

Fragments as Islands: a Synthesis of Faunal Responses to Habitat Patchiness

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Abstract: *Scientific interest in the impact of habitat fragmentation on biodiversity is increasing, but our understanding of fragmentation is clouded by a lack of appreciation for fundamental similarities and differences across studies representing a wide range of taxa and landscape types. In an effort to synthesize data describing ecological responses of animals to fragmentation across two classes of independent variables (taxonomic group and landscape), we sampled 148 studies of five major faunal groups from the primary literature and analyzed data on 13 variables extracted from those studies. We focused our analyses on three classes of dependent variables (effects of area and isolation on species richness, z values, and nestedness and species composition). Area ranged over more orders of magnitude than isolation and tended to explain more variation in species richness than isolation. There were few matrix or taxon effects on the patterns we investigated, although we did find that sky islands tended to manifest isolation effects on both species richness and nestedness more frequently than other patch types. Sky islands may offer insight into the future of habitat patches fragmented by contemporary habitat loss, and because they show a stronger effect of isolation than other patch types, we suggest that isolation will play an increasing role in the biology of habitat fragments. We use multiple lines of evidence to suggest that our understanding of the role of isolation on community assembly in fragmented landscapes is inadequate. Finally, our observation that consistent taxonomic differences in community patterns were minimal suggests that conservation actions intended to mitigate the negative effects of extinction may have far-reaching effects across taxonomic groups.*

Keywords: habitat fragmentation, habitat isolation, islands, matrix habitat, nestedness, species richness

Los Fragmentos como Islas: una Síntesis de las Respuestas de la Fauna a la Heterogeneidad de Hábitats

Resumen: *El interés de científicos en el impacto de la fragmentación del hábitat sobre la biodiversidad está aumentando, pero nuestro entendimiento de la fragmentación está ensombrecido por la falta de apreciación de similitudes y diferencias fundamentales en los estudios que representan a una amplia gama de taxa y tipos de paisaje. En un esfuerzo por sintetizar los datos que describen las respuestas ecológicas de animales a la fragmentación mediante dos clases de variables independientes (grupo taxonómico y paisaje), muestreamos 148 estudios de cinco grupos mayores de fauna en la literatura primaria y analizamos los datos de 13 variables extraídas de esos estudios. Concentramos nuestro análisis en tres clases de variables dependientes (efectos del área y el aislamiento sobre la riqueza de especies, valores de z, anidamiento y composición de especies). El área varió en más órdenes de magnitud que el aislamiento y tendió a explicar más variación en la riqueza de especies que el aislamiento. Hubo pocos efectos de la matriz o el taxón sobre los patrones que investigamos, aunque si encontramos que las islas elevadas tendían a manifestar efectos del aislamiento sobre la riqueza de especies y el anidamiento más frecuentemente que los otros tipos de fragmento. Las islas elevadas pueden ofrecer una panorámica del futuro de los parches de hábitat fragmentados por la pérdida de hábitat, y porque muestran un mayor efecto del aislamiento que otros tipos de parche, sugerimos que el aislamiento tendrá un papel cada vez mayor en la biología de los fragmentos de hábitat. Utilizamos líneas múltiples de evidencias para sugerir que nuestro entendimiento del papel del aislamiento en el ensamble de comunidades en paisajes fragmentados es inadecuado. Finalmente, nuestra observación de que la consistencia*

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en las diferencias taxonómicas fue mínima sugiere que las acciones de conservación para mitigar los efectos negativos de la extinción pueden tener efectos de gran repercusión en diferentes grupos taxonómicos.

Palabras Clave: aislamiento del hábitat, anidamiento, fragmentación del hábitat, hábitat matriz, islas, riqueza de especies

Introduction

Habitat loss and fragmentation are among the principal threats to current levels of terrestrial biodiversity (e.g., Brooks et al. 2002; Stockwell et al. 2003; Reed 2004), and this realization has resulted in a dramatic increase in the number of scientific articles devoted to the study of habitat patchiness. Although anthropogenic habitat fragmentation is the stimulus for much of the research on patchy landscapes, a thorough understanding of the implications of habitat fragmentation requires data from a variety of patchy habitats (e.g., oceanic islands, habitat remnants, forest islands; see Table 1 for definition of terms used throughout our review). The theoretical underpinning of most studies of anthropogenic habitat fragmentation is provided by the equilibrium theory of island biogeography (ETIB), a theory intended to explain patterns of species richness on oceanic islands (MacArthur & Wilson 1967). The use of the ETIB as a tool to understand community assembly in modified terrestrial landscapes may be problematic if patterns on virtual habitat islands do not mimic those observed on real islands. Although problems with the ETIB have been identified (reviewed in Gilbert 1980), and it has been recognized that key patterns underlying the ETIB may be more complicated than is often recognized (Lomolino & Weiser 2001), we are unaware of a systematic investigation of the analogy between oceanic islands and habitat remnants.

