

Testing macroecology models with stream-fish assemblages

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ABSTRACT

We measured species-level probabilities of colonization and extinction from a decade (1976–86) of stream-fish censuses at 10 sites on the Cimarron River, Oklahoma. In a macroecological analysis that controlled for phylogenetic relationships among the 41 species, we used body size, average population size, area of geographic range and distance to the centre of the geographic range as correlates of colonization and extinction probabilities. Average population size was the single best predictor of both colonization and extinction probabilities. Additionally, extinction probabilities were marginally greater for large-bodied than small-bodied species, and larger for species in which the census sites were closer to the edge than the centre of the geographic range. Ignoring phylogeny masked the edge-of-range and body size effects on extinction. Overall, our results confirm that species-level traits are correlated with standardized estimates of extinction and colonization probabilities within large assemblages of species. These analyses may be useful in applied conservation problems where direct estimates of extinction and colonization probabilities cannot be obtained.

Keywords: abundance, body size, colonization, extinction, freshwater fishes, geographic range, macroecology.

INTRODUCTION

Predicting the colonization and extinction potential of species is an important research focus of basic and applied ecology (Pimm, 1991). The macroecology paradigm potentially offers new insights into these processes. As summarized by Brown (1995), macroecology seeks to describe extinction as a species-level trait that can be linked to other species-level traits such as body size, geographic range and average population size. These traits cannot usually be measured for extinct species (but see Jablonski, 1987; Foote, 1991). Instead, patterns of covariation among these traits are analysed for extant taxa (Brown and Maurer, 1986, 1987, 1989; Gaston, 1990; Blackburn and Gaston, 1998). Trait combinations are sought that are likely to lead to extinction, or be unlikely to evolve in the first place. However, validating the macroecological approach has been problematic, because it is rarely possible to link species-level traits to good-quality data on extinctions. ‘Historical’ records

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of extinctions are often unsatisfactory because of inconsistent sampling effort, non-standard definitions of what constitutes an extinction, errors or changes in species-level taxonomy, and limited sample sizes (Gotelli and Graves, 1996).

An alternative approach is to analyse an assemblage of species and ask which species-level traits best predict background probabilities of colonization and extinction of individual populations. This sort of analysis requires data collected at a large enough spatial and temporal scale so that extinctions and colonizations can legitimately be considered species-level traits. In this study, we analyse a decade of annual censuses of fish species of the Cimarron River, Oklahoma. In a companion paper, we analyse these data from a metapopulation perspective and try to predict local extinction on the basis of landscape occupancy and site location (Gotelli and Taylor, 1999).

Here, we ignore this small-scale spatial and temporal variability in extinction and colonization, and instead extract overall average values of extinction and colonization probabilities for each species. We then use these probabilities to ask two questions: (1) How well do species-level attributes such as body size, average population size, and area and position of the geographic range predict colonization and extinction? (2) Does a consideration of phylogenetic constraints substantially alter the outcome of the macroecological analysis?

MATERIALS AND METHODS

Censuses and cladogram construction

Fish collections were made by J. Pigg from May 1976 to November 1986. At each of the 10 sites, he sampled fishes two to three times a year with a seine and gill net. Site descriptions, census methods and criteria for defining presence and absence of populations are described by Pigg (1988) and by Gotelli and Taylor (1999). A total of 41 native species were recorded and used in our analyses. We discarded data on five introduced species, although the results were similar with and without the inclusion of non-natives. To examine the degree to which phylogenetic relationships affected correlations of distribution, colonization and extinction, we constructed a cladogram on hypothesized relationships among these 41 taxa (Fig. 1). Cladograms from Mayden (1989), Lundberg (1992), Smith (1992) and Wainwright and Lauder (1992) were used in conjunction with Nelson (1994) to create a composite topology for Cimarron River fishes. All cladograms were based on morphological data (mostly osteological characters) and were constructed using maximum parsimony methods. Nelson (1994) provides a current synthesis of fish systematics under a cladistic framework that was used to build the composite topology for Cimarron fishes. The resulting tree represents the phylogenetic relationships among species that co-occur in this taxonomically diverse assemblage.

