RARITY, FRAGMENTATION, AND THE SCALE DEPENDENCE OF EXTINCTION RISK IN DESERT FISHES

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Abstract. Attributes of a species' spatial distribution, such as the number of occurrences and the spatial distribution of those occurrences, can affect extinction risk. Extinction risk, however, is scale dependent, and it is unclear how scale dependency affects linkages between species' distributions and extinction risk. Here, we evaluate the relationships between number of occurrences, distributional fragmentation, and extinction risk for a diverse assemblage of desert fishes across multiple spatial scales. We used the SONFISHES biodiversity database, which details occurrence patterns of 25 native fishes to contrast the species' historical distributions with their much-reduced modern distributions. Defining occurrences (and losses to extinction) at each of five scales (5, 25, 100, 500, and 2500 km of stream reach), we found that range fragmentation was a stronger predictor of extinction risk than the number of occurrences for all scales of analysis. Furthermore, we detected scale dependence in the strength of the predictive relationship between fragmentation and extinction, with loss of occurrences at intermediate scales (~100 km of stream reach) being most closely tied to range fragmentation. Importantly, our results proved insensitive to our definition of the historical and modern periods. These findings highlight the value of multiscale analyses to investigations of extinction in species assemblages.

Key words: Colorado River; desert fishes; distribution scale; extinction risk; fragmentation of range; scale–area slope statistic; SONFISHES biodiversity database; Sonoran Desert; stream metapopulation.

INTRODUCTION

Of the many factors that can influence a species' vulnerability to extinction (e.g., life history traits, population size), aspects of spatial distribution are considered some of the most important (Gaston 1994, Hanski 1998). A species' spatial distribution has several components, with range size, the number of occurrences, and the arrangement of those occurrences being the most frequently considered. Spatial arrangement of occurrences is of particular concern because of the extensive array of studies linking habitat fragmentation or the fragmented distribution of species to declines in population size and/or increases in extinction risk (Robinson et al. 1995, Davies et al. 2000, Jager et al. 2001, Morita and Yamamoto 2002, Knapp et al. 2003, Cox et al. 2004). For example, for 25 species of desert fishes, Fagan et al. (2002) demonstrated that the degree to which a species' historical range was fragmented was a stronger predictor of local extinction risk than was the number of historical occurrences.

Extinction risk, however, is a scale-dependent measure (Thomas and Abery 1995, Hartley and Kunin 2003), meaning that it may be valuable to view extinction dynamics from both a large network- or system-wide perspective and a local, site-by-site basis

(e.g., Skelly et al. 1999, 2003). Furthermore, it is by no means clear that the same factors that drive losses of local populations are of comparable importance for extinction risk at larger spatial scales. For example, generalist predators intruding into a forest remnant from the surrounding farmland may extirpate a local population of birds, whereas the disruption of metapopulation dynamics caused by habitat loss and fragmentation may eliminate that species of bird from the landscape (Robinson et al. 1995). Consequently, a major need when investigating spatial dynamics is to understand how the linkages between species' spatial distributions and their risks of extinction vary as a function of spatial scale.

To address this knowledge gap, we use the SONFISHES database (Fagan et al. 2002), which documents the historical and modern occurrence patterns for native freshwater fishes of the Sonoran Desert. Members of this faunal assemblage, many of which are now gravely endangered (Minckley and Deacon 1968, 1991), historically exhibited large interspecific differences in spatial distribution due to a complex array of factors. For example, hydrologic factors (e.g., flow connectivity), water temperature tolerances, habitat preferences, as well as differing life history attributes (e.g., dispersal abilities, parental care strategies) all contributed to interspecific variation in spatial connectivity (e.g., Tibbets and Dowling 1996). Historically, some species were broadly distributed within the biogeographic re-

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gion and exhibited little fragmentation of their historical ranges. In contrast, other species had highly fragmented ranges due to some combination of biophysical and ecological factors. The end result was a system that exhibited a wide degree of interspecific variability in range fragmentation, but where no single process was responsible for the historical distributional fragmentation. Recent anthropogenic modifications of stream networks and their surrounding landscapes, largely via dam building, water diversion, and species introductions, have disrupted the ecology of the region, have driven populations and/or species extinct, and continue to threaten species' persistence (e.g., Fradkin 1983, Minckley and Deacon 1991, Kowalewski et al. 2000).