In an effort to clarify the understanding of habitat patchiness in all its forms, attempts have been made to synthesize knowledge of fragmented systems and suggest frameworks for the study of habitat patchiness (e.g., McGarigal & Cushman 2002; Watson 2002; Brotons et al. 2003). In a similar spirit of reviewing and synthesizing existing knowledge of habitat patchiness, we surveyed 148 studies from the primary literature to identify patterns among taxonomic groups and patch and matrix types with respect

to (1) species richness, (2) z values, and (3) nestedness and species composition. We believe that identification of broad patterns can serve to identify gaps in existing knowledge, provide a foundation for future research, and suggest empirical guidelines based on general trends. To that end, we discuss the relevance of the results revealed by our analyses to the field of conservation science.

Because area and isolation are the main correlates of the extinction and colonization processes theorized to drive species richness patterns, we quantified several aspects of the relationships among species richness, area, and isolation. The analysis and interpretation of z values, the slope estimate resulting from a log-log species-area regression ($\log S = \log k + z \log A$, where S is species richness, A is area, and k and z represent the intercept and slope of the species-area regression) has been a contentious area of fragmentation and island biogeography research, with some authors interpreting z values biologically and others suggesting no biological meaning can be attributed to z (Preston 1962; Connor & McCoy 1979; Gilbert 1980). Because z values continue to feature in discussions of the conservation implications of the ETIB (e.g., Desmet & Cowling 2004), we compared z values across matrix types and taxa to investigate whether z is consistently different across levels of these two factors.

Biotic nestedness describes a particular type of structure among assemblages in which the biota of species-poor patches represents a perfect (i.e., nested) subset of the fauna of species-rich patches (Patterson & Atmar 1986; Worthen 1996). Nestedness is characteristic of many taxa and landscape types, but relatively few attempts have been made to elucidate general trends resulting from studies of nestedness since the metric was formalized (but see Boecklen [1997] and Wright et al. [1998] for quantitative syntheses of nestedness patterns). We included analyses of nestedness as one type of compositional pattern but also included more general analyses of

Table 1. Definitions of terms used throughout the review of faunal responses to habitat patchiness.

<i>Term</i>	<i>Definition</i>
Patch	any discrete habitat unit surrounded by a distinct habitat ("matrix") from which it is easily distinguishable
Matrix	habitat surrounding a patch
Oceanic island	terrestrial patch surrounded by an aquatic matrix that has not been connected to a more continuous "mainland" since at least the Pleistocene epoch
Landbridge island	terrestrial patch surrounded by an aquatic matrix that was connected to a more continuous "mainland" during the Pleistocene
Virtual or habitat island	terrestrial patch surrounded by a terrestrial matrix; in contrast to a landbridge or oceanic island

species composition and test for differences in these two dependent variables across area and isolation gradients and among faunal groups.

Methods

We sampled the primary literature on habitat fragmentation and island biogeography for case studies. In an effort to collect as representative a data set as possible, we conducted a keyword search for *species richness and area and isolation* and *habitat fragmentation and nestedness* in the Web of Science on line database in April 2005, and acquired publications resulting from those searches. Of 185 articles only 45 included analyses from which we could build our data base or that had the raw data necessary to calculate the desired statistics. We supplemented the studies resulting from on line searches with articles that included data we could use for our analyses, many of which were obtained from a recent synthesis of the species-area relationship (SAR) (Lomolino & Weiser 2001). These combined approaches resulted in data from a total of 148 studies, a list of which is available from J.I.W.

We collected data on 13 variables for our analyses (Table 2). If only analyzed data were included in an article, we used the authors' results in assembling our database. If raw data were included (most often in the form of tables with area, isolation, and species richness values, or species-by-site matrices appropriate for calculation of a nestedness index and species richness totals by sites), we analyzed the data ourselves and used our results, even

if they differed slightly from the authors' original estimates. For taxon, we lumped amphibians and reptiles into one category because the studies we examined included several different data partitions, including lizards, amphibians, amphibians and reptiles separately, and amphibians and reptiles together. Because snakes are embedded within lizards (Pough et al. 2001), rendering lizards a nonphylogenetic group, existing data were confounded. Thus, rather than analyzing natural groups represented by small sample sizes, we grouped all terrestrial poikilothermic vertebrates together.

