A Large-Scale Deforestation Experiment: Effects of Patch Area and Isolation on Amazon Birds

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As compared with extensive contiguous areas, small isolated habitat patches lack many species. Some species disappear after isolation; others are rarely found in any small patch, regardless of isolation. We used a 13-year data set of bird captures from a large landscape-manipulation experiment in a Brazilian Amazon forest to model the extinction-colonization dynamics of 55 species and tested basic predictions of island biogeography and metapopulation theory. From our models, we derived two metrics of species vulnerability to changes in isolation and patch area.

A large-scale deforestation experiment, Dimona, Brazil. This aerial photograph of a 10-ha and a 1-ha fragment was taken shortly after isolation. Gaps between the fragment edge and the continuous forest are less than 1 km wide.

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Our analysis follows three steps, all of which are based on fitting models for each species. First, we ask what covariates appear in the top-ranking models of each species. Second, we focus on the single model that fits best across species and examine the signs and magnitudes of covariate effects (slope parameters). Finally, we select one best-fitting model per species and draw inferences based on the estimated local extinction and colonization parameters.

Patch isolation appears as a covariate of colonization and/or local extinction in high-ranking models \((wj > 0.2)\) of nearly all, but not all, species (Table 1 and table S3). Patch size, regardless of isolation, seems sufficient to explain the observations on three exception species: Geotrygon montana, Dendrocopelates certhia, and Hypocnemis cantator. Fifteen species have high-ranking models with an effect of isolation only on local extinction, and five species have high-ranking models with that effect only on colonization. Regrowth enters high-ranking models in two-thirds of the species. Contrary to our expectation, we cannot reject the null hypothesis that regrowth enters high-ranking models of high- and low-dispersal species in the same proportions (one-tailed \(z\) test, \(P = 0.33\)). Likewise, there is no evidence to sustain the prediction that isolation would appear more frequently in high-ranking models of low-dispersal species (one-tailed \(z\) test, \(P = 0.97\)). Inferences are qualitatively the same if high-ranking models are redefined as having \(wj > 0.1\) or \(wj > 0.25\).

Comparison of estimated slope parameters for area and isolation across species is facilitated by use of a single model, so we focus on model 6 (Table S2 and Fig. 2), which has the highest average \(wj\) across species. Model 6 hypothesizes fixed colonization and an additive effect of size and isolation on local extinction. There is a negative effect of patch size on \(\epsilon\): For all species, larger plots have lower \(\epsilon\) values. Isolation shows more variable results, with 36 of 55 species showing a positive slope. As predicted, the effect of isolation on local extinction is positive more often than negative (one-tailed \(z\) test, \(P < 0.01\)), but for roughly one-third of the species, slope estimates are very close to zero (or even negative). We found no evidence to suggest that poor dispersers show positive isolation effects on extinction more often than do good dispersers (one-tailed \(z\) test, \(P = 0.49\)). Confirming previous inferences (12, 13), all obligate ant-followers (Pithys albifrons, Gymnornis rufugula, and Dendrocmaela merula) and many mixed-species–flock attendants (14) showed evidence of a positive effect of isolation on local extinction, despite their high dispersal ability (Table S3). Model 6 concentrates the effects of size and isolation on only one of the dynamic rate parameters (local extinction). The support for this model suggests that many species would be equally good at colonizing isolated and continuous forest patches. However, our ability to infer changes in colonization may be limited by the greater opportunity to see extinctions than colonizations in our data (8). It is very possible that more data may lead to more evidence of effects on colonization.

By selecting the best-fitting model for each species, we can account for the effect of regrowth and for the possible interaction between the effects of size and isolation on local extinction (Table S4) (8), which are two aspects that model 6 did not address. We select only from the subset of 10 models that includes the covariate isolation affecting local extinction to ensure that we always estimate an effect of isolation on occupancy parameters, no matter how small. For each species-model combination, our analyses provided estimates of local extinction and colonization, expressed as functions of the pertinent covariates (Fig. S1). These two parameters combine into a single population-dynamic metric that predicts equilibrium patch occupancy \(\psi^*_c\), where \(c\) denotes isolation and \(s\) denotes patch size (3, 4). Figure 3 illustrates how \(\psi^*_c\), estimated for isolated and nonisolated patches of different sizes, may reflect different responses to landscape change. From the ensemble of each species’ \(\psi^*_c\) values, obtained from the best-fitting model for the species, we compute two metrics that separate specific effects of patch size and isolation. Species that have large territories or are otherwise sparsely distributed should have relatively low \(\psi^*_c\) values in small patches of continuous forest. Accordingly, we formulate an index of area sensitivity \(A\) (Fig. 3C) as the relative reduction in \(\psi^*_c\) from the largest to the smallest continuous-forest \((cf)\) patch:

\[
A = 1 - \frac{\psi^*_c}{\psi^*_c^{cf}}
\]

with the numerical subscript denoting patch size (in hectares). The uncommon black-throated antshrike (Frederickena viridis), a forest-interior antbird with narrow habitat requirements, exemplifies a species that is highly sensitive to area (Fig. 3, D to F). Poor colonizers that rarely cross open areas, or species that do not survive well in isolation, should have relatively low \(\psi^*_c\) values in isolated patches. Thus, we measure vulnerability to isolation \(I\) (Fig. 2C) as the relative reduction in \(\psi^*_c\) from 1-ha continuous-forest to 1-ha isolated (isol) patches:

\[
I = 1 - \frac{\psi^*_c^{isol}}{\psi^*_c^{1-ha}}
\]

The white-chinned woodcreeper (D. merula), a bird that forages by following swarms of army ants, is highly vulnerable to isolation but not sensitive to area (Fig. 3, A to C).

