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Effects of urbanization on California's fish diversity: Differentiation, homogenization and the influence of spatial scale

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ABSTRACT

Human development of freshwater ecosystems has lead to drastic changes in freshwater fish faunas, including the loss of many native species and the gain of non-natives. Typically conservation ecologists view these two opposing forces as contributing to biological homogenization, and consider homogenization as one of the principle negative consequences of urbanization. However, homogenization is only one outcome out of many that can result from the loss and gain of species. In particular, it is possible for invasions and extinctions to lead to differentiation; a process whereby two (or more) regions become less similar to one another through time. Using the freshwater fishes of California, we show that urbanization is highly positively correlated to both the endangerment of native fish and the invasion of non-native fish within watersheds. Despite this, the fish faunas of California's watersheds have differentiated from one another through time. Furthermore, the degree of differentiation is positively correlated with measures of urbanization, which is contrary to expectation. We suggest that this result reflects: (1) the haphazard manner in which non-native fishes have been introduced into California watersheds, (2) the difficulty that both native and non-native fishes have in expanding their geographical ranges, and (3) the continued presence of vestiges of formerly distinct regional faunas. This pattern of differentiation among watersheds is likely a matter of scale, as previous work on freshwater fishes has demonstrated homogenization at both larger and smaller spatial scales. In addition the observed pattern is probably a short-term (temporal) phenomena and will disappear with continued invasion and extinction. We suggest that similar patterns may occur for other taxa that have limited natural dispersal abilities and that are idiosyncratically released as non-natives via human activities (e.g. herptiles).

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1. Introduction

Freshwater fish assemblages around the world have been irreversibly altered in the last 100 years (Lever, 1996; Gido and Brown, 1999; Rahel, 2000, 2002; Moyle, 2002), and as we enter a new century, it is important to ask questions regarding the fate of our remaining aquatic heritage. One of these questions should be; do we want all of our rivers, streams, lakes and estuaries to be dominated by the same suite of cosmopolitan species? There is good evidence that freshwater

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fish assemblages are becoming homogenized across the United States (Rahel, 2000) and within US watersheds (Scott and Helfman, 2001; Marchetti et al., 2001). These authors suggest increased urbanization tends to favor the persistence of a relatively few native species, the introduction and establishment of already widespread non-natives, and the extinction (or extirpation) of unique natives (see also Blair, 2001 and this issue). However, homogenization is only one outcome among several that can result from the combined effects of extinction and invasion (Olden and Poff, 2004 and this issue). It is theoretically possible that urbanization can promote faunal differentiation if the loss and gain of species across geographic units (e.g. states or watersheds) follows one of several mechanistic pathways outlined by Olden and Poff (2003). Here, we provide the first empirical example of how urbanization can lead to faunal differentiation.

Although California has a relatively small number of native freshwater fish species (66), it has a disproportionately large number of endemic taxa (24, or 36%). This is due in large part to the geographical isolation of the state and the physical diversity of habitats within the state (Moyle, 2002). This within-state physical diversity has resulted in the native fish assemblages often being regionally distinct. For example, in the Southern California zoogeographic province 40% (6) of the native species (15) are endemic solely to that province.

After the 1850 discovery of gold in California, the state experienced a rapid boom in its human population density; an upward trend in urban growth that continues to this day. Along with this influx of humans came the introduction of 50 non-native fish species (Dill and Cordone, 1997), and the statewide extinction of 7 native species (Moyle, 2002). In addition there are 32 fish species (48% of state natives) that are considered in danger of becoming extinct in the near to medium future (i.e. within the next 100 years). Considering such a large imbalance between invasions and extinctions, it should not be surprising that overall California has experienced a 76% increase in species richness (see Sax et al., 2002 and Lockwood, 2004 for similar examples).

Marchetti et al. (2001) explored how this increase in species richness altered spatial diversity patterns across several geographical scales. They found that freshwater fish assemblages have become more similar at very local scales (i.e. along stream reaches) and at very large scales (i.e. between zoogeographic provinces). However, they note that watersheds within zoogeographic regions sometimes became less similar to each other through time, although there is much variation across watershed comparisons (Marchetti et al., 2001). We build on this work and test whether or not a suite of urbanization measures correlate with the number of non-native fishes per watershed and the number of extinct or threatened species per watershed. We then go on to test whether urbanization can explain across-watershed variation in degree and direction of homogenization.