For some analyses with matrix type and patch type, we excluded poorly represented types (<5 case studies) or collapsed them into broad categories (e.g., aquatic vs. terrestrial matrices or real islands vs. virtual islands). Because few studies included details on the intensity or type of farming occurring in agricultural matrices (i.e., use of pesticides, extent of fallow land, periodicity of harvest), we did not attempt to incorporate these data into our analyses. In cases where cropland was mixed with pasture or other land use, we categorized the matrix as agriculture unless it was not clear what the dominant land use in the matrix was, in which case we simply categorized the matrix as terrestrial. Range in patch isolation was measured as either distance to continuous "mainland" habitat, nearest patch, or nearest larger patch depending on which variable provided the strongest species-isolation relationship. If only one isolation metric was included in a study, we used that estimate of isolation. The R^2 of the regression equation describing the relationship between area and isolation was a test of the strength of colinearity

Table 2. The 13 variables used to characterize fragmented landscapes in this study.

<i>Variable</i>	<i>Categories</i>
Taxon	(1) bats, (2) birds, (3) herps (amphibians and/or reptiles), (4) invertebrates, (5) nonvolant mammals
Matrix type	(1) water, (2) agriculture (includes pastures and plantations), (3) grassland, (4) scrub, (5) urban, (6) desert, (7) ghost forest (standing trees surrounding hilltop islands formed by flooding of low-lying areas), (8) forest, and (9) terrestrial (if matrix type was not specified)
Patch type	(1) landbridge islands, (2) oceanic islands, (3) mixed oceanic and landbridge islands, (4) barrier islands, (5) terrestrial remnants, (6) islands resulting from flooding, (7) sky islands (high-elevation vegetation formations, usually forest, surrounded by a lowland "sea" of distinct habitat, usually desert), (8) Carolina bays, (9) lakes, (10) coral reef heads, (11) salt marshes, (12) bushes, (13) forest islands, (14) calcerous grasslands, (15) temporary wetlands, and (16) pine plantations
Number of species	
Number of patches	
Range in patch area (ha)	
Range in patch isolation (m)	
R^2 value resulting from species-area regression	
R^2 values resulting from species-isolation regression	
z value (slope) of species-area regression	
R^2 of area-isolation regression	
Nestedness temperature	
Significance of regression between isolation and residuals of the species-area relationship	

between area and isolation. We included significance of the regression equation describing the relationship between isolation and the residuals of the SAR if isolation was not related to species richness itself to see whether there was a relationship between isolation and species richness after accounting for the variation in species richness explained by area.

When possible, we calculated regression equations describing the relationship between natural log-transformed values of species richness, area, and isolation. Although there is not a strong theoretical framework for quantifying the relationship between species richness and isolation, the literature on the SAR suggests that the best fit between variables is not necessarily achieved by log transformation of data (Connor & McCoy 1979; He & Legendre 1996; Tjørve 2003). However, log-log transformation is probably the single most common transformation used to describe the SAR, so we log transformed all variables to provide a standard comparison across studies. In cases with no relationship between isolation and species, we saved the residuals of the species-area regressions and calculated regressions between those residuals and isolation to see whether isolation explained variation in species richness after removing the effect of area on richness. We also used regression analyses to test for intercorrelation between patch area and isolation within studies.

We compared differences in the range of area and isolation values represented in studies by using the number of orders of magnitude spanned by area or isolation as the dependent variable. We also tested for an association between the range of area or isolation values included in a study and the amount of variance in species richness explained by area or isolation, respectively. For all species-area and species-isolation equations, we recorded R^2 values to determine whether one variable consistently explained more variation in species richness than the other. We used t tests or analyses of variance (ANOVA) to quantify variation in the explanatory power of area and isolation on species richness across matrix types and taxa. If ANOVA revealed a significant difference in a variable across factor levels, we used Tukey's honestly significant difference (HSD) post hoc test to determine which factor levels differed significantly from one another.

We used parametric tests to test for differences in z values (the slope of the SAR) across matrix types and taxa. Because z has been interpreted as a metric of the "strength" of the SAR, we tested for the association between z and the amount of variance in species richness explained by area, an alternative metric of the strength of the SAR.

