Effect of habitat area and isolation on fragmented animal populations

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Habitat destruction has driven many once-contiguous animal populations into remnant patches of varying size and isolation. The underlying framework for the conservation of fragmented populations is founded on the principles of island biogeography, wherein the probability of species occurrence in habitat patches varies as a function of patch size and isolation. Despite decades of research, the general importance of patch area and isolation as predictors of species occupancy in fragmented terrestrial systems remains unknown because of a lack of quantitative synthesis. Here, we compile occupancy data from 1,015 bird, mammal, reptile, amphibian, and invertebrate population networks on 6 continents and show that patch area and isolation are surprisingly poor predictors of occupancy for most species. We examine factors such as improper scaling and biases in species representation as explanations and find that the type of land cover separating patches most strongly affects the sensitivity of species to patch area and isolation. Our results indicate that patch area and isolation are indeed important factors affecting the occupancy of many species, but properties of the intervening matrix should not be ignored. Improving matrix quality may lead to higher conservation returns than manipulating the size and configuration of remnant patches for many of the species that persist in the aftermath of habitat destruction.

incidence function | island biogeography | logistic regression | metaanalysis | occupancy

Habitat loss and fragmentation are major threats to terrestrial biodiversity (1). Globally, ≈40% of land has been converted for agricultural use (2), and regions as diverse as the eastern United States, the Philippines, and Ghana have lost >90% of their natural habitat (3, 4). Conservation theory and practice are founded on the principle that large habitat patches have more species than small ones and connected patches have more species than isolated ones (5). Although few would dispute this basic premise, we still do not know the general value of patch area and isolation as predictors of species occupancy in fragmented terrestrial systems. Despite hundreds of patch occupancy studies over >4 decades, there has been no quantitative synthesis of these findings. Several syntheses have examined species-area and diversity relationships (6, 7), but the species occupancy patterns that underlie diversity patterns in fragmented landscapes have been overlooked (8). How important is patch isolation relative to patch size in determining where species occur, and how consistent are these effects across diverse taxonomic groups? These are foundational, yet unanswered, questions for ecology and conservation biology.

We synthesized patch occupancy data from 89 studies of terrestrial fauna on 6 continents (Table S1) to determine how patch area and isolation affect species' occurrence patterns. Collectively, these studies recorded the occurrence of 785 animal species (Table 1) in 1,015 population networks surveyed in 12,370 discrete habitat patches. We use the term "population network" to refer to a spatially-structured population that occupies habitat patches embedded in a matrix of land cover deemed unsuitable for the species. Most of the population networks in our analysis were probably metapopulations linked by dispersal events, but few studies provided the necessary evidence for these linkages. Animals ranged in size from the 0.2-mm false spider mite (*Pentamerismus* sp.) to the 500-kg American bison (*Bos bison*), and habitat patches varied in isolation and area by 8 and 12 orders of magnitude, respectively (within-study order of magnitudes ranged from 0.2 to 4.4 for isolation and 0.8 to 5.4 for area). The dataset presents a global representation of faunal occurrence patterns in ecosystems made patchy both by humans (via agriculture, forestry, and urbanization; 72% of studies) and natural processes (28% of studies). We begin with the broad question: are patch area and isolation good predictors of occupancy for animals in terrestrial habitat fragments?