This paper builds upon previous research (Fagan et al. 2002) to examine how strongly the number of occurrences and the spatial arrangement of those occurrences determine extinction risk across multiple spatial scales. Based on our previous work, we expected that these alternative measures of spatial rarity would be differentially useful as predictors of extinction risk and expected that their predictive utility would vary with spatial scale. However, we were uncertain as to the exact nature of this scale dependence. As it turned out, scale-dependent variation in the strength of the relationships between distribution and extinction risk helps us to focus on the processes most important to species' persistence system-wide.

MATERIALS AND METHODS

The SONFISHES database

To test the influence of rarity on extinction risk, we used the "SONFISHES" biodiversity database, which details the distributions of fishes from the drainages of the Sonoran Desert and portions of adjacent ecoregions of northwestern Mexico and southwestern United States (Fagan et al. 2002, Unmack 2002, Unmack and Fagan 2004). For brevity we will refer to this area as the Sonoran Desert ecoregion, although we recognize that terrestrial ecologists associate that term with geographic boundaries different than the ones we adopt on a hydrologic basis. SONFISHES encompasses 150 years of ichthyological research and summarizes the complete holdings of the major museum collections from this region, numerous smaller collections, plus records from the Non-Game Branch of Arizona Game and Fish, and some peer-reviewed and "gray" literature sources. SONFISHES comprises thousands of georeferenced locality records (representing millions of specimens) for all 52 native freshwater fish taxa in the Sonoran ecoregion. For this analysis, we focus on the most thoroughly studied portion of this ecoregion, the "Lower Basin" of the Colorado River, which includes both Mexican and U.S. reaches, including all tributaries between Glen Canyon Dam and the Gulf of California, except the Salton Sea. Here we analyze the distribu-

tional data for 25 native species within the Lower Basin, excluding three additional native fish species (*Rhinichthys deaconi*, *Moapa coriacea*, and *Crenichthys baileyi*) that are completely dependent on spring discharge and hence have spatial distributions that do not conform to the stream network map that forms the basis for our analyses. Occurrence records stemming from artificial translocations and reintroductions were also excluded.

Evaluating distributional patterns and extinction events

To assess fish distributional patterns, we assigned each locality record for each of the 25 native fishes onto a particular 5-km stream reach. We then applied a stream-order approach (Strahler 1967, Hynes 1970, Fisher 1986) to aggregate these 5-km reaches into a series of nested hierarchical spatial scales of 25-, 100-, 500-, and 2500-km reaches (Fagan et al. 2002). For comparison, the 5-km, or local, scale corresponds to the spatial scale on which direct resource management would take place, whereas the 2500-km scale roughly corresponds to major river basins.

To estimate the proportion of occurrences that have been extirpated at each of the nested scales, we contrasted the historical and modern distributions for each species. As detailed in Fagan et al. (2002), we developed historical distributions by cumulating occurrence records from 1843 to 1980, whereas modern records were cumulated from 1981 to 2001. To calculate the extinction probability at the local scale for each taxon, we determined the proportion of historical records at the 5-km scale that yielded no modern records. Extinction probabilities were then calculated via a similar historical–modern comparison at each of the larger scales for each species. For Lower Basin fishes, absences during the modern period clearly constitute actual extinction events. This is because modern records in the SONFISHES database are almost exclusively byproducts of intensive efforts by federal and state agencies to determine species' complete distributions prior to listing decisions under the U.S. Endangered Species Act. Reaches with modern records of a species, but no historical records, were treated as occupied historically under the assumption that this scenario reflected insufficient historical sampling. This situation was rare. For example, it occurred for only 58 out of the 1107 species × reach combinations at the 100-km scale. Given increasing fragmentation (i.e., desiccation, dams) of aquatic systems through human water use, the alternative explanation of fish dispersal and colonization of a new site during the modern period is unlikely except perhaps in very localized cases (Minckley et al. 1986).