We used the nestedness temperature calculator (Atmar & Patterson 1993) to quantify nestedness of species-by-site matrices. The nestedness temperature calculator provides a nestedness score (T) that ranges from 0 to 100, with low scores ("cool temperatures") indicating nested matrices. We compared T across matrix types and taxa, in addition to testing for relationships between T and patch

area and isolation gradients (i.e., determining whether nestedness was more pronounced in studies with relatively large ranges in patch area and isolation). For associations between nestedness and area and isolation (i.e., whether matrices were nested along area or isolation gradients), we calculated regression equations describing the relationship between area and isolation and the rank order of patches in the maximally nested matrix [see Patterson and Atmar (2000) for an explanation of the approach]. It has been pointed out that T may be prone to Type I statistical errors (i.e., it overestimates the degree and significance of nestedness; Fischer & Lindenmayer 2002). However, because we were concerned with the comparative aspects of nestedness rather than the actual nested values themselves, we consider T to be a useful statistical tool. In all cases where raw data were provided, we created species-by-site matrices and ran all analyses ourselves; in a few cases we relied on analyses provided by the authors.

We used the same species-by-site matrices as in the nestedness analyses to test for differences in species composition. Compositional data were analyzed in program Primer (Clarke & Warwick, 2001) in which analyses of similarity (ANOSIM) tested for differences in species composition between area and isolation classes based on the presence-absence data. The ANOSIM uses a resampling approach to estimate the significance of compositional differences among factor levels. We tested for compositional differences between two factors (area and isolation) with two levels each (large or small and near or far). We divided patches into large and small or near and far by assigning half the patches in a study to one category and the other half to the other category. It was not possible to assign global estimates of patch size or isolation based on the range of values observed across all studies because the range of patch size (or isolation) included within a study would fall into only one size (or isolation) category, making it impossible to compare differences in species composition between patch types. The ANOSIM procedure results in a test statistic (global R) that describes the separation of compositional data among factor levels. We utilized univariate statistics to test for differences in global R by matrix types and taxa. We used a t test to determine whether there was a difference in global R when sites were separated into area classes versus isolation classes (i.e., to determine whether there was greater separation of patch composition by area or by isolation). Finally, we tested for an association between global R and the range of area and isolation values included in a study to determine whether species composition was more distinct between size or isolation classes when the range in size or isolation was relatively large.

Results

The specific questions we addressed and their answers based on our analyses are summarized in Table 3. Below

Table 3. Summary of results describing differences in area and isolation gradients, species richness, z values, and nestedness across matrix types and taxa.

	<i>Area & isolation</i>	<i>Species richness</i>	<i>z values</i>	<i>Nestedness</i>
General patterns				
Difference in range of values included in a study?	yes, area ranges over more orders of magnitude than isolation			
Difference in amount of variance in species richness explained by area versus isolation?	yes, area explains more variance in richness than isolation			
Increase in amount of variance in species richness explained with increasing range of area values?	yes			no
Increase in amount of variance in species richness explained with increasing range of isolation values?	no			yes
Difference in nestedness with size of species-by-site matrix				no
Increase in nestedness with increasing range of area values?				yes
Increase in nestedness with increasing range of isolation values?				no
Matrix & patch effects among all matrix types				
Difference in amount of variance explained by isolation?		no	weakly significant, lower z values in agricultural matrices than other matrix types	no
Difference in amount of variance explained by area?		no		
Difference between terrestrial patches and real islands?			yes, z values are greater on real islands than terrestrial patches	weakly significant, with islands more nested than terrestrial patches
Difference in amount of variance explained by isolation?		no		
Difference in amount of variance explained by area?		no		
Difference between landbridge and oceanic islands?		no		no
Difference in amount of variance explained by isolation?		no		
Difference in amount of variance explained by area?		no		no
Taxon effects				
Difference in amount of variance explained by isolation?		no		
Difference in amount of variance explained by area?		yes, area explains more variance in species richness of birds than invertebrates		

we describe our results across the three broad categories of variables analyzed: area and isolation effects on species richness, z values, and nestedness and species composition.

Area and Isolation

We analyzed 118 studies with data on the SAR, which was significant and positive in 91% of cases, significant and negative in 1% of cases, and not significant in 8% of cases. There was no clear trend in the type of study that failed to reveal a significant SAR. A total of 81 studies provided data on the relationship between species richness and isolation. Of the 81 studies, 54 (67%) showed no relationship between species richness and isolation. In the remaining 27 studies (33%), the relationship between variables was significant and negative, and most of these studies (19 of 27) occurred on true islands. However, of the eight terrestrial studies that had a significant relationship between richness and isolation, five were of sky islands, and only two out of seven studies of sky islands failed to show a relationship between richness and isolation.