Results and Discussion

Patch area and isolation were surprisingly poor predictors of occupancy across species. All together, 38% of patches were occupied (n = 55,855 occupancy records). We ran 4 logistic regression models for each population network to determine how well patch area and isolation predicted occupancy: (*i*) area only, (*ii*) isolation only, (*iii*) area + isolation, and (*iv*) area × isolation (see *Methods*). The amount of deviance (i.e., variation) in occupancy explained by each model ($pseudoR^2$, or pR^2) represents the ability of patch area and/or isolation to predict species occurrence patterns; this statistic is analogous to the R^2 of linear regression (9). The pR^2 values from each of the 1,015 population networks created distributions that were skewed toward 0, and few species were strongly influenced by patch area or isolation (Fig. 1*A*). The full area × isolation model accounted for a median of 25% of the deviance in occupancy, indicating that at least 75% of occupancy deviance was caused by other factors for most population networks. Area was a better predictor of occupancy than isolation: area alone accounted for a median of 13% of the deviance in occupancy versus 3% accounted for by isolation alone. These results raise 2 questions: first, why does area explain more deviance in occupancy than isolation, and second, why are both metrics such poor predictors of occupancy, given that habitat destruction is the dominant threat to species persistence?

The stronger effect of patch area can be explained by examining the type of isolation measure used in the analysis. Patch isolation is measured in many ways (10), and we used 3 categories to define the isolation measure used in each study: distance to nearest habitat patch of any size (*NH*); distance to nearest large

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Table 1. Numbers of species included in the metaanalysis

Taxon	Species	Families	Orders
Birds	370	75	18
Mammals	166	38	11
Invertebrates	167	49	9
Reptiles	50	7	1
Amphibians	32	7	3
Total	785	176	42

The full list of species is available in Table S2.

patch, or "mainland" (*NM*); or distance to nearest occupied source patch (*NS*). *NH* and *NM*, which are landscape isolation measures, were used for 94% of the population networks, whereas *NS* (a demographic isolation measure) was used for only 6%. When we limited analyses to studies that used *NS*, the importance of isolation in predicting occupancy was equal to that of area (Fig. S1). Likewise, for the 82 population networks for which we could calculate both *NS* and *NH*, *NS* had a much stronger effect on occupancy (paired *t* test on slopes of logistic regression, $P < 0.0001$). Previous studies that found stronger effects of area on occupancy often used landscape isolation measures (7, 11) or "isolated/not isolated" categories for each patch (12). *NS* is more relevant to metapopulation dynamics because the proximity of source populations, not habitat patches per se, affects colonization probabilities.

Although demographic isolation was a better predictor of occupancy than landscape isolation, area and demographic isolation were still poor predictors: the full area × isolation model explained a median of only 24% of the deviance in occupancy across the subset of studies (Fig. 1*B*). *NS* may be superior to *NND* as an isolation measure, but a previous study (10) indicated that *NS* was inferior to more complex measures that take into account the areas and distances of all potential source patches, known as model S_i. Data were available to calculate S_i for 24 population networks (including the 2 metapopulations used in the previous study), and our larger analysis showed that S_i did not explain any more variance in occupancy than *NS* did (see *SI Text*). Thus, *NS* appears to be as good a measure of isolation as the more complex measures that have been developed.

The overall poor performance of area and isolation as predictors of species occupancy could be caused by limitations of the data, ecological factors, or a combination of both. Snapshot occupancy data contain less information than population density or turnover data and may fail to capture the demographic advantages of large, highly connected habitat patches. Indeed, population networks that were monitored over multiple years had stronger relationships with area than those monitored for only 1 year (mean $pR^2 = 0.27$ for multiyear records vs. 0.17 for single-year, $F_{1,952} = 44.5, P < 0.0001$). However, the relationship with isolation did not improve with additional years of monitoring (mean $pR^2 = 0.09$ for both types of studies, $F_{1,699} = 0.02$, $P = 0.90$). Although this limitation likely explains some of the poor model fit, detailed examinations have suggested that occupancy data captures much of the information provided by population density data (13, 14). We propose 4 additional explanations for the low predictive power of patch area and isolation: (*i*) patches studied were of an inappropriate scale, such that areas and distances were not matched to focal species' body sizes and dispersal abilities; (*ii*) particular taxonomic groups or species with certain life history traits were less sensitive than others; (*iii*) most of the species were "survivors," able to tolerate disturbance and not threatened with extinction; or (*iv*) the habitat island paradigm is not adequate in fragmented terrestrial

