Homogenization, Differentiation, and the Widespread Alteration of Fish Faunas

Frank J. Rahel*

Department of Zoology and Physiology and the Program in Ecology
Department 3166, 1000 East University Avenue
University of Wyoming, Laramie, Wyoming 82071, USA

Abstract.—Widespread introduction of common species coupled with extirpation of endemic species can cause fish assemblages to lose much of their regional uniqueness. This process of biotic homogenization contrasts with biotic differentiation, whereby initially similar fish faunas diverge due to introductions of different species. The relative importance of homogenization and differentiation in altering fish faunas has been examined across the world. Synthesis of these studies indicates that homogenization of fish faunas has been widespread and that introductions, especially of sport fishes, have played a bigger role in altering fish faunas than extirpations. In the United States, pairs of states now average 15.4 more species in common than before European settlement. Additionally, the 89 pairs of states that formerly had no fish species in common now share an average of 25.2 species. While homogenization is prevalent at large spatial scales, differentiation of fish faunas is evident at intermediate spatial scales such as among watersheds within an ecoregion. This differentiation is largely the result of the idiosyncratic nature of fish introductions among individual lakes and streams. In general, translocated species (i.e., species that are native somewhere in the region but that have been moved to new locations) cause homogenization, whereas exotic species (species not native to the region) cause differentiation. Habitat and flow homogenization are major drivers of biotic homogenization because altered habitats create conditions that favor a few generalist species at the expense of more-specialized endemic species.

Introduction

Homogenization and differentiation are two processes by which humans have altered spatial patterns in the similarity of biotic assemblages. Homogenization refers to an increase in the similarity of biotas and differentiation to a decrease in the similarity of biotas over time. Natural processes such as glaciation, stream capture, the formation of land bridges,

and speciation can alter spatial patterns in biotic similarity, but these operate over relatively long periods. By contrast, humans have greatly accelerated changes in biotic similarity by increasing colonization and extinction rates, by simplifying and degrading habitats, and by enabling species to bypass historic biogeographic barriers (Olden 2006; Rahel 2007). Whether homogenization or differentiation occurs depends on the relative frequency of introductions versus extirpations, the spatial scale of

* Corresponding author: frahel@uwyo.edu

the analysis, and the types of species being introduced. Biologists are concerned about homogenization because it often signals the loss of unique species and their replacement by cosmopolitan generalists (McKinney and Lockwood 1999; Scott 2006). Although local biodiversity may be enhanced through species introductions, such artificial diversity often involves taxa that are already widespread, tolerant of degraded habitats, and considered to be a nuisance by humans (Angermeier 1994; Pimentel et al. 2000; Scott and Helfman 2001). Biotic differentiation is of concern because it is usually the result of disparate localized introductions of species that often spread beyond the original introduction site (Rahel 2004; Clavero and García-Berthou 2006). Loss of native species and gain of nonnative species moves communities away from their natural state and thus away from the conditions that are most desired from a conservation perspective (Angermeier 2000).

Much of the literature on biotic homogenization has focused on quantifying how the species composition of disjunct regions has become more similar. However, the process of homogenization extends across multiple levels of biological organization, including genetic, taxonomic, and functional homogenization (Olden et al. 2004). Habitat homogenization has resulted in similar aquatic habitats across North America, such as eutrophic urban ponds, warmwater reservoirs, cold tailwaters below dams, and streams with relatively constant flow regimes (Moyle and Mount 2007). In these human-created habitats, endemic species typically are replaced by cosmopolitan species with the result that entire ecosystems resembling each other now occur in disparate parts of the country. Thus, common carp *Cyprinus carpio*, bullheads *Ameiurus* spp., and aquarium fishes such as goldfish *Carassius auratus* inhabit many city ponds (Copp 2005;

Chizinski et al. 2006). Popular sport fish such as largemouth bass *Micropterus salmoides* and walleye *Sander vitreus* are the dominant species in reservoirs across North America (Rahel 2000; Taylor et al. 2001; Marchetti et al. 2006). Even southern regions in the United States can boast of trout fisheries where reservoirs release cold hypolimnetic water throughout the summer (Quinn and Kwak 2003). At the genetic level, homogenization of gene pools is of concern for taxa subject to artificial propagation and widespread stocking, such as many species of salmonids (Williamson and May 2005).

