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# Distinguishing between Invasions and Habitat Changes as Drivers of Diversity Loss among California's Freshwater Fishes

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**Abstract:** *Many of California's native populations of freshwater fish are in serious decline, as are freshwater faunas worldwide. Habitat loss and alteration, hydrologic modification, water pollution, and invasions have been identified as major drivers of these losses. Because these potential causes of decline are frequently correlated, it is difficult to separate direct from indirect effects of each factor and to appropriately rank their importance for conservation action. Recently a few authors have questioned the conservation significance of invasions, suggesting that they are "passengers" rather than "drivers" of ecological change. We compiled an extensive, watershed-level data set of fish presence and conservation status, land uses, and hydrologic modifications in California and used an information theoretic approach (Akaike's information criterion, AIC) and path analysis to evaluate competing models of native fish declines. Hydrologic modification (impoundments and diversions), invasions, and proportion of developed land were all predictive of the number of extinct and at-risk native fishes in California watersheds in the AIC analysis. Although nonindigenous fish richness was the best single predictor (after native richness) of fishes of conservation concern, the combined ranking of models containing hydrologic modification variables was slightly higher than that of models containing nonindigenous richness. However, the path analysis indicated that the effects of both hydrologic modification and development on fishes of conservation concern were largely indirect, through their positive effects on nonindigenous fish richness. The best-fitting path model was the driver model, which included no direct effects of abiotic disturbance on native fish declines. Our results suggest that, for California freshwater fishes, invasions are the primary direct driver of extinctions and population declines, whereas the most damaging effect of habitat alteration is the tendency of altered habitats to support nonindigenous fishes.*

**Keywords:** Akaike's information criterion, aquatic invasions, extinction, fish conservation, hydrologic alteration, information-theoretic approach, nonindigenous fishes, path analysis

Distinguiendo entre Invasiones y Cambios de Hábitat como Conductores de la Pérdida de Diversidad en Peces Dulceacuícolas de California Light & Marchetti

**Resumen:** *Tal como sucede con faunas dulceacuícolas en todo el mundo, muchas de las poblaciones nativas de peces dulceacuícolas en California están declinando seriamente. La pérdida y alteración de hábitat, la modificación hidrológica, la contaminación del agua y las invasiones han sido identificadas como los principales factores de estas pérdidas. Debido a que estas potenciales causas de declinación frecuentemente están correlacionadas, es difícil separar los efectos directos de los indirectos de cada factor y clasificar su importancia para acciones de conservación. Recientemente, algunos autores han cuestionado el significado de las invasiones, sugiriendo que son "pasajeros" y no "conductores" del cambio ecológico. Compilamos un extenso conjunto de datos a nivel de cuenca sobre la presencia de peces y su estatus de conservación, formas de uso de suelo y modificaciones hidrológicas en California y utilizamos un método teórico-informático (criterio de información*

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*de Akaike (CIA) y análisis de trayectorias para evaluar modelos de las declinaciones de peces nativos. En el análisis CIA, la modificación hidrológica (represas y desvíos), las invasiones y la proporción de tierras desarrolladas pronosticaron el número de especies de peces nativos extintas y en riesgo en las cuencas hidrológicas de California. Aunque la riqueza de especies no nativas fue el mejor pronosticador individual (después de la riqueza nativa) de peces de interés para la conservación, la clasificación combinada de modelos conteniendo variables de modificación hidrológica fue ligeramente mayor que la de otros modelos conteniendo riqueza no nativa. Sin embargo, el análisis de trayectorias indicó que los efectos tanto de las modificaciones hidrológicas como del desarrollo sobre peces de interés para la conservación fueron mayormente indirectos, a través de sus efectos positivos sobre la riqueza de especies de peces no nativos. El modelo trayectoria que ajustó mejor fue el modelo conductor; que no incluyó efectos directos de la perturbación abiótica sobre las declinaciones de peces nativos. Nuestros resultados sugieren que, para peces dulceacuícolas de California, las invasiones son el principal conductor primario de las extinciones y declinaciones poblacionales, mientras que el efecto más perjudicial de la alteración del hábitat es la tendencia de hábitats alterados a soportar peces no nativos*

**Palabras Clave:** Alteración hidrológica, análisis de trayectorias, conservación de peces, criterio de información de Akaike, extinción, invasiones acuáticas, método teórico-informático, peces no nativos

## Introduction

Nonindigenous species invasions are commonly cited as the number two cause, after habitat alteration, of biodiversity loss (e.g., Vitousek et al. 1996; Mack et al. 2000; Ricciardi 2004). This one-two ranking of habitat alteration and invasions has been repeated so often that it has entered the abbreviated canon of conservation biology taught in introductory biology and environmental science classes (e.g., Wright 2005; Campbell & Reece 2005). Nevertheless, several authors have recently questioned the conservation importance of invasions, pointing out that the high correlation between nonindigenous species dominance and habitat alteration makes it difficult to determine which of the two is the cause of extinctions (Gurevitch & Padilla 2004; Didham et al. 2005; MacDougall & Turkington 2005). These authors propose that invasive species, rather than being the drivers of diversity loss, are in many cases merely passengers of more fundamental causes of extinctions and ecosystem change. Appropriate conservation action requires that we accurately identify the causes of species declines (Gurevitch & Padilla 2004). It is particularly difficult to distinguish between the driver and passenger models of invasive species effects in systems where there has been a long history of extensive habitat modification, frequent and widespread introductions of nonindigenous species, and an acknowledged association between invasive dominance and habitat alteration. This is unfortunately the situation for freshwater systems in much of the world (Poff et al. 1997).

