ECOLOGICAL PROCESSES DRIVING BIOTIC HOMOGENIZATION: TESTING A MECHANISTIC MODEL USING FISH FAUNAS

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Abstract. Biotic homogenization, the process of gradual replacement of native biotas by nonindigeous and locally expanding nonnative species, is rapidly diminishing the regional distinctiveness of global terrestrial and aquatic ecosystems. Although the empirical study of biotic homogenization is substantial and growing, the mechanisms underlying its dynamics remain poorly understood. We recently developed a theoretical model that predicts levels of biotic homogenization or differentiation (i.e., decreased community similarity) according to a series of distinct mechanisms that describe the outcomes of various interactions between native species, nonnative species, and the environment. Here, we test this model using empirical data for freshwater fish faunas in the United States at three spatial scales: the entire continent, zoogeographic provinces in California, and watersheds within these provinces. Our analysis reveals that, in general, mechanisms depicting widespread introductions of cosmopolitan species and either no or differential spatial patterns of native-species extirpations explain fish-community homogenization across multiple spatial scales. Our results also highlight the potential effect of spatial grain on the perceived importance of different invasion–extinction scenarios shaping patterns of homogenization and differentiation. Next, we discuss the utility of the model for providing insight into the dominant ecological processes likely driving the homogenization of other major taxonomic groups that currently lack quantitative estimates of community change. Our study is the first to quantitatively examine the relative importance of different ecological mechanisms that can generate observed patterns of biotic homogenization. Using this model may allow advance prediction of future patterns of homogenization by explicitly considering underlying ecological processes and mechanisms.

Key words: beta diversity; biodiversity; biotic differentiation; community similarity; distinctiveness; fish communitites, biotic-homogenization likelihood; fish fauna; species extinctions; species invasions; species richness; taxonomic homogenization.

INTRODUCTION

The regional distinctiveness of biological communities reflects historical factors that have restricted species ranges via physical isolation, ecological interactions, and evolutionary diversification (Huston 1994). In contrast to the paleontological record that reveals only episodic mixing of isolated biotas, such as during the Great American Interchange after the formation of the Panama isthmian land bridge (Vermeij 1991), global biotic exchange has been dramatically accelerated by humans in historical times. Charles Elton (1958) was perhaps the first to recognize this phenomenon when he discussed the dissipation of Wallace's Faunal Realms by global commerce during European settlement. In the past few decades humans have hastened the mixing process by dissolving natural biogeographic barriers through activities such as canal building, international commence, exotic pet trade, intentional translocations, aquaculture, and horticulture (Courtenay and Stauffer 1990, Carlton and Gellar 1993, Litvak

and Mandrak 1993, Naylor et al. 2001, Reichard and White 2001). The introduction of cosmopolitan, nonnative species, in conjunction with the loss of native (often endemic) species is causing the breakdown of regional distinctiveness of the Earth's biota, a process termed *biotic homogenization* (Vitousek et al. 1997, McKinney and Lockwood 1999).

Patterns of biotic homogenization (or, more specifically, taxonomic homogenization) are defined simply as an increase in species similarity among a set of communities through time. This phenomenon has received increased attention in recent years for numerous taxonomic groups, including plants (Rooney et al., *in press*), birds (Lockwood et al. 2000, Jokimäki 2003), insects (Blair 2001), reptiles and mammals (Wilson 1997), marine algae (Carlton 1996), mussels and amphibians (Duncan and Lockwood 2001*b*), snails (Cowie 2001), zooplankton (Beisner et al. 2003), and fish (Radomski and Goeman 1995, Rahel 2000, Marchetti et al. 2001, Scott and Helfman 2001), although only quantified for a small subset of these groups. Despite this wealth of interest, our understanding of the process remains very limited. For instance, biotic homogenization can arise from a number of ecological mecha-

nisms representing specific, often quite distinct, interactions among native species, nonnative species, and the environment. Several factors can regulate patterns and rates of homogenization, including the degree of initial differences in species similarity among the communities coming in contact (reflecting zoogeographic history), the taxonomic identities of the introduced and extirpated species, and the spatial distribution and number of species introductions and extirpations across the landscape (reflecting both natural and anthropogenic factors related to vectors of introduction and habitat modification). Our inability to distinguish among these various ecological and environmental drivers of biotic homogenization impedes our ability to explain current patterns or predict future rates of homogenization and thus intervene to minimize the potentially serious ecological and evolutionary consequences (Olden et al. 2004).