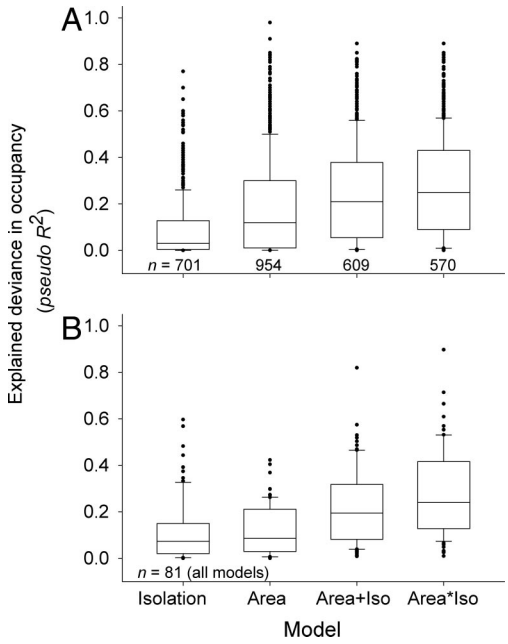

Fig. 1. Strength of patch area and isolation effects on fragmented animal populations. Area explained more deviance in occupancy than isolation when all measures of isolation were included (*A*), whereas effects were equal when analyses were restricted to studies that used distance to nearest source population (*NS*) as the isolation measure (*B*). Isolation was measured as the distance to nearest patch, mainland, or source population in *A*. Four logistic regression models were run for each population network (when possible), with the following predictors of occupancy: (*i*) patch area, (*ii*) isolation, (*iii*) area + isolation, or (*iv*) area × isolation. The pR^2 value (a goodness-of-fit measure analogous to R^2 of linear regression) was recorded for each model. Box plots show medians (horizontal lines), interquartile ranges (boxes), the extent of nonoutlier datapoints (whiskers), and outliers (points).

systems because of strong effects of the matrix surrounding patches. We consider each of these.

Scale. Assuming that researchers chose patch sizes that were appropriate to the body size of the study species, we would expect population networks from multispecies studies to be less sensitive to patch area, on average, than population networks from single-species studies. Most studies in this metaanalysis recorded the occupancy of multiple species in a single landscape, with body size ranges of up to 5 orders of magnitude, thus reducing the likelihood that patch sizes could be scaled appropriately for all species studied. Contrary to expectation, there was no relationship between the number of species in a study and the sensitivity of those species to patch area ($n = 86$ studies, $R^2 = 0.002, P = 0.68$). In addition, mean patch area was roughly scaled to body size across population networks ($r = 0.52, n = 971$). The small effect of area on occupancy therefore does not appear to be caused by inappropriate scaling.

Likewise, isolation sensitivity was not strongly influenced by dispersal limitation. A dispersal limitation index was calculated as:

$$\log\left(\frac{dist_{\max}}{disp_{\max}}\right),$$

where $dist_{\max}$ is the maximum distance between patches in the landscape and $disp_{\max}$ is the maximum recorded dispersal distance for the species ($n = 189$). A species with a negative limitation index should not be dispersal limited. For example, a limitation index of −2 indicates that dispersal ability is 2 orders

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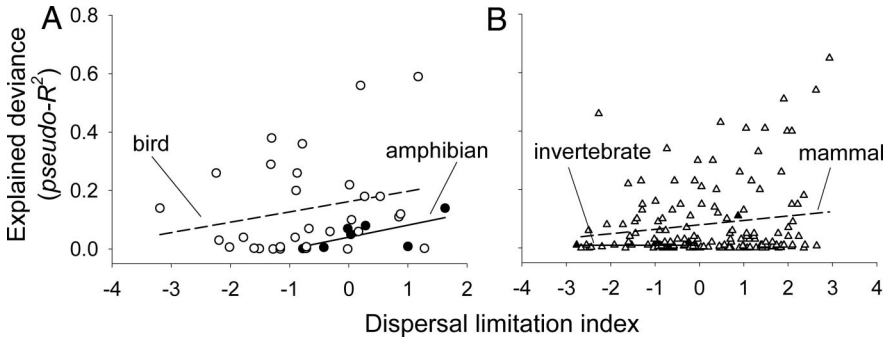

