

TRAIT SYNERGISMS AND THE RARITY, EXTIRPATION, AND EXTINCTION RISK OF DESERT FISHES

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Abstract. Understanding the causes and consequences of species extinctions is a central goal in ecology. Faced with the difficult task of identifying those species with the greatest need for conservation, ecologists have turned to using predictive suites of ecological and life-history traits to provide reasonable estimates of species extinction risk. Previous studies have linked individual traits to extinction risk, yet the nonadditive contribution of multiple traits to the entire extinction process, from species rarity to local extirpation to global extinction, has not been examined. This study asks whether trait synergisms predispose native fishes of the Lower Colorado River Basin (USA) to risk of extinction through their effects on rarity and local extirpation and their vulnerability to different sources of threat. Fish species with “slow” life histories (e.g., large body size, long life, and delayed maturity), minimal parental care to offspring, and specialized feeding behaviors are associated with smaller geographic distribution, greater frequency of local extirpation, and higher perceived extinction risk than that expected by simple additive effects of traits in combination. This supports the notion that trait synergisms increase the susceptibility of native fishes to multiple stages of the extinction process, thus making them prone to the multiple jeopardies resulting from a combination of fewer individuals, narrow environmental tolerances, and long recovery times following environmental change. Given that particular traits, some acting in concert, may differentially predispose native fishes to rarity, extirpation, and extinction, we suggest that management efforts in the Lower Colorado River Basin should be congruent with the life-history requirements of multiple species over large spatial and temporal scales.

Key words: dams; functional diversity; life history; Lower Colorado River Basin (USA); native fishes; river regulation; species attributes; species invasions.

INTRODUCTION

The escalation of anthropogenic pressures confronting natural ecosystems underscores the urgency with which we must identify and protect species facing the greatest risk of extinction (Pimm and Jenkins 2005). This is a challenging task, in large part, because we lack direct estimates of extinction risk for most species. Consequently, ecologists have increasingly turned to using predictive suites of ecological and life-history traits as rule-of-thumb proxies to triage vulnerable species (O’Grady et al. 2004). Such rules are based on a wealth of empirical evidence from a diverse set of taxa which suggests that a number of intrinsic biological traits can render species more vulnerable to extinction (reviewed by McKinney 1997). The identification of such “extinction-prone traits” has helped to prioritize management strategies aimed at safeguarding native species with the greatest risk of extinction (Purvis et al. 2000).

By integrating the landscape activities of humans, fresh waters are subjected to a panoply of anthropogenic

threats, including the pervasive effects of hydrological alteration, agricultural and urban land-use, invasive species, and climate change (Dudgeon et al. 2006). The nexus of these threats are well documented in the Lower Colorado River Basin, USA, where the century-long exploitation of water resources for human consumption, irrigation, and hydroelectricity has resulted in one of the most controlled rivers in the world (Fradkin 1981, Carlson and Muth 1989). Historically, the Lower Colorado River was characterized by extreme seasonal variations in flow, flash flooding, and warm, turbid waters in which native fishes responded over evolutionary time by developing particular behavioral patterns, morphologies, and life-history traits (Deacon and Minckley 1974, Smith 1981). However, since European settlement, hydrologic alteration from extensive dam building and irrigation and the deleterious effects of invasive species have caused the precipitous decline of many native fishes (Minckley and Deacon 1968, 1991, Fagan et al. 2005b, Olden and Poff 2005). Conservation of native biodiversity in the Lower Colorado River Basin will require management strategies that focus on identifying and conserving those fish species that are considered to be at the greatest risk to extinction.

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TABLE 1. Native fishes of the Lower Colorado River Basin, USA, examined in our study.

Scientific name	Common name
Catostomidae	
<i>Catostomus clarkii</i> †	desert sucker
<i>Catostomus discobolus</i>	bluehead sucker
<i>Catostomus insignis</i> †	Sonora sucker
<i>Catostomus latipinnis</i>	flannelmouth sucker
<i>Xyrauchen texanus</i>	razorback sucker
Cyprinidae	
<i>Gila cypha</i>	humpback chub
<i>Gila elegans</i>	bonytail
<i>Gila intermedia</i> †	Gila chub
<i>Gila nigra</i> †	headwater chub
<i>Gila robusta</i>	roundtail chub
<i>Lepidomeda mollispinis</i> †	Virgin River spinedace
<i>Lepidomeda vittata</i> †	Little Colorado River spinedace
<i>Meda fulgida</i> †	spikedace
<i>Plagopterus argentissimus</i> †	woundfin
<i>Ptychocheilus lucius</i>	Colorado pikeminnow
<i>Agosia chrysogaster</i>	longfin dace
<i>Rhinichthys osculus</i>	speckled dace
<i>Rhinichthys cobitis</i> †	loach minnow
Cyprinodontidae	
<i>Cyprinodon macularius</i> †	desert pupfish
Poeciliidae	
<i>Poeciliopsis occidentalis</i>	Gila topminnow
Salmonidae	
<i>Oncorhynchus gilae apache</i> †	Apache trout
<i>Oncorhynchus gilae gilae</i> †	Gila trout

† Species endemic to the Lower Colorado River Basin.

