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RARITY, FRAGMENTATION, AND EXTINCTION RISK IN DESERT FISHES

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Abstract. Theoretical efforts and small-scale experiments have given rise to the widespread belief that the fewer occurrences a species has or the more fragmented its distribution is, the more vulnerable that species should be to extinction. Lacking, however, are large-scale multi-species studies exploring the connection between rarity and local extinction risk. Here we present a landscape-level biogeographic test of this widely assumed linkage. Using a unique data set detailing the occurrence patterns of freshwater fishes of the Sonoran Desert (a gravely endangered fauna) we obtained for each of 25 species a measure of rarity that was independent of spatial scale. We found that fragmentation was consistently associated with elevated extinction risk, whereas the number of occurrences exerted a significant effect only if fragmentation had not already been accounted for. Specifically, desert fish species with the most fragmented historic distributions were nearly five times more likely to suffer local extirpations (since 1980) than were species with more continuous distributions. These findings underscore what a strong link exists between spatial distribution and vulnerability to extinction, clarifying that the link exists even at the landscape level and across an entire biogeographic fauna.

Key words: *Catostomidae; Colorado River, Lower Basin; Cyprinidae; desert fish species; extinction vulnerability; rarity and local extinction; scale–area curves; Sonoran Desert.*

INTRODUCTION

From diverse perspectives, researchers have argued that rare species (defined variously as rare in terms of geographic range, frequency of occurrence, or local abundance) have a greater likelihood of extinction than common ones (e.g., Karr 1982, Jablonski 1987, Pimm et al. 1988, Laurance 1991, Gaston and Blackburn 1996, Musick 1999). Rabinowitz and colleagues (Rabinowitz and Rapp 1985, Rabinowitz et al. 1989) found that historically rare species exhibited a variety of traits (e.g., decreased reproductive variability), buffering them from vagaries of small population size, thus decreasing risk of extinction despite rarity. However, interpretation of the relationship between rarity and extinction is difficult because the nature of the linkage appears to depend strongly on the spatial scale of individual studies (Gaston 1994).

When one focuses on spatial rarity (i.e., rarity in terms of spatial distribution), a commonly held belief is that the fewer occurrences a species has or the more fragmented its distribution is, the more vulnerable that species should be to extinction (Gaston 1994, Hanski 1998). A range of ecological evidence supports this view, including both theoretical work (Hess 1996) and small-scale experimental studies (e.g., Gonzalez et al. 1998). Other rarity-related issues, such as the importance of fragmentation on very large spatial scales and

the degree to which interspecific differences in distributional fragmentation translate into differences in extinction risk remain unclear (Gaston 1994). In addition, a taxonomic bias exists regarding ecologists' understanding of the connections between rarity and risk because of the preponderance of studies involving mammals and birds.

Here we present a large-scale biogeographic test of the widely assumed connection between rarity or fragmentation and local extinction risk. Using a unique data set detailing the occurrence patterns of freshwater fishes of the Sonoran Desert, a gravely endangered fauna (Minckley and Deacon 1968, 1991), we obtained for each species a measure of rarity that was independent of spatial scale (Kunin 1998). We found that fragmentation was consistently associated with elevated extinction risk, whereas the number of occurrences exerted a significant effect only if fragmentation had not already been accounted for. As we detail below, desert fish species with the most fragmented historic distributions were nearly five times more likely to suffer local extirpations (since 1980) than were species with more continuous distributions. These landscape-level findings underscore what a strong link exists between spatial distribution and vulnerability to extinction, reinforcing understanding gained from studies conducted on smaller scales or other taxa.

MATERIALS AND METHODS

The SONFISHES database

To test hypotheses regarding the influence of distribution patterns on local extinction, one needs a data set of widespread occurrences that spans a long time