However, it is important to recognize that our phylogeny is incomplete in two ways. First, we are dealing with a regional species pool that includes one to several members of many distantly related clades. In other words, Fig. 1 does not depict the evolutionary process of speciation; it merely links species and clades to their sympatric sister groups. The second problem concerns the measurement of branch lengths in units of expected evolutionary change. For all of our macroecological variables except body size, there is no simple underlying model of character change, or any reason to assume that the traits of interest are directly heritable. Despite these difficulties, our topology provided us with an hypothesis of

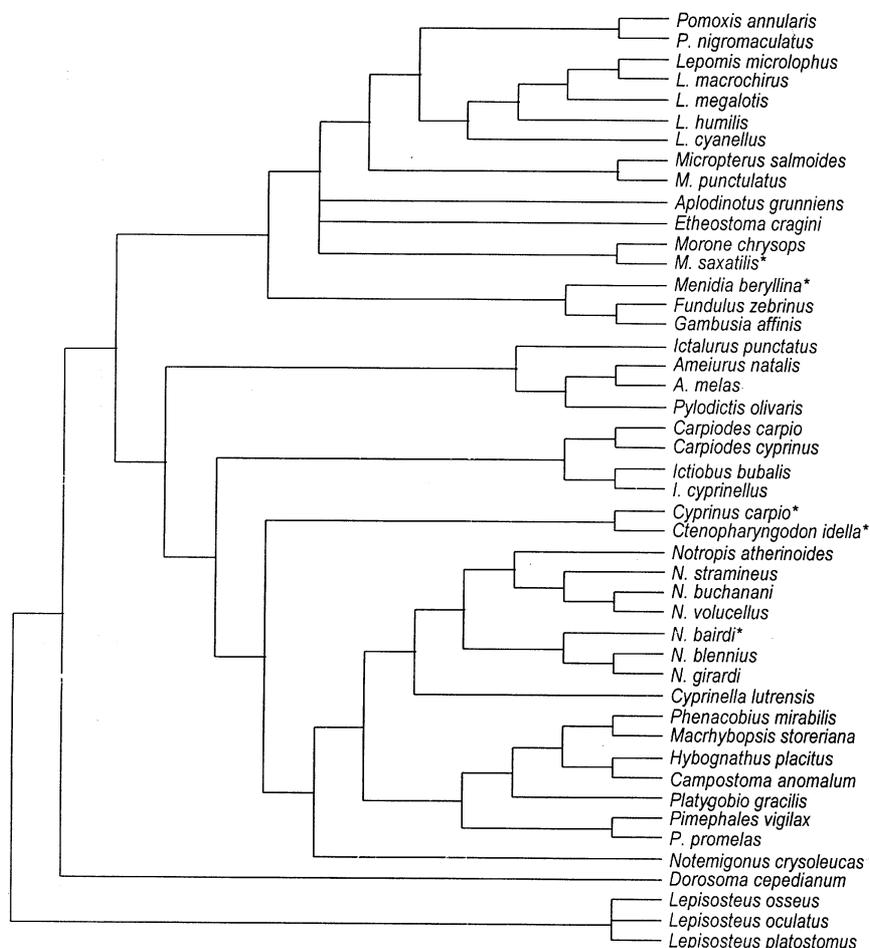


Fig. 1. Cladogram of taxa collected from the Cimarron River. Asterisks indicate introduced taxa, which were not included in the analyses.

species relationships that we were able to take into account before performing macroecological analyses on species-level attributes.

Quantifying colonization and extinction

To carry out macroecological analyses, we had to measure extinction and colonization as species-specific traits, rather than as probability measures that applied to a particular time or a particular site. We estimated the species-specific probability of extinction as:

$$p_e = \frac{\text{number of times an occupied site in year } (t) \text{ was unoccupied in year } (t + 1)}{\text{total number of occupied sites censused in years 1–9}}$$

Similarly, the species-specific probability of colonization was calculated as:

$$p_c = \frac{\text{number of times an unoccupied site in year } (t) \text{ was occupied in year } (t + 1)}{\text{total number of unoccupied sites censused in years 1–9}}$$

p_e and p_c are equivalent to a weighted average of the yearly probabilities, with the weights being proportional to the number of sites censused in a particular year. These measures average the spatial and temporal variability in colonization and extinction probabilities.

Measuring species-level traits

We used data on geographical distribution and body size from Lee *et al.* (1980). Measuring adult body size in fishes is problematic because they are indeterminate growers, minimum adult reproductive size is unknown for most species, and interpopulation variability in body size is common. Because 'normal' size is highly variable, maximum adult size may be a better measure for interspecific comparisons, and we have used maximum standard lengths listed in Lee *et al.* (1980) as our measure of body size for each species.