Fig. 2. Relationship between the dispersal limitation of a species and its sensitivity to patch isolation. The ability of patch isolation to predict occupancy was weakly related to dispersal limitation for all species combined ($F_{1,192} = 4.04$, $R^2 = 0.02$, $P = 0.05$). See *Scale* in *Results and Discussion* for calculation of dispersal limitation. Relationships were stronger for amphibians and birds (*A*) than for invertebrates and mammals (*B*) but were not significant for any individual taxonomic group (amphibians: $n = 7$, $R^2 = 0.45$, $P = 0.1$; birds: $n = 31$, $R^2 = 0.06$, $P = 0.2$; mammals: $n = 142$, $R^2 = 0.02$, $P = 0.06$; invertebrates: $n = 13$, $R^2 < 0.001$, $P = 0.98$). Patch isolation included all 3 measures (nearest patch, mainland, or source). When restricted to nearest source, the relationship was similarly weak ($F_{1,30} = 3.31$, $R^2 = 0.10$, $P = 0.08$). Alternative analyses using the slope parameter as a measure of effect size rather than pR^2 showed no relationship between dispersal limitation and isolation sensitivity ($F_{1,175} = 1.82$, $R^2 = 0.01$, $P = 0.18$ with all measures; $F_{1,30} = 1.25$, $R^2 = 0.04$, $P = 0.27$ with nearest source only).

of magnitude greater than the maximum distance between patches. Limitation indices ranged from −3.2 for the red-tailed hawk (*Buteo jamaicensis*) in Mexico (41) to 2.9 for the northern pocket gopher (*Thomomys talpoides*) in Washington (42), and nearly half (49%) of the species were not dispersal-limited according to this index. Dispersal records are notoriously poor and often rely on chance observations, so maximum dispersal distances are likely underestimated for many species. Thus, the number of dispersal-limited species may be fewer than indicated by this index. If a lack of dispersal limitation explains the low influence of isolation on occupancy, then sensitivity to isolation should increase as dispersal limitation increases. There was a positive relationship between isolation sensitivity and dispersal limitation across species, indicating that the poor performance of isolation as a predictor of occupancy may be caused due by inappropriate scaling. However, the relationship between isolation sensitivity and dispersal limitation was weak, particularly for mammals and invertebrates (Fig. 2). Use of mean dispersal distances and mean or minimum patch distances to create the dispersal limitation index produced similar results. Although the scale of patch area and isolation may have been inappropriate for some species, scale issues are insufficient to explain the weak overall effect of area and isolation on species occurrence patterns.

Species Traits. Sensitivity to area and isolation may have been low if particularly sensitive taxonomic groups, or species with certain life history traits, were poorly represented in the database. We examined the effects of taxonomic group, diet, specialization, habit (terrestrial or arboreal), and fecundity on area and isolation sensitivity by using general linear models. None of these factors significantly affected isolation sensitivity, but area sensitivity was affected by taxonomic group, diet, and habit (Fig. 3). Birds and mammals were most sensitive to area whereas amphibians were least sensitive, carnivores (including insectivores) were more sensitive than omnivores, and arboreal species were more sensitive than terrestrial species. It is notable that specialists, which should be more restricted to habitat patches than generalists, did not have increased sensitivity to patch area or isolation, despite inclusion of several individual studies that showed higher area sensitivity of specialists (e.g., ref. 43). This finding contrasts the idea that the habitat island paradigm fits terrestrial systems best when species that use matrix habitats are excluded from analyses (15, 16). The groups with relatively high area sensitivity (birds, mammals, and carnivores) were those