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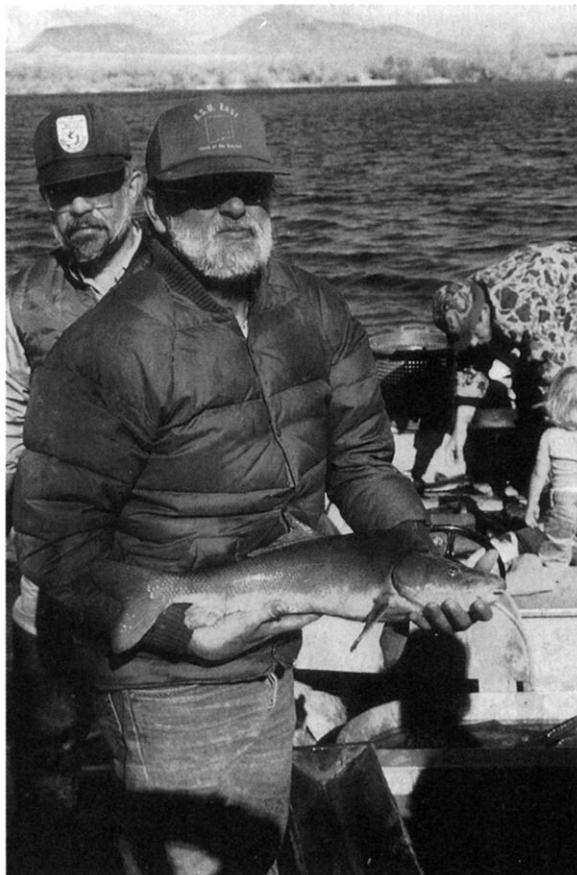


PLATE 1. The late W. L. Minckley is pictured here on the shore of Lake Mohave, holding a specimen of *Xyrauchen texanus* (razorback sucker). Minckley spent 38 years at Arizona State University studying this fish and many other species from the deserts of North America, where he began making extensive collections in 1963. These records comprise a substantial proportion of the SONFISHES database he initiated in 1994. He will be sorely missed, but never forgotten.

period and includes strikingly contrasting patterns of distributions among species. Such a database is SONFISHES, which details the distributions of native freshwater fishes in the Sonoran Desert ecoregion of northwestern Mexico and the southwestern USA over ~160 yr of research. The "SONFISHES" database contains incidence, identity, and collecting data for the complete holdings of the major museum collections of Sonoran fishes (ANSP, AMNH, ASU, BYU, MCZ, MSW, UANM, UANL, UMMZ, UNLV, USNM [abbreviations adopted from Leviton et al. 1985]), numerous lesser collections, plus records from peer-reviewed and "gray" literature sources. In total, SONFISHES comprises >20 000 locality records (representing millions of specimens) for all 52 native freshwater fish taxa in the Sonoran ecoregion (see Plate 1). Digitized localities are correct to within ~1.0 km of a collecting site and routes of early collectors have been retraced (e.g., Minckley 1999), matching outdated place names with

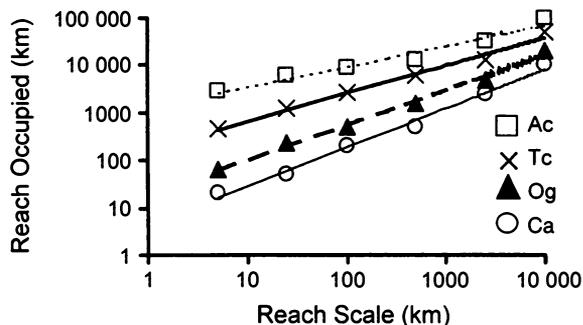


FIG. 1. Scale–area curves (Kunin 1998) for representative species of the Lower Basin of the Colorado River. Species key: Ac = *Agosia chrysogaster*, Tc = *Tiaroga cobitis*, Og = *Oncorhynchus gilae*, Ca = *Cyprinodon arcuatus*. Note logarithmic scales on both axes.

present-day equivalents and excluding all suspicious records.

We focus on the most thoroughly studied portion of this ecoregion, the "Lower Basin" of the Colorado River, which includes both Mexican and United States reaches, including all tributaries between Glen Canyon Dam and the Gulf of California. A total of 25 970 km of reach (much of which lacks perennial water due to the interplay between water discharge and substrate (Brown et al. 1981)) drains 331 500 km² of landscape. SONFISHES contains 18 271 georeferenced locality records of the 25 native species for the Lower Basin. Watershed summaries of the database's contents are available at the Desert Fishes Council website.³ Native fishes within this landscape are broadly characterized as resilient; being adapted to unpredictable extremes of drought and flood, they historically persisted on a regional basis but greatly fluctuated in abundance at individual localities (Minckley and Deacon 1968). However, massive anthropogenic alterations of the Sonoran landscape during the last few decades—including dam building, water diversion, and introduction of exotic species—have profoundly disrupted the ecology of the region (Fradkin 1983, Minckley and Deacon 1991, Kowalewski et al. 2000).