The first mechanistic investigation of biotic homogenization was recently provided by Olden and Poff (2003), who developed a predictive model that forecasts trajectories of biotic homogenization or differentiation (i.e., decreased community similarity) according to a series of distinct mechanisms that describe the outcomes of various interactions between native species, nonnative species, and the environment. In this paper we test this mechanistic model using freshwater fish faunas, the only taxonomic group for which quantitative estimates of homogenization are published. We analyze three data sets at three spatial scales: the continental United States (Rahel 2000), zoogeographic provinces in California (Marchetti et al. 2001), and the watersheds within these California provinces (Marchetti et al. 2001). To test the model, we hypothesized a priori which specific mechanisms would best describe the interactions between native fish species, nonnative fish species, and environmental modification at the three scales. Next, we applied the model to generate model predictions of changes in community similarity according to a suite of ecological mechanisms and compared them to the published findings of fish-fauna homogenization and differentiation.

Our empirical validation of the mechanistic model provides important insight into the dominant ecological processes driving contemporary changes in fish-community similarity within and across the United States. For major taxonomic groups currently lacking quantitative estimates of biotic homogenization, we discuss the utility of the model for exploring different invasion and extirpation processes likely to be dominant shapers of community change in those groups. Identifying the possible ecological processes leading to observed patterns in community similarity is the first step toward a mechanistic understanding and prediction of biotic homogenization and our paper is the first quantitative investigation of specific mechanisms responsible for patterns of biotic homogenization in a major taxonomic group. The mechanistic model provides an important framework for interpreting the growing number of studies documenting patterns of biotic homogenization across a broad number of taxonomic groups.

An Overview of the Theoretical Model of Biotic Homogenization (Olden and Poff 2003)

Taxonomic homogenization (the most commonly studied form of biotic homogenization; Olden et al. 2004) refers to an increase in species similarity among a set of communities and is quantified as the change in the pair-wise community similarity (based on species presence or absence) over a specified time interval (Rahel 2002). The model of Olden and Poff (2003) describes 14 ecological mechanisms by which different rates and patterns of species invasions and extinctions (or extirpations, hereafter used interchangeably) can cause changes in community similarity. These 14 scenarios, summarized in Table 1, represent possible outcomes resulting from unique combinations of interactions among species and the environment that are well supported in the aquatic and terrestrial literature (see Olden and Poff [2003] for empirical examples for each scenario). The invasion–extinction scenarios are divided into three groups depending on whether only species invasions (scenarios I1–I2), only species extinctions (scenarios E1–E4), or both species invasions and extinctions (scenarios IE1–IE8) occur in the recipient communities.

For each invasion–extinction scenario the model systematically varies: (1) the number of introduced and extinct species; (2) the initial similarity among the communities (hereafter referred to as J_i); and (3) the initial species richness of the communities; to generate predictions of change in community similarity based on Jaccard's coefficient of similarity (hereafter referred to as "ΔCS"). The number of introduced species ranged from 0 to initial species richness, whereas the maximum possible number of extinct species was constrained by the number of species that the communities originally shared or did not share and the number of species that were available to become extinct, and therefore varied depending on the initial community similarity and the particular scenario. A positive ΔCS represents biotic homogenization and a negative ΔCS represents biotic differentiation.

Empirical Evidence for Fish-Fauna Homogenization Throughout the United States

Elimination of the regional distinctiveness of fish faunas across the United States is the best quantitative documentation of biotic homogenization to date (e.g., Radomski and Goeman 1995, Rahel 2000, Duncan and Lockwood 2001b, Marchetti et al. 2001, Scott and Helfman 2001, reviewed by Rahel [2002]). The estimates of fish homogenization and differentiation reported by Rahel (2000) and Marchetti et al. (2001) are among the only published in the literature (but see Radomski and

TABLE 1.   A summary of the 14 invasion–extinction scenarios of the mechanistic model of Olden and Poff (2003) representing different ecological mechanisms by which species invasions and extinctions can drive biotic homogenization (i.e., increased community similarity) and differentiation (i.e., decreased community similarity).