2. Methods

2.1. Fish data

We gathered presence/absence data on every freshwater fish species inhabiting California's watersheds (Fig. 1) as of January 2000 (Moyle, 2002). From these data a number of fish metrics were tallied for each watershed: the number of native species, the number of established non-native species (both from outside California and intra-state introductions), the number of native species considered either extinct or threatened with extinction. A full accounting of all the fish species in California by watershed can be found in Moyle (2002). Some watersheds within the state were excluded from the analysis either because there are no fish in the watershed, or because the watershed extended significantly outside the state boundaries (Table 1, Fig. 1).

Within California's boundaries, there are several aquatic zoogeographic provinces (Moyle, 2002; Moyle and Cech, 2004), each with distinctive climates, tectonic settings, and hydrologic regimes (Mount, 1995). All watersheds in the state fall into one of six provinces defined by Moyle (2002): Klamath, Sacramento-San Joaquin, North Coast, Great Basin, South Coast, and the Salton Sea (Table 1). Moyle's divisions, based primarily on freshwater fish distributions, are comparable to divisions based solely on hydrologic factors (Mount, 1995; Moyle, 2002). Two of these provinces contains $\leqslant 2$ watersheds (Klamath and Salton Sea) and were excluded from the Bray–Curtis analysis below.

2.2. Measurement of watershed-scale habitat data

A Geographic Information System and digital map data were used to measure 11 habitat attributes for the 44 watersheds included in the analysis (Table 2). We examined variables related to hydrologic alteration (dams, reservoir area, ditch density, and aqueduct density), land use (proportion developed, proportion agriculture, and proportion with high protection status), and natural environmental characteristics (mean elevation, mean rainfall, stream length, and watershed area). Several other variables examined early in the study were excluded due to their high correlations ($r > 0.7$) with retained variables. For example, we excluded road density (highly correlated with proportion developed), mean latitude (highly correlated with mean rainfall), and elevational range (highly correlated with watershed area). In each case, we retained the variable that seemed more inclusive (watershed area, development) or more likely to be directly related to fish diversity in California (rainfall). Variables were scaled to watershed area where appropriate and transformed for (approximate) normality as indicated in Table 2. All variables were examined for collinearity and no variable pairs had linear correlation coefficients greater than 0.67. The highest correlations were between the following pairs of variables: reservoir area/dams = 0.67, reservoir area/ditch density = 0.62, watershed area/elevation = 0.66, and watershed area/ditch density = 0.66. We also included the variable 'richness' as a measure of the original (pre-1850) native fish diversity per watershed (Table 2) as this has been shown elsewhere (Marchetti et al., 2004a) to be an important variable explaining fish invasions.

2.3. Statistical analysis

We used multiple regression models to examine the relationship for three dependant variables of interest per watershed:

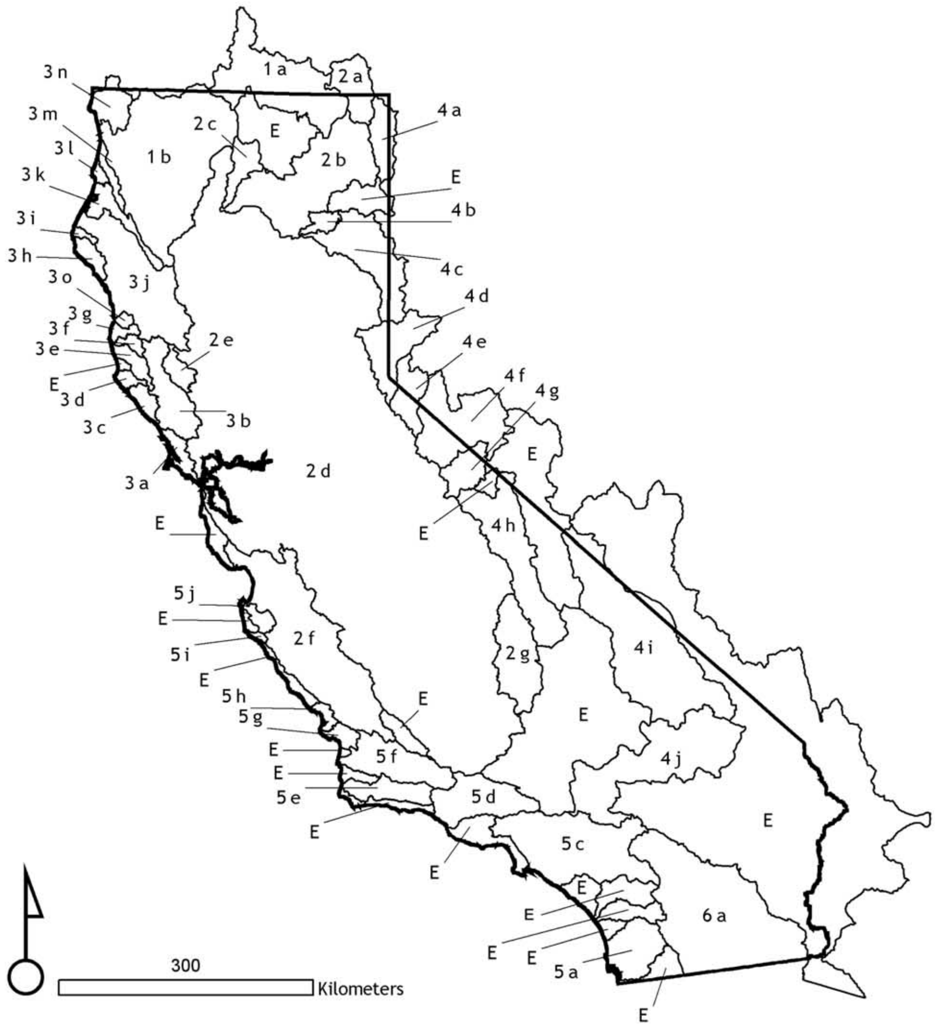

Fig. 1 – Watersheds of California. See Table 2 for watershed codes. All watersheds bearing the letter 'E' were excluded from the analysis (see Section 2 for details).

the number of non-native species, the number of native species showing some anthropogenic impact, and the averaged change in Bray–Curtis scores through time (see below for explanation of this variable). In separate analyses, these three dependant variables were regressed against the 11 independent variables of interest (Table 2). For each multiple regression model, we performed a stepwise forward model selection procedure using Wald test P-values, with inclusion criteria for the Wald test requiring $P \leqslant 0.10$ (Hosmer and Lemeshow, 2000). If a final model contained a pair of highly correlated variables (see above), each of the variables was removed in sequence and the best model containing only one of the variables was retained.

To explore changes in compositional similarity (i.e. homogenization) between the watersheds, we calculated Bray–Curtis Scores for all watershed pair wise combinations within each zoogeographic province at two time periods. The first time period (historical) represented the pre-1850 non-invaded freshwater fish fauna, where we included all extant natives and those natives that have gone extinct. The second time period (current) represents the existing freshwater fish fauna in that we included all established non-native fishes and we excluded all extinct native fishes.

Using the Bray–Curtis scores, we employed Kruskal's nonmetric multidimensional scaling (MDS) algorithm to portray the compositional differences between watersheds within

Table 1 – Diversity of native and non-native fish species in California watersheds