Starting from a digital base map of drainages in the Sonoran ecoregion (ESRI 1993), we subdivided drainages into 5-km reach segments. We then used a stream-order approach (Strahler 1967) to aggregate these 5-km reach segments into a hierarchy of reach segments at the 25-, 100-, 500-, 2500-, and 10 000-km scales. We mapped Lower Basin records onto individual 5-km reach segments prior to scale–area analyses, yielding 3276 total occurrences at that scale. Occurrence records stemming from artificial translocations and reintroductions were excluded from analysis. Also excluded were three fish species completely dependent on spring discharge whose spatial distributions consequently did not conform to our dendritic landscape map.

³ URL: (<http://www.desertfishes.org/na/gis/index.html>)

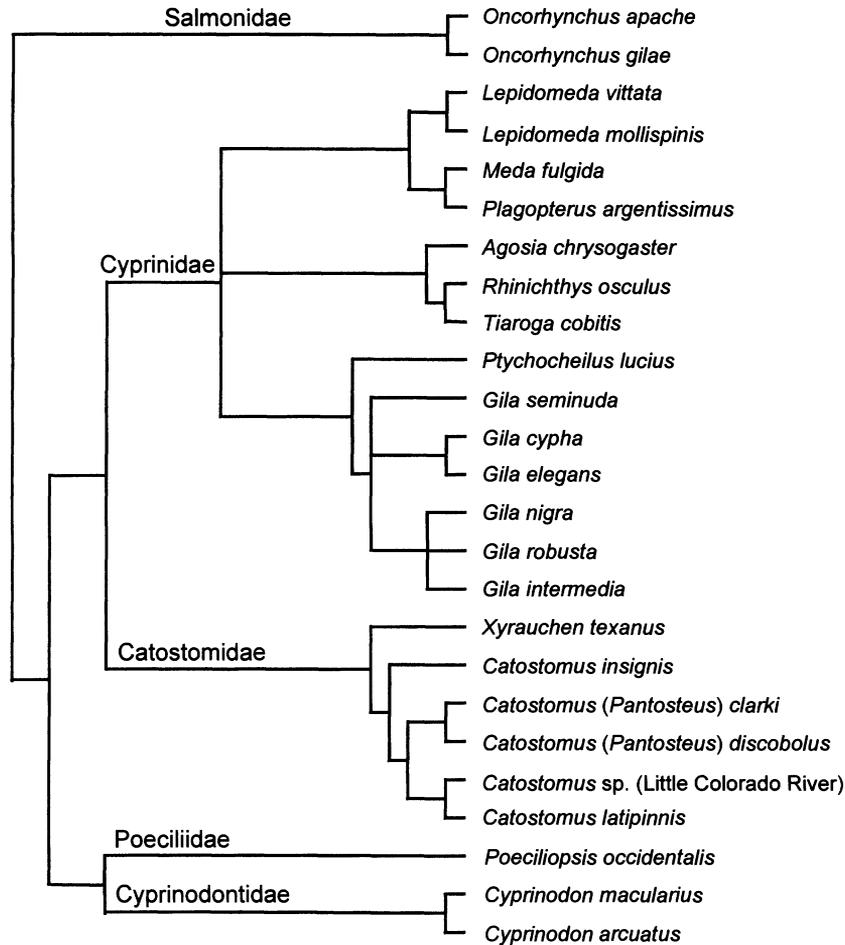


FIG. 2. Qualitative phylogeny of all native freshwater fishes of the drainages for the Lower Basin of the Colorado River except for three species completely restricted to springs (Smith 1992, T. E. Dowling, G. J. P. Naylor, and C. A. Tibbetts, *unpublished manuscript*). Branch lengths carry no quantitative meaning. Analyses indicate a strong dependence of local-extirpation risk on scale–area slope, even after the effects of phylogenetic relatedness have been controlled for.

Utilizing “scale–area” curves to overcome complications of scale

Unfortunately, even with a database like SONFISHES, analyses of distributional fragmentation are not straightforward because of the confounding issue of scale (Rahel 1990, Levin 1992), which influences one’s ability to detect change (Thomas and Abery 1995, Leon-Cortes et al. 1999). In particular, the presence (or absence) of an occurrence depends on the spatial scale of a record—a species may be absent from a specific reach but present in a river. In the arena of freshwater fish conservation, issues of scale are especially important because of the constrained connectivity in hierarchical river–creek networks (Dunham et al. 1997) and because habitats suitable for particular fish species are often patchily distributed (Pringle et al. 1988, Johnston 2000), resulting in substantial among-species variation in distributional fragmentation (Tibbetts and Dowling 1996).