| | | | Supporting evidence‡ | |
Scenario	Description	Predictions†	Qualitative	Quantitative
Invasion-only events				
I1	Same species invade, no extinction of resident species	C, P, W	C, P	**P̲**
I2	Different species invade, no extinction of resident species	W, w	w	**w̲**
Extinction-only events				
E1	No species invasion, extinctions in both communities involve same species		W	W
E2	No species invasion, extinctions in both communities involve different species			
E3	No species invasion, extinction in one community of a species that was originally shared by both communities			
E4	No species invasion, extinction in one community of a species that was originally not shared by both communities			
Invasion-and-extinction events				
IE1	Same species invade, extinctions in both communities involve same species	C, P, W	C, P	
IE2	Same species invade, extinctions in both communities involve different species			
IE3	Same species invade, extinction in one community of a species that was originally shared by both communities	C, P, W	C, P, W	**C̲, W̲**
IE4	Same species invade, extinction in one community of a species that was originally not shared by both communities		C, P	
IE5	Different species invade, extinctions in both communities involve same species			
IE6	Different species invade, extinctions in both communities involve different species	W, w	W	W
IE7	Different species invade, extinction in one community of a species that was originally shared by both communities			
IE8	Different species invade, extinction in one community of a species that was originally not shared by both communities	W, w	w	**w̲**

Note: The scenarios are divided into three groups, depending on whether changes in community similarity are driven by only species invasions events (scenarios I1–I2), only species extinctions events (scenarios E1–E4), or both species invasion and extinction events (scenarios IE1–IE8).

† The a priori predictions of invasion–extinction scenarios playing dominant roles in driving fish community change at each scale: C = continental United States, P = California's provinces, W = California's watersheds, and w = California's South Coast province watersheds.

‡ Supporting evidence refers to those model predictions showing the strongest agreement with empirical estimates of community change at each scale based on qualitative (Fig. 1) and quantitative (Fig. 2) assessments. Boldface underlined values for quantitative support indicate those scenarios with the strongest overall agreement (see *Empirical evidence for fish-fauna homogenization . . .* for details).

Goeman 1995). These two data sets are optimal for testing the model because they were collected over a similar time period (approximately the last century), which minimizes potential bias in estimates of homogenization resulting from length of observation period (Olden and Poff 2003). Using current ecological thought we generated several a priori hypotheses regarding the most plausible ecological mechanisms driving patterns of fish-fauna homogenization or differentiation in the United States at three different spatial scales (see Table 1).

At the continental scale, Rahel (2000) compared present-day to pre-European-settlement fish faunas across the 48 conterminous United States. On average, pairs of states were reported to have 15.4 more species in common than before European settlement, which resulted in an average homogenization of 7.2%. Rahel (2000) attributed patterns of homogenization to the widespread introduction of cosmopolitan species and only the limited extirpation of native species, a hypothesis that is also supported for the major drainages of North America (see Gido and Brown 1999). Evidence also suggests that a common suite of species comprise most widespread introductions (Gido and Brown 1999, Rahel 2000) and that particular species are more prone to extinction (Angermeier 1995, Duncan and Lockwood 2001*a*). Based on this understanding, we hypothesized that continental fish-fauna homogenization is driven primarily by scenarios involving introductions of the same species, accompanied by either no species extinctions (I1), extinction of the same species (IE1), or differential extinction of species that were originally shared by the communities (IE3) (Table 1). More precisely, we hypothesized that patterns of homogenization would most closely fit the mechanisms depicted in IE3 because species extinctions are likely to occur differentially across the landscape in response to nonrandom patterns of habitat deg-

radation (Moyle 1986, Richter et al. 1997), and that the large spatial grain (i.e., political states) at which homogenization is quantified will increase the diversity of habitats and communities sampled, thereby increasing the probability that pairs of states will historically share the same species.

Next, we use the data of Marchetti et al. (2001) to test the model at two finer spatial scales: zoogeographic provinces of California and watersheds within these provinces. Given the different spatial grains at which homogenization was quantified and California's unique geographic and hydrologic history (Mount 1995), we expected different invasion–extinction scenarios to vary in importance in shaping patterns of fish community composition between provinces and between watersheds.

At the provincial scale, Marchetti et al. (2001) found zoogeographic provinces to exhibit, on average, a 20.3% increase in community similarity ($n = 6$ provinces). Analogously to continental-scale homogenization, province-scale changes in fish-community similarity are expected to be driven by the introduction of a common group of species and minimal extinction of native species (Moyle 2002). We therefore hypothesized that change in provincial similarity will be driven by scenarios I1, IE1, or IE3, and of these scenarios (Table 1) we predicted scenario I1 to be of primary importance given the minimal number of species extinctions in California (Moyle 2002).