Watershed	Watershed Code	Zoogeographic province	Non-native fish diversity	Number of native species showing anthropogenic impact	Averaged change in Bray–Curtis score[a]
Lower klamath river	1a	Klamath	14	8	NA
Goose lake	2a	Sacramento–San Joaquin	11	4	7.99
Pit river	2b	Sacramento–San Joaquin	15	2	8.40
Mc Cloud river	2c	Sacramento–San Joaquin	4	4	−6.91
Sacramento–San Joaquin river	2d	Sacramento–San Joaquin	41	12	−0.64
Clear lake	2e	Sacramento–San Joaquin	18	6	7.58
Monterey	2f	Sacramento–San Joaquin	20	7	3.78
Kern river	2g	Sacramento–San Joaquin	7	1	9.12
Tomales	3a	North coast	7	2	−18.85
Russian river	3b	North coast	19	8	−18.47
Gualala river	3c	North coast	0	1	−5.45
Garcia river	3d	North coast	0	2	−8.08
Navarro river	3e	North coast	0	1	−5.77
Big river	3f	North coast	0	1	−6.31
Noyo river	3g	North coast	0	1	−4.68
Matolle river	3h	North coast	0	2	−7.10
Bear river	3i	North coast	0	2	−7.34
Eel river	3j	North coast	10	8	−15.91
Mad river	3k	North coast	8	6	−14.77
Little	3l	North coast	0	3	−7.02
Redwood	3m	North coast	6	5	−16.66
Smith river	3n	North coast	0	6	−6.33
Ten mile creek	3o	North coast	0	1	−5.97
Surprise valley	4a	Great basin	2	3	−5.36
Eagle lake	4b	Great basin	2	1	−14.62
Susan river	4c	Great basin	7	2	−18.48
Truckee river	4d	Great basin	15	2	−10.61
Carson river	4e	Great basin	14	2	−10.52
Walker river	4f	Great basin	13	2	−1.49
Mono lake	4g	Great basin	6	0	NA
Owens river	4h	Great basin	14	4	−7.29
Amargosa river	4i	Great basin	2	2	−3.28
Mojave river	4j	Great basin	23	1	6.02
San Diego	5a	South coast	26	4	−25.24
Santa Margarita	5c	South coast	12	5	−20.04
Los Angeles	5d	South coast	34	7	−15.08
Santa Clara	5e	South coast	24	3	−24.66
Santa Inez	5f	South coast	16	3	−18.931
Santa Maria	5g	South coast	8	3	−22.65
San Luis Obispo	5h	South coast	8	4	−21.79
Morro	5i	South coast	10	3	−24.77
Big sur	5j	South coast	0	1	−42.19
Carmel river	5k	South coast	12	1	−14.76
Salton sea	6a	Salton sea	24	4	NA

[a] Averaged change in Bray–Curtis scores given as ‘NA’ indicates that the watershed was not included in the ΔCS analysis because it was either the only watershed in the zoogeographic province (Klamath and Salton Sea) or it contained no native species (Mono).

each time period. The resulting MDS graphs provide a visual indication of how similar watersheds are to one another within one time period. Because we calculated these scores at two time periods, we can also examine how between-watershed similarity has changed through time.

Clarke and Warwick (2001) present a Monte Carlo procedure for evaluating whether or not groups of sites are statistically different in respect to their relative similarities. This test, called analysis of similarity (ANOSIM), mimics the procedures for a standard univariate ANOVA. In the context of this paper, ANOSIM provides a mechanism to statistically test whether between-watershed similarities have significantly shifted through time. To accomplish this, ANOSIM calculates the average of all rank similarities among watersheds within one time period (r_w), and the average of rank similarities arising from all watershed comparisons made between time periods (r_b). A test statistic, R, is then calculated as, $R = \frac{r_b - r_w}{1/2M}$, where $M = \frac{n(n-1)}{2}$ and n is the total number of samples (Clarke and Warwick, 2001). The test statistic R will thus vary between +1 and −1, and will take the value of +1 when all the watersheds at one a time period are more similar to each other than any of the watersheds from different time periods, with the reverse being true if R equals −1. R will equal zero if the null hypothesis that there are no differences in between-watershed

Table 2 – Name, description, data source, and transformations of variables used in the models

Variable	Description	Transformation
Dams	Number of dams per area (#/1000 km^2); includes dams >7.6 m in height or with a storage capacity of 61,681 m^3 or more	ln (x + 1)
Reservoir area	Total surface area of reservoirs per watershed area (100 m^2/km^2)	arcsine-sqrt
Ditch density	Total length of ditches and unlined canals per watershed area (m/km^2)	ln (x + 1)
Aqueduct density	Total length of aqueducts per watershed area (m/km^2)	ln (x + 1)
Development	Proportion of watershed developed: commercial, industrial, urban, suburban, transportation, mines, and quarries	arcsine-sqrt
Agriculture	Proportion of watershed in agriculture: cropland, pasture, feeding lots, orchards, groves, vineyards, and nurseries	arcsine-sqrt
Protected	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	arcsine-sqrt
Elevation	Mean elevation of the watershed (m)	ln (x)
Rainfall	Mean annual rainfall (mm), averaged spatially and temporally (1961–1990 data)	ln (x)
Stream length	Total length of natural streams per watershed area (m/km^2)	ln (x)
Ws area	Total area of watershed (including portions of the watershed outside California) (km^2))	ln (x)
Richness	Original number of fish species in the watershed, including present native species plus extinct native species	None

Full normality could not be achieved for the variables dams, reservoir area, ditch density, aqueduct density, developed, agriculture, protected, and elevation.

similarities across the two time periods is true (i.e. we cannot distinguish the two groups, historical and current, from one another). We conducted 10,000 random permutations to produce a distribution of *R*-values for comparison to the overall, or global, observed *R*-value.

