and at least 100 years to recover mature biomass levels (36). Conservation managers would want to have forest fragments large enough to protect species until they can be "rescued" by forest regrowth. Our results relating time to area suggest that "large enough" (for the understory birds considered here) must be measured on a scale of $\geq 1,000$ ha (≥ 10 km^2). This is unfortunate when one considers that for some species-rich areas of the planet, a large proportion of remaining forest is in fragments $<1,000$ ha (4). Such fragments will have limited conservation value for forest-dependent birds, at least. An even more challenging question is how large fragments should be if there is no hope of forest regrowth rescuing their stranded species. Our scaling results suggest that even fragments as large as 10,000 ha (100 km^2) lose many species (likely the ones of most conservation concern) when isolated for a century.

Minimum size is important in itself, but choosing an appropriate scale for assigning conservation priority also is important.

A common procedure selects the minimum set of areas that, if protected, would conserve some predefined set of species (such as all endemic or all threatened species). Such techniques depend on the widely varying resolution of the available data in species ranges. They are susceptible to the "Noah's Ark effect" (37), in which the total area needed to protect all species becomes vanishingly small (and politically tempting) provided one accepts an unreasonably small resolution (the area occupied by a pair, in the case of the Noah's Ark). Conversely, too large a spatial resolution results in the selected areas being too large to meet the economic or political constraints on reserve establishment. Without knowing the appropriate spatial resolution that scaling rules provide, priority setting can fall into either ecological irrelevance or practical impossibility. Our results provide a lower bound to the minimum fragment size for birds. Determining the fragment sizes required to slow the losses of other taxa to manageable levels will require more estimates similar to the ones presented here.

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