At the watershed scale, Marchetti et al. (2001) reported that the watersheds within the four major zoogeographic provinces in California exhibited, on average, a 10.7% decrease in community similarity ($n = 7, 10, 11$, and 15 watersheds). This smaller spatial grain implies an increased probability of observing species introductions and extinctions of different or originally unshared species in the communities, because finer sampling resolution should accentuate among-site habitat and species differences. Therefore, at this scale, in addition to the scenarios discussed above for provinces, we expected scenarios IE6 and IE8 to be potentially important for driving patterns of community change (Table 1).

Last, to further explore the model's utility, we examined the 11 watersheds within the South Coast province, the unique zoogeographic history of which suggests additional invasion–extinction scenarios may operate to drive homogenization. Historical fish communities of this province are believed to be very similar due to the presence of many anadromous species and Pleistocene connections during periods of low sea level (Moyle 2002). Indeed, Marchetti et al. (2001) reported an average historical community similarity of 63.3% among the watersheds. Further, these watersheds have likely experienced haphazard species introductions from multiple sources (e.g., aquaculture, aquarium escapees). Together, these two lines of evidence led us to hypothesize the predominance of scenario I2, in ad-

dition to the potential contributions of scenarios IE6 and IE8 (as suggested for the watershed scale, above) (Table 1).

GENERATING MODEL PREDICTIONS OF FISH-FAUNA HOMOGENIZATION AND DIFFERENTIATION

We extended the mechanistic model of Olden and Poff (2003) to generate predictions of change in community similarity (i.e., predicted levels of homogenization and differentiation) according to each of the 14 invasion–extinction scenarios. Input parameters of the model include: (1) the initial level of community similarity (J_i), (2) the number of introduced and extinct species, and (3) the initial species richness of the communities. First, given the wide range of initial similarities reported across the sampling units of states ($J_i = 0.00$ to 0.89), provinces ($J_i = 0.00$ to 0.58), and watersheds ($J_i = 0.00$ to 1.00), we generated model predictions for all levels of J_i from 0.00 to 1.00, increasing by increments of 0.01. These incremental predictions allow a detailed exploration of the model's utility. Second, to account for varying rates of species invasions and extinctions both within and among the sampling units, we averaged ΔCS (the change in Jaccard's coefficient of similarity) across all possible combinations and numbers of introduced and extinct species. Third, because model predictions have been shown to be independent of species richness values exceeding 20 (Olden and Poff 2003), we set initial species-richness to 100, a reasonable estimate of the mean number of fish species across all data sets. All simulations were conducted using computer macros in MatLab (The MathWorks, Natick, Massachusetts, USA) written by J. D. Olden.

Predicted ΔCS for each of the invasion–extinction scenarios are illustrated in Fig. 1A–C, and show either linear or unimodal relationships with J_i. Invasion-only (I1 and I2), extinction-only (E3), and both invasion and extinction scenarios (IE1–IE8) reduce community similarity (i.e., differentiation) with increasing J_i, whereas the magnitude of ΔCS for the remaining scenarios (E1, E2, E4) initially increases and then decreases with J_i. Independent of J_i the model predicts homogenization for scenarios I1, E2, E4, IE1, IE2, and IE4 and differentiation for scenarios I2, E1, E3, and IE5–8; only scenario IE3 leads to both homogenization and differentiation.