Freshwater faunas are among the most threatened in North America, with extinction rates greatly exceeding those of marine or terrestrial vertebrates and within the range of those estimated for tropical rainforest communities (Riccardi & Rasmussen 1999). In California some 10% of the largely endemic fish fauna is extinct and another 48% is listed as endangered, threatened, or of special concern (Moyle 2002). Eighteen of California's 46 major

watersheds have lost one or more species, for a total of 38 watershed-wide extinction events in the state since about 1850 (Moyle 2002). In a survey of fishes considered extinct, declining, or endangered in California, Moyle and Williams (1990) identified water diversions as the principal cause, followed closely by introduced species and other forms of habitat modification and more distantly by pollution and overexploitation. Similarly, habitat alteration is the most commonly cited cause of fish extinctions throughout North America (73%), followed by introductions (68%) (Miller et al. 1989).

These rankings, like those of Richter et al. (1997) and Wilcove et al. (1998), rely on vote counting of the number of times particular causes are mentioned in accounts of extinct or endangered species. The science underlying these accounts tends to be fairly anecdotal, often relying on professional judgments, although on occasion experimental or other well-documented evidence clearly points to one cause or another. Frequently, conservation scientists are in the position of assessing the effects of historic events that happened nearly simultaneously or in quick succession, as when dam building or major channel alterations are accompanied by stocking of nonindigenous sport and forage fishes (Miller et al. 1989; Moyle 2002). In these instances it may be difficult or impossible to separate the effects of habitat alteration from those of species introductions. Distinguishing between the driver and passenger models in these situations requires methods that break the correlational linkages between habitat alteration and invasive dominance to distinguish between causes and correlates of species decline (Didham et al. 2005).

In California watersheds, both the richness of nonindigenous fishes (Marchetti et al. 2004) and overall homogenization of the fish fauna (Marchetti et al. 2001, 2006) are positively associated with a variety of measures of habitat alteration, including urbanization, agriculture, and hydrologic modification (impoundments and

diversions). It is unclear, however, how much of the decline of California's native fishes is due to each of these correlated causes. To address this question, we analyzed an extensive data set of fish presence, absence, and conservation status; land uses; and measures of hydrologic modification in California's major watersheds. Our goal was to distinguish among invasions and anthropogenic changes as proximate causes of extinctions and declines of native fishes in California. We used an information theoretic approach to evaluate and rank competing models predicting extinctions and declines of native fish. We then used path analysis to further refine the models, to distinguish between direct and indirect effects, and to explicitly compare the driver and passenger models of invasion effects on native fish declines.

## Methods

### Data Set

We used fish presence, absence, and conservation status data from Moyle (2002) to determine, for each major

California watershed ( $n = 43$ ), (1) the number of native fish extinctions and watershed-wide extirpations, (2) the number of fishes at risk of watershed-wide extirpation, and (3) the number of established nonindigenous fish species (NIS) (from outside California and from intrastate introductions). Some watersheds within the state were excluded from the analysis either because they lacked native fishes or because the watershed extended significantly outside the state boundaries (Marchetti et al. 2004). We added the number of fishes at risk of extinction in each watershed (Moyle 2002) to the number of extirpations to determine the number of fish species of conservation concern (FCC) in each watershed. For each watershed we also determined the historic (pre-1850) native species richness by adding the number of extant and extinct native species (Table 1).

We used a geographic information system and digital map data to measure seven watershed-scale habitat attributes for each of the 43 watersheds (Table 1). Some available variables were not included in the main analysis because of high correlations with included variables (e.g., road density with proportion developed, reservoir

**Table 1.** Variable names, categories, descriptions (including units), and data transformations for variables used in the models of native fishes of conservation concern.<sup>a</sup>

<i>Variable</i>	<i>Variable category</i>	<i>Description</i>	<i>Transformation</i>
Extinct fishes	response variable	number of native fishes extirpated from each watershed since 1850	$\sqrt{(x + 1)}$
Fishes of conservation concern (FCC)	response variable	number of native fishes extinct or at risk of extinction in each watershed	$\sqrt{(x + 1)}$
Native richness	diversity	original richness of fishes in the watershed, including present native fishes plus extinct native fishes	$\sqrt{(x + 1)}$
Nonindigenous richness (NIS)	invasions	number of established nonindigenous fishes in the watershed	$\ln(x + 1)$
Dams	hydrologic modification	number of dams per area (no./1000 km <sup>2</sup> ); includes dams >7.6 m (25 feet) in height or with a storage capacity of at least 61,681 m <sup>3</sup> (50 acre-feet)	$\ln(x + 1)$
Ditch density	hydrologic modification	density of unlined ditches and canals per watershed area (m/km <sup>2</sup> )	$\ln(x + 1)$
Aqueduct density	hydrologic modification	density of lined aqueducts per watershed area (m/km <sup>2</sup> )	$\ln(x + 1)$
Proportion developed	land use	proportion of watershed developed: commercial, industrial, urban, suburban, transportation, mines, quarries	arc-sine $\sqrt{x}$
Proportion agriculture	land use	proportion of watershed in agriculture: cropland, pasture, feeding lots, orchards, groves, vineyards, nurseries	arc-sine $\sqrt{x}$
Proportion protected	land use	proportion of watershed with high protection status: USFS wilderness areas or research natural areas; NPS national parks, preserves, monuments, seashores, and wilderness areas; BLM wilderness areas; state park wilderness areas and reserves; State Fish and Game ecological reserves; University of California natural reserves; Nature Conservancy preserves; Audubon sanctuaries <sup>b</sup>	arc-sine $\sqrt{x}$
Watershed area		area of watershed, or of California portion for watersheds that cross state lines (km <sup>2</sup> )	$\ln(x)$

<sup>a</sup>Data sources are given in Marchetti et al. 2004.

<sup>b</sup>USFS, U.S. Fish and Wildlife Service; NPS, National Park Service; BLM, Bureau of Land Management.

area with number of dams). We also excluded variables describing the natural environment (stream density, elevation, rainfall) because we lacked specific predictions regarding their relationships with fish extinctions and declines. For this study, we examined variables related to hydrologic alteration (number of dams, ditch density, and aqueduct density) and land use (proportions developed in agriculture and proportions with high protection status; Table 1). Watershed area was used in the path analysis because previous analyses (Gido & Brown 1999; Marchetti et al. 2004) show it to be highly predictive of nonindigenous fish richness.