The year 1980 was chosen as the primary breakpoint between historical and modern portions of the SONFISHES database because that year corresponds to a shift in sampling regimes. Changes occurred in the purposes for the surveys and in the personnel carrying

REPORTS

them out; however, methodologies remained largely the same. In particular, prior to 1980, sampling was conducted primarily by academicians for research and museum purposes. After 1980, state and federal agencies undertook intense sampling in the context of legal and resource management issues. Although we continue to adopt 1980 as our standard breakpoint between historical and modern time periods, we also explore here how sensitive assemblage-level patterns emerging from the database are to our choice of the 1980 breakpoint. We do this by analyzing the interspecific relationships between spatial distribution and extinction risk using a series of breakpoints from 1955 to 1980, by five-year steps.

Linking extinction probability and historical rarity

Our analyses here focus on assemblage-level results that characterize how extinction risk depends on spatial distribution on multiple spatial scales. A previous paper (Fagan et al. 2002) explored the implications of spatial distribution for local-scale extinction dynamics (i.e., on the 5-km reaches) and also documented that the strong relationship between range fragmentation and extinction risk is insensitive to phylogenetic relationships among species. A separate manuscript addresses the scope and conservation consequences of species-level losses (W. F. Fagan, C. M. Kennedy, and P. J. Unmack, *unpublished manuscript*).

To assess the connections between spatial distribution and extinction dynamics, we used logistic regression to relate a species' realized probability of extinction on a particular scale (i.e., 5-, 25-, 100-, 500-, and 2500-km scales) against: (1) the number of historical occurrences on that scale, (2) the number of historical occurrences at each of the four other spatial scales, and (3) the historical scale–area slope. The scale–area slope statistic, which derives from area-occupancy perspectives on biogeographic range size (Gaston 1991), provides a scale-independent measure of the degree of fragmentation of a species' distribution (Kunin et al. 2000, Fagan et al. 2002, Hartley and Kunin 2003). Values of the scale–area slope statistic range from 0 to 1, with steep scale–area slopes (i.e., higher values) occurring when a species is sparsely distributed over a large area. Shallow slopes characterize species whose occurrences are clustered across scales. Calculation of this fragmentation metric in the context of the SONFISHES database is detailed in Fagan et al. (2002).

We used two approaches to quantify how well our two measures of spatial distribution (scale–area slope and number of occurrences) performed as predictors of extinction risk. First, when making comparisons *within* a particular combination of spatial scale and historical–modern breakpoint, we conducted logistic regressions of extinction risk against the predictor variables using an analysis of deviance framework. Specifically, we used generalized linear modeling to fit the binary extinct/extant data by maximum likelihood using a logit-link function (McCullagh and Nelder 1989, Venables and Ripley 2002). For each of the 30 combinations (i.e., 5 scales $\times$ 6 historical–modern breakpoints), we then used a likelihood-ratio test to evaluate whether there was a significant benefit to including scale–area slope as a predictor variable in the logistic regression.

When comparing the relative utility of scale-area slope or number of occurrences as predictors of extinction risk across scales, we have to contend with an additional statistical problem, namely, that the null deviance for the extinction data being explained changes substantially from one scale to the next (see Fig. 1). To make these comparisons, we undertook a series of cross-validation analyses in which we assessed the predictability of extinction risk as a classification problem. That is, under the logit link, we asked the question ''which covariate does the better job of explaining the observed extinction risk at particular scales and across time?'' The cross-validation (specifically K-fold cross-validation; Davidson and Hinckley 1997) involved splitting the data for a given scale and historical–modern breakpoint up into different groups, dropping one group, fitting the model on the remaining data, and then comparing model predictions for the withheld group to its actual values. For each cross-validation sample, we computed a cost function for the misclassifications made (Davidson and Hinckley 1997):

$$c(y, \hat{y}) = \begin{cases} 1 & |y - \hat{y}| > 0.5 \\ 0 & \text{otherwise} \end{cases} \qquad (1)$$

in which y is the observed extinction or non-extinction event within each reach (i.e., 1 and 0), and $\hat{y}$ is the associated predicted extinction or non-extinction event obtained using the logistic regression model. We then computed the expected aggregated prediction error by averaging the cost function across the cross-validation groups. Because we have a binary response, the average cost was the chance that a classification error would be made under the given model. We compared predictive accuracy for scale-area slope and number of occurrences (separately) against a ''random guess rule'' based solely on the observed probability of extinction. Specifically, if the observed probability of extinction for a given species over all reaches at a given scale for some historical–modern breakpoint was p, the probability of misclassifying a randomly chosen occurrence simply by guessing that it went extinct with probability p is $2p(1 - p)$. Thus, in the context of the cross-validation analyses, the relative performance of the two predictor variables could be judged against the random guess rule using a common and easily understandable metric, i.e., the probability of mispredicting whether a particular occurrence went extinct or not.