VALIDATING THE MODEL USING FISH FAUNAS OF THE UNITED STATES AT THREE SPATIAL SCALES

We used two approaches to test the model and differentiate among the alternative ecological processes driving the homogenization of fish faunas. First, using regression analysis we qualitatively compared (i.e., visual inspection) model predictions of the change in Jaccard's coefficient of similarity, ΔCS (Fig. 1A–C) to empirical patterns of ΔCS (Fig. 1D–E) as they vary across the entire range of J_i. Polynomial regression
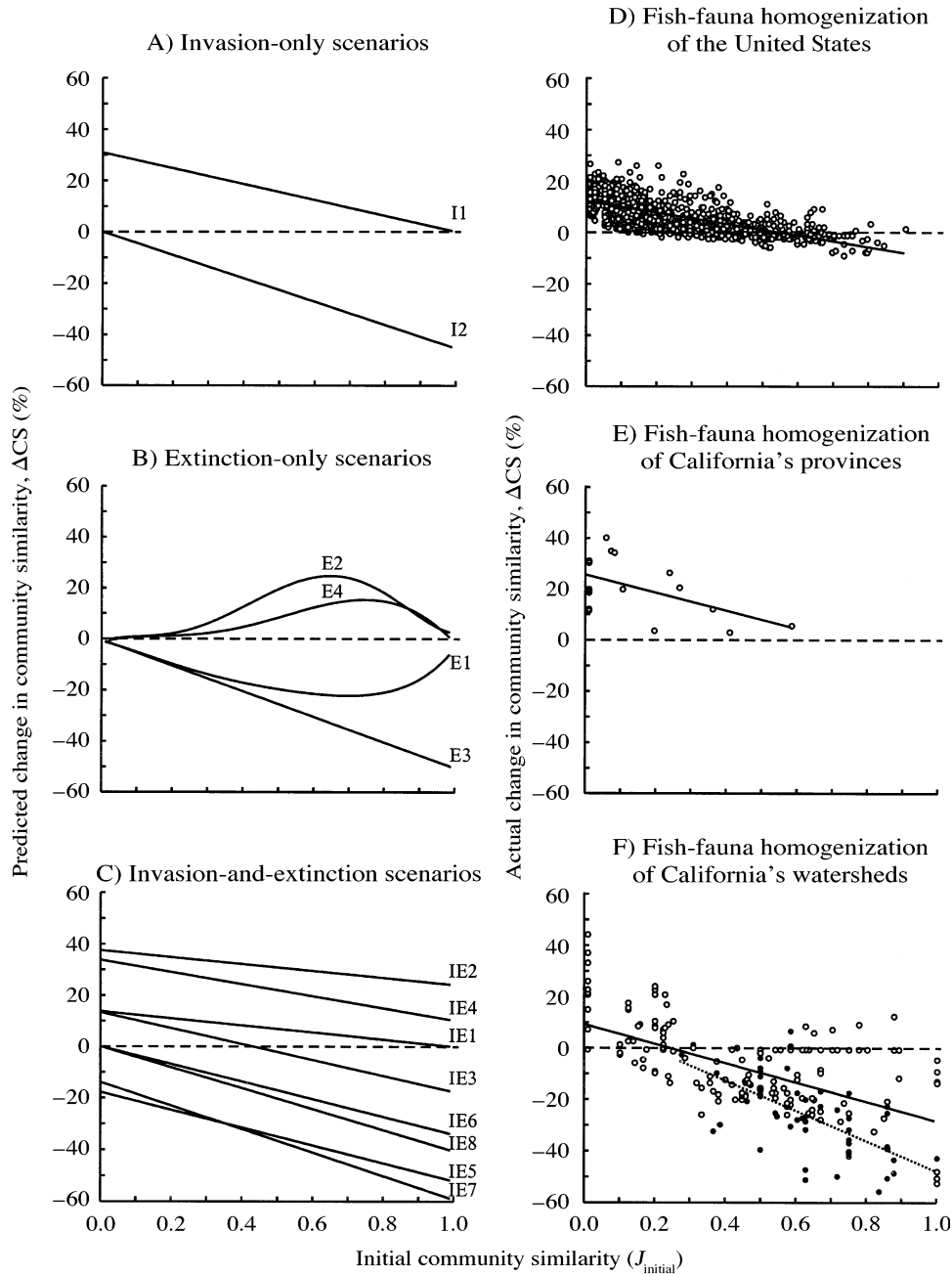
FIG. 1. Patterns of change in community similarity (ΔCS) as a function of the initial similarity among communities (J_i) (both represented by Jaccard's coefficient of similarity expressed as a percentage) based on model predictions for three different invasion–extinction scenarios: (A) only species-invasion scenarios (I1–I2), (B) only species-extinction scenarios (E1–E4), and (C) both species-invasion and extinction scenarios (IE1–IE8), and based on empirical values for (D) the continental United States, (E) the zoogeographic provinces of California, and (F) the watersheds of the four major provinces of California (open circles, solid line) and the watersheds of the South Coast province (solid circles, dotted line).