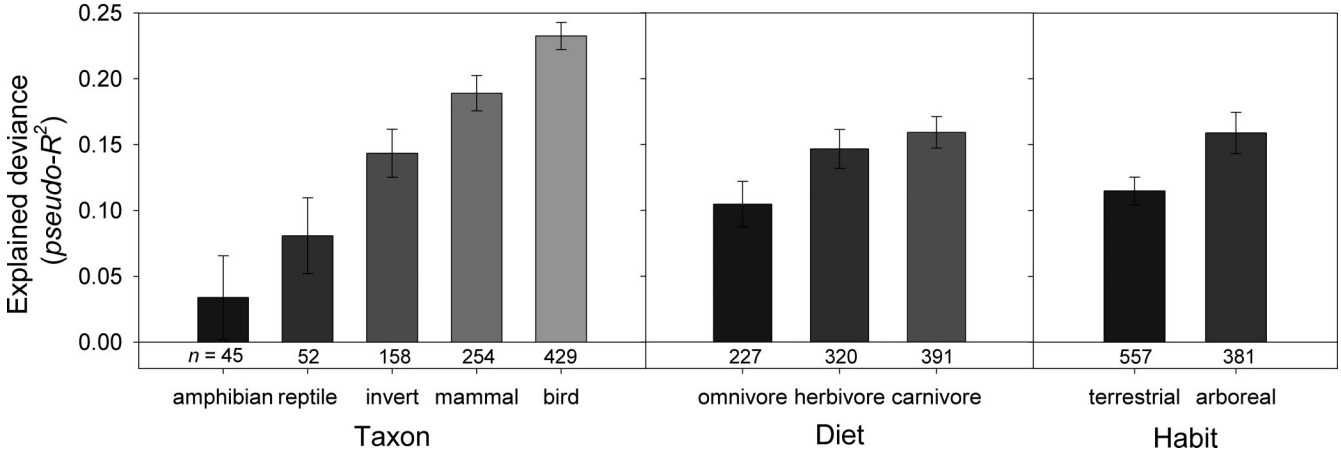

Fig. 3. Influence of species traits on the strength of patch area effects. The ability of patch area to predict occupancy was affected by the taxonomic group, diet, and habit of the species (full model $F_{7,930} = 14.2$, $R^2 = 0.10$, $P < 0.0001$; taxon $F_4 = 12.5$, $P < 0.0001$, diet $F_2 = 5.2$, $P = 0.005$, habit $F_1 = 7.7$, $P = 0.007$). Diets were grouped such that ''carnivore'' included insectivores and parasitoids and ''herbivore'' included frugivores, nectivores, granivores, and detritivores. Habit was grouped such that ''terrestrial'' included fossorial and semiaquatic species. Least-squared means and SE bars are shown.

with relatively high metabolic requirements rather than those with habitat restrictions; arboreal species were the only area-sensitive group with obvious ties to habitat requirements. Difficulty in defining and delineating habitat may partially explain the low area sensitivity of amphibians, because different habitats are often used during different life stages. Thus, delineated patches may underestimate the habitat actually used. These traits explain some of the variation in area sensitivity across species, but they do not explain the overall low effect of area on occupancy: area-sensitive groups were not poorly represented in the database and in fact tended to be better represented (Fig. 3).