We transformed fish diversity and environmental variables to improve normality and meet assumptions of constant variance (Table 1). After transformation, most variables still deviated somewhat from normal according to the Shapiro-Wilk test. The variable extinct fishes was particularly far from normal (Shapiro-Wilk  $W = 0.667$ ,  $p < 0.0001$ ), probably because of the large number of watersheds (26) with no recorded extinctions. For this reason, we focused most analysis on the number of fishes of conservation concern. In the final path analysis, we compared the path models for number of extinct species to those for fishes of conservation concern to evaluate the ability of the models to predict extinctions alone. The residuals of all models presented here were normally distributed (Shapiro-Wilk  $W > 0.94$ ,  $p > 0.05$ ).

### Regression Analysis

Our goal in model building was to explicitly compare models that included subsets of variables representing three hypothesized drivers of native fish declines: invasions, hydrologic modification, and land-use modification. Rather than focus on a single best model, we used the information-theoretic, model-selection approach of Burnham and Anderson (2002) to rank and evaluate a set of 72 proposed linear-regression models. Our candidate models included a global model (including all eight explanatory variables), eight single-variable models, and a set of multivariable models that included native richness plus all possible combinations of up to three additional variables. All multivariable models included the variable native richness because we expected the number of declining species to be greater in watersheds containing more species. This approach seemed to preserve more information than the alternative of modeling the proportion of species of conservation concern, relative to native richness, in each watershed. Diagnostics from a multiple-regression fit of the global model indicated a reasonable fit to the data with no deviations from the underlying regression assumptions and showed no evidence of overdispersion as measured by the variance inflation factor (VIF).

We ranked the models with a small-sample size variant of Akaike's information criterion ( $AIC_c$ ) to gauge the relative support for each model. The  $AIC_c$  estimates the

Kullback–Leibler distance between the model at hand and the (unknown) theoretical underlying mechanism generating the data; lower  $AIC_c$  values indicate a better fit (Burnham & Anderson 2002). We calculated the difference between each  $AIC_c$  value and the  $AIC_c$  value of the top-ranked model ( $\Delta_i$ ). This AIC difference estimates the fit of each model compared with the best-fitting model. We used JMPIN (SAS Institute 2002) to perform multiple regressions and obtain AIC values and the formulas of Burnham and Anderson (2002) to calculate  $AIC_c$  values.

We inspected the model ranking to determine whether more than one model had reasonable support. Models with  $\Delta_i \leq 2$  are typically considered to have substantial support and those with  $\Delta_i$  between 2 and 7 to have some support (Burnham & Anderson 2002). For the current analysis, we examined in detail the set of models with  $\Delta_i$  values of  $\leq 7$ . Although 36 candidate models met this initial criterion, we eliminated all models in which one or more variables failed to contribute to the fit of the model. These models all represented variants of higher-ranked models that differed only in including an additional variable or two that reduced the fit of the model. On a post hoc basis, each remaining model was tested to see if adding additional variables would contribute to the fit of the model (none did). For the resulting set of models ( $n = 7$ ), we calculated the Akaike weight ( $w_i$ ), which represents the relative likelihood of each model, given the data. It is calculated as the ratio of each model's likelihood to the sum of all the model likelihoods. We then determined the standardized regression parameter values and their significance, and the model-averaged regression parameters (calculated by summing the product of  $w_i$  and the regression parameter for each variable across all models; Burnham & Anderson 2002). We calculated cumulative Akaike weights ( $\Sigma w_i$ ), a measure of variable importance (Burnham & Anderson 2002), for each variable by summing the  $w_i$  for each model containing the variable. To compare the relative importance of hydrologic alteration, land-use disturbance, and invasions as predictors of native fish declines, we calculated, for each category, the cumulative  $w_i$  for models containing any variables from that category.

### Path Analysis

Multiple regression, including the model-selection approach outlined earlier, has the drawback that parameters can be treated only as independent (predictor) or dependent (response) variables. In the analysis earlier, the dependent (response) variable was number of FCC, and all other variables are predictors and were assumed to be independent of one another. However, we already know from earlier analyses (Marchetti et al. 2004) that the number of introduced fish species per watershed can be predicted from watershed area, native richness, and some of the land use and hydrologic modification variables. To

better model the system as we understand it (e.g., by treating nonindigenous fish richness as both a dependent and independent variable), we performed a path analysis using SYSTAT (SYSTAT 1999). This also allowed us to separate the direct effects of watershed disturbance variables on number of fishes of conservation concern from their indirect effects via nonindigenous species richness. Path analysis, like the information-theoretic approach, requires the explicit statement of a prior hypothesis in the form of a path diagram. It differs from multiple regression in that variables may be treated as simultaneously dependent and independent, and it allows explicit testing of direct versus indirect effects (Mitchell 1993; Shipley 2000).

To minimize the number of variables in the analysis, we created the composite variable "water development in-

dex" (WDI) by summing the standardized values of number of dams, aqueduct density, and ditch density (McDonald 1996). As a check on the WDI, we reran each path model, replacing WDI by each of the hydrologic modification variables (dams, reservoir area, ditch, aqueduct) in turn. Each of these models was consistent with the data (likelihood ratio test) and gave results qualitatively similar to those using the WDI (T.L., unpublished analysis).