RESULTS

For Sonoran Desert fishes, the among-species relationships between spatial distribution and extinction
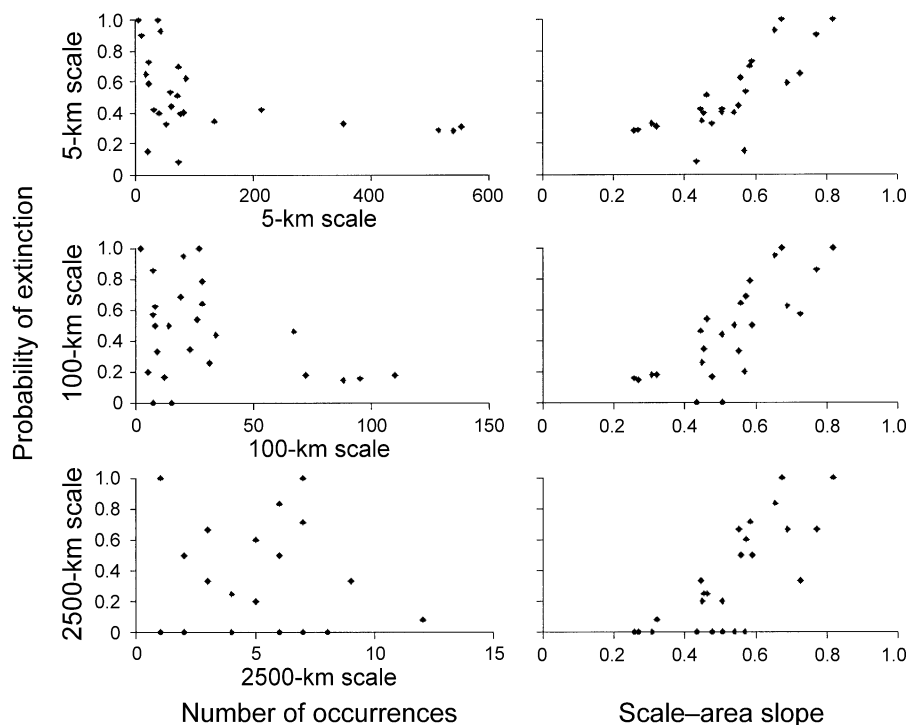
FIG. 1. Extinction risk as a function of spatial distribution for 25 species of fishes native to the Sonoran Desert ecoregion. For each panel, each black diamond represents a species. Panels on the left document the influence of the number of occurrences per species, whereas panels on the right demonstrate the importance of spatial arrangement of occurrences in terms of the scale–area slope statistic, which is a measure of fragmentation.

risk depend on spatial scale (Fig. 1). This is because both the number of occurrences for a species and the probability that a species went extinct at a site are scale-dependent traits. Thus, the predictive utility of a scale-independent metric like the scale–area slope statistic (which provides a scale-independent measure of the spatial clustering of a species' occurrences across the landscape) may change across scales because frequencies of extinction events are changing across scales even if the measure of fragmentation does not (Fig. 1).

Across species, extinction risk increased incrementally as a function of the historical scale–area slope statistic and did not exhibit a strong threshold-like effect (Fig. 1). Based on the logistic regression models, fish species with the most fragmented historical distributions were approximately three times more likely to suffer extinctions at the 5-km scale than species with less fragmented distributions. On the 100-km scale, extinction risks for species with highly fragmented distributions averaged nearly eight times those for the species with the least fragmented distributions (Fig. 1).