To overcome complications of scale, we used “scale–area” curves (Kunin 1998; see He and Gaston 2000), which provide a scale-independent quantitative measure of spatial rarity. Briefly, to derive a species’ scale–area curve, one breaks a landscape into a series of equal-sized cells at each of several resolutions (with a fixed number of fine-scale cells nested inside each coarser-scale cell). At each resolution, a detailed and comprehensive biodiversity database is used to determine a species’ presence or absence for each cell. Assuming a cell with at least one incidence record is “filled,” plotting the total map portion filled at a given resolution vs. cell size at each resolution generates an approximately power-law curve from which one can estimate a scale–area slope (Kunin 1998). Though the technique was initially applied to terrestrial, grid-based landscapes (Kunin 1998), we adopted the methodology to characterize rarity within dendritic, riverine landscapes at 5-, 25-, 100-, 500-, 2500-, and 10000-km reach scales.

We next determined historic occupancy patterns at each of the six spatial resolutions using SONFISHES and, using plots of segment-length occupied vs. reach scale (i.e., reach length), calculated a historic scale–area slope for each species via power-law regression (Fig. 1). These slopes are equivalent (in both interpretation and calculation) to their two-dimensional counterparts. For consistency with prior work, we retain the adjective “scale–area,” even though “scale–reach length” is more appropriate for our riverine landscapes.

Steep historic scale–area slopes characterize species with fragmented distributions whose historic occurrences were sparsely distributed over a large region, whereas shallow slopes identify species whose former occurrences were more compactly distributed (Kunin 1998). To determine the proportion of occurrences (at the 5-km scale) for each species that has been extirpated, we contrasted historic and modern distributions for each species. Specifically, to calculate extirpation probability for each taxon, we determined the proportion of “historic” records at the 5-km reach scale that have yielded no “modern” records. Historic distributions were developed by cumulating occurrence records from 1843 to 1980, whereas modern records were cumulated over 1981–1998. For Lower Basin taxa, such absences clearly constitute actual extirpation events because modern records in the SONFISHES database are almost exclusively by-products of intensive efforts by federal or state agencies to determine species’ complete distributions prior to listing decisions under the U.S. or Mexican Endangered Species Acts. Those reaches with modern records of a species, but no historic records, were considered occupied historically. Given habitat, elevational distributions, etc., there is every reason to expect that “absent” species were actually present in such reaches historically, and that their absence from the database merely reflects incomplete historical collecting (e.g., some subdrainages were not visited by virtue of their remoteness). (Excluding these reaches did not qualitatively affect results.) To assess the connections between historic rarity and extinction dynamics, we used logistic regression to relate the realized probability of local extirpation against first, the number of historic occurrences at the 5-km scale and, second, the historic scale–area slope.

Because certain fish taxa are particularly well represented within the Sonoran ecoregion (e.g., families Cyprinidae and Catostomidae, genera *Gila* and *Catostomus*) (Fig. 2), it was important to account for possible phylogenetic contributions to the observed dependence of local extinction risk on the details of species’ spatial distribution. Evolutionary branch lengths can be estimated via molecular markers for only limited portions of the phylogeny. Consequently, we developed a surrogate measure of distance quantifying phylogenetic structure among the species in the database following the concept of independent contrasts (Felsenstein 1985) using a currently accepted phylogeny (Fig. 2). We ob-