In this chapter, I discuss empirical patterns in the homogenization and differentiation of fish faunas and consider the mechanisms that produce these patterns. Next, I discuss why we should be concerned about human-mediated changes in biotic similarity. In particular, what are the ecological and evolutionary consequences of altering spatial patterns in biodiversity? Finally, I explore options for slowing the rate of biotic homogenization and differentiation and consider if these processes can be reversed. Much of the literature on homogenization is focused on fish, but the principles apply to other aquatic faunas and, in many cases, to terrestrial taxa as well.

Quantifying Homogenization and Differentiation

A variety of methods have been used to examine changes in spatial patterns in similarity among fish assemblages (Table 1). Because only presence–absence data are usually available, most studies have used a binary coefficient to quantify changes in similarity among sites. The most commonly used coefficient is Jaccard's index, which is calculated as $S = [a/(a + b + c)] \times 100$, where S is the similarity between two sites and a = the number of species found in both sites, b = the number of species

Table 1. Studies examining homogenization and differentiation of fish faunas.

	Author	Study area	Similarity metric	Findings
1.	Radomski and Goeman 1995	72 lakes in Minnesota	Jaccard Index	Homogenization due to cosmopolitan introductions
2.	Rahel 2000	48 coterminous states in the United States	Jaccard index	Homogenization due to cosmopolitan introductions
3.	Duncan and Lockwood 2001	7 geographic provinces in Tennessee	Spatial turnover index (Ts)	Homogenization predicted to occur
4a.	Marchetti et al. 2001	6 zoogeographic provinces in California	Jaccard index	Homogenization due to cosmopolitan introductions
4b.	Marchetti et al. 2001	watersheds within provinces in California	Jaccard index	Differentiation due to idiosyncratic introductions
5.	MacRae and Jackson 2001	14 lakes in Ontario	Ordination by correspondence analysis	Homogenization due to predator introductions
6.	Gido et al. 2002	14 sites in Big Blue River basin, Kansas	Jaccard index	Homogenization mainly due to species introductions
7.	Walters et al. 2003	30 streams in Etowah River basin, Georgia	Ratio of endemic to cosmopolitan species	Homogenization due to loss of rheophilous species
8a.	Taylor 2004	13 Canadian provinces and territories	Jaccard index	Homogenization due to cosmopolitan introductions
8b.	Taylor 2004	8 ecoregions within British Columbia	Jaccard index	Differentiation due to idiosyncratic introductions
9.	Clavero and García-Berthou 2006	10 Iberian basins in Europe	Jaccard index	Homogenization due to cosmopolitan introductions
10.	Habit et al. 2006	Longitudinal patterns along Biobio River, Chile	Shannon-Wiener diversity index (H')	Homogenization due to introductions and extirpations
11.	Marchetti et al. 2006	Watersheds in 4 California zoogeographic provinces	Ordination by multidimentional scaling	Differentiation due to idiosyncratic introductions
12.	Eberle 2007	2 river basins in Kansas	Unnamed similarity coefficient	Homogenization due to introductions and extirpations
13a.	Hoagstrom et al. 2007	2 zoogeographic provinces in South Dakota	Jaccard & Sorenson	Homogenization due to introductions and extirpations
13b.	Hoagstrom et al. 2007	16 river drainages in South Dakota	Jaccard & Sorenson	Homogenization due to introductions and extirpations
14.	Leprieur et al. 2008	25 river basins across Europe	Jaccard index	Homogenization due to translocated species
15a.	Olden et al. 2008	12 primary river basins across Australia	Sorensen index	Homogenization due to cosmopolitan introductions
15b.	Olden et al. 2008	53 secondary river basins in northeast Australia	Sorensen index	Differentiation due to idiosyncratic introductions
16.	Gido et al. 2008	Streams versus reservoirs in Midwestern USA	Bray-Curtis coefficient, Jaccard index, ordination by nonmetric multidimensional scaling	Faunal homogenization followed conversion of stream habitat to reservoir habitat
17.	Casatti et al. 2009	Agricultural versus natural to stream reaches in Brazil	Bray-Curtis coefficient	Habitat homogenization led faunal homogenization by nonnative species

found only in the first site, and c = the number of species found only in the second site. Values of Jaccard's index range from 0% (no species in common) to 100% (complete overlap in species composition). Typically, the average similarity among a set of sites based on historical fish species composition is subtracted from the average similarity based on present-day fish species composition. Positive values indicate increased similarity (i.e., homogenization), whereas negative values indicate decreased similarity (i.e., differentiation).