The relative performance of the number of historical occurrences and the scale–area slope statistic as predictors of extinction risk was rather insensitive to our choice of breakpoint between the historical and modern portions of the database (Fig. 2). Analysis of deviance from the logistic regression models indicates that on

local, intermediate, and large spatial scales, the historical scale–area slope was a significantly better predictor of extinction risk on each scale than was the number of historical occurrences on that scale, provided that we used a historical–modern breakpoint of 1965 or later (Fig. 2). Prior to 1965, the two measures of spatial distribution did not differ as predictors of extinction risk, in large part because relatively few extinctions of Sonoran fishes had accumulated before the 1960s. Thus our analyses indicate that, in general, the historical degree of fragmentation clearly explains more of the observed interspecific variation in extinction risks over the last few decades (Fig. 2).

Results from K-fold cross-validation analyses (in which the scale–area slope statistic or the number of occurrences on a particular spatial scale was used to predict extinction events on other spatial scales) indicate that, as predictors of extinction, both measures of spatial distribution offer improvements over random guessing (Fig. 3). Results of these classification-style statistical analyses indicate that, for understanding extinctions at larger spatial scales ($\geq$100 km of stream reach), the scale–area slope statistic predicts extinction events most accurately. For example, knowing only the scale–area slope statistic for a species would allow one to determine correctly the post-1980 fate of a particular occurrence on the larger
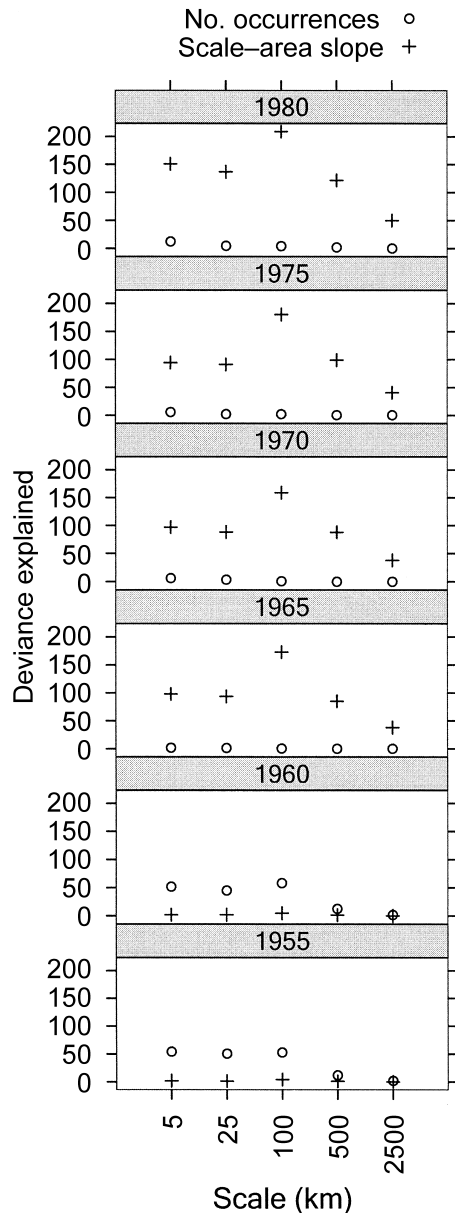
FIG. 2. Among-species relationships between spatial distribution and extinction risk depend on spatial scale. Results are shown for six alternative historical–modern breakpoint years over which extinction losses were assessed. Analysis of deviance from logistic regressions indicates that a species' scale–area slope statistic was a significantly better predictor of extinction risk than was the number of occurrences on all spatial scales for all historical–modern breakpoints of 1965 and after (likelihood ratio tests, $P < 10^{-8}$ in all 20 cases). Prior to 1965, the two measures of spatial distribution did not differ as predictors of extinction risk ($P > 0.42$ in all 10 cases), in large part because relatively few extinctions of Sonoran fishes had accumulated before the 1960s.

scales (i.e., 100, 500, or 2500 km of reach) with ~80% accuracy. In contrast, if one only knows the number of occurrences of that species in the landscape, one's ability to predict correctly the post-1980 fate of an

occurrence declines to 59% to 72%, depending on the scale on which occurrences are scored. If one only knows how often that species has actually gone extinct, then post-1980 predictions made under the random guess rule fall to 52–55% correct.