Previous studies have shed considerable insight into the ecological and life-history correlates of extinction risk for freshwater fishes (e.g., Angermeier 1995, Parent and Schriml 1995, Reynolds et al. 2005, Olden et al. 2006, 2007). However, an important knowledge gap remains with respect to the specific pathways that biological traits may operate to predispose species to extinction. We believe that our understanding and prediction of fish species extinctions would be improved by explicitly considering how biological traits collectively predispose species to the primary components of the extinction process: rarity, risk of local extirpation, and vulnerability to global extinction. Unfortunately, progress in this research area has been limited for at least two reasons. First, previous studies across many taxonomic groups have principally examined the independent effects of individual traits, not interactions among traits that may influence a species' extinction risk. Ecological theory supports the importance of such trait interactions, or synergisms, for species extinction (Lawton 1994), but there is little empirical support (Davies et al. 2004, Cardillo et al. 2005). Second, past research has concentrated primarily on establishing trait linkages with estimated risk to global extinction, without considering the specific mechanisms by which traits may confer risk. For example, traits associated with rarity and local extirpation or with vulnerability to extinction from habitat loss or interactions

with invasive species may differ (Duncan and Young 2000, Owens and Bennett 2000, Olden et al. 2007).

In the present study, we provide the first investigation of how trait synergisms may predispose fish species to risk of extinction through their effects on rarity and local extirpation and their interactions with different ecological mechanisms that underlie the extinction process. We characterize a suite of ecological and life-history traits for native fishes of the Lower Colorado River Basin, and ask if synergistic trait combinations provide greater predictive insight into the overall extinction process compared to the additive effects of individual traits considered in isolation. In doing so we have the opportunity to examine the widely held, yet rarely examined, assumption that attributes of species that contribute to their rarity will further predispose them to greater risk of local extirpation and ultimately global extinction (Pimm et al. 1988, Gaston 1994, Johnson 1998). We then assess the degree to which trait combinations can be used to distinguish the relative contribution to extinction risk arising from anthropogenic habitat alteration vs. interactions with nonindigenous fishes. By addressing these objectives we aim to improve our understanding of the linkages between fish species' extinction, biological traits, and specific drivers of environmental change in the highly-modified Lower Colorado River Basin.

MATERIALS AND METHODS

Ecological and life-history traits

The Lower Colorado River Basin is home to a unique ichthyofauna that exhibits a distinct suite of behavioral, morphological, and life-history characteristics. Our study focuses on 22 native fish species (out of the 28 species present in the lower basin) for which reliable trait data were available (Table 1). Of these species, 12 are endemic to the lower basin and six are endemic to the Colorado River Basin. We collated data for 10 traits, including (1) maximum total body length (cm); (2) swim factor, the ratio of minimum depth of the caudal peduncle to the maximum depth of the caudal fin, where small factors are indicative of strong swimmers (following Webb 1984); (3) trophic guild, the adult feeding mode based on published diet analyses and classified as herbivore–detritivore (~>25% plant matter), omnivore (~<5% plant matter), invertivore, or invertivore–piscivore; (4) diet breadth, the total number of major diet items consumed at any time during a fish's lifetime, including inorganic material, vegetative material, plankton, aquatic/terrestrial insects, oligochaetes/crustaceans/molluscs, fish/fish eggs, and amphibians/mammals/birds (range 1–7); (5) longevity, the maximum potential life span (years); (6) female age at maturation (years); (7) female length at maturation (cm); (8) fecundity, the total number of eggs or offspring per breeding season; (9) parental care, a metric representing the total energetic contribution of parents to their offspring (following Winemiller 1989); and (10) reproductive guild, described as non-guarders (open substra-

tum spawners, brood hiders), guarders (substratum choosers, nest spawners), or bearers (external) (following Balon 1975). We selected these attributes from a larger trait database because they reflect the main dimensions of the species ecological niches in this region (Olden et al. 2006).

Trait assignments were based on a comprehensive review of state fish textbooks, primary literature, state agency reports, university reports, graduate theses, and electronic databases available on the World Wide Web (see Olden et al. 2006 for more details). Expert knowledge of regional specialists was used to assign values to a small number of trait states (<2%) that could not be obtained from the previous methods (mainly inferred from congenetics). To account for interdemic variation in biological traits, values were based on research conducted in the study region whenever possible. Ordinal and nominal trait values were assigned a single state based on a majority-of-evidence rule according to adult preferences, and median values for continuous traits were used when ranges were presented. Although we recognize the sensitivity of trait estimates to factors including sample size and geographic location, the assembled database reflects the best available information for this group of species.