Ordinations also can be used to visualize changes in similarity patterns. Ordination axes represent gradients of fish assemblage change, and thus fish assemblages that are similar in composition will cluster together in the ordination plot, whereas fish assemblages that differ in their composition will be dispersed. For example, the close positioning of historical fish assemblages in 10 Southern California watersheds indicates that they had similar fish faunas (Figure 1). By contrast, the dispersion of the watersheds today indicates reduced similarity among their fish faunas. Marchetti et al. (2006) attributed this differentiation to the id-

iosyncratic nature of fish species introductions among the watersheds. Gido et al. (2009) used ordination to compare the similarity of fish assemblages in reservoirs versus streams in the Great Plains, USA. In the ordination plot, reservoirs were clustered and stream sites were dispersed, indicating that reservoirs contained more homogenous fish faunas than streams within the same drainages. Gido et al. attributed this to the fact that reservoirs were dominated by a small group of species introduced for sportfishing, whereas stream sites retained the diverse fish faunas that reflected the historical biogeography of the region.

Walters et al. (2003) used the ratio of endemic to cosmopolitan fish species to examine homogenization of fish faunas throughout the Etowah River basin in Georgia, USA. The ratio declined with increases in sedimentation and eutrophication because unique benthic fishes were replaced by widespread fishes tolerant of degraded water quality. The loss of endemics resulted in the homogenization of fish assemblages throughout the basin. An advantage of the ratio used by Walters et al. is that it did not require historical data on species composition. However, there may be some subjectivity in defining "endemic" versus "cosmopolitan" species. Using the ratio of endemic to cosmopolitan species based on abundance information would be a way to detect the early stages of homogenization related to habitat degradation. Sensitive species would be expected to decline and generalist species would be expected to increase well before extirpations of natives or introductions of nonnatives becomes widespread.

Whatever method is used to quantify homogenization, it is important to recognize that species changes do not necessarily cause predictable changes in assemblage similarity. Introductions and extirpations can lead to either homogenization or differentiation, depending
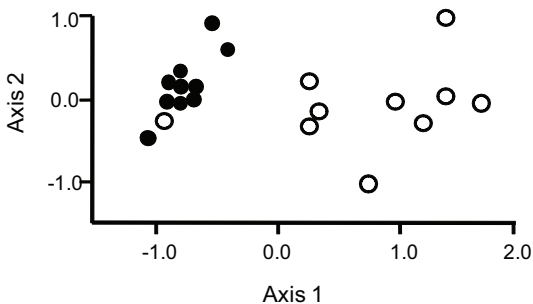

Figure 1. Ordination using nonmetric multidimensional scaling for 10 watersheds in Southern California based on fish species composition at two time periods. Historical (pre-1850) watershed species composition is given as closed circles and present-day species composition is given as open circles (from Marchetti et al. 2006). The stress value for the plot is 0.07.

upon the spatial interplay of these two processes (Rahel 2002). Problems in assessing changes in assemblage can arise when species identity is not considered (i.e., increased species richness is used as a surrogate measure of homogenization) or contemporary patterns of community similarity are determined without reference to historical patterns (Olden and Rooney 2006).