Overall, at larger spatial scales, predictions based on the scale–area slope statistics are least likely to misclassify an extant occurrence as extinct or misclassify an extinction event as a persisting population. The pattern is different if one's goal is to predict extinction risk at smaller spatial scales (i.e., 5 or 25 km of reach). In these cases, the scale–area slope statistic and number of occurrences performed comparably well as predictors of extinction risk in the cross-validation analyses (Fig. 3).

DISCUSSION

In a system like the Sonoran ecoregion, where connectivity may be determined largely by in-stream proximity of individual populations, it is intuitive that the extent of fragmentation in populations is a strong predictor of extinction risk. Our analysis revealed that species whose distributions were more fragmented historically had greater risks of extinction, whether losses were measured at the local scale (reaches 5 km long), intermediate scales (100 km of reach), or on the scale of river basins (2500 km of reach). In contrast, species whose historical distributions were more compact (less fragmented) were apparently at an advantage with regard to subsequent extinction losses, presumably due to increased opportunities for local recolonization on decadal time scales. Proximity must play a key role in long-term persistence of these species because increases in only the number of occurrences clearly did not carry the same benefits (Figs. 2 and 3).

The multiscale analysis presented in this paper allowed for the identification of the scale at which the effects of fragmentation were most clear at the assemblage level. The strongest links between historical fragmentation and extinction risk for Sonoran fishes were at intermediate and large spatial scales (100–2500 km of reach), which correspond geographically to tributaries through river basins (Fig. 3). Our results suggest that it is on these scales that differences in the degree to which species' spatial distributions are fragmented translate most cleanly into differential susceptibility to extinction loss. To prevent further losses of this already endangered fauna, we need to understand how the processes operating at intermediate and large spatial scales (or alternatively, processes that used to operate at these scales but no longer do) contribute to extinction mechanisms for Sonoran fishes. A prime suspect, of course, involves limitations on dispersal. In that case, reaches of 100–2500 km in length may represent roughly the scale over which recolonization dynamics may have taken place fast enough to offset historical rates of population losses. However, we must also consider the degree to which human activities, such as dam building,
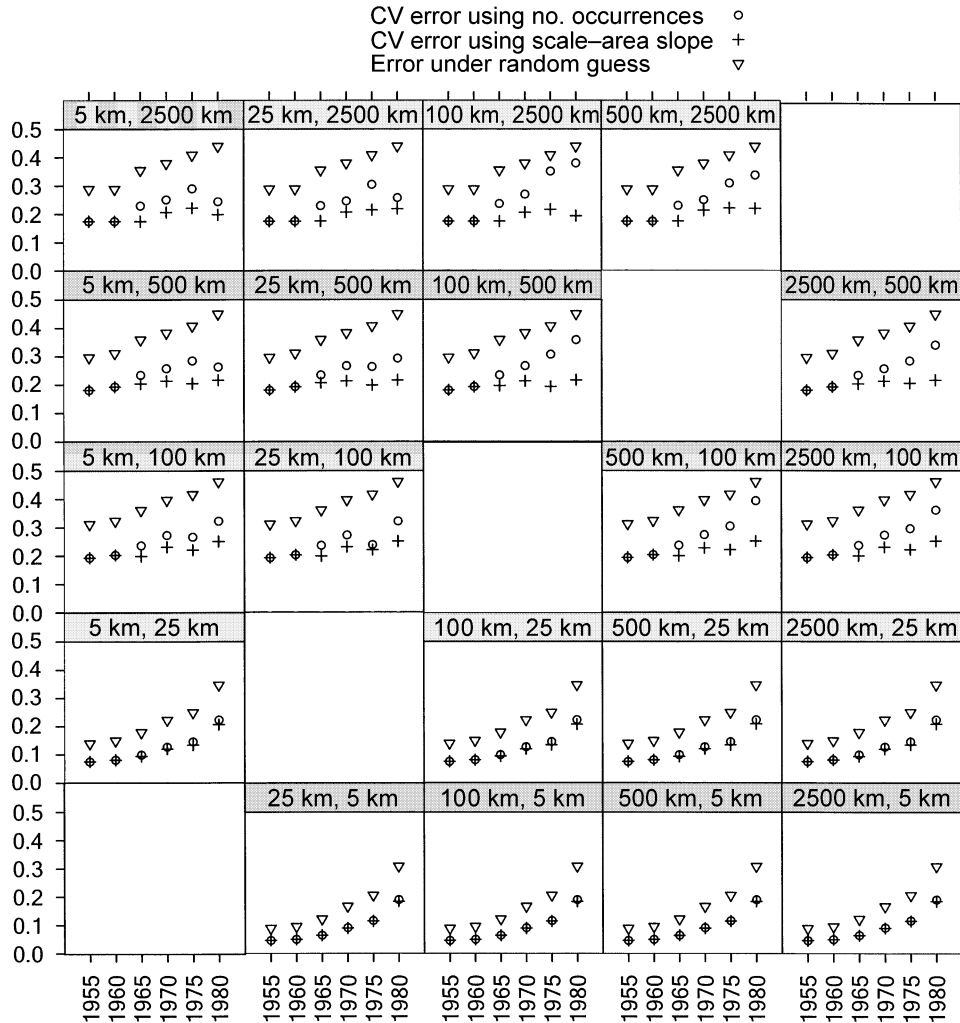
REPORTS