Phylogenetic inertia

It is expected that species share similar life-history attributes through descent from common ancestry, thus necessitating the need to account for phylogeny effects when exploring patterns in ecological data (Fisher and Owens 2004). Approaches for controlling the effects of phylogeny typically involve the method of independent contrasts (Felsenstein 1985); however, this technique cannot accommodate combinations of nominal, ordinal, and continuous variables that are present in our data set. Therefore, we employed the eigenvector method proposed by Diniz-Filho et al. (1998) to quantify the degree of phylogenetic inertia in our species pool. This involved constructing a qualitative phylogeny of native fishes (see Appendix A) and assembling a phylogenetic distance matrix by tabulating the total number of nodes separating the species in the tree (following Webb et al. 2002). Next, a principal coordinate analysis (Gower 1966) was computed from the phylogenetic distance matrix to represent species in reduced multivariate space expressing variation in their phylogenetic relatedness. The first two principal coordinates, which accounted for 90.2% of the original variation (70.8 and 19.4%, respectively), were statistically significant based on the broken-stick model (Peres-Neto et al. 2003) and provided two indices of phylogenetic relatedness.

Species' rarity, frequency of extirpation, and perceived extinction risk

We obtained empirical estimates of species' rarity and frequency of local extirpation from Olden and Poff (2005) and Fagan et al. (2002), respectively (Appendix

B). Both studies used the Sonoran Fishes (or SONFISHES) database; a comprehensive data source containing incidence, identity, and collection records for the complete holdings of major museums, numerous smaller holdings, records from the state agencies, and peer-reviewed and "gray" literature sources. Together, SONFISHES contains 20 000+ unique occurrence records collected over a 150-year period (1843–1998) providing information on past and present distributions of fishes in the region (Unmack 2002). Olden and Poff (2005) estimated present-day range size (inversely related to species' rarity as defined by the size of a species' geographic range) as the total kilometers of stream reach occupied by each species during the modern record (1981–1998). Fagan et al. (2002) quantified extirpation probabilities as the proportion of fish occurrence records at the 5-km river-segment scale in the historic period (1843–1980) that were absent during the modern record (1981–1998). Sampling effort (number of collections per kilometer of stream network) increased through time due to the intense sampling adopted post-1980 by resource managers and government agencies, therefore estimates of extirpation are unlikely to be overestimated (Olden and Poff 2005). Recent work supports the robustness of extirpation estimates based on 1980 as the threshold for delineating the historical and modern periods (Fagan et al. 2005a, b).

To estimate perceived extinction risk for native species of the Colorado River Basin, we developed a questionnaire to survey 20 professional fish biologists with decades of research experience in the region (see *Acknowledgments*). Based on the findings of Fagan et al. (2005b), we decided to survey local experts rather than rely on conservation rankings compiled in national (U.S. Fish and Wildlife Service 1999) or international assessments (2006 IUCN Red List of Threatened Species, *available online*).⁵ Using the SONFISHES database, Fagan and colleagues examined spatial distributions of Lower Colorado River fishes at three scales for historical and modern time periods, and compared these trends to U.S. Fish and Wildlife Service and IUCN listings. The authors found poor correspondence between long-term distributional trends and both ranking systems. Using the IUCN ranking protocols with the long-term data available from the SONFISHES database, they suggested a revised IUCN ranking for 14 out of 15 endemic fish species. For this reason, we were not confident that either ranking system accurately reflects the current conservation status of native species in this region.

We asked each survey respondent to classify all species according to two criteria: present-day "perceived risk" of extinction using four levels (none, low, moderate, or high), and the primary source of imperilment (altered flow regimes, altered temperature regimes,

⁵ (www.iucnredlist.org)

altered physical habitat conditions, predation by non-native fishes, competition with nonnative fishes, or other biological interactions, e.g., hybridization or disease). From the questionnaire results we used a majority rule to place each species into one of five categories that combined perceived level of extinction risk and primary source of threat over their lifetime (Appendix B): (1) none/low risk; (2) moderate risk–environmental degradation (first three sources listed above); (3) moderate risk–species invasions (last three sources listed above), (4) high risk–environmental degradation, and (5) high risk–species invasions. We assessed inter-respondent reliability by comparing the actual assignment to random assignments of the species to the five extinction level–source categories according to Fleiss' kappa (1971). Fleiss' kappa is interpreted as the extent to which the observed amount of agreement among raters exceeds what would be expected if all raters made their ratings completely randomly (complete agreement then $\kappa = 1$, no agreement then $\kappa \leq 0$). For the 22 fish species, we found that $\kappa = 0.41$ (representing a mean concordance among participants of 66.8%); a value significantly greater than chance ($P = 0.038$). This indicates good inter-respondent consistency for assigning species to one of the five extinction level–source categories.

Statistical analyses

We used classification and regression trees (CART; Breiman et al. 1984) to model species' rarity (expressed as total kilometers of stream reaches occupied), frequency of local extirpation (probability between 0 and 1), and perceived level and source of extinction risk (five nominal categories) as functions of the 10 biological traits and two indices of phylogenetic relatedness. CART is particularly powerful for ecological analyses because it allows the modeling of nonlinear, nonadditive relationships among mixed variable types, it is invariant to monotonic transformations of the data that are often required prior to using traditional methods, and it facilitates the examination of intercorrelated variables in the final model (De'ath and Fabricius 2000). Thus, the CART methodology is well suited for analyzing trait synergisms among inherently correlated biological traits that are both continuous and categorical.