Evidence for Homogenization or Differentiation

Changes in similarity patterns of fish faunas have been examined at a variety of spatial scales across the United States, Canada, Europe, and Australia (Table 1). Overall, homogenization is a more common phenomenon than differentiation (Figure 2). A high degree of homogenization was reported among six zoogeographic provinces in California where the average similarity, as measured by Jaccard's index, increased by 20.3% (Marchetti et al. 2001). Similarly, the average similarity among fish faunas in 10 major drainage basins in Iberia increased by 17.1% (Clavero and García-Berthou 2006) and between two river basins in Kansas by 15.4% (Eberle 2007). An example of a high degree of differentiation involves watersheds within the south coast zoogeographic province in California where the average similarity, as measured by Jaccard's index, decreased by 25.7% (Marchetti et al. 2001). It should be noted that while the average change in similarity among pairs of fish faunas in a region may indicate homogenization, some of the pairwise comparisons may show differentiation. For example, in Australia, the average change in similarity among the 12 primary drainages was 3.0%, indicating overall homogenization (Olden et al. 2008). However, 14 of the 66 pairwise combinations had a small negative change in similarity, indicating slight differentiation in fish faunas between some drainages.
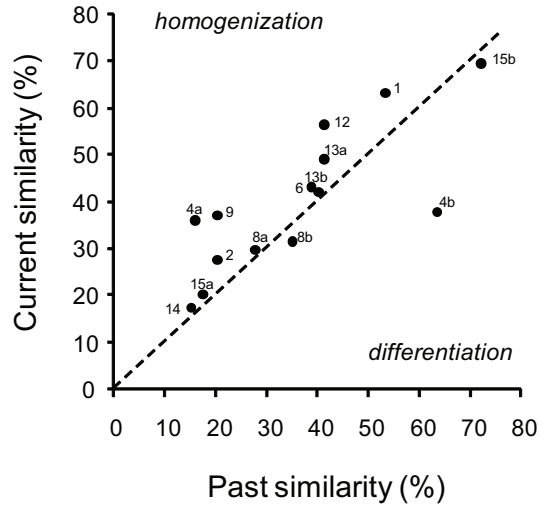

Figure 2. A plot of past versus current average similarities of fish faunas for various regions of the world. The numbers refer to the study identification numbers in Table 1. Points above the diagonal indicate that fish faunas are more similar today than in the past, thus homogenization has occurred. Points below the diagonal indicate fish faunas are less similar today than in the past, thus differentiation has occurred. All the studies used Jaccard's index to quantify assemblage similarity except for studies 12 (an unnamed similarity index) and 15 (Sorensen's index).

Although changes in the percent similarity among fish faunas provide a way to quantify homogenization, the significance of a given change in similarity can be reinforced if additional data are presented. For example, Rahel (2000) noted that the average change in fish faunas among the 48 contiguous states in the United States was 7.2%. This change means that, on average, any pair of states now shares 15.4 more fish species in common than they did historically. Additionally, the 89 pairs of states that had zero similarity (no species in common), now have an average similarity of 12.2% and an average of 25 species in common. Among 10 river basins in Iberia, the mean Jaccard similarity increased by 17% from the pristine situation largely due to species

introductions (Clavero and García-Berthou 2006). The magnitude of this change is apparent when you consider that, on average, more than half (52.5%) of the species in each basin are now nonnative.

Empirical Patterns and Mechanisms Driving Homogenization and Differentiation

Spatial Scale Dependence of Homogenization versus Differentiation

Whether faunas have become more or less similar over time may depend on the spatial scale of the analysis. In several studies, homogenization was evident across larger spatial scales, whereas differentiation occurred at intermediate spatial scales. For example, homogenization was evident among the six faunal provinces spanning California where the average similarity increased from 15.7% to 36.0% (Marchetti et al. 2001). By contrast, within some of the provinces, differentiation among watersheds occurred. An example is the south coast province where average similarity among the 55 watersheds declined from 63.3% to 37.6% (compare 4a and 4b in Figure 2). In Canada, similarity increased at the provincial scale, but within the province of British Columbia, similarity decreased among the eight ecoregions (compare 8a and 8b in Figure 2; Taylor 2004). In Australia, the similarity of fish faunas increased among 12 major drainage divisions spanning the continent but decreased among the 53 watersheds within the northeast coast drainage division (compare 15a and 15b in Figure 2; Olden et al. 2008).