Species Are Survivors. The landscapes in this metaanalysis had been fragmented for at least 30 years, so it is possible that area and isolation effects were weak because the most sensitive species had disappeared before surveys. Indeed, only 5% of the mammals, birds, and amphibians in the metaanalysis were classified as threatened by the International Union for Conservation of Nature (IUCN). Worldwide, 20% of species in these taxonomic groups are threatened (17). However, IUCN threat status was unrelated to area and isolation sensitivity ($n = 641$, $R^2 = 0.001$, $P = 0.39$), indicating that low pR^2 values were not caused by a lack of threatened species in the database. For example, the critically endangered mountain yellow-legged frog (*Rana muscosa*) and the endangered Amani sunbird (*Anthreptes pallidigaster*) were both insensitive to patch area ($pR^2 = 0.01$ and 0.0003, respectively). Conversely, the 2 most area-sensitive species (the wood thrush, *Hylocichla mustelina*, and the veery, *Catharus fuscescens*) are ranked as "least concern" by the IUCN but are experiencing declines throughout their large ranges (ref. 18 and http://bna.birds.cornell.edu/BNA). Species in the database are "survivors" in that they have persisted through initial habitat destruction, but many of their populations are far from secure. Doomed populations can take far >30 years to disappear after fragmentation (19). This extinction debt could also lessen area effects, but we found that the reverse was true: population networks in systems with a natural matrix, which have generally been fragmented for thousands of years, were actually the least sensitive to area.

Patches Are Not Islands. Unlike true oceanic islands, terrestrial habitat islands are not surrounded by a uniformly hostile matrix. Animals venturing outside of patches may find sufficiently benign conditions to live and reproduce, rendering the notion of the patch less relevant. We found strong effects of the matrix type on area and isolation sensitivity (Fig. 4). These broad patterns are particularly striking because the hostility of a matrix can vary widely among species within a landscape (20), and we therefore did not expect to find consistent effects of matrix type across species. Area sensitivity was higher in landscapes with human-dominated matrix types than in areas with natural matrix types. In contrast, isolation sensitivity was highest for population networks in forest patches surrounded by clear cuts. In these forestry-dominated landscapes, isolation effects were actually stronger than area effects even when landscape isolation measures were included.

The patch/nonpatch dichotomy appears to be a gross oversimplification for many species in fragmented landscapes. Irrespective of matrix effects, habitat patches often vary substantially in quality (21, 22). Many studies in this metaanalysis reported a strong influence of habitat quality on occupancy patterns. For example, patch area and isolation had little effect on the occupancy of most amphibians, whereas local habitat factors had stronger effects (45, 46). If habitat quality varies among patches, patch area may be a poor proxy of population size and thus unable to predict extinction probabilities accurately (23).

Habitat heterogeneity not only affects occupancy probabilities, but it also increases the difficulty of defining and delineating

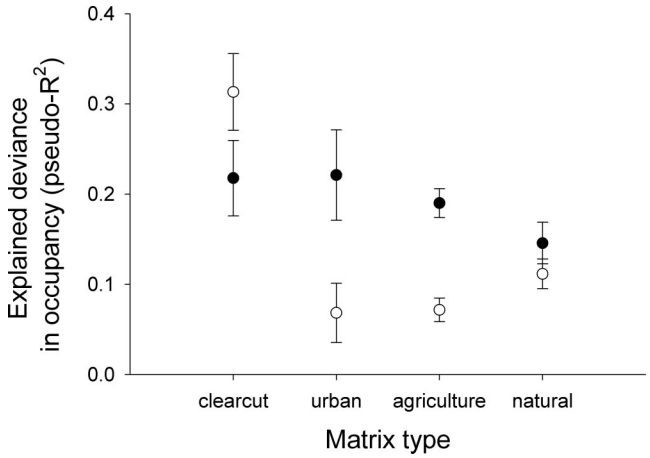

Fig. 4. Effect of predominant land cover in the matrix surrounding habitat patches on the sensitivity of species to patch area (●) and isolation (○). Sensitivity was measured as the proportion of deviance in occupancy accounted for by patch area or isolation in logistic regression analyses (pR^2). Analyses were weighted such that each study (i.e., landscape) contributed equally to the results ($n = 52$ agricultural landscapes, 7 forestry clearcut, 5 urban, and 25 natural). Patch area was a better predictor of occupancy in landscapes made patchy by human activities (agriculture, forestry, urbanization) than by natural processes ($F_{3, 950} = 5.2$, $P = 0.002$). Patch isolation (all measures included) best predicted occupancy in forest patches surrounded by clear cuts ($F_{3, 697} = 40.3$, $P < 0.0001$). Results were the same when analyses were restricted to studies using a demographic isolation measure ($F_{3, 77} = 11.7$, $P < 0.0001$). Error bars show 95% confidence intervals.