We considered three alternative path models. The full model (Fig. 1a) included direct paths from the variables WDI, proportion developed, and native richness to both NIS and FCC, and a direct path from NIS to FCC. We used the full model to examine the direct effects of NIS and environmental variables on FCC and to separate the direct effects of the environmental variables on FCC from their

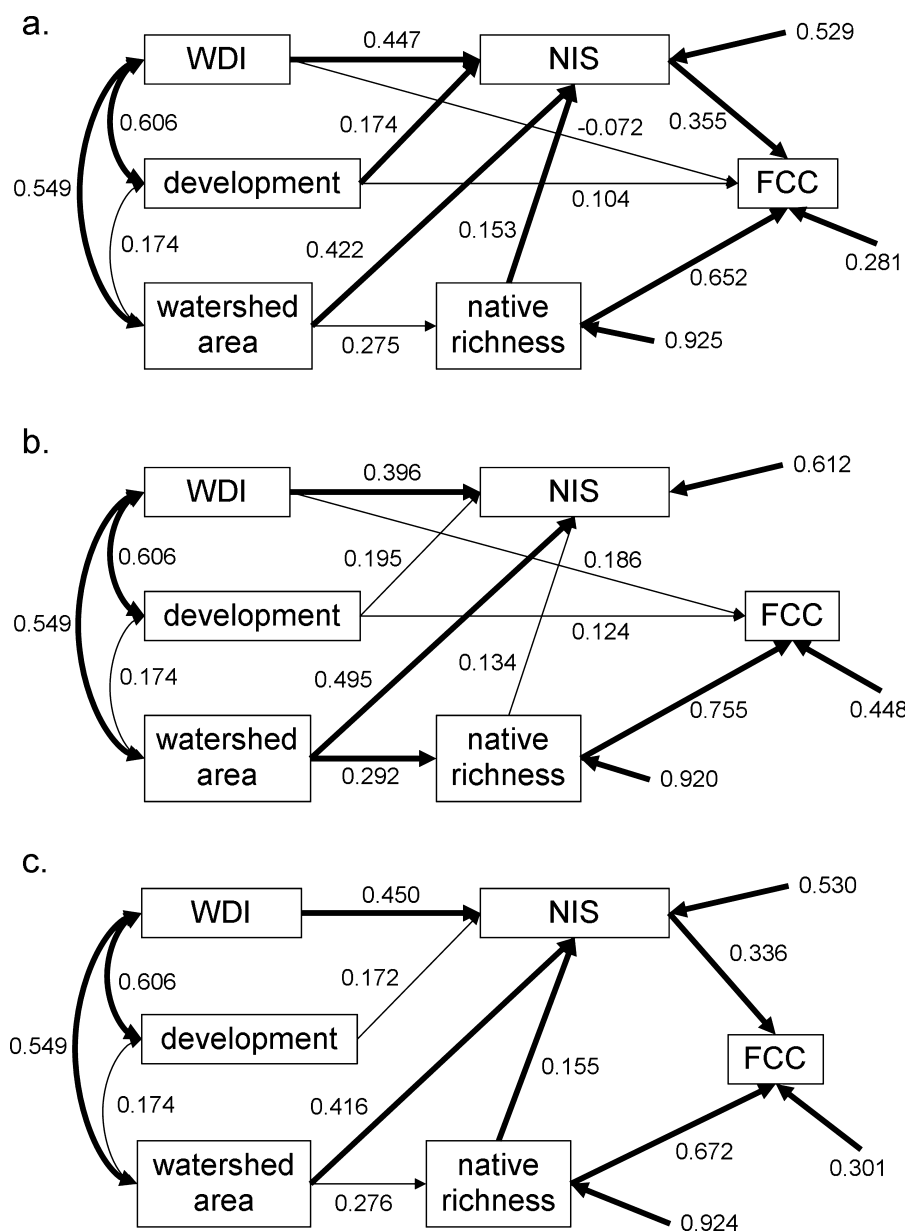


Figure 1. Path diagrams of three models of effects of hydrologic development (WDI), proportion developed land (development), watershed area, native richness, and nonindigenous fish richness (NIS) on the number of fishes of conservation concern (FCC) in 43 California watersheds: (a) full model incorporating all hypothesized paths among variables, (b) passenger model hypothesizing no direct effect of invasions on FCC, (c) driver model hypothesizing direct effects of invasions but no direct effects of WDI or development on FCC. Models a and c are consistent with the data; model b is not (likelihood ratio test). The numeric values (path coefficients) are the maximum likelihood values of the free parameters based on centered and standardized variables. Units are standard deviations from the mean (Shipley 2000). Thick arrows indicate significant effects ( $p < 0.05$ ). The significant positive association of nonindigenous with native richness in models a and c is consistent with previous findings, and is discussed elsewhere (Marchetti et al. 2004).

indirect effects via NIS. We then compared the full model to two nested models. In the first (the passenger model, Fig. 1b), the direct effect of NIS on FCC was deleted (i.e., fixed at zero). In this model, all association between invasions and native fish declines was assumed to be due to shared causes, specifically, the environmental variables and native richness. In the second (the driver model, Fig. 1c), the direct effects of WDI and proportion developed on FCC were deleted, while the direct effect of NIS was retained. This model assumes no direct effect of environmental alteration on native fish declines, with any association due mainly to indirect effects via NIS. We evaluated all models for collinearity using the VIFs and condition indices (CIs) (Petraitis et al. 1996), and found no major problems (largest VIF = 3.36, largest CI = 3.7; both for model 1 [Fig. 1a]).

We used the likelihood ratio test to evaluate the fit of all three models, and the difference between likelihood ratios to compare the nested and full models. The likelihood ratio test (maximum likelihood  $\chi^2$  statistic) provides a measure of the fit between model and data in a path analysis by measuring the probability that the observed and expected correlation (or covariance) matrices differ by more than would be expected because of random sampling errors (Mitchell 1993; Shipley 2000). The likelihood ratio difference test allows comparisons among models, so long as the models are nested (Mitchell 1993; Shipley 2000). Nested models differ in that a path that is free to vary in the more comprehensive model is constrained to a certain value (usually zero) in the nested model (Mitchell 1993; Shipley 2000).