The CART methodology uses a recursive partitioning algorithm to repeatedly partition the data set according to the explanatory variables (i.e., biological traits) into a nested series of mutually exclusive groups, each as homogeneous as possible with respect to the response variable (i.e., rarity, extirpation, extinction). The branching topology of the resulting decision tree reveal nonadditive (or synergistic) trait effects, and the primary splits represent the most important predictor traits as well as indicating the best competitive traits (called surrogate splits) that show similar classification power. Therefore, the CART methodology has the favorable characteristic of allowing the simultaneous examination of biological traits (e.g., age and length at maturity) that

may have similar predictive roles in the final model. We used the Gini impurity criterion to determine the optimal variable splits (minimum parent node size: $n = 5$; minimal terminal node size: $n = 2$), and we determined the optimal size of the decision tree by constructing a series of cross-validated trees and selecting the smallest tree based on the one-standard-error rule (De'ath and Fabricius 2000). Cohen's κ coefficient of agreement (classification tree) and Pearson's moment correlation coefficient (regression tree) were used to assess the predictive performance of the decision trees compared to random expectations (Fielding and Bell 1997). Analyses were conducted using CART 5.0 (Salford Systems, San Diego, California, USA).

RESULTS

Rarity

Species rarity varied as a function of ecological and life-history traits ($R = 0.72$, $P = 0.0002$, Fig. 1). The branching sequence of the regression tree indicates that trophic specialization and reproductive strategy were the most important trait predictors of species' present-day range size (inversely related to rarity). Species with an herbivore/detritivore feeding behavior—considered a generalist trophic guild that consumes living and dead plant matter in benthic habitats—were three times more widespread compared to the other species (Fig. 1, node A). Of the species in the remaining trophic guilds ($n = 18$), two groups had high rarity: those providing a low degree of parental care (surrogate split: non-guarders spawning on open substrates, i.e., low energetic contributions to reproduction with respect to guarding and nest building; node B), and those having high parental care coupled with low diet breadth (node C). In contrast, species characterized by relatively high parental care and high diet breadth occupied considerably larger ranges (node D).

Because the regression tree was optimized to separate species into relatively homogenous groups with respect to their level of rarity, it is useful to examine species that contribute the greatest to terminal node impurity (i.e., model error). By comparing predicted to actual species range sizes (Appendix C), we found that the range sizes of *Catostomus clarkii* (desert sucker, node A) and *Gila robusta* (roundtail chub, node B) were underestimated by the model (i.e., according to the model these species should exhibit greater rarity), whereas the range sizes of *C. latipinnis* (flannelmouth sucker, node A), *Oncorhynchus gilae apache* (Gila trout, node C) and *Poeciliopsis occidentalis* (Gila topminnow, node D) were overestimated by the model (i.e., according to the model these species should exhibit lower rarity).

Frequency of extirpation

Species frequency of local extirpation was highly predictable as a function of multiple, interacting biological traits ($R = 0.87$, $P < 0.0001$, Fig. 2). Fish species with the highest frequency of local extirpation