Model predictions are averages for all combinations of numbers of introduced and extinct species for each J_i (see *Generating model predictions of fish-fauna homogenization* for more details). Dashed lines demarcate homogenization (positive ΔCS) from differentiation (negative ΔCS).

Least-squares regression lines are as follows: I1, $y = 30.94 - 0.31J_i$; I2, $y = 0.0 - 0.45J_i$; E1, $y = 2.36 - 0.78J_i + 0.006J_i^2$; E2, $y = -11.26 + 1.03J_i - 0.009J_i^2$; E3, $y = 0.0 - 0.50J_i$; E4, $y = -5.58 + 0.46J_i - 0.003J_i^2$; IE1, $y = 13.70 - 0.14J_i$; IE2, $y = 37.50 - 0.13J_i$; IE3, $y = 13.32 - 0.13J_i$; IE4, $y = 33.78 - 0.24J_i$; IE5, $y = -17.76 - 0.34J_i$; IE6, $y = 0.0 - 0.34J_i$; IE7, $y = -13.92 - 0.45J_i$; IE8, $y = 0.0 - 0.41J_i$; United States, $y = 11.79 - 0.23J_i$; California provinces, $y = 25.92 - 0.36J_i$; California watersheds, $y = 9.20 - 0.38J_i$; and California South Coast province, $y = 10.49 - 0.57J_i$.
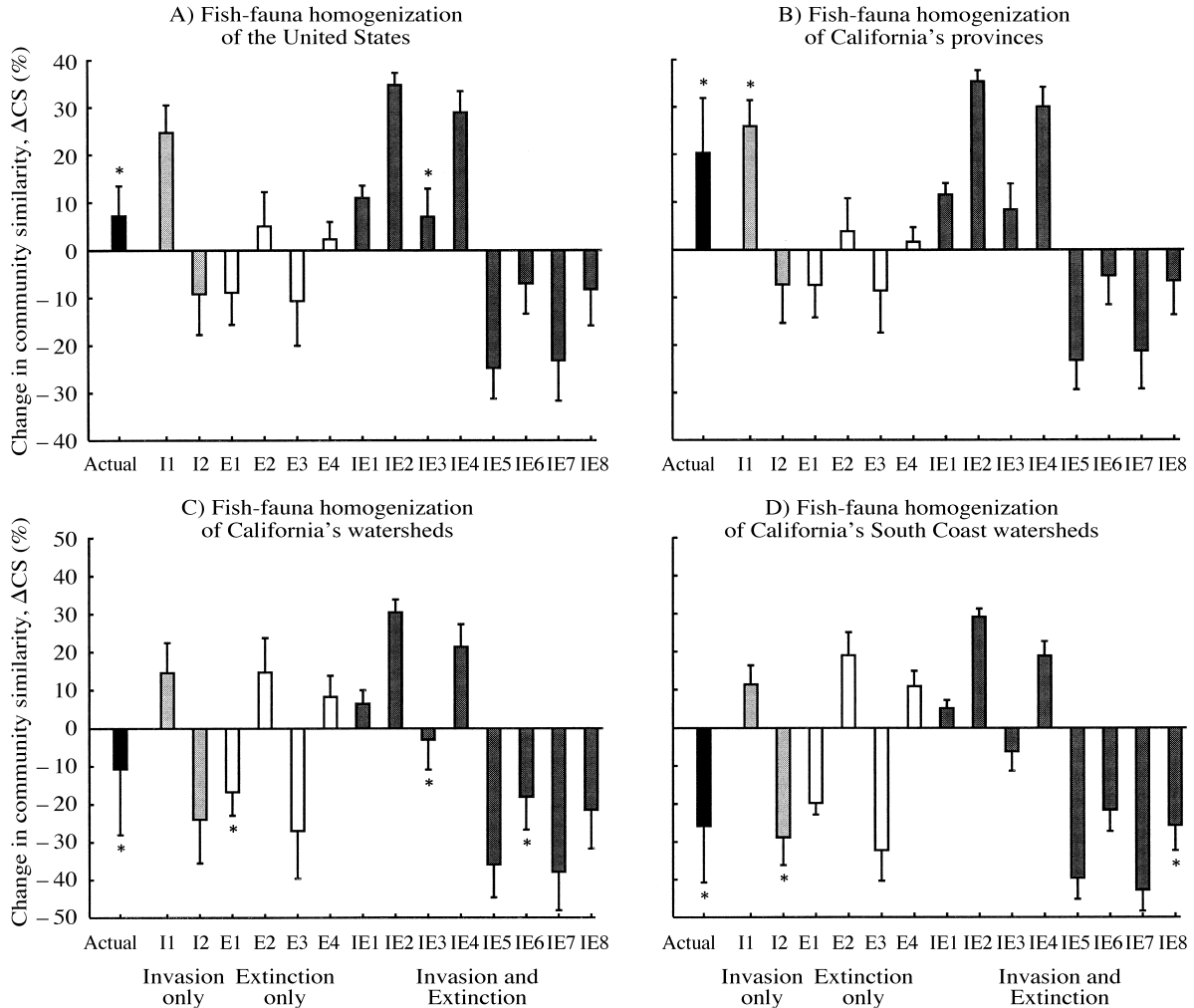
FIG. 2. Changes in community similarity (ΔCS) for model predictions based on each of the 14 invasion–extinction scenarios (generated using actual values of initial fish community similarities) and for empirical values across the continental United States (A), the zoogeographic provinces of California (B), the watersheds of the four major provinces of California (C), and the watersheds of the South Coast province (D). Data are means and 1 SD; asterisks represent nonsignificant differences between actual and predicted ΔCS based on a Student's t test, thus providing support for the importance of the particular scenario. The solid horizontal lines demarcate homogenization (positive ΔCS) from differentiation (negative ΔCS).