## Results

### General and Univariate Results

Fish species richness and species composition in California watersheds have been markedly altered over the last 150 years by both invasions and extinctions, and these alterations were associated with many forms of watershed alteration, including development, agriculture, and hydrologic alteration (Table 2). The average California watershed has experienced 0.75 fish extinctions (range 0–4), has 2.6 at-risk species (range 0–8), and has gained 10.3 nonindigenous species (range 0–41). Meanwhile, some 1165 dams over 7.6 m in height have been constructed in the portions of the state covered by our analysis, the average watershed is about 14% (range 0–63%) developed and 20% (range 0–57%) in various forms of agriculture. There were significant positive univariate correlations between most forms of watershed disturbance and both nonindigenous fish richness and number of native fishes of conservation concern in each watershed. Nonindigenous fish richness was also highly positively correlated with number of fishes of conservation concern in each watershed (Table 2).

### Regression Analysis

The top-ranked multivariate model ( $AIC_c = -46.6$ ) explaining number of fishes of conservation concern in a watershed included the variables native richness, nonindigenous richness, dams, and aqueduct density (Table 3). Five other models had strong support ( $\Delta_i < 2$ ) and

**Table 2.** Univariate (Pearson) correlations<sup>a</sup> among variables in the analysis of fishes of conservation concern, showing high positive correlation between invasions and number of fishes of conservations concern, and between measures of hydrologic and land-use modification and both invasions and native fish declines.<sup>b</sup>

	<i>Fishes of conservation concern</i>	<i>Nonindigenous richness</i>	<i>Dams</i>	<i>Ditch density</i>	<i>Aqueduct density</i>	<i>Proportion developed</i>	<i>Proportion agriculture</i>	<i>Proportion protected</i>	<i>Native richness</i>
Nonindigenous richness	0.537***	1.000							
Dams	0.212	0.545***	1.000						
Ditch density	0.443**	0.736***	0.430**	1.000					
Aqueduct density	0.221	0.569***	0.230	0.464**	1.000				
Proportion developed	0.375*	0.535***	0.515***	0.347*	0.526***	1.000			
Proportion agriculture	0.601***	0.567***	0.421**	0.572***	0.282	0.423**	1.000		
Proportion protected	-0.152	0.060	-0.293	0.037	0.064	-0.153	-0.141	1.000	
Native richness	0.772***	0.299*	0.235	0.274	-0.140	0.191	0.539***	-0.303*	1.000
Watershed area	0.509***	0.736***	0.212	0.661***	0.385**	0.174	0.394**	0.193	0.276

<sup>a</sup>Significance of correlations: \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$ . Correlations were calculated after transformation (detailed in text).

<sup>b</sup>Examination of scatterplots revealed no major deviation from bivariate normality ( $n = 43$  watersheds).

**Table 3. Standardized regression coefficients, their 95% confidence intervals (in parentheses), and model diagnostics for the seven top-ranked models predicting number of fishes of conservation concern in each watershed.<sup>a</sup>**

Model rank (category) <sup>b</sup>	Native richness	Nonindigenous richness	Dams	Ditch density	Aqueduct density	Proportion developed	Model diagnostics <sup>c</sup>			
							AIC <sub>c</sub>	Δ <sub>i</sub>	w <sub>i</sub>	adj. R <sup>2</sup>
1 (I,W)	0.746 (0.54, 0.95)	0.285 (0.026, 0.54)	-0.171 (-0.37, 0.042)		0.209 (-0.020, 0.43)		-46.6	0.000	0.218	0.691
2 (I,W)	0.725 (0.52, 0.93)	0.187 (-0.045, 0.42)			0.232 (0.0034, 0.46)		-46.5	0.137	0.203	0.678
3 (W)	0.793 (0.60, 0.98)				0.349 (0.17, 0.53)		-46.2	0.396	0.179	0.665
4 (I,W,L)	0.712 (0.51, 0.90)	0.368 (0.15, 0.58)	-0.256 (-0.48, -0.038)			0.182 (-0.030, 0.39)	-46.2	0.417	0.177	0.688
5 (I,W)	0.697 (0.50, 0.90)	0.433 (0.22, 0.64)	-0.190 (-0.40, 0.019)				-45.6	0.984	0.133	0.672
6 (I)	0.664 (0.46, 0.86)	0.337 (0.15, 0.52)					-44.6	1.981	0.081	0.652
7 (W,L)	0.726 (0.52, 0.94)		-0.204 (-0.43, 0.024)	0.238 (0.035, 0.44)		0.266 (0.050, 0.48)	-40.4	6.162	0.010	0.643
Average <sup>d</sup>	0.731 (0.51, 0.94)	0.250 (-0.092, 0.59)	-0.110 (-0.37, 0.15)	0.002 (-0.008, 0.012)	0.155 (-0.16, 0.47)	0.035 (-0.092, 0.16)				
∑w <sub>i</sub> <sup>e</sup>	1.000	0.811	0.537	0.010	0.599	0.187				

<sup>a</sup>Blank entries indicate the variable was not included in the model (i.e., regression coefficient = 0). Calculation of confidence intervals follows Burnham and Anderson (2002).

<sup>b</sup>Model categories: I, invasions; W, hydrologic modification; L, land-use modification.

<sup>c</sup>The AIC<sub>c</sub> is the small-sample variant of Akaike's information criterion; Δ<sub>i</sub> (AIC difference) is the difference between each AIC<sub>c</sub> value and that of the best-performing model; w<sub>i</sub> (Akaike weight or model probability) is calculated as the ratio of each model's likelihood to the sum of all model likelihoods (Burnham & Anderson 2002). The adjusted R<sup>2</sup> value is provided for comparison with less-familiar model diagnostics.

<sup>d</sup>Model-averaged regression coefficients were calculated by multiplying each standardized regression coefficient by the corresponding w<sub>i</sub> and summing the results.

<sup>e</sup>The cumulative Akaike weight (cumulative rank) for each variable was calculated by summing the Akaike weights (w<sub>i</sub>) for each model containing that variable.