Following the methodology of Taylor and Gotelli (1994), we digitized the range maps in Lee *et al.* (1980) to estimate the geographic range of each species. This measure of geographic range is independent of our local measure of the fraction of sites occupied by each species in the Cimarron River data set. We also calculated an 'edge-of-range' index for each species to quantify the position of the Cimarron River census sites relative to the edge of each species' geographic range (see also Enquist *et al.*, 1995). First, we defined each species' distributional centre within the Cimarron River as the midpoint of the most upstream and downstream occurrences among the 10 sample stations. We then defined the centre of each species' geographical distribution as the longitudinal and latitudinal midpoint of the geographical range (Taylor and Gotelli, 1994). Finally, for each species, we divided the distance from the geographical range centre to the distributional centre in the Cimarron River by the square root of the geographical range area. These 'edge-of-range' indices ranged from 0.05 to 1.30; the smaller the index, the closer the distributional centre in the Cimarron River was to the geographic range centre of a species.

Statistical analyses

We used maximum body size, average abundance in occupied sites, area of the geographic range and position within the range as independent variables in multiple regression models to predict p_e and p_c . Because the macroecological variables for closely related species will be more similar than for distantly related species, it is necessary to control for phylogenetic effects that would otherwise inflate the degrees of freedom in the analysis (Pagel, 1992).

To accomplish this, we computed standardized independent contrasts (Felsenstein, 1985), implemented with PDTREE software (Garland *et al.*, 1993), for all macroecological variables. Felsenstein's (1985) method of pairwise independent contrasts for the analysis of continuous variables is based on the idea that species or higher nodes sharing a common ancestor make valid comparisons for traits, and assumes that evolution of traits proceeds according to a specified model of evolutionary change. The method requires a true branching phylogeny and branch lengths measured in units of expected evolutionary change. For our analyses, only body size can be reasonably viewed as a heritable trait, so we

have used Pagel's (1992) method of setting branch lengths arbitrarily. All variables were checked for normality with probability plots (Systat, 1996). Before standardized contrasts were computed, we used a log-10 transformation on all variables except p_e , p_c and the fraction of sites \times times occupied.

To calculate independent contrasts between two species or nodes, it is necessary to subtract the values in question in an arbitrary direction. Because we were uncertain of the sign of the contrasts, we forced the multiple regressions through the origin (Garland *et al.*, 1993). Because condition indices (Systat, 1996) indicated little collinearity among our macroecological variables, we computed entire multiple regression models, rather than relying on stepwise procedures.

RESULTS

Figure 2 depicts the relationships among body size, geographic range size and population size, the traditional species-level traits in macroecological analysis. The phylogenetic regression model controls for the degree of relatedness among species and identifies which of these species-level traits are the best predictors of extinction and colonization probabilities (Table 1).

The full model indicates that extinction is negatively correlated with abundance and with the edge index. Species for which the Cimarron River sites were near the edge of their geographic range had a greater risk of extinction than species for which the sites were closer to the centre of their geographic range. Body size was also positively correlated with extinction risk, although the result was statistically marginal ($P = 0.088$). Abundance was the only significant predictor of the probability of colonization.

Results were similar when phylogenetic relationships were ignored, but there were some changes in the relationships. For extinction, the edge-of-range effect became non-significant. For colonization, ignoring phylogeny generated marginally non-significant effects of edge-of-range and area of geographic range. In this model, colonization probabilities were greater for species that had their range centres located closer to the Cimarron sites, and colonization probabilities were greater for species that had large geographic ranges. In both the phylogenetic and non-phylogenetic analyses, the strongest effect on both colonization and extinction was average population size.

DISCUSSION

Testing macroecology models

In spite of the success of macroecology and its popularity as a framework for understanding extinctions, there are some important challenges to this approach (Blackburn and Gaston, 1998). First, past extinctions have usually been inferred, but not measured directly. Second, it may be difficult to statistically disentangle the correlated macroecological variables that are associated with extinction risk (Blackburn *et al.*, 1990; Taylor and Gotelli, 1994). Third, early studies of macroecology often ignored phylogenetic constraints and treated species as being statistically independent of one another (Felsenstein, 1985). We have followed the lead of more recent studies (Nee *et al.*, 1991; Gaston and Blackburn, 1996; Poulin and Rohde, 1997) and have incorporated the degree of relatedness among species into our analyses of extinction risk.