(second-degree) was used for scenarios E1, E2, and E4 because they were clearly nonlinear, and simple linear regression was used for the remaining scenarios. Second, we quantitatively validated the model by seeding it with the actual values of J_i for each pair-wise comparison for each scale (i.e., state–state, province–province, watershed–watershed pairs) to estimate mean and variance of ΔCS for each scenario. Empirical values of ΔCS were then compared to the predicted ΔCS for each scenario using a Student's t test with significance based on a Bonferroni-corrected significance level of $\alpha = 0.004$ (note: a noncorrected $\alpha = 0.05$ produced similar results) (Fig. 2). Scenarios that showed concordance with empirical patterns of ΔCS for both approaches implicate their importance in fish-fauna homogenization.

At the continental scale, model predictions of ΔCS according to the 14 invasion–extinction scenarios showed variable agreement with observed levels of ΔCS reported by Rahel (2000). The comparison of regression lines showed that predicted ΔCS model predictions for scenarios I1, IE1, IE3, and IE4 have highest concordance with observed patterns of ΔCS, thus supporting the importance of these ecological processes for driving broad-scale biotic homogenization (Fig. 1A,C, and D). Of these scenarios, three match our a priori hypotheses (Table 1). However, only model predictions of ΔCS for scenario IE3 did not differ significantly from empirical values of ΔCS ($t = 1.37$, df = 1127, $P > 0.004$; Fig. 2A). Scenario IE3 is further supported by the fact that predictions for the other three scenarios failed to detect biotic differentiation, a phe-

nomenon observed for 130 of the 1128 pair-wise state comparisons (Fig. 1D).

At the provincial scale, scenarios I1, IE1, IE3, and IE4 agree well with observed patterns of changes in fish community similarity (Fig. 1A,C, and E). Again, three of these four scenarios match our a priori hypotheses (Table 1). The strongest correspondence was for scenario I1, in which the slope and y intercept were very similar to empirical patterns of ΔCS (Fig. 1A and E) and only model predictions from this scenario did not differ significantly from empirical values ($t = -2.28$, df = 14, $P > 0.004$; Fig. 2B).

At the watershed scale, model predictions for scenarios E1, IE3, and IE6 showed strong concordance with empirical patterns of community change (Fig. 1B and C). Predicted ΔCS for all these scenarios did not significantly differ from observed ΔCS ($t = -7.81 - 7.14$, df = 225, $P > 0.004$; Fig. 2C). Scenarios IE3 and IE6 match our a priori hypotheses (Table 1); however, strongest evidence was for scenario IE3 because visual inspection of Fig. 1F shows that scenarios E1 and IE6 failed to predict biotic homogenization, a phenomenon that was observed for 44 of the 226 pair-wise watershed comparisons (Fig. 1F).

Within the South Coast province specifically, observed changes in fish community similarity among watersheds (Fig. 1F) were consistent with predictions provided by the model for scenario I2 (Fig. 1A) and scenario IE8 (Fig. 1C). Model predictions for both these scenarios were the only that did not significantly differ from actual ΔCS ($t = -0.03 - 1.87$, df = 54, $P > 0.004$; Fig. 2D).