**Table 4.** Observed (below diagonal) and expected (above diagonal) correlations among fish and environmental variables in the path analysis.<sup>a</sup>

	FCC <sup>b</sup>	Native richness	NIS <sup>c</sup>	Water development	Proportion developed	Watershed area
Fishes of conservation concern (FCC)	—	0.748	0.515	0.376	0.278	0.420
Native richness	0.772	—	0.269	0.151	0.048	0.275
Nonindigenous richness (NIS)	0.537	0.299	—	0.807	0.525	0.740
Water development	0.383	0.161	0.807	—	0.606	0.549
Proportion developed	0.375	0.191	0.535	0.606	—	0.174
Watershed area	0.509	0.276	0.736	0.549	0.174	—

<sup>a</sup>Expected correlations are calculated from the path diagram, and are based on the full model (Fig. 1a).

<sup>b</sup>Fishes of conservation concern.

<sup>c</sup>Nonindigenous fish richness.

one had moderate support ( $\Delta_i < 7$ ) (Table 3). Native richness and nonindigenous richness were strongly predictive of number of fishes of conservation concern in most highly ranked models. The hydrologic modification variables aqueduct density, dams, and ditch density and the land-use variable proportion developed entered some top models, while the remaining variables (proportion agriculture and proportion protected) did not contribute to the fit of any top-ranked models (Table 3). Among the model-averaged regression coefficients, only the coefficient of native richness had a 95% confidence interval that did not include zero (Table 3).

In the analysis of variable importance, native richness was the most important single predictor of number of fishes of conservation concern in a watershed, entering every highly ranked model. The variable nonindigenous richness was next in importance, followed by the variables aqueduct density and dams (Table 3). In the analysis of category importance, the cumulative rank of all models including water development variables (0.919) was the highest, followed closely by models including nonindigenous richness (0.811), and more distantly by models including land-use variables (0.187).

### Path Analysis

The full path model detailed in Fig. 1a produced a good fit with the data (likelihood ratio test = 4.58,  $df = 3$ ,  $p = 0.21$ ). The likelihood ratio tests the null hypothesis that the observed and expected (under the model) correlation matrices are identical (Table 4), so the non-

significant result indicated that the data were consistent with the causal model depicted in Fig. 1a. The passenger model (Fig. 1b), with no direct effects of nonindigenous richness on fishes of conservation concern, was not consistent with the data (likelihood ratio test = 16.97,  $df = 4$ ,  $p = 0.002$ ). The driver model, with direct effects of NIS on FCC but no direct effects of WDI or proportion developed, also fit the data well (likelihood ratio test = 6.21,  $df = 5$ ,  $p = 0.29$ ). The difference between likelihood ratios for the full and driver models was also nonsignificant (likelihood ratio difference test = 1.63,  $df = 2$ ,  $p = 0.44$ ). The driver model should therefore be preferred to the full model as it is more parsimonious. The full model explained 92% of the variance in FCC; 13% of that variance was due to the direct effects of NIS. The driver model similarly explained 91% of the variance in FCC, with 11% of that due to direct effects of NIS. However, because native richness alone explains 45% of the variance in FCC, nonindigenous diversity directly explains about 20% of the variance in fish diversity declines that has a meaningful cause (i.e., is not due just to larger numbers of fishes declining in more diverse watersheds).

The path analysis revealed strong and significant direct effects only of native richness and nonindigenous richness on fishes of conservation concern (Figs. 1a & 1c; Table 5). The majority of the association between NIS and FCC in model 1a was accounted for by this direct effect, whereas a minority was accounted for by indirect effects due to shared causes (e.g., in the path analytic framework of model 1a, a portion of the univariate correlation between NIS and FCC would be due to the shared

**Table 5.** Decomposition of direct and indirect effects and effects due to shared causes of nonindigenous fish richness and environmental variables on native fish extinctions and declines in California watersheds.<sup>a</sup>

Variable affecting fishes of conservation concern	Direct effect	Indirect effect via NIS <sup>b</sup>	Total of other indirect effects	Effects due to shared causes	Total effect	Observed correlation
Nonindigenous fish richness	0.355	—	—	0.160	0.515	0.537
Water development	-0.072	0.159	0.289	—	0.376	0.382
Proportion developed	0.104	0.062	0.112	—	0.278	0.375

<sup>a</sup>Based on the full model (Fig. 1a).

<sup>b</sup>Nonindigenous fish richness.

predictor native richness) (Table 5). The positive correlations of water development variables and proportion developed land with native fish declines were, according to this model, mainly due to their indirect effects via non-indigenous richness. The direct effects of both variables on native fish declines were weak and nonsignificant (Table 5; Figs. 1a & 1c). Measures of water development, proportion developed land, watershed area, and native richness all had positive direct effects on nonindigenous fish richness (Figs. 1a & 1c).

Substituting number of extinct fishes per watershed for fishes of conservation concern produced qualitatively similar results in all three models. Although all models initially showed an acceptable fit with the data (likelihood ratio test: full model = 2.03,  $df = 3$ ,  $p = 0.57$ ; passenger model = 6.43,  $df = 4$ ,  $p = 0.17$ ; driver model = 6.17,  $df = 5$ ,  $p = 0.29$ ), the difference between likelihood ratios for the full and passenger models was significant (likelihood ratio difference test = 4.40,  $df = 1$ ,  $p = 0.036$ ), leading to rejection of the nested passenger model. The full model explained 67% (7% due to NIS), and the driver model explained 62% (12% due to NIS) of the variance in number of extinct fishes.