Following Olden and Poff (2004) and Rahel (2000), we further characterized the degree of homogenization experienced by each watershed by calculating the change in Bray–Curtis Score between pre-1850 (historical) and current compositions for all between-watershed comparisons (ΔCS). A positive ΔCS represents biotic homogenization and a negative ΔCS represents differentiation. However, this produces as many values of ΔCS per watershed as there are pair wise comparisons to be made (i.e. *N*! comparisons where *N* is the number of watersheds in the province). To reduce this complexity, and to understand how each watershed changed relative to all others in the province, we averaged each watershed's values of ΔCS (Koleff et al., 2003). This does not change the interpretation of ΔCS. Positive scores still represent homogenization and negative scores differentiation. The averaged ΔCS per watershed are given in Table 1. These scores were then entered into the univariate and multiple linear regression analyses described above as dependent variables.

3. Results

The multiple regression model that aimed to predict the number of non-native species per watershed was significant, explaining 76% of the variance (Table 3). The following independent variables were included in the final model: reservoir area, development, and watershed area (Table 3). For example, the Los Angles watershed (Fig. 1, 4d) has a large number of introduced fishes (34) and the highest proportion of developed land (63%) of any watershed.

Table 3 – Stepwise multiple regression model examining the number of non-native species per California watershed with the set of 11 independent variables (Table 2)

Variable	DF	Parameter estimate	*F* ratio	P-value
Reservoir area	1	4.945	11.24	0.0018
Development	1	3.942	10.91	0.0020
Watershed area	1	0.578	29.53	<0.001

The table presents likelihood ratio tests for each of the four significant variables included in the final model. The final model has an adjusted $R^2 = 0.759$ and $P < 0.0001$.

The multiple regression model that aimed to predict the number of native species considered extinct or threatened with extinction per watershed was significant, explaining 72% of the variance (Table 4). The following independent variables were included in this final model: richness, aqueduct density, and watershed area (Table 4). For example, the Sacramento–San Joaquin watershed (Fig. 1, 2d) has a high number of species at risk (12) as well as a high diversity of native species (29) and the largest watershed area (>140,000 km^2) in the state.

The MDS plots of each zoogeographic province are presented in Fig. 2, with points in each graph representing the watersheds within that province. Stress values for the MDS plots are all below 0.20 (Sacramento–San Juaquin = 0.17, Southern California = 0.07, North Coast = 0.09, Great Basin = 0.13), at value which Clarke and Warwick (2001) suggest as an upper limit to an acceptable goodness-of-fit of the underlying non-parametric regression to the original similarity data. The two key pieces of information from these graphs (relative to our goals) are: (1) the difference in locations

Table 4 – Stepwise multiple regression model examining the number of native species considered extinct or threatened with extinction per California watershed with the set of 11 independent variables (Table 2)

Variable	DF	Parameter estimate	*F* ratio	*P*-value
Richness	1	0.541	73.24	<0.0001
Aqueduct density	1	0.132	7.32	0.0100
Watershed area	1	0.091	4.81	0.0342

The table presents likelihood ratio tests for each of the three significant variables included in the final model. The final model has an adjusted $R^2 = 0.718$ and $P < 0.0001$.

(composition) between the historical (pre-1850) points and the current points and (2) the changing dispersion of the points between the two time periods. In nearly all provinces, the historical points form a distinct group as compared to the current points, thus indicating that species composition in these watersheds has drastically shifted through time (see also Marchetti et al., 2001). This is confirmed statistically from the ANOSIM results (Table 5). The most extreme shifts in composition have occurred in the Sacramento–San Joaquin and Southern California provinces (Fig. 2). The North Coast province does not show much shift in composition; the two sets of points (historical and current) often overlap in the MDS space (Fig. 2).

Despite this shift in composition, the watersheds within each province have not become more similar to one another through time. In all cases, the dispersion of current points is at least as broad, if not broader, as the dispersion of historical points. Indeed, in nearly all cases the watersheds show decreased similarity to one another through time; that is, they have differentiated in composition. This result is reinforced when we review the averaged ΔCS for each watershed (Table 1). Only 6 out of 41 watersheds show a positive value of averaged ΔCS, and most of these values are half the magnitude as the negative averaged ΔCS values observed.