habitat patches in terrestrial landscapes (24). For example, extremely small patches may be ignored, and omission of small patches could lead to underestimates of area effects if those patches are empty. Furthermore, if some "nonhabitat" matrix areas are used by the animals, used patches may be both larger and closer together than those identified a priori by the researchers, thus contributing to the poor predictive power of area and isolation we detected.

Because habitat loss and fragmentation frequently co-occur, patch area and isolation may combine to reflect the influence of total habitat amount on a species (25). Previous work indicates that the total amount of habitat in a landscape may be the main determinant of population size and viability (26), and the spatial configuration of habitat does not influence occupancy until the proportion of habitat falls below a threshold (27–29). We were unable to test this hypothesis quantitatively because the total amount of habitat and nonhabitat in each landscape was unknown for most studies. However, maps of study areas in our metaanalysis generally showed that delineated habitat patches represented a small proportion of each landscape's total area. It is therefore unlikely that the poor predictive power of patch metrics across studies was caused by large amounts of identified habitat in each landscape.

Our empirical analysis of hundreds of animal species occurring in fragmented terrestrial landscapes throughout the world shows that patch area and isolation are poor predictors of occupancy in many cases. This finding does not mean patch metrics should be ignored altogether. Most species were more likely to be found in larger and less isolated patches, and some species were highly sensitive to patch area and isolation. However, the characteristics of intervening areas between patches, and of patches themselves, should not be ignored. The potential value of matrix areas for conservation has long been recognized (30–32), and our synthesis shows that landscape context has a strong effect on occupancy patterns across many taxonomic groups and ecosystems worldwide. The burgeoning body of research addressing

matrix attributes should greatly increase our ability to predict and enhance species' persistence probabilities in fragmented systems (33–36). Identification of key features that determine whether a species will occupy an area should also improve both occupancy modeling and habitat restoration efforts. Minimizing the impact of threats that accompany habitat destruction, such as the spread of exotic species, overexploitation, and degradation of habitat within patches may have larger conservation returns than focusing on the amount and configuration of remaining habitat (37, 38), at least for those populations that persist in the aftermath of habitat destruction.

Methods

Data Acquisition. In contrast to traditional metaanalyses, which are constrained by the often inconsistent statistical summaries reported in original publications, we maximized the size, accuracy, and standardization of our dataset by obtaining raw data directly from authors and conducting statistical analyses ourselves. Studies were found by a comprehensive search using the Web of Science in March 2005 with the terms ''patch occupancy,'' ''habitat occupancy,'' ''metapopulation,'' ''island biogeography,'' and ''incidence function.'' Forward and backward citations of articles found in these searches were also used to locate studies. Studies were included if 10 or more discrete terrestrial habitat patches (of the same general habitat type) were surveyed and raw occupancy data for birds, mammals, invertebrates, reptiles, or amphibians could be obtained. True island archipelagos were excluded. Hundreds of articles were screened, and 280 were examined in detail, 109 of which were found to be suitable for inclusion. Twenty of these studies were not included because raw data could not be obtained from the authors or their papers. The landscapes of the 89 studies included in the metaanalysis had been fragmented for a minimum of 30 years before surveys.