Because only one-third of studies showed a relationship between species richness and isolation, we tested for a relationship between isolation and the residuals of the SAR to see whether isolation could explain variation in species richness across islands with the effect of area on richness removed. The 56 studies used in this analysis did not include studies from which we reported a significant species-isolation relationship above. Twelve out of the 56 studies (21%) showed a significant or suggestive relationship between isolation and the residuals of the SAR, suggesting that a substantial minority of cases may indeed exhibit an isolation effect, albeit indirectly. Ten of the 12 cases with an association between isolation and the residuals of the SAR occurred in studies of true islands.

Seventy-six studies provided data on both patch area and isolation, and in 21 of 76 studies (28%) there was significant intercorrelation between area and isolation. In 12 cases, the relationship between patch area and isolation was negative (i.e., smaller islands were more isolated from source habitat than larger islands), but there was no clear trend in the patch type represented by these studies. Nine of the 21 cases showed a positive relationship between area and isolation, and all of these studies occurred on patches surrounded by aquatic matrices (landbridge or oceanic islands or, in one case, patches created by the flooding of low-lying terrain).

Across all studies, patch area ranged over more orders of magnitude than patch isolation ($F_{1,279} = 125.588$, $p < 0.001$; area mean = 2.750 ± 0.083 , isolation mean = 1.391 ± 0.088). This was true for islands ($F_{1,168} = 113.681$, $p < 0.001$; area mean = 3.057 ± 0.109 , isolation mean = 1.390 ± 0.112) and terrestrial patches ($F_{1,115} = 29.600$,

$p < 0.001$; area mean = 2.302 ± 0.114 , isolation mean = 1.389 ± 0.123). Area explained more of the variance in species richness than isolation ($F_{1,224} = 136.181$, $p < 0.001$; area mean = 0.547 ± 0.017 , isolation mean = 0.232 ± 0.021) across all studies and in terrestrial patches ($F_{1,92} = 42.396$, $p < 0.001$; area mean = 0.542 ± 0.029 , isolation mean = 0.230 ± 0.038) and true islands ($F_{1,128} = 97.319$, $p < 0.001$; area mean = 0.553 ± 0.020 , isolation mean = 0.236 ± 0.025).

Because the range in patch area tended to be greater than the range in patch isolation, and area explains more variance in species richness than isolation, we wanted to determine if the amount of variance in species richness explained depended on the range in values of area and isolation included in a study. Across all studies, there was a significant, positive relationship between the amount of variance in species richness explained by area and the range in island areas represented in a study ($F_{1,136} = 6.577$, $p = 0.011$), but this was not true for isolation ($F_{1,84} = 2.163$, $p = 0.145$). The relationship between R^2 and range in area across studies was driven by results from studies of true islands ($F_{1,77} = 5.059$, $p = 0.027$) because terrestrial patches showed no such pattern ($F_{1,57} = 2.308$, $p = 0.134$). The relationship between R^2 and range in isolation values was not significant on true islands ($F_{1,50} = 2.479$, $p = 0.1217$) or terrestrial patches ($F_{1,32} = 0.180$, $p = 0.674$).

There was no difference in the amount of variation in species richness explained by area across different matrices (agriculture, urban, desert, water; $F_{3,113} = 0.228$, $p = 0.877$). Distinguishing between real and virtual islands revealed no difference in the amount of variance in species richness explained by area ($t = -0.245$, $df=136$, $p = 0.871$), nor did distinguishing between landbridge and oceanic islands ($t = 1.469$, $df=61$, $p = 0.147$). Similarly, there were no differences in the amount of variation in species richness explained by isolation among matrix types ($F_{3,72} = 0.462$, $p = 0.710$), between real and virtual islands ($t = -0.085$, $df=86$, $p = 0.933$), or between landbridge and oceanic islands ($t = -0.652$, $df=37$, $p = 0.518$).

Across taxa (bats, birds, amphibians and reptiles, invertebrates, and nonvolant mammals), we found a difference in the amount of variation in species richness explained by area ($F_{4,133} = 3.977$, $p = 0.004$), and Tukey's HSD post hoc test indicated that area explained significantly more difference in species richness among patches for birds (mean $R^2 = 0.626$) than invertebrates (mean $R^2 = 0.452$). No other comparisons among taxa were significantly different. There were no differences in the amount of variance in species richness explained by isolation across taxa ($F_{4,83} = 0.567$, $p = 0.688$). To determine whether there was a taxon-by-matrix-type interaction in the ability of area or isolation to explain variation in species richness, we used a two-way ANOVA to test for differences across levels of the independent variables and the interaction

between them. Because of lost degrees of freedom in the analyses as a result of the large number of factor levels included in the analyses, for two-way ANOVAs, we collapsed taxa into two categories (volant vs. nonvolant, excluding invertebrates) and matrices into two classes (terrestrial vs. aquatic). In both cases, the overall models were not significant ($F_{3,92} = 0.829$, $p = 0.481$ and $F_{3,56} = 0.166$, $p = 0.919$ for area and isolation, respectively) and effects tests indicated no significant effect of taxa, matrix type, or the interaction between the two on the amount of variance explained by patch area or isolation.