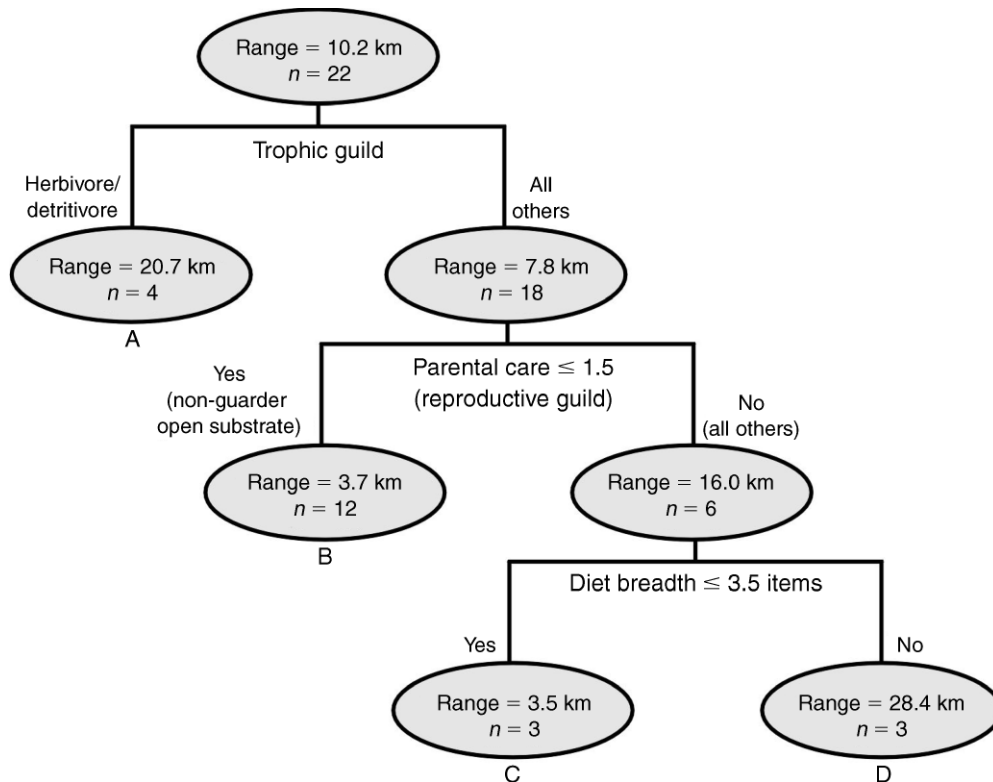


FIG. 1. Regression tree discriminating among native species of the Lower Colorado River Basin, USA, according to empirical estimates of species rarity (defined according to range, the total river kilometers occupied). According to the tree-branching topology, we also interpret the best competitive surrogate splits (indicated in parentheses) that showed similar classification power to the primary split. Note that, for continuous traits, the specific split-defining values in the tree should not be interpreted as distinct thresholds, but as a relative threshold compared to the remaining species. Letters A–D indicate terminal nodes; n is the number of species. Parental care refers to an index (range 1–3) of total energetic contribution of parents to their offspring according to the specificity of zygote placement, length of time given protection, and degree of nutrition contribution (see Winemiller 1989).

were grouped into two terminal nodes located close to the root of the regression tree (Fig. 2, nodes A–B), whereas species exhibiting near or below average frequencies were situated on longer branches (nodes C–F). Trait combinations leading to the highest extirpation probabilities included either large body size at maturity (four species in node A) or smaller size at maturity coupled with extremely low fecundity (three species in node B). Of the remaining 15 species, biological traits describing diet breadth, parental care, and longevity discriminated among species with predicted extirpation frequencies between 0.30 and 0.52. Species having the lowest probability of extirpation exhibited either a combination of diet specialization and a reproductive strategy of higher parental care to offspring (node D), or a combination of broad diet breadth plus a relatively short life span (node E). Notable species that significantly contribute to terminal node impurity included the under-prediction of extirpation frequencies for Gila trout (node B) and *O. g. apache* (Apache Trout, node D), and the overprediction for Gila topminnow (node B) and *G. intermedia* (Gila chub, node C) (Appendix C).

Level and source of extinction risk

Species perceived level and source of global extinction risk were correctly classified for 19 of 22 native species (86.4% correct classification, $\kappa = 0.878$, $P < 0.0001$; Fig. 3). The branching sequence of the classification tree indicates that traits describing body morphology, reproductive strategy, and trophic specialization were the most important predictors of extinction risk. Similar to the regression trees for species rarity and extirpation, the phylogenetic relatedness indices were not present in the final classification tree for species extinction. Maximum body size was the primary splitting variable in the classification tree. Larger-bodied species were identified as being under moderate threat to extinction (Fig. 3, node A), whereas smaller-bodied species were considered at high extinction risk from interactions with nonnative species (node B). The remaining 17 species of intermediate body sizes formed a diverse group of fishes under different levels and sources of extinction threat. These species were split into two large branches according to species reproductive strategies, specifically the degree of parental care provided to offspring.