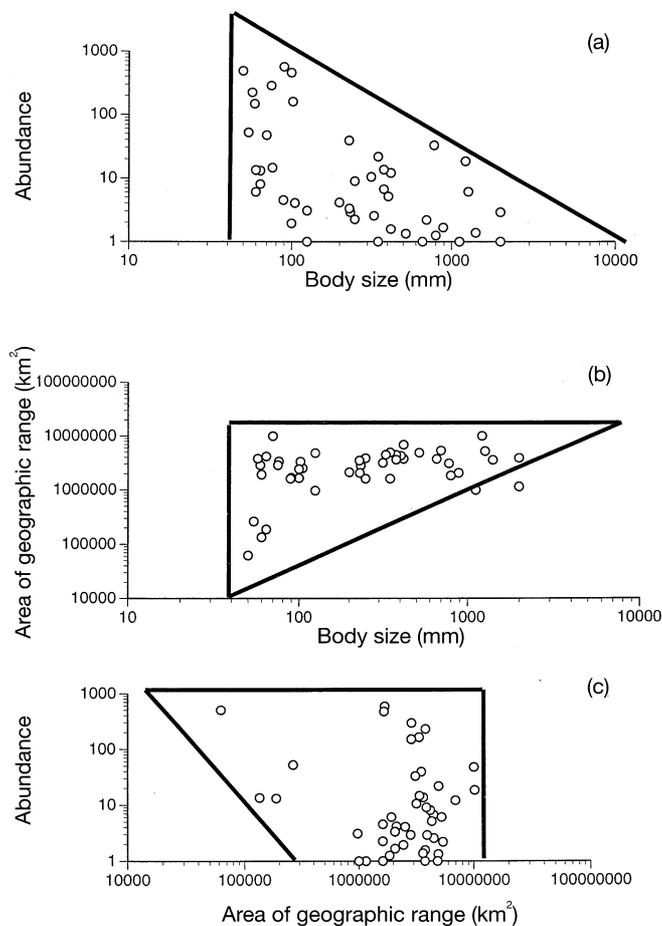


Fig. 2. Macroecological relationships among body size, population density and area of geographic range for Cimarron River fishes. Each point represents a different species.

Table 1. Ordinary and phylogenetic regression models for extinction and colonization probabilities

	Phylogenetic regression		Ordinary regression	
	Extinction	Colonization	Extinction	Colonization
Adjusted multiplier r^2	0.514	0.328	0.495	0.364
Edge-of-range	0.293 (0.045)	-0.143 (0.269)	0.072 (0.654)	-0.192 (0.059)
Abundance	-0.644 (<0.001)	0.482 (<0.001)	-0.315 (<0.001)	0.091 (0.047)
Body size	0.247 (0.088)	-0.018 (0.889)	-0.033 (0.785)	-0.056 (0.456)
Range size	-0.081 (0.521)	0.001 (0.995)	-0.109 (0.324)	0.125 (0.072)

Note: The regression coefficient is given for each independent variable, and the significance level is in parentheses. Ordinary regression models treat each species as an independent data point. Phylogenetic regression models were adjusted for the relationships in Fig. 1. Phylogenetic regressions were based on standardized contrasts and forced through the origin (Garland *et al.*, 1993).

The second and third problems are statistical in nature, and they have been largely solved by the use of phylogenetic regressions and more sophisticated statistical analyses. Traditional macroecological analyses have been based on bivariate plots of the relationships between body size, population size and geographic range of extant species (Brown, 1995). For stream fishes of Oklahoma, this analysis is relatively non-informative. There is little concordance between the patterns in the Cimarron data (Fig. 2) and the original predictions of Brown and Maurer (1987). The exception is the relationship between body size and area of geographic range (Fig. 2b), which displays the triangle-shape also found in the North American avifauna. Brown and Maurer (1987) have interpreted this relationship as indicating that species with large body sizes and small geographic ranges are prone to extinction. Our regression analyses confirm that body size contributes to extinction risk, but we could find no effect of geographic range *per se* (Table 1). Instead, the significance of geographic range is the position of the sites relative to the edge or centre of the range.