Because these changes in between-watershed similarities are driven by the loss of native species and the gain of non-native species, we should expect to see a correlation between averaged ΔCS and the urbanization variables albeit likely less strong as it subsumes two relatively independent mechanisms (Fig. 3). The results of the multiple regression to predict the averaged ΔCS per watershed was significant, explaining 33% of the variance (Table 6). The following independent variables were included in this final model: development, protected areas, and watershed area (Table 6). For example, San Luis Obispo watershed (5h on Fig. 1) has a negative averaged ΔCS score (−21.8), is one of the smaller watersheds in this analysis (823 km^2), has a relatively high proportion of developed land (28%) and a relatively high proportion of the watershed is protected (32%).

4. Discussion

4.1. *Linking urbanization with changes in diversity*

Most of the papers in this special volume will find links between some aspect of urbanization and the establishment

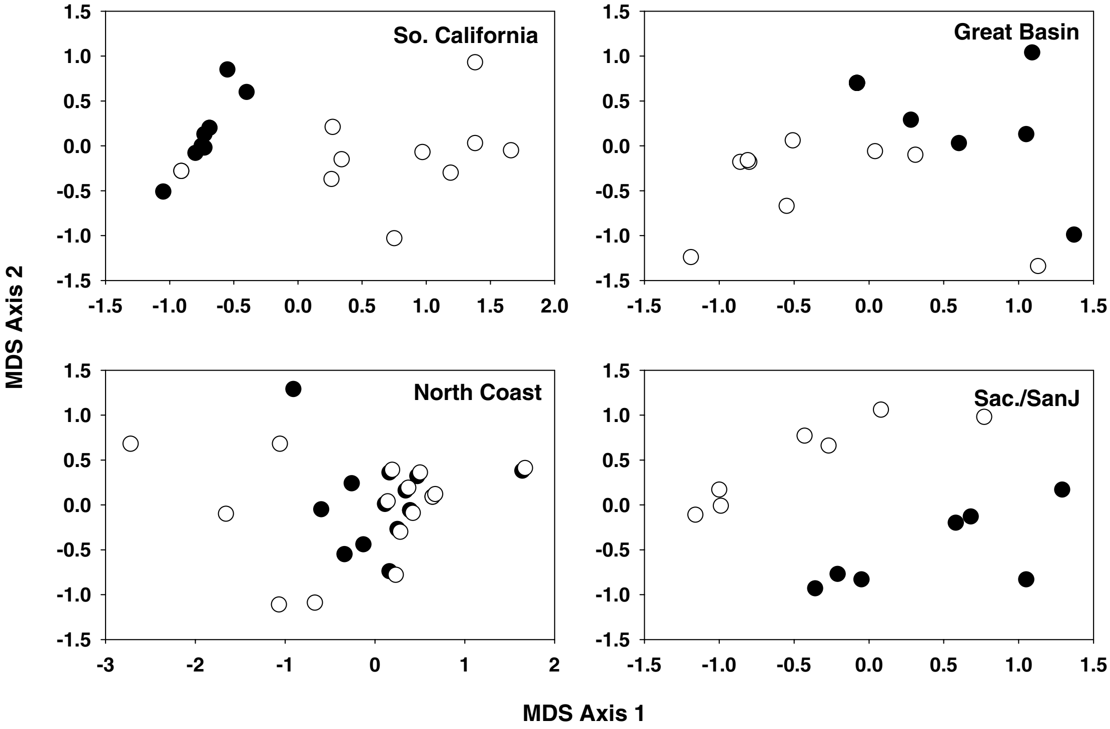

Fig. 2 – Multidimensional scaling (MDS) plots for each zoogeographic province. Historical (pre-1850) watershed composition given as closed circles and current composition given as open circles. The points in this graph are determined by their relative similarity (Bray–Curtis Score) to all other points. In the North coast zoogeographic province, eight watersheds scores for the current time period were slightly altered to better indicate their relative position.