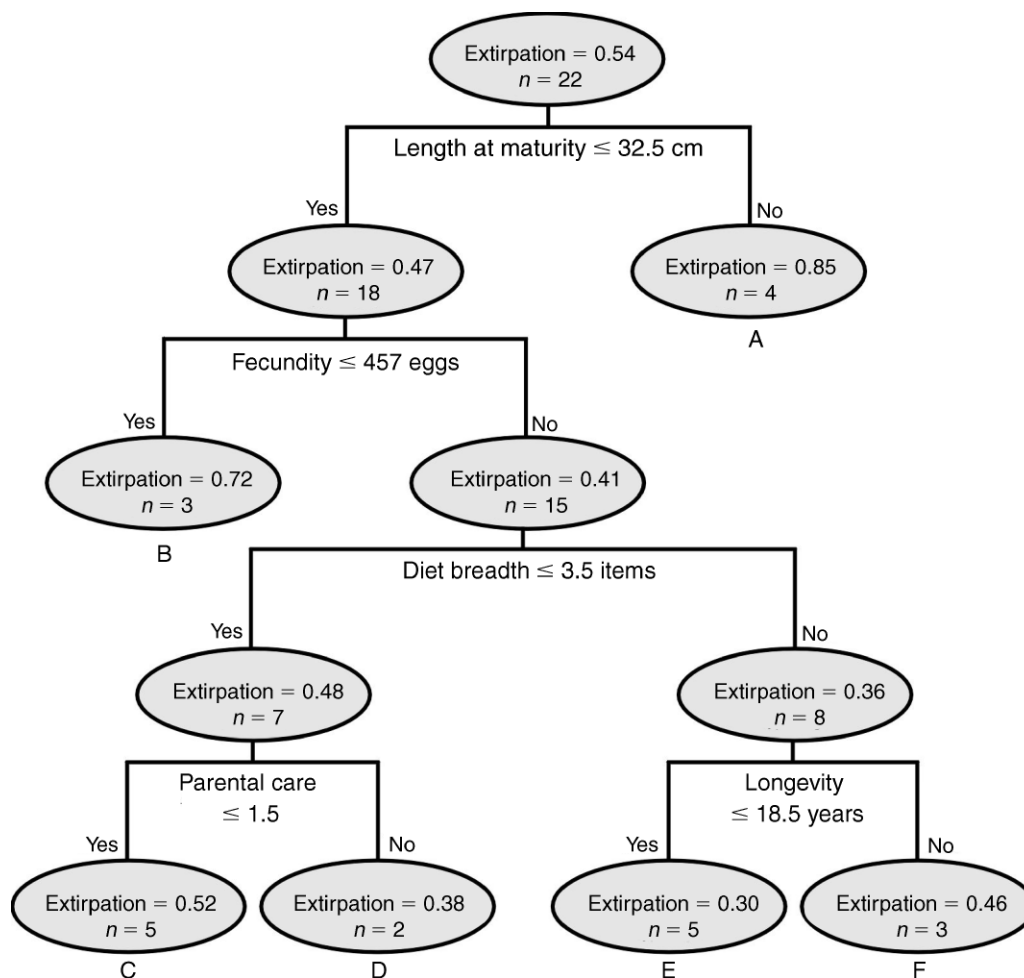


FIG. 2. Regression tree discriminating among native species of the Lower Colorado River Basin according to empirical estimates of local extirpation frequency (values between 0 and 1). Letters A–F indicate terminal nodes; n is the number of species.

In the right-hand branch, species with more parental care (surrogate split: all reproductive guilds excluding non-guarders spawning on open substrates) that mature at relatively younger ages and smaller body sizes were identified as having no or low risk of extinction (node F). In contrast, species with high parental care but delayed maturity (i.e., long-lived species that mature at older ages and at larger body sizes) were classified as having a high threat of extinction from biological invasions (node G). In the left-hand branch, species with low parental care (surrogate split: non-guarders spawning on open substrates) and herbivory/detritivory were classified to be at minimal risk of extinction (node E). Of the remaining species, body morphology discriminated between fishes subjected to different levels and sources of extinction risk. Species with body shapes indicative of strong swimming ability (i.e., small swim factor) were considered to be threatened from biological invasions (node C), whereas weaker swimming species (i.e., large swim factor) were primarily under high risk of extinction from environmental alteration (node D).

An examination of model predictions (Appendix C) shows that fish species were misclassified according to either their level or source of extinction risk, but never both. *Gila cypha* (humpback chub) and *G. elegans* (bonytail) were predicted to be under moderate extinction threat from non-native species (node C) rather than the high threat assessed by local experts, whereas *Lepidomeda vittata* (Little Colorado River spinedace) was correctly classified to its level of extinction risk, but the source of threat was misclassified as environmental alteration (node D).

DISCUSSION

For the highly endemic fish fauna of the Lower Colorado River Basin, our study points to the importance of trait synergisms for increasing the susceptibility of native fishes to multiple stages of the extinction process. Body size, an essential organismal trait correlated with many other life-history characteristics (Peters 1983) and important to the functioning of aquatic ecosystems (Layman et al. 2005), showed a strong