Logistic Regression Models. Patch occupancy data were analyzed in the program *R* by using logistic regression models. In each model, presence/absence was used as the dependent variable for single-year studies ($n = 67$) and years present versus years surveyed was used for multiyear studies ($n = 22$). A binomial distribution was assumed, and data were generally not overdispersed or underdispersed (dispersion = 1.08 ± 0.51 SD). When patch area and isolation were both available, 4 models were run for each population network with the following predictors: (*i*) patch area only, (*ii*) patch isolation only, (*iii*) area plus isolation (additive), and (*iv*) area × isolation (interactive). Univariate models were run when only area or isolation was available. Patch area (hectares) and isolation (meters) were log-transformed before analyses to allow for direct comparison of area and isolation regression coefficients; these coefficients (i.e., slopes of the logistic regressions) indicate the change in occupancy probability given an order of magnitude change in area or isolation. Analyses were also conducted on untransformed data, and results were similar. Population networks were treated independently; adding ''study'' as a random effect did not change results.

In addition to the slopes, intercepts, and associated errors, we also calculated the pR^2 of each model as:

$$\frac{\text{null deviance} - \text{residual deviance}}{\text{null deviance}}.$$

Null and residual deviances are analogous to the sum-of-squares estimates of linear regression (39). Although pR^2 does not have all of the statistical properties of the ordinary least-squares R^2 (such as a straightforward connection to the *F* statistic), it provides analogous goodness-of-fit estimates (9).

Paired *t* Tests on Slopes. To determine the relative strength of area and isolation effects, we used paired *t* tests of the coefficients (i.e., slopes) of univariate logistic regression models by using area and isolation as predictors ($n = 590$ population networks with both variables). A paired *t* test of area and isolation slopes should not differ from 0 if the strengths of area and isolation effects on occupancy are equal, because area slopes should be positive (occupancy increases with patch area) and isolation slopes should be negative (occupancy decreases with patch isolation). Positive differences in slopes indicate stronger area effects.

Weighting. In traditional metaanalyses, effect sizes are weighted by the inverse of the associated error estimates, so that studies with more precise estimates are given more weight in analyses (40). We did not weight analyses presented here, but see Figs. S2–S4 and *SI Text* for alternative analyses with weighted effect sizes. Weighting was not possible when comparing area and isolation slopes because there were 2 estimates of error (1 for each slope) and 1 estimate of effect size (the difference between the slopes). We did not weight pR^2 values shown in Figs. 1–3 to facilitate ease of interpretation and display the distribution of pR^2 values. Results from weighted and unweighted analyses were very similar.

Species and Landscape Traits. The effect of species traits on sensitivity to patch area and isolation was examined by using general linear models. Because body size, maximum lifespan, and fecundity were highly correlated ($r = -0.65$ for body size and fecundity, $r = 0.76$ for body size and lifespan), only fecundity was included in models because it had the strongest relationship with area and isolation sensitivity. The starting model included the following predictors: taxonomic group, diet, fecundity, specialization, and habit (see Table S2 for a full list of species and traits). Habit was categorized as arboreal (species primarily living in trees) and terrestrial (species primarily living on the ground, below ground, or in low shrubs). Diet was categorized as carnivorous (including insectivores and parasitoids), herbivorous (including frugivores, nectivores, granivores, and detritivores), or omnivorous (consuming plant and animal material). Reclassifying detritivores as omnivores did not affect results. Species were classified as specialists (primarily use 1 habitat or food item, e.g., monophagous insects) or generalists (use several habitats or foods). Sources for all species traits are available on request. The stepAIC modeling function in program *R* was used for analyses, in which forward and backward stepwise regression and Akaike Information Criterion (AIC) values were used to rank models. A Gaussian link was used. The model with the lowest AIC value was retained as the best model (Fig. 2 and Fig. S4).

The effect of matrix quality on area and isolation sensitivity was examined by an ANOVA comparing the pR^2 values among population networks in landscapes with different matrix types. Matrix types were classified as natural (e.g., meadows, forests), urban, agricultural, or clearcut. Landscapes containing multiple matrix types were classified according to the most prevalent type. ANOVAs were weighted such that each landscape contributed equally to the analysis to avoid overrepresentation of landscapes with occupancy records for large numbers of species (16).

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