Position within the geographic range

The non-significant effect of geographic range area may reflect the fact that our measurements of extinction probabilities are not continental, but are based on observations within a relatively restricted area (see fig. 1 in Gotelli and Taylor, 1999). At this scale, the position of the sites within the geographic range of a species is an important predictor of extinction: the closer the sites are to the edge of the species geographic range, the greater the probability of extinction (Table 1). This result is consistent with a large body of data suggesting that, at the edge of the geographic range, population size decreases (Hengeveld and Haeck, 1981, 1982; Brown *et al.*, 1995) and environmental conditions become more harsh (Andrewartha and Birch, 1954; Terborgh, 1973). Our findings closely mirror those of Enquist *et al.* (1995), who showed that the abundance of contemporary and Pleistocene molluscs was lower and more variable near the edge of the geographic range. Moreover, species-level turnover (extinctions and colonizations) are also more likely near the edge of the geographic range.

With the exception of Enquist *et al.* (1995), the effects of geographic range edges have been neglected in studies of extinction risk. For example, Pimm *et al.* (1988) analysed island extinction records for birds of the British Isles and concluded that, after controlling for effects of population size, large-bodied species were less prone to extinction at small population sizes than small-bodied species. This conclusion was challenged on several methodological and statistical grounds (Tracy and George, 1992; Haila and Hanski, 1993), and the results do not seem clear-cut (Diamond and Pimm, 1993; Tracy and George, 1993).

However, none of these authors considered the effects of position within the geographic range of a species as important. For example, the Pied Flycatcher (*Ficedula hypoleuca*) is one of the species that Pimm *et al.* (1988) record as having the greatest risk of extinction in the British Isles, and the geographic centre of its distribution is roughly in the Ukraine. In contrast, extinctions were never recorded for the Rock Pipit (*Anthus petrosus*), which has its geographic range centred approximately in the British Isles. Unless extinctions and colonizations are measured across the entire geographic range of a species, the position of the sites within the range will be a potentially important variable, as our analyses have demonstrated.

Distribution and abundance

The correlation between distribution (fraction of sites occupied) and abundance (average density in occupied sites) is ubiquitous in nature, and at least eight hypotheses have been proposed to account for it (Hanski *et al.*, 1993; Gaston *et al.*, 1997). The pattern also holds for Oklahoma stream fishes (Fig. 3), and we can use the data to address some of these hypotheses.

The simplest null hypothesis is that individuals are distributed randomly in space by a Poisson process, and then sampled in fixed areas such as quadrats. Under these circumstances, a plot of the natural logarithm of the frequency of absences ($\ln(1-f)$) versus the average abundance in all sites should yield a line with a slope of -1.0 and an intercept of 0.0 (Wright, 1991). However, clumping effects, as expressed in a negative binomial distribution, can lead to a variety of expected curves. Our data are organized as abundance in occupied sites, and our definition of occurrence is one or more occurrences within a year, so we cannot test Wright's (1991) model quantitatively.

However, the random sampling model implies a static distribution of individuals determined solely by a Poisson process. In contrast, populations of Oklahoma stream fishes underwent frequent extinction and recolonization (see fig. 3 in Gotelli and Taylor, 1999), suggesting that this simple model cannot explain the correlation between distribution and abundance at this scale. We can also eliminate the hypothesis that the correlation is spurious and is caused by the non-independence of species. Our phylogenetic regressions controlled directly for the degree of relatedness among the species.

At a slightly larger spatial scale, correlations between distribution and abundance can arise if sampling occurs over a limited area, and different portions of species geographic ranges are sampled. Those species for which the sample sites occur near the centre of the range will be recorded as widespread and abundant, whereas those species for which the sample sites occur near the periphery of the range will be perceived as patchily distributed and not very abundant (Bock and Ricklefs, 1983). We have already shown that position

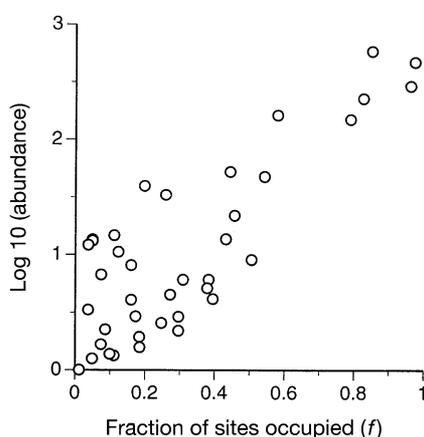


Fig. 3. The relationship between distribution (fraction of sites occupied) and abundance (average abundance in occupied sites) for fishes of the Cimarron River. Each point represents a different species.