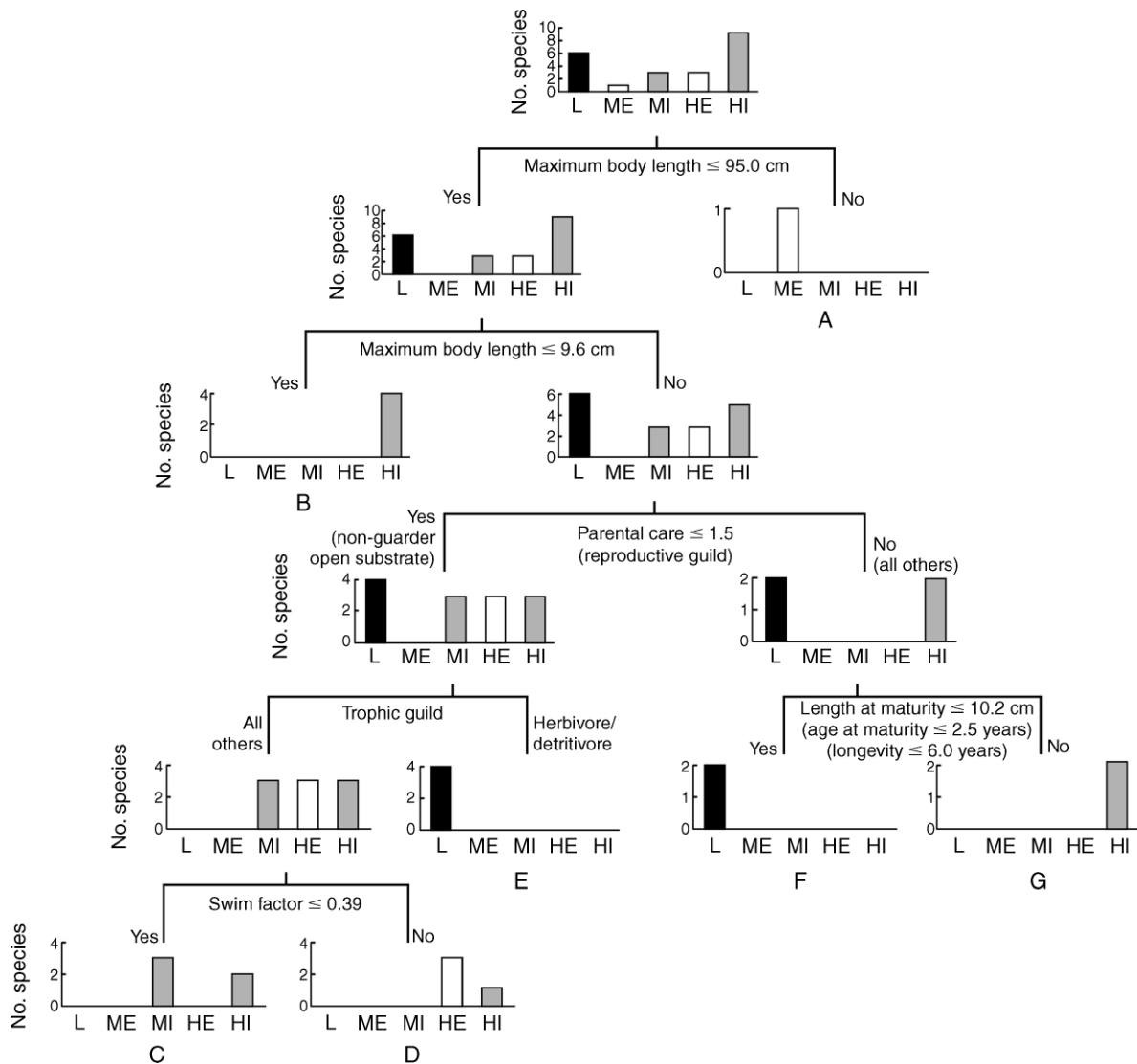


FIG. 3. Classification tree discriminating among native species of the Lower Colorado River Basin according to level and source of threat to extinction: none/low risk (L) indicated by black bars, moderate risk (ME) and high risk (HE) from environmental alterations indicated by white bars, and moderate risk (MI) and high risk (HI) from species invasions indicated by gray bars. In all panels, the y-axis represents the number of species. According to the tree branching topology, we also interpret the best competitive surrogate splits (indicated in parentheses) that showed similar classification power to the primary split. Letters A–G indicate terminal nodes.

bimodal relationship with extinction vulnerability whereby both small- and large-bodied native fishes were more at risk. The same relationship is evident for the world's freshwater fishes; globally imperiled species exhibit a bimodal size–frequency distribution indicating that small- and large-bodied species are relatively more threatened (Olden et al. 2007). We found that lack of parental care and specialized feeding behavior also were associated with elevated extinction risk, but their effects were only apparent for intermediate body sizes. These results suggest that the manner in which species traits are related to the extinction risk of Lower Colorado River fishes is both complex and sensitive to other life-

history attributes, including body size. Broader support for this finding comes from Cardillo et al. (2005) who showed that the relationship between extinction risk of mammals and life-history traits varies as a function of body size.

By partitioning overall extinction risk according to different sources of threat, we improved our understanding of the linkages between fish species traits and specific drivers of environmental change in the Lower Colorado River Basin. An important finding was that species under threat to environmental alteration are characterized by body morphologies indicative of weaker swimming ability (and potentially poor dispersal

capability) compared to species principally threatened by invasive species. This finding supports the idea that the interaction between habitat loss/fragmentation and the differential dispersal ability of fish (for example to recolonize areas after disturbance) is an important mechanism driving the extinction vulnerability of native fishes in the Lower Colorado River Basin (Fagan et al. 2002).