Z Values

The z values were significantly higher on true islands (mean = 0.256) than in terrestrial patches (mean = 0.202; $t = -2.675$, $df=134$, $p = 0.008$). Further analyses across four matrix types (agriculture, desert, urban, and water) showed a weakly significant difference across factor levels ($F_{3,111} = 2.659$, $p = 0.052$), with the highest z values on true islands and lowest in agricultural matrices (mean $z = 0.259$ and 0.183 , respectively). There were no differences in z values between landbridge and oceanic islands ($t = 1.190$, $df=61$, $p = 0.239$) and no differences across taxa either when groups were combined into an analysis of volant versus nonvolant taxa ($t = 0.865$, $df=93$, $p = 0.389$) or across the five taxonomic groups ($F_{4,131} = 0.763$, $p = 0.551$). A two-way ANOVA with combined categories for both independent variables (true islands vs. terrestrial patches and volant vs. nonvolant taxa) confirmed the patterns described from the univariate models above. Although the overall model was not significant ($F_{3,91} = 1.632$, $p = 0.187$), effects tests indicated no effect of taxon ($F_{1,91} = 0.396$, $p = 0.531$), a weakly significant effect of matrix ($F_{1,91} = 3.732$, $p = 0.057$), and no interaction between main effects ($F_{1,91} = 0.322$, $p = 0.572$). Across all studies, z values and the R^2 of the species-area regression were significantly associated ($F_{1,134} = 20.401$, $p < 0.001$).

Nestedness and Species Composition

Of the 67 studies including data suitable for analysis of nestedness, 63 (94%) of the species-by-site matrices were significantly nested. Fifty studies included data with which we could calculate correlations between nestedness and area and nestedness and isolation. Nestedness was correlated with island area in 42 (84%) of the cases. There was no apparent trend to the identity of the eight studies in which nestedness was significant but not correlated with area. Thirty-four studies included sufficient data with which to test for an association between nestedness and patch isolation, and this relationship was significant in nine cases (26%), although in all nine cases in which nestedness was associated with isolation, it was also associated with area. Six of the nine cases that show a significant association between nestedness and isolation were studies of sky islands. The only study of sky islands

that did not show a relationship between nestedness and isolation did not include the data with which to test for a relationship.

Studies occurring on true islands were more nested than studies of terrestrial patches ($t = 1.919$, $df=75$, $p = 0.059$; mean nestedness temperature on islands = 13.60 ± 1.48 and 17.76 ± 1.58 on terrestrial patches). Differences in nestedness temperature were not significant when we expanded our analysis to differentiate between desert, urban, agricultural, and aquatic matrices ($F_{3,64} = 2.107$, $p = 0.108$). Similarly, there was no difference in nestedness temperature between oceanic and landbridge islands ($t = -0.687$, $df=23$, $p = 0.499$). Nestedness temperature did not vary by taxon ($F_{3,72} = 1.396$, $p = 0.251$). Bats were not included in the previous analysis because only one study provided data with which to calculate a nestedness temperature. We found no difference in nestedness temperature when we compared studies of volant versus nonvolant taxa (excluding invertebrates, $t = -0.015$, $df=56$, $p = 0.988$). In a two-way ANOVA comparing nestedness scores between matrix type (aquatic/terrestrial) and taxon (volant/nonvolant) and their interaction, the overall model was weakly significant ($F_{3,54} = 2.458$, $p = 0.073$), with a significant main effect of matrix type ($F_{1,54} = 7.184$, $p = 0.010$) but no effect of taxon ($F_{1,54} < 0.001$, $p = 0.996$) and no interaction between main effects ($F_{1,54} = 0.004$, $p = 0.952$).

The sizes of the species-by-site matrix and nestedness temperature were not associated ($F_{1,72} = 0.036$, $p = 0.851$). Although nestedness temperature was not related to the range in patch isolation ($F_{1,69} = 2.526$, $p = 0.117$), nestedness temperature was negatively related to the range in patch area represented ($F_{1,75} = 8.603$, $p = 0.004$). In other words, nestedness was more pronounced (i.e., lower nestedness temperature) in studies where the range of patch areas was relatively high.