## Discussion

Diversity loss among California freshwater fishes was strongly associated with the extent of invasions, hydrologic modification, and land-use disturbance. However, because the abiotic disturbances were also strongly predictive of invasion extent, it was not immediately obvious which of these hypothesized causes was most directly responsible for the declines and extinctions of native fishes. The regression analysis gave nearly equal importance to hydrologic modifications (as a group) and invasions as predictors. In contrast, the path analysis identified invasions as the key direct driver of native fish declines and extinctions. The most parsimonious path model was the driver model, which included no direct effect of either hydrologic modification or land disturbance on native fish declines. Instead, it indicated that the overall association of both variables with native fish declines was due to indirect effects via fish invasions and other correlated factors, such as watershed area and native diversity. This model suggests that, at least for California fishes, the most damaging aspect of aquatic habitat modification may be the tendency of modified habitats to support nonindigenous fishes, which often do not prosper in the highly fluctuating natural flow regimes of unaltered streams (Baltz & Moyle 1993; Marchetti & Moyle 2001).

Although the two analyses appear to lead to conflicting conclusions, they are not asking precisely the same questions. The regression analysis assumes all predictors of native fish declines to be independent direct drivers of

those declines. The path analysis treats the variable non-indigenous richness as simultaneously dependent (with regard to environmental modification variables) and independent (with regard to native fish declines), better reflecting the hypothesized causal relationships among variables in this system. Although the data are observational, and both analyses ultimately rely on correlational linkages among variables of unknown true causal relationships, path analysis does allow us to explicitly test alternative causal hypotheses (the full, passenger, and driver models). Path analysis of quantitative empirical data has been suggested as one approach to testing the driver versus passenger models of invasion effects on native species (Didham et al. 2005). In large systems involving mobile species, manipulative experiments at relevant scales may be nearly impossible. This leaves statistical approaches such as the above, and examination of historic case studies, or "natural experiments" (Diamond 1984).

Some particularly well-documented cases in California support the idea that modified habitats frequently continue to support native species in the absence of invasions. For example, many mid-elevation reservoirs of the Central Valley contained abundant native Sacramento suckers (*Catostomus occidentalis*), Sacramento pikeminnows (*Ptychocheilus grandis*), and hardheads (*Mylopharodon conocephalus*) for the first few years after filling. As non-native fishes, especially centrarchid basses, were introduced and became abundant, recruitment of pikeminnows and hardheads declined, and they were eventually extirpated (though typically they have maintained populations in streams where these are not too altered by reservoir operations). Suckers remain abundant (sometimes more than before reservoir creation) in many of these reservoirs (Moyle 2002). In some cases, reservoirs may even provide beneficial habitat to otherwise rare fishes. The rough sculpin (*Cottus asperimus*) of the Pit River drainage, the first fish to be officially protected by the California Fish and Game Commission, is typically an inhabitant of springs and large spring-fed rivers. Hydroelectric power development of the Pit River drainage has led to the extirpation of rough sculpins from some dewatered reaches; meanwhile, it has successfully colonized several reservoirs, extending its former range some 22 km downstream (Moyle 2002). However, the more common pattern, at least in California, is the dominance of altered habitats by introduced fishes—including large predators such as the black basses (*Micropterus* spp.), intermediate predators such as sunfishes (*Lepomis* spp.) and crappies (*Pomoxis* spp.), and introduced forage fishes such as golden shiners (*Notemigonus crysoleucas*) and threadfin shad (*Dorosoma petenense*)—and the subsequent limitation of native fishes to less-altered stream reaches (when these remain), where few introduced fishes can maintain large populations (Baltz & Moyle 1993; Moyle 2002).

Other cases, however, demonstrate that local extinctions of California fishes can also be due to habitat alteration alone. Dam building with its associated diversions and dewatered stream reaches has led fairly directly to extirpation and decline of large-river salmonids, particularly certain runs of chinook salmon, *Oncorhynchus tshawytscha* (Moyle 2002). Sedimentation due to poor logging practices has resulted in extirpation and decline of many northern coast salmonid populations, particularly coho salmon, *O. kisutch*, and steelhead, *O. mykiss*. This impact was not well captured in our models, due to lack of available spatially explicit (i.e., GIS) data on logging and sediment loading. This omission may limit the usefulness of our models for predicting losses in parts of California (e.g., the North Coast bioregion), which are heavily affected by logging. While these losses have had major ecological and economic impacts, they are dwarfed in sheer numbers by declines and extinctions that are associated at least in part with invasions (Moyle 2002; this analysis).

## Other Systems

How representative are the California fish data of other systems and taxa? Several lines of evidence suggest that the relative importance of invasions and habitat alteration as drivers of freshwater species declines may differ in other regions of North America. According to the surveys of resource managers and other experts, exotic invasions top the list of threats to western aquatic species, whereas eastern species are most threatened by altered sediment loads and nutrient pollution, threats that were rarely mentioned for western species (Richter et al. 1997). Introduced fishes make up a relatively small proportion of fish species richness (2–25%) in typical eastern North American drainages, compared to western drainages (25–70%) (Meador et al. 2003). While overall fish assemblage change (including both invasions and extirpations) in eastern drainages is associated with altered land uses (Ross et al. 2001; Scott & Helfman 2001; Argent & Carline 2004) and reduced water quality (Meador et al. 2003), to our knowledge no analysis has jointly examined abiotic changes and fish invasions as drivers of fish diversity losses in eastern North America.

The fish faunal composition, hydrology, and threats common to California stream systems may be more similar to streams of the Mediterranean regions of southern Europe than to those of eastern North America (Moyle 1995). Mediterranean systems share the high endemism, seasonal flow patterns, high degree of invasions, and profound modification by dams, diversions, and channelization characteristic of California streams. Quantitative analyses of native fish declines, invasions, and habitat alteration in this region reveal that dams, channelization, and

water pollution are associated with both native species decline and with the richness and abundance of introduced fishes (Aparicio et al. 2000; Corbacho & Sánchez 2001; Clavero et al. 2004). However, none of these analyses separately quantify the impact of introduced fishes on native diversity or conservation status.