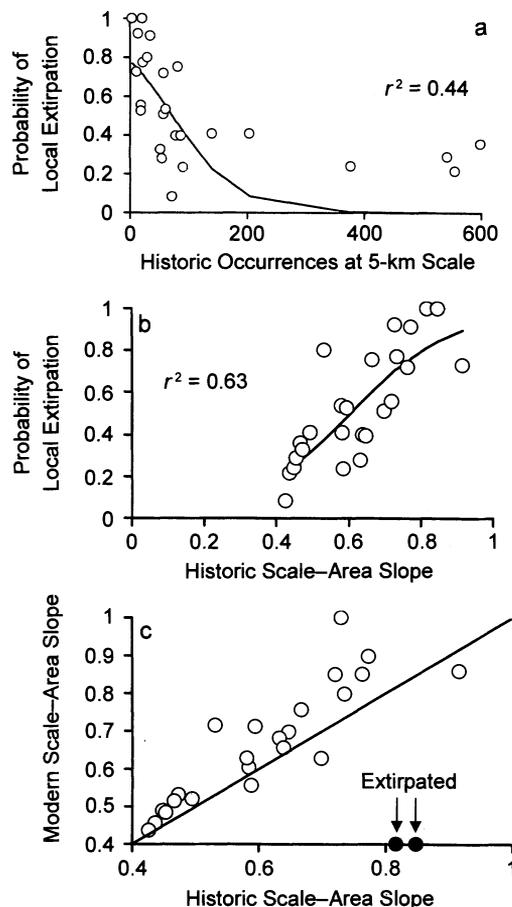


FIG. 3. Relating historic spatial distributions to extinction risk for native Sonoran Desert fishes. (a) Logistic regression of local-extirpation probability on number of historic occurrences. (b) Logistic regression of local-extirpation probability on historic scale–area slope. The strong dependence of extirpation risk on this slope measure, which provides a scale-independent measure of distributional fragmentation, indicates that the arrangement of populations in space can markedly influence extinction risk. (c) Modern scale–area slopes show increased fragmentation compared to historic distributions; 1:1 line shown for comparison. Extirpated species lack modern scale–area slopes.

tained a fine-grained correction for phylogenetic relatedness by quantifying how many phylogenetic nodes separated each pair of taxa. Distributional output from the SONFISHES database was then used to build matrices of interspecific distance in units of occurrence number (5-km reach scale), scale–area slope, and local-extirpation risk. Naturally, the node-based distances we calculated would change if we included species from outside the Lower Basin of the Colorado River in the phylogeny.

Having constructed matrices of phylogenetic relatedness and measures of rarity, we then performed a series of partial Mantel tests (Smouse et al. 1986, Rosenberg 2001) to explore the significance of correlations between matrices of extirpation risk and occurrence

TABLE 1. Rarity and extinction dynamics of native freshwater fishes in the Lower Basin of the Colorado River (United States and Mexico).

Taxon†	Official status‡		Total locality records§	Historic Occurrences	Historic scale–area slope¶	Probability of local extirpation
	U.S.	Mexico				
<i>Agosia chrysgaster</i> ^a	N	T	3024	554	0.44	0.21
<i>Catostomus insignis</i> ^b	N	E	2538	377	0.45	0.24
<i>Catostomus latipinnis</i>	N	N	307	81	0.67	0.75
<i>Catostomus</i> sp. (Little Colorado River) ^b	N	A	273	72	0.43	0.08
<i>Catostomus (Pantosteus) clarki</i> ^b	N	N	3077	542	0.45	0.29
<i>Catostomus (Pantosteus) discobolus</i>	N	A	688	140	0.49	0.41
<i>Cyprinodon macularius</i> ^b	E	E	24	11	0.92	0.73
<i>Cyprinodon arcuatus</i> ^b	X	A	20	4	0.82	1
<i>Gila cypha</i>	E	A	229	18	0.72	0.56
<i>Gila elegans</i>	E	E	122	34	0.77	0.91
<i>Gila intermedia</i> ^b	C	E	489	86	0.65	0.40
<i>Gila nigra</i> ^b	N	A	257	54	0.63	0.28
<i>Gila robusta</i>	N	R	1108	204	0.58	0.41
<i>Gila seminuda</i> ^b	E	A	162	19	0.59	0.53
<i>Lepidomeda mollispinis</i> ^b	N	A	183	30	0.53	0.8
<i>Lepidomeda vittata</i> ^b	T	A	260	52	0.47	0.33
<i>Meda fulgida</i> ^b	T	A	755	78	0.64	0.40
<i>Oncorhynchus apache</i> ^b	T	A	226	60	0.58	0.53
<i>Oncorhynchus gilae</i> ^b	E	A	41	13	0.73	0.92
<i>Plagopterus argentissimus</i> ^b	E	A	85	22	0.74	0.77
<i>Poeciliopsis occidentalis</i> ^a	E	T	522	57	0.70	0.51
<i>Ptychocheilus lucius</i>	E	E	38	21	0.85	1
<i>Rhinichthys osculus</i>	N	E	2783	599	0.47	0.36
<i>Tiaroga cobitis</i> ^b	T	E	770	90	0.59	0.23
<i>Xyrauchen texanus</i>	E	E	290	57	0.76	0.72

† Nomenclature follows Minckley (*in press*) and Miller (*in press*). One genetically differentiated but unnamed species is designated according to its best-known locality. Superscript letters are defined as follows: a, taxa endemic to Sonoran Desert Ecoregion; b, taxa endemic to the Lower Basin of the Colorado River within the Sonoran Desert Ecoregion.