In 29 studies (63% of the total tested), there was a significant or weakly significant effect of area on species composition, whereas only 33% showed a significant effect of isolation on species composition. There were no clear trends in the type of studies demonstrating significant relationships between variables. Species composition showed greater separation between patch-size classes (mean global $R = 0.290 \pm 0.035$) than for isolation classes (mean global $R = 0.141 \pm 0.042$; $t = 2.715$, $df=77$, $p = 0.008$). There was no effect of taxon or matrix type on the differentiation of patches between size classes ($F_{3,34} = 0.220$, $p = 0.882$) or isolation classes ($F_{3,23} = 2.184$, $p = 0.117$).

Discussion

Area and Isolation

One of the clearest results to emerge from our analyses was that the range in patch area represented in studies

was well over an order of magnitude greater than range in isolation. This raises the possibility that area effects on species richness may be more widely reported in the literature than isolation effects at least in part because of differences in the scale over which the two variables are measured. That is, the relatively narrow range in isolation values included in studies may preclude the recovery of strong species-isolation relationships simply because there is not enough variation in isolation to drive a response in species richness. Furthermore, area and isolation were intercorrelated in one-fifth of studies tested. Approximately half of these studies showed a negative relationship between the two variables, and half showed a positive relationship. In approximately one-fifth of studies in which there was not a significant relationship between species richness and isolation, there was a relationship between the residuals of the SAR and isolation. We do not believe the observation that area exerts a stronger influence on species richness than isolation is solely the result of statistical artifact, but we do suggest that the role of isolation on species richness may be underappreciated because of methodological and analytical procedures.

A greater understanding of the importance of isolation on species richness is of practical as well as theoretical interest. An increase in habitat loss results in an increase in the distance separating neighboring fragments (Andr n 1994), a pattern seen throughout species-rich tropical forests (S nchez-Azofeifa et al. 2003; DeFries et al. 2005). As protected areas become more isolated, it may be expected that the importance of isolation as a driver of patch richness will increase. This implies an increase in the importance of conservation actions designed to mitigate the negative effect of isolation on patch biota. Small reserves, although they may not be capable of supporting sustainable populations of target taxa, may be important stepping stones linking larger protected areas (Baum et al. 2004). Although the conservation value of corridors and stepping-stone reserves is debated (e.g., Hannon & Schmiegelow 2002; Baum et al. 2004), repeated calls for more research into the biology of corridor use underscore our suggestion that the biology of isolation should be a focus of fragmentation research.

A growing literature attests to the importance of matrix effects on patch dynamics (Ricketts 2001; Cook et al. 2002), and the results of several studies demonstrate single-species responses to variation in matrix type (Gobeil & Villard 2002; Haynes & Cronin 2003; Stevens et al. 2004), yet we found no matrix effect on the ability of area and isolation to explain variation in species richness on patches. Our data therefore raise the question as to how the matrix affects community-level patterns in patchy landscapes. Several processes have been invoked to explain SARs (reviewed in Hill et al. 1994), although we are not aware of a similarly well-developed literature underlying species-isolation relationships. If there are systematic differences across matrix types in the processes driving relationships between patch characteristics and species

richness (i.e., richness is driven by energetic relations on true islands but by disturbance processes in agricultural matrices), overall matrix effects on community patterns may be obscured. More important, explicit recognition of the processes underlying the distribution of species richness will help inform conservation initiatives in fragmented landscapes. If species richness in one system is driven by the maintenance of a mosaic of successional stages, this implies a different set of conservation strategies than in a system in which species richness is driven by population dynamics as postulated by the ETIB. Therefore, more explicit consideration of the process underlying species-area and species-isolation relationships may help illuminate the importance of the matrix on community assembly and the utility of alternative conservation strategies.

Z Values

We found no evidence for consistent taxonomic differences in z values. It has often been assumed that differences in z may be interpreted as a relative metric of immigration rates (with lower z values, or shallower slopes indicating greater matrix permeability and therefore increased immigration rates; Connor & McCoy 1979; Rosenzweig 1995; Krauss et al. 2003). If this is true, our results imply that taxonomic groups do not show consistent differences in their capacity for immigration. In contrast, many authors assume that dispersal capabilities vary consistently among taxonomic groups (e.g., birds and invertebrates are often assumed to be good dispersers, whereas amphibians and reptiles are often assumed to be poor dispersers; Quinn & Harrison 1988; Cook & Quinn 1995). We believe that our observation that isolation may be systematically underappreciated (see above) coupled with the observation that common assumptions about dispersal abilities are not reflected in community-level patterns reinforce our suggestion that a deeper understanding of the implications of isolation and dispersal abilities on patch assembly is needed.