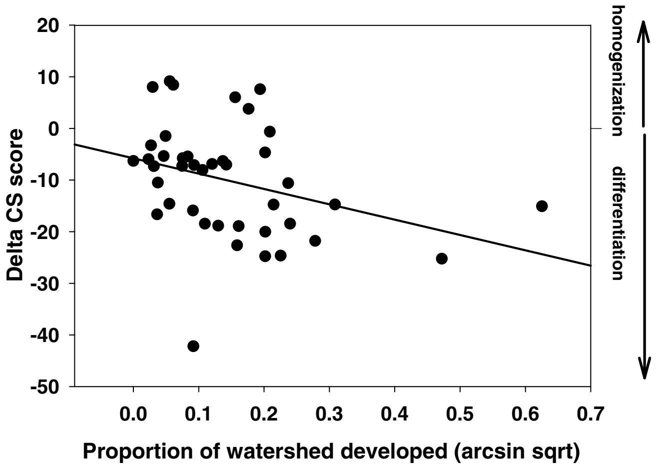

Fig. 3 – Linear relationship between proportion of watershed developed and ΔCS scores. Note that positive values for ΔCS indicate homogenization and negative values indicate differentiation. Regression line equation: ΔCS = −5.80 − 29.68 [arcsin-sqrt (development)]. $R^2 = 0.11$, $P = 0.0335$.

Table 5 – ANOSIM results from Kruskal's non-metric multidimensional scaling (MDS) analysis

Zoogeographic province	*R*-value[a]	Number of random *R*-values greater than observed	Significance level[b]
Southern California	0.644	2	0.0002
Great basin	0.261	22	0.0022
North coast	−0.007	5158	0.5158
Sacramento–San Joaquin	0.54	1	0.0001

[a] Large *R*-values indicate that the between-watershed similarities have significantly shifted through time.

[b] Significance is judged by comparing the number of randomly generated *R*-values out of 10,000 that are greater than the observed.

of non-native species or the endangerment of natives. It seems to follow that these authors will also find a correlation between urbanization and homogenization. Typically urbanization results in the loss of unique native species and replaces them with non-native species that are already widespread either because they have been introduced widely or because they have expanded their ranges in response to the expanding human footprint (Olden and Poff, 2003).

Our results confirm the underlying connection between urbanization and invasion, and urbanization and extinction. Urbanization drastically alters the physical nature of watersheds and waterways through a variety of mechanisms. We show that the integrity of native assemblages is often compromised by the presence of aqueducts which create linkages among watersheds that were formerly isolated, thereby promoting biological movement and a more homogenous ecosystem. Yet aqueducts are only found in 21 of 44 watersheds so alterations of this sort are limited to certain parts of the state (Marchetti et al., 2001).

Conversely, the warm lentic waters of reservoirs and ditches provide ideal habitat for many non-native species that are pre-adapted to this type of environment, while the native fauna is not. In addition, locations that are close to human activity (highly developed urban areas) tend to have many non-native species introduced through careless acts (aquaria releases) and intentional stocking (Marchetti et al., 2004b) further driving up the numbers of non-native species within these urban watersheds.

Despite these connections among urbanization, species additions and species deletions, the watersheds within California provinces have not greatly homogenized at this time. Instead, they have differentiated from one another. This means that the addition of non-native fishes, and the extinction of natives, has served to make each watershed more unique in relation to one another. Furthermore, higher levels of differentiation are associated with a measure of urbanization (i.e. development). To our knowledge this is the first time urbanization has been associated with differentiation, and illustrates the complex relationship among the activities of people and the alterations to diversity they bring about. The history of freshwater fish introductions in California illustrates that the distribution of non-native species is tightly associated with human preferences and actions, and that these activities can vary substantially across space and time (Marchetti et al., 2004a,b).

Table 6 – Stepwise multiple regression model examining the averaged ΔCS with the set of 11 independent variables (Table 2)

Variable	DF	Parameter estimate	*F* ratio	P-value
Development	1	−43.293	13.02	<0.001
Protected areas	1	−16.018	7.03	0.0117
Watershed area	1	3.733	12.49	0.0011

The table presents likelihood ratio tests for each of the three significant variables included in the final model. The final model has an adjusted $R^2 = 0.333$ and $P < 0.001$.

4.2. Mechanisms of differentiation

There are three mechanisms adding to this counterintuitive result that we will discuss individually: (1) the idiosyncratic introduction of various fish species across California ensures that each watershed receives a unique set of non-natives (Marchetti et al., 2004b), (2) the difficulty for non-native fishes to spread substantially beyond their watershed of original introduction when compared with other taxa such a plants or birds, and (3) the retention of a limited number of endemic natives within zoogeographic provinces serves to retain some natural differentiation among watersheds.