The passenger model receives some of its strongest support from the recent plant literature. Harrison et al. (2006) used structural equation modeling (a more general form of path analysis) to examine a data set from serpentine grasslands in California. The authors demonstrate that, while natural environmental variables and disturbance influence both exotic cover and native richness, exotic cover has no significant effect on native richness or on the richness of endemic or rare species once the environmental variables are accounted for. In an experimental study (MacDougall & Turkington 2005), a 3-year removal of dominant non-native grasses in garry oak (*Quercus garryana*) meadows had little effect on the richness or cover of native species. Because fire suppression is the main cause of non-native grass dominance, and competition with the dominant grass is not the only factor limiting native herbaceous species, this study has been upheld as an example of the invasive-species-as-passengers idea (Didham et al. 2005). Other removal experiments with plants, however, reveal positive effects on native richness and cover (e.g., D'Antonio et al. 1998; Alvarez & Cushman 2002). A recent study of New England (USA) coastal marshes indicates that shoreline development facilitates *Phragmites* invasion, while *Phragmites* is strongly implicated in reducing native plant diversity (Silliman & Bertness 2004). With the exception of Harrison et al. (2006), however, none of these studies was explicitly designed to separate the effects of disturbance from that of invasions. Because serpentine grasslands occupy a particularly stressful habitat that is fairly resistant to invasion (Harrison et al. 2006), it is difficult to assess how well they represent other plant assemblages.

## Implications for Conservation

The driver and passenger models have distinctly different implications for conservation policies and practices. In systems best described by the passenger model, native species should be adequately protected by restoration and protection of habitat and natural ecosystem processes. In systems best described by the driver model, as we suggest is the case for California freshwater fishes, the situation is more complex. Habitat protection and restoration are still important in these systems, as nonindigenous species are frequently facilitated by altered habitats. In aquatic systems, restoring natural flow patterns and disturbance regimes can sometimes favor native over introduced fishes, leading to at least partial restoration of

historic fish communities (Schmidt et al. 1998; Trexler et al. 2000; Marchetti & Moyle 2001). Not all restoration efforts are so successful, however. For example, evidence so far suggests that ongoing, multimillion-dollar efforts to restore shallow-water habitat in the Sacramento-San Joaquin Delta (CA) may end up benefiting primarily non-indigenous fishes and invertebrates (Brown 2003; Feyrer et al. 2004). In such systems, careful fine tuning of restoration efforts may be required to tip the balance toward native species. For example, Crain et al. (2004) showed that early inundation of restored floodplains along the Cosumnes River, California, favors predominantly native larval fishes, whereas later flooding and warmer water temperatures favor introduced fishes.

Where restoration alone cannot reduce populations of invasive species, serious consideration should be given to aggressive eradication efforts, coupled with education and legislation designed to prevent or at least slow the rate of new introductions. Eradicating established nonindigenous species, however, is generally feasible only at the earliest invasion stages and/or over a small geographic area (Drake & Naiman 2000; Saunders et al. 2002; Simberloff 2003). In aquatic systems, eradication attempts have typically used nonselective poisons, particularly the piscicide rotenone, which is increasingly running afoul of public concerns about impacts on drinking water safety, nontarget biodiversity issues, conservation values, and managed sport fisheries (e.g., eradication efforts for northern pike [*Esox lucius*] in California, Moyle 2002). The generally low success, high expense, and unpopularity of eradication efforts suggest that preventing further invasions should be a high priority to conservation (Saunders et al. 2002). Analyses that have considered the economic costs of invasions versus the cost of prevention have also made this point (e.g., Mack et al. 2000; Leung et al. 2002).

Supporting the idea that habitat protection alone will not preserve native fish diversity in California, we found no evidence that diversity losses are less likely in watersheds with a high proportion of protected land area. We previously showed that protected status has a similar lack of association with the richness of nonindigenous fishes (Marchetti et al. 2004). Protected areas in California typically are located at high elevations, have low native fish diversity, and are rarely managed for native fish conservation. Furthermore, the cultural practice of stocking sportfishes is common in most parks and wilderness areas (Moyle 2002). Successful protection of native aquatic diversity in California will require a suite of conservation strategies: shifting management of protected lands to the watershed or bioregional scale, identifying and protecting watersheds with largely intact fish communities, restoring natural hydrographs, preventing further introductions, and locally eradicating (where possible) established nonindigenous fishes (Moyle & Yoshiyama 1994; Saunders et al. 2002).

## Conclusions

We concur with Gurevitch and Padilla (2004) that the causes of extinction and species declines should be examined carefully before they are used to guide conservation action and the allocation of scarce resources. These authors point out that habitat alteration and invasion are often linked and that this linkage can make it difficult to discern the most important cause(s) of biodiversity declines. The large-scale systems of conservation interest are rarely amenable, practically or ethically, to manipulative experimentation, the ecologist's preferred tool for breaking correlational linkages and confidently assigning causation. However, path analysis can be used to assess the relative fit of different causal models to correlational data, though it cannot exclude the possibility that the patterns observed may be due to causes not included in the models (Shipley 2000). Many data sets of invasions, native diversity declines, and habitat change exist that could be assessed with this approach. Such analyses would improve our understanding of broad patterns in biodiversity loss, and are likely to identify important regional and taxonomic differences in the drivers of diversity declines. Exotic species may well be primarily passengers of habitat alteration in some systems, such as California's serpentine grasslands (Harrison et al. 2006). In other systems, however, high correlations between invasions and disturbance may obscure the fact that habitat alteration is actually *less* directly responsible for species declines than it appears. Managers and policy makers must be able to distinguish between these possibilities to predict whether protection and restoration of natural habitats and ecosystem processes, in the absence of active efforts to exclude or remove invasive species, will be sufficient to restore species of conservation concern.

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## Queries

- Q1** Author: The abbreviation AIC appears both with and without the subscript “c” to the letter “C.” Is it OK?
- Q2** Author: Reference “Vitousek (1996)” has been changed to “Vitousek et al. (1996)” per list. Is it OK?
- Q3** Author: Reference “Campbell and Reece (2006)” has been changed to “Campbell and Reece (2005)” per list. Is it OK?
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