Studies of true islands tended to have higher z values ($z = 0.259$) than studies of terrestrial patches, and this result was primarily driven by the relatively low z values reported from studies of patches in agricultural matrices ($z = 0.183$). Although Preston (1962) considered slope values of 0.17–0.33 to fall within the “canonical range” predicted from a log-normal relative abundance distribution, Connor and McCoy (1979) argue that slope values outside the range 0.20–0.40 may be interpreted biologically. If so, the low-average slope value seen in many studies of agricultural matrices may suggest higher immigration rates in that matrix type and underscore the importance of matrix effects on species richness patterns in patchy landscapes. Specifically, the maintenance of populations in agricultural matrices may serve to maintain sufficient movement throughout the landscape to keep patch-level extinction rates lower than in other matrix types (e.g.,

Knutson et al. 2004; Silva et al. 2005). This provides support for calls for active management of the matrix around protected areas as a means of maintaining the biological integrity of reserves (Mazerolle & Villard 1999; Baum et al. 2004). We recognize that this result is at odds with our finding that the ability of area and isolation to explain variation in species richness is not affected by matrix type and suggest that this discrepancy warrants further investigation.

Nestedness and Species Composition

Nestedness was associated with area much more frequently than with isolation. If we assume that area is associated with extinction processes (MacArthur & Wilson 1967; Gilpin & Diamond 1976; Rosenzweig 1995), our data indicate that nestedness is most often a result of extinction processes rather than colonization processes. Because nestedness did not vary among taxonomic groups, our data imply that extinction trajectories are similar across taxa. This observation is supported by data indicating that the characteristics associated with extinction proneness are similar across taxonomic groups (Henle et al. 2004).

Our failure to uncover consistent taxonomic differences in our analyses may indicate that organismal responses to habitat patchiness are so variable that it is not possible to make general conservation recommendations on anything but a species-by-species or site-by-site basis (e.g., Schmiegelow & Monkkonen 2002). Alternatively, our observation may imply that conservation actions taken to prevent species losses in a landscape will have broad impacts across a range of taxa. For example, given a reserve (or series of reserves), actions taken to mitigate extinction-based processes (i.e., stepping-stone reserves, corridors, and management of the matrix surrounding reserves) may have broad effects across many taxonomic groups. This is particularly relevant to conservation of biodiversity hotspots, where species richness and endemism are concentrated (Brooks et al. 2002). Studies describing species responses to corridors and other landscape features designed to increase "connectivity" are rare, and few researchers have investigated responses of multiple taxa to such manipulations. Although we are aware that any generality is likely to generate numerous exceptions, we believe that data suggesting that community-level responses to habitat patchiness do not discriminate among taxa (and the potential conservation benefits this implies) are worthy of further consideration.

The Case of Sky Islands

Our analyses indicated that sky islands are more likely to show a significant effect of isolation on species richness compared with other patch types, and they are also more likely to be nested along an isolation gradient. Thus, although we found that isolation effects on patch patterns

were generally secondary to area effects, two independent lines of evidence attest to the importance of isolation on sky islands. A recent classification system distinguished eight types of patchy landscapes on the basis of three patch characteristics: origin (island or fragment), contrast (the structural difference between a patch and its surrounding matrix, categorized as low contrast or high contrast), and age (Watson 2002). Within the context of this classification system, habitat patches resulting from anthropogenic habitat loss are generally classified as young, low-contrast fragments, whereas sky islands are old, low-contrast fragments. The difference between anthropogenic habitat fragments and sky islands is one of age, and we suggest that sky islands may serve as a window to the future of forest remnants resulting from contemporary habitat loss. Our observations that isolation plays an elevated role on community-level patterns on sky islands compared with other patch types reinforces our earlier call for an improved understanding of the biology of immigration in patchy landscapes.

We found that area consistently exerted a stronger influence on the ecology of fragmented landscapes than isolation: area explained more variance in species richness than isolation, was more often correlated with nestedness than isolation, and explained more of the differentiation in species composition among patches than isolation. We argue that at least some of the primacy in area over isolation may be the result of the greater range in patch areas included in studies relative to isolation and suggest that the role of isolation may be underappreciated because of statistical reasons rather than biological ones. When isolation was found to affect patch ecology, it did so more frequently on sky islands than in other patch types, and we argue that sky islands may provide a relevant window to the future awaiting habitat fragments resulting from contemporary anthropogenic fragmentation. Finally, our observation that community-level responses to habitat patchiness were quite similar across taxonomic groups and terrestrial matrices suggests that conservation actions to mitigate species losses will benefit a large proportion of the fauna in target areas.

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