Fish have been introduced into and around California's watersheds as the result of intentional human activities (stocking for game, food, biocontrol or conservation) and as the unintended byproduct of human activities (ballast water, aquaria release, bait bucket release or bulk water transfer in aqueducts or canals; Moyle, 1999). Beyond this variation, the particular reason for an individual species' introduction to a watershed can often vary between watersheds or even drainages within a watershed. For example, the fathead minnow (*Pimephales promelas*) has been variously introduced into California waters intentionally as a forage fish, as unintentional release from bait buckets, and as an escapee from aquaculture facilities (Dill and Cordone, 1997). This variety in the mode of transport within a single species is not unique to the fathead minnow and in fact is quite common among California's introduced fishes (Dill and Cordone, 1997; Moyle, 2002). Variability in transport mode among and within species, as well as among and within watersheds, has produced a seemingly haphazard pattern of introductions, although Marchetti et al. (2004b) have shown that intentionally stocked fish have significantly different habitat associations than other introductions.

Adding to the differentiation of California's watersheds is the fact that in general, fish do not easily move beyond the natural boundaries of their particular watersheds. This includes both native fish within their natural zoogeographic boundaries and introduced species within their watershed(s) of introduction. Dispersal in aquatic systems is a longitudinal process along stream and river courses. The definition of watershed generally precludes aquatic organisms, lacking a terrestrial or aerial dispersal phase, from movement outside of the watershed boundaries. Therefore in the absence of extraordinary circumstances (i.e. human-aided dispersal) it is not likely that fish placed in one watershed will be able to colonize adjacent watersheds. Colonization and spread within watersheds is however, extremely likely and has been seen for many introduced species in California (Moyle, 2002). This may account for the difference in the degree and direction of homogenization across spatial scales observed by Marchetti et al. (2001). At an intermediate geographical scale (e.g. within watersheds) we see differentiation, whereas at smaller (e.g. within watersheds) and larger scales (e.g. between watersheds) we see the reverse pattern (Marchetti et al., 2001). This suggests that the relationship between urbanization and homogenization is much more complicated than generally appreciated, and examples that show homogenization may not be representative of changes happening at all spatial scales.

Finally, interpretation of the trends we see across California's watersheds, requires us to examine some of the details of the processes of extinction. It is important to note that some native fishes in California have been extirpated from a portion or even a majority of their native range, yet retain populations in a few watersheds (Moyle, 2002). When coupled with the additional fact that there have been very few global or state-wide extinctions of California endemic fish species (7 species), the natural spatially-variable pattern of native fish diversity across the state is still somewhat intact (Moyle, 2002), or at least it retains vestiges of its pre-European (1850) structure. The remnants of spatial endemism that remain help to explain the faunal differentiation we observe.

5. Conclusions

We are clearly witnessing the loss of diversity not only through global reductions in richness but also by the reorganization of species through invasions. Some of this reorganization results in homogenization, and certainly we see the most reorganization within urban and urbanizing landscapes. However, as we have shown here, homogenization is not the only outcome of this process. Depending on aspects of both the invasion process (introduction vectors, modes of transport, and dispersal constraints) and the regional patterns of extinction we can see periods of differentiation following urbanization and anthropogenic change.

The current pattern observed in this study should not be taken to imply continued differentiation into the near future. In fact, current data suggest the opposite. In the foreseeable future California is likely to loose a large proportion of its remaining native fish diversity as the result of an onslaught of anthropogenic changes (Moyle, 2002; Marchetti et al., 2004b). Currently 48% of the state's native fish fauna is listed as threatened, endangered or as species of special concern (Moyle, 2002), suggesting more extinctions in the near future. In a similar manner the current rate of exotic species introductions will likely continue or increase in the foreseeable future (Cohen and Carlton, 1998). If the losses of native species occur, and the wave of invasions continues, the differentiation we currently see will be a tiny blip in a downward spiral of increasing homogeneity among regional fish faunas.

Our research shows that urbanization in California promotes the introduction of non-native species, but these species are introduced haphazardly across the landscape and may fail to spread much beyond their initial watershed of introduction. This may be a unique feature of freshwater fish introduction, but more likely it is a feature of introduction of species that are not particularly vagile (or are not spread through human actions once established like zebra mussels) but are a common by-product introduction of human activities (e.g. pet owners). Similar results may hold for other commonly introduced but sedentary taxa such as reptiles and amphibians.

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