We found that fish species with “slow” life histories (e.g., large body size, long life, delayed maturity), minimal parental care to offspring, and specialized feeding behaviors face greater frequency of local extirpation and perceived extinction risk than would be predicted by simple additive effects of these traits. These species have low maximum rates of population growth and are therefore intrinsically more vulnerable to environmental change and, ultimately, extinction (Minckley 1991). Similarly, the synergistic effects of limited parental care and high trophic specialization (depicted by low diet breadth) were associated with both elevated rarity and greater frequency of local extirpation, a relationship observed for freshwater fishes in other regions of North America and the world (Angermeier 1995, Parent and Schriml 1995, Reynolds et al. 2005). Our findings also suggest that multiple traits may operate to reduce extinction risk via what could be considered trait antagonisms. As examples, fish species with “slow” life histories appear buffered from higher probabilities of extirpation if they have relatively higher fecundity, and species with low parental care may have lower extinction risk if they are feeding generalists or have a body morphology that is indicative of stronger swimming ability. Given that extinction is rarely catastrophic, but occurs incrementally as local populations are lost or extirpated from portions of their geographic range, we believe that the subtle manner in which trait synergisms and antagonisms influence different stages of extinction risk requires further investigation.

Our results reveal strong concordance between traits associated with “slow” life histories, low parental care and specialized diets, and levels of species rarity, decreased population persistence (i.e., frequency of extirpation) and decreased species persistence (i.e., extinction risk). This finding lends support to ecological theory positing that the attributes of species associated with their rarity (in this case referring to species range size and not low abundance) will further predispose them to local extirpation and global extinction (Pimm et al. 1988, Gaston 1994, Johnson 1998). Species possessing such traits may, therefore, be prone to the multiple jeopardies resulting from the combination of smaller population size, narrow environmental tolerances, and long recovery times following environmental change (Lawton and May 1995). Indeed, many of the most imperiled native fishes in the Lower Colorado River Basin that exhibit these trait syndromes, including *G. cypha* (humpback chub), bonytail, *Ptychocheilus lucius*

(Colorado pikeminnow) and *Xyrauchen texanus* (razorback sucker), have shown precipitous declines over the past century (Fagan et al. 2005b, Olden and Poff 2005).

Native fish populations of the American Southwest are adversely impacted by three major factors: loss and fragmentation of riverine habitats, hydrologic alteration and water development, and invasive species. Resource managers and ecologists are faced with the difficult task of identifying those species and watersheds having greatest need for conservation, while being constrained by limited biological and environmental data. Our study suggests that the conservation of native fish species in the Lower Colorado River Basin would be informed by a trait-based approach that assesses the multiple stages and sources of extinction risk (see also Winemiller 2005). The ability to reliably predict rarity and likelihood of extirpation of a species on the basis of biological traits will allow more efficient prioritization of conservation initiatives. For example, we found that a number of fish species have trait compositions that apparently predispose them to higher eventual extinction risk than they are currently facing, including desert sucker, roundtail chub and Gila chub. These species are currently not listed by U.S. Fish and Wildlife Service (1999) and are considered not threatened or not evaluated by the IUCN (with the exception of Gila chub which is ranked as “lower risk”; see footnote 5). Our analysis of the intrinsic attributes of these species indicates that their conservation ranking should be reconsidered. This trait-based recommendation is supported by Fagan et al. (2005b), who convincingly showed, using century-long distributional data and the IUCN ranking scheme, that Gila chub should be re-ranked as critically endangered and desert sucker should be added to the lower risk category.

CONCLUSION

Meeting conservation challenges in the Lower Colorado River Basin will require strategies that identify and conserve fish species that face the greatest risk of extinction. Management strategies should be based on a fundamental understanding of how species' ecological attributes interact with fluvial habitats to influence population persistence in the face of environmental change. Local habitat restoration and removal/exclusion of invasive species from critical native habitats, such as spawning and nursery floodplains (Minckley et al. 2003), will only be successful if other environmental impacts that contribute to rarity, such as dam-altered flow or thermal regimes, are also mitigated (Olden et al. 2006). In short, integrative conservation plans that aim to inform and prioritize management efforts in the Lower Colorado River Basin require actions that are congruent with the life-history requirements of multiple species over large spatial and temporal scales.

Our results point strongly to the need to explicitly consider trait interactions when making predictions about species vulnerability on the basis of intrinsic

biological characteristics. Failing to do so may provide only a limited perspective for identifying extinction-prone traits and may, in some cases, mask higher-order synergisms among suites of traits, as suggested by Davies et al. (2004). Moreover, there are likely multiple means to an "extinction end" in the sense that species with different trait combinations may be predisposed to similar levels of risk to rarity, extirpation, and extinction. We cite the need for more research involving other taxa and ecosystems that examines the manner in which trait synergisms influence patterns and rates of population decline, local extirpation, and global extinction.

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APPENDIX A

Qualitative phylogeny of the native freshwater fishes of the Lower Colorado River Basin examined in our study (*Ecological Archives* E089-048-A1).

APPENDIX B

Values of range size (species' rarity), frequency of local extirpation, and perceived level/source of extinction risk for native fishes of the Lower Colorado River Basin examined in our study (*Ecological Archives* E089-048-A2).

APPENDIX C

Terminal node predictions of the decision trees for species' rarity from Fig. 1, frequency of local extirpation from Fig. 2, and perceived level/source of extinction risk from Fig. 3 (*Ecological Archives* E089-048-A3).