‡ Official status in United States and Mexico according to each country's Endangered Species Act: N = no official status, A = no occurrences, E = endangered, X = extinct, T = threatened, C = candidate for listing, R = rare.

§ The total number of unique sites at which the fish was found.

|| At 5-km scale. In many cases there are ≥ 2 locality records within a 5-km reach; hence the number of historic occurrences at 5 km is always less than or equal to the number of locality records.

¶ For all species, the scale–area regressions yielded $r^2 \geq 0.90$, with 23 species having $r^2 \geq 0.96$. For dendric riverine landscapes, the “scale–area slope” is really the “scale–reach length slope.”

number or scale–area slope while holding our measure of phylogenetic relatedness constant across taxa.

RESULTS

Historic scale–area slope, a scale-independent measure of the spatial clustering of a species' occurrences across the landscape, was a stronger predictor of extinction risk than was the number of those occurrences (Fig. 3a, b). Across the assemblage, fish species with the most fragmented historic distributions were nearly 5 times more likely to suffer local extirpations than were species with the most nearly continuous distributions. These local extirpations resulted in further fragmentation of species distributions (Fig. 3c), increasing the average scale–area slope of the 23 extant species by 0.06 ± 0.02 (mean ± 1 SE) (a 9% increase in proportional terms) and, we predict, setting the stage for further losses into the future. Species names, historical data, and federal listing status for the native fishes of the Lower Basin are provided in Table 1.

Even more telling than the simple regressions of Fig. 3 are results of stepwise logistic regression analyses.

When scale–area slope entered the regression equation first, adding occurrence number as a second predictor variable did not improve model fit ($r^2 = 0.63$ vs. 0.63), despite the additional degree of freedom. In contrast, adding scale–area slope as the second predictor variable did improve the fit ($r^2 = 0.44$ vs. 0.63). Thus, whereas fragmentation consistently exerted a striking influence on extinction risk, the number of occurrences had no effect after the influence of fragmentation had been factored out.

The phylogenetically controlled test makes the dependence of local-extirpation risk on the spatial disconnection among occurrences clearer still. When phylogenetic distances are calculated in terms of nodes, differences in scale–area slope strongly reflect differences in extirpation risk (Mantel correlation = 0.55, $P < 0.001$), whereas differences in numbers of occurrences do not (Mantel correlation = 0.01, $P = 0.86$).

DISCUSSION

Recent decades have witnessed extensive anthropogenic landscape alterations, widespread introduction

of nonnative species, and a general decrease in surface waters in the Sonoran ecoregion (Minckley and Deacon 1968, 1991, Fradkin 1983, Kowalewski et al. 2000). For native fishes, our analyses indicate that a spatial distribution involving more compactly distributed occurrences was a key to weathering these changes.

The mechanism for this effect is likely simple: clustered occurrences aid successful recolonization, thereby increasing the probability by which extant local populations could repopulate extirpated ones. Among those fish species in which detailed studies of dispersal have been made, strongly leptokurtic dispersal kernels appear the rule (Gerking 1959, Johnston 2000, Rodriguez 2002). Thus most individuals do not move, but those that do may move great distances. This dispersal pattern facilitates rapid recolonization of defaunated areas (Peterson and Bayley 1993), especially during periods of high discharge (Minckley and Deacon 1968, Horwitz 1978).

The notion of a strong limitation on dispersal accords with the striking effect we report here regarding the influence of fragmentation on extirpation risk. However, habitat connectivity is critical to successful dispersal (Hess 1996), and connectivity among patches in river systems, already severely restricted in comparison with terrestrial habitats where two-dimensional movement is possible (Fagan 2002), is a sad casualty of human modifications like dam building, water diversion, and introduction of exotic species. Though especially pronounced in the Colorado River system, such human interference with fish dispersal is common throughout river systems worldwide (e.g., Moyle 1995, Harris and Gehrke 1997). Indeed, human barriers to dispersal are increasingly common in many landscapes. If our finding that the clustering of occurrences is key to species persistence over a wide range of landscape scales proves general, then the interplay between habitat fragmentation and habitat loss may be even more ruinous than currently predicted.

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