FIG. 3. Results from K-fold cross-validation analyses in which the scale–area slope statistic or the number of occurrences on a particular spatial scale (the first scale mentioned in the title bar of each subpanel) were used to predict extinction risks on another scale (the second scale mentioned in the title bars) for an assemblage of 25 fish native to the Sonoran Desert ecoregion. Results are presented for each of six alternative historical–modern breakpoint years. (Note that "CV error" is cross-validation error.)

water diversion, and the introduction of nonnative species, may have created ecological barriers on intermediate and large spatial scales, potentially aggravating the spatial subdivision of an already fragmented system.

Results in this paper document the overriding influence that distributional fragmentation has played in determining interspecific variation in extinction losses to date. Proximate mechanisms for particular losses range from the mundane (dewatering of stream reaches [Fradkin 1983]) to biophysical problems (reproductive failure due to altered riverine temperature regimes [Valdez and Ryel 1995]) to biological interactions (elimination of recruitment via larvivory by introduced species [e.g., Marsh and Douglas 1997]). The 25 species in this diverse assemblage are not equally susceptible to this

assortment of anthropogenic modifications, and as in other studies (e.g., Davies et al. 2000, Fagan et al. 2001), we expect that interspecific variation in fish life history traits will contribute to variation in extinction risk. However, in this system we expect that the primary effects of interspecific variation in life history traits will be to explain species-specific departures from the overall assemblage-level relationship between distributional fragmentation and extinction risk. Work in this direction is progressing.

Understanding linkages between historical distributions and extinction risks may help us to forecast future losses based on species' current distributions. Knowledge of which species are more likely to go extinct, on what scale such extinctions are likely, and what occurrences are most at risk would greatly aid in

the prioritization of management actions to protect extant occurrences or to design translocation activities to restore lost populations. Such detailed information is urgently needed because human modifications to stream networks and the surrounding landscapes have fragmented species' modern distributions beyond the levels of fragmentation present historically (Fagan et al. 2002), suggesting that further extinction events are likely.

Finally we note that, in general, the temporal structure of the SONFISHES database was not critical to our results. Provided that our chosen historical–modern breakpoint fell after the onset of major extinction losses (which accelerated starting in the late 1950s and 1960s (Minckley 1973, 1991), the assemblage-level relationship in which species with more fragmented ranges have suffered greater losses was not sensitive to the breakpoint (Figs. 2 and 3). Thus, even though any analysis concerning the loss of particular occurrences or changes in the distribution of an individual species might suffer from idiosyncrasies in database structure, our broad-scale analyses, which deal with the response of an entire biogeographic fauna to landscape-level change, appear robust to our analytical assumptions. Consequently, an additional general contribution of this study is to demonstrate that even seemingly simple information such as presence–absence data can play an important role in conservation planning. In many conservation problems, such simple data may be all that are available for analysis, and it is important to find ways of exploiting such data to test ecological hypotheses.

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REPORTS