within the geographic range affects the probability of extinction (Table 1), so it may also account for the correlation between distribution and abundance. However, a phylogenetic multiple regression revealed that the correlation between distribution and abundance was still significant, even after accounting for position within the geographic range (partial correlation $r = 0.569$, $P < 0.001$). Thus, the geographic sampling effect cannot account entirely for the correlation between distribution and abundance.

The fourth explanation is that metapopulation dynamics, and specifically a rescue effect, lead to the correlation between distribution and abundance (Hanski, 1982). Early studies accepted the between-species correlation as evidence in favour of metapopulation dynamics (Hanski, 1982; Gotelli and Simberloff, 1987), but the inference is probably not valid because the assumption that the dynamics of all species is similar is almost never true (Gotelli and Graves, 1996). In a separate analysis of these data, we were unable to detect much evidence within species in favour of simple metapopulation dynamics (Gotelli and Taylor, 1999), so this explanation cannot account for the between-species pattern.

The remaining hypotheses (table 1 of Gaston *et al.*, 1997) – resource breadth, resource availability, density-dependent habitat selection, and variation in vital rates – require additional ecological data that we do not have for this system. The most prominent explanation is Brown's (1984) hypothesis of variation in species niches (resource breadth). Consistent with Brown's (1984) hypothesis is the finding that, for most species, colonization and extinction probabilities varied predictably with position in the stream gradient (Gotelli and Taylor, 1999). However, we still do not have the critical data needed to evaluate this hypothesis – independent measures of resource specialization, tolerance, and niche breadth of widespread versus restricted species (Gaston *et al.*, 1997; Scheiner and Rey-Benayas, 1997).

Phylogenetic effects

Since the publication of Harvey and Pagel's (1991) influential book, controlling for phylogenetic effects has become an accepted statistical practice in the analysis of species assemblages. In some cases, phylogenetic analysis can reveal new insights, particularly when correlations vary dramatically between versus within clades (Nee *et al.*, 1991). On the other hand, Ricklefs and Starck (1996) suggested that published phylogenetic analyses have not revealed large biases and may serve merely to broaden confidence bounds and weaken statistical significance. In the study of macroecology, Brown (1995) has also suggested that biotic and abiotic effects on species may sometimes be more important than historical or phylogenetic constraints.

How important were phylogenetic effects in our analysis? In contrast to Ricklefs and Starck's (1996) conclusions, we found that ignoring phylogeny would have caused us to miss the important body size and edge-of-range effects on extinction. However, our interpretation must be tempered by the fact that the phylogeny we have used is not well-resolved. A proper analysis based on a complete phylogeny with branch length estimates might magnify or diminish phylogenetic correlations in these data sets. Although phylogenetic considerations are important in the analysis of macroecology, the method is limited by the fact that good phylogenies are not available for many taxa, especially invertebrates and plants.

CONCLUSIONS

For fishes of the Cimarron River, the strongest correlate of both colonization and extinction was average population size. This pattern certainly reflects the fact that, in a variable environment, extinction risk always increases for small populations (Richter-Dyn and Goel, 1972). Similarly, we expect high abundance to be the proximate cause leading to successful colonization of empty sites. Nevertheless, even after controlling statistically for abundance and phylogenetic relationships, we find that macroecological variables (position in range and body size) contribute importantly to average annual extinction probabilities. This finding supports the idea that species-level traits should be considered when trying to understand ecological processes of colonization and extinction.

Directly measuring extinction and colonization in the field is time-consuming and difficult, and there are few examples like the Cimarron data set, in which colonization and extinction were measured at multiple sites for over a decade using standardized sampling methods. Our analyses demonstrate that the relative extinction risk of different fish species can be determined from trait measurements of species and sites that are relatively easy to obtain: average population size, body size, position within the geographic range and position within the stream gradient (Gotelli and Taylor, 1999). Such an approach may be very effective for conservation biologists trying to quantify extinction risk in assemblages of related species. Future studies should attempt to validate these patterns for other taxa with different life histories and habitat requirements.

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