We use approximate 95% confidence intervals (Fig. 4) to assess whether each metric is significantly different from zero. In agreement with results based on slope parameters and \(wj\), a substantial proportion (29/54) of species is not significantly vulnerable to isolation. There is a 

### Table 1. Contribution of isolation and regrowth covariates to high-ranking models of 50 species, grouped by dispersal ability. Isolation is a binary variable (“1” for isolated patches and “0” for otherwise). Regrowth counts the number of years since isolation. Five species had no models with \(wj > 0.2\).

<table>
<thead>
<tr>
<th>Dispersal ability of species</th>
<th>Does the isolation or regrowth covariate enter any part of a model with (wj \geq 0.2)?</th>
<th>Number of species</th>
</tr>
</thead>
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<tr>
<td></td>
<td>Isolation</td>
<td>Regrowth</td>
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<tr>
<td>High</td>
<td>22</td>
<td>0</td>
</tr>
</tbody>
</table>

**Fig. 2.** Slope parameter estimates for the effect of isolation (A) and patch size (B) on local extinction, as according to model 6. Low- and high-dispersal species (table S3) appear on the left and right sides of the dashed line, respectively. Error bars indicate approximate 95% confidence intervals, assuming normally distributed parameter estimates. Points without confidence intervals on the upper or lower edges of the plot indicate point estimates beyond the limits of the y axis. Confidence intervals could not be estimated for all points.
Our finding that local extinctions are always sensitive to area is reminiscent of similar variation reported for avian communities in temperate forests of North America (15). Both the North American study and our more realistic modeling approach report interspecific variation, but they differ in that our finding demonstrated a relatively stronger effect of area than of isolation. We qualify this finding by noting that our data come from a landscape that is dominated by forest. The distance between isolated patches and continuous forest ranges from 150 to 900 m (16). Further forest destruction is expected to result in additional species loss and larger effects of isolation (7, 17).

**Fig. 3.** Example of patch-occupancy parameters estimated by the best-fitting models for two species. Solid and open circles show estimates for continuous forest and isolated patches, respectively; error bars and lines without symbols show 95% confidence intervals. V(I) (C and F) is a function of e (A and D) and γ (B and E). D. merula [(A) to (C)] shows a marked effect of isolation both on local extinction and colonization and a stronger effect on V(I). Estimates for F. viridis [(D) to (F)] vary mostly with patch area. Arrows in (C) illustrate two sensitive to area.

**Fig. 4.** Values of A and I for 54 species grouped by uncertainty over the two metrics (table S4). Open and solid circles indicate that the approximate 95% confidence intervals of both metrics or of neither metric overlap zero, respectively. Upward and rightward pointing triangles indicate that only the confidence interval of A or I does not overlap zero, respectively. Symbols with arrows indicate point estimates outside the plotted range of the x axis.

higher proportion (36/54) of species with area sensitivity that is significantly different from zero, with two-thirds of these species not being significantly vulnerable to isolation. This result suggests that many species fail to occur in small isolated patches, not because they succumb to the effects of isolation in reducing any rescue effect but because they rarely occupy any small patch (even in continuous forest) just because of their pattern of space use. Management aimed at curbing the effects of isolation (e.g., corridors and edge protection) will have reduced effectiveness for those species that are highly sensitive to area.

Our finding that local extinctions are always more probable in small than in large patches is predicted by demographic theory and is evident from the slope parameters of model 6. The role of isolation is less obvious: A predominantly positive but variable effect of isolation on local extinction under model 6 must be qualified by the many low and uncertain estimates of I. Our knowledge of the dispersal abilities of species in undisturbed conditions does not explain the variation in the signs of the slope parameters or in the contributions of the isolation and regrowth covariates to high-ranking models. Either we do not know enough about dispersal abilities—a notion that is widely supported by neotropical ornithologists—or those abilities change in disturbed landscapes to the extent that we cannot use them to predict occupancy parameters under disturbance.

Deforestation results in forest-area reduction and isolation of remaining forest patches, and both factors affect occupancy dynamics. This study shows the generality of these effects by showing that they apply to tropical forest landscapes in addition to the temperate landscapes from which most previous inferences have come. The interspecific variation in the effects of isolation on the studied tropical bird community is reminiscent of similar variation reported for avian communities in temperate forests of North America (15). Both the North American study
Distinct Populations of Primary and Secondary Effectors During RNAi in C. elegans

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RNA interference (RNAi) is a phylogenetically widespread gene-silencing process triggered by double-stranded RNA. In plants and Caenorhabditis elegans, two distinct populations of small RNAs have been proposed to participate in RNAi: “primary siRNAs” (derived from DICER nuclease-mediated cleavage of the original trigger) and “secondary siRNAs” [additional small RNAs whose synthesis requires an RNA-directed RNA polymerase (RdRPI)]. Analyzing small RNAs associated with ongoing RNAi in C. elegans, we found that secondary siRNAs constitute the vast majority. The bulk of secondary siRNAs exhibited structure and sequence indicative of a biosynthetic mode whereby each molecule derives from an independent de novo initiation by RdRP. Analysis of endogenous small RNAs indicated that a fraction derives from a biosynthetic mechanism that is similar to that of secondary siRNAs formed during RNAi, suggesting that small antisense transcripts derived from cellular messenger RNAs by RdRP activity may have key roles in cellular regulation.

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8. Materials and methods are available as supporting material on Science Online.
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Supporting Online Material
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Materials and Methods
Fig. S1
Tables S1 to S4
References
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