DISCUSSION

The empirical homogenization and differentiation of fish communities at different spatial scales provides strong support of the mechanistic model of Olden and Poff (2003). The strength of this model is that it is simple enough to be tractable analytically yet realistic enough to be applicable to the study of biotic homogenization at a variety of spatial scales. Our results strongly support current scientific evidence implicating both widespread introduction of cosmopolitan species and the differential extinction of native species (likely caused by the loss or modification of critical habitat) as determinants of fish community change across the United States (e.g., Richter et al. 1997, Rahel 2000). In contrast, at the finest spatial scale (watersheds within the South Coast Province of California) we found strong evidence for the importance of different species invasions and either no extinction (I2) or differential extinction (IE8) of unshared native species for shaping patterns of biotic differentiation. This agrees with the hypothesized sporadic introduction of aquarium fishes throughout this province (Marchetti et al. 2001), as well as the fact that decreased spatial grain likely increases the probability of observing the introduction of different species and the extinction of different or un-

shared species, because finer sampling resolution accentuates among-site habitat and community differences (Olden and Poff 2003).

The mechanistic model can also be extended to gain insight into the likely dominant invasion and extinction processes shaping community change in taxonomic groups for which adequate, quantitative estimates of homogenization are unfortunately lacking (Fig. 1A–C). Such an examination could be guided by current information regarding how the particular taxonomic group is being threatened by nonnative introductions and human disturbance. For example, the global avifauna continue to lose their regional distinctiveness due to the widespread introduction of cosmopolitan bird species, coupled with the extinction of endemic species via habitat alteration and the effects of introduced nonavian predators (Lockwood et al. 2000). Therefore, we would predict large-scale patterns of avian homogenization to be driven primarily by mechanisms describing the invasion of the same nonnative species and the differential extinction of native species (i.e., IE3 or IE4). Quantitative tests of such hypotheses will require the explicit consideration of the spatial and temporal scales at which both the data were collected and the ecological mechanisms are believed to be operating for the particular taxonomic group. In summary, based on the robust performance of our model for fish communities we believe it offers a framework for predicting future patterns of homogenization for a variety of taxonomic groups.

We acknowledge that multiple invasion and extinction processes are likely important for driving biotic homogenization and differentiation. Indeed, rates and taxonomic identities of species invasions and extinctions (i.e., different invasion–extinction scenarios) vary nonrandomly across the landscape with respect to existing patterns of human-caused habitat degradation and species introductions (e.g., Seabloom et al. 2002), as is seen for many taxonomic groups (e.g., Case 1996, McKinney 2001a, b). Further, mechanisms of homogenization may vary even within taxonomic groups that experience different rates of invasions and extinctions in different environments (e.g., island vs. continental biota, Case 1996, Lonsdale 1999; or between-island biota, Sax et al. 2002). For example, fish faunas in the eastern United States appear to have adjusted to nonnative invasions without much loss of native species (i.e., invasion-only scenarios), whereas for more disturbed aquatic ecosystems in the western United States, introduced species appear to have greater negative impacts on native communities (i.e., both invasion and extinction scenarios) (Moyle 1986). Therefore, given the likely existence of multiple drivers of homogenization we expect imperfect correspondence between model predictions that are based on only single invasion–extinction scenarios and observed patterns of fish community change. Despite this, the model shows an excellent fit to the empirical data, strongly implicating

specific invasion–extinction mechanisms in shaping patterns of homogenization and differentiation in fish faunas of the United States.

Conclusion

Biotic homogenization of communities is an emergent property of species invasion and extinction, and its quantification is sensitive to the specific ecological mechanisms operating across the landscape. Although many studies have qualitatively documented biotic homogenization in both aquatic and terrestrial ecosystems, we still lack a solid quantitative understanding of the underlying invasion and extinction processes driving patterns of community change. Consequently, our ability to predict future patterns of biotic homogenization will continue to be limited unless we begin to employ more mechanistically based models (e.g., Olden and Poff 2003) that account for differential rates of species introductions and extinctions that vary both spatially and taxonomically (Collins et al. 2002). Gaining this knowledge will define not only the manner in which this process threatens global biotas, but also the proactive management scenarios required to suppress it.

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