The most common explanation for the differentiation of faunas at intermediate spatial scales is the idiosyncratic nature of species introductions. At larger spatial scales, it is likely that a given nonnative species will be introduced somewhere within each major basin, even if it involves only one or a few sites. This means that the introduced species will be counted as present in most major basins and contribute to an increase in similarity at that large spatial scale. Within each major basin, the species may be present in only a subset of watersheds, thus contributing to differentiation at intermediate spatial scales when the similarity among watersheds is analyzed. However, this differentiation may be a transitory phenomenon as fish eventually spread through natural and human-assisted means (Rahel 2004; Unmack, and Fagan 2004; Johnson et al. 2008). For example, a strong positive relationship between time since introduction and the number of occupied basins was reported for nonnative fishes in the Iberian Peninsula (Clavero and García-Berthou 2006).

At small spatial scales, homogenization is considered a more likely occurrence than differentiation (Marchetti et al. 2006). For example, stream sites within a single watershed are likely to share many of the same introduced species when movement barriers are absent and habitat degradation favors a few generalist species at the expense of habitat specialists. Thus, homogenization of fish faunas has been reported for sites in the Seine River basin in France (Boët et al. 1999), along the Biobio River in Chile (Habit et al. 2006) and in the Etowah River basin in Georgia, USA. (Walters et al. 2003). Despite these generalities, the relationship between spatial scale and changes in similarity can be complex and dependent on historical biogeography (which influences the initial similarity of faunas), the vagility of the species (which influences their ability to spread), and the cultural history of a region (which determines which species were introduced) (Cassey et al. 2007).

Role of Introductions versus Extirpations

In theory, homogenization and differentiation can be caused by introductions, extirpations, or

a combination of both processes (Rahel 2002; Olden and Poff 2003). In practice, changes in faunal similarity seem to be mainly driven by introductions that are much more common than extirpations across a wide range of spatial scales and geographic regions (Table 1). One way to assess the relative importance of introductions versus extirpations is to determine the change in similarity among faunas that would occur due to each process acting separately. For example, if only introductions had occurred among the 48 contiguous states of the United States, the average change in similarity would be 7.3% (Figure 3). The change due to extirpations alone would be –0.3%. The effect of the two processes combined is 7.2%, indicating that introductions are the major factor altering state fish faunas.

One place where extirpations appear to play an important role in altering fish faunas is in streams of the Great Plains of the United States. These streams are naturally prone to intermittency and extreme abiotic conditions (Eberle 2007). These stresses have been exacerbated by water withdrawals and land use activities with the result that many native species have been extirpated. In Kansas, introductions or extirpations caused similar levels of homogenization, but their combined effects were synergistic (Figure 3).

Translocated Species Cause Homogenization; Exotic Species Cause Differentiation

In studies of biotic homogenization, a distinction is often made between translocated species (i.e., species that are native somewhere in the region but that have been moved to new locations), and exotic species (i.e., species not native to the region under study). For example, of the 901 fish introductions within the 48 coterminous United States reported by Rahel (2000), 673 involved translocated species
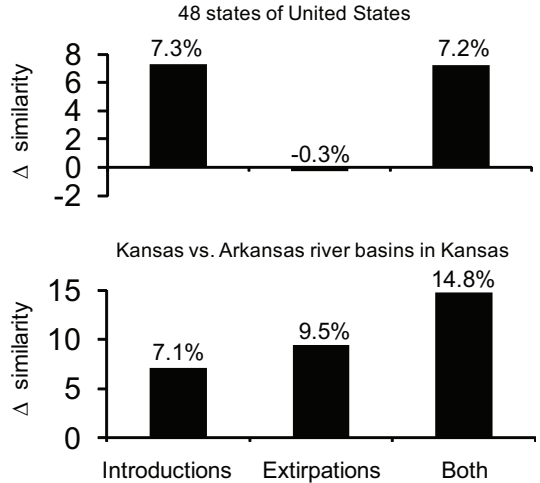

Figure 3. Change in similarity due to introductions only, extirpations only, or both processes combined. Top panel: Average change in similarity among 1,128 pairwise combinations of the 48 continuous United States involving 901 introduction events and 196 extirpation events (data from Rahel 2000). Bottom panel: Change in similarity between the Kansas River and Arkansas River drainages within the state of Kansas involving 26 introduction events and 13 extirpation events (data from Eberle 2007).

such as largemouth bass, which are native to eastern North America, whereas 228 involved exotic species such as brown trout *Salmo trutta*, which are native to Europe.

Some authors have reported that exotic species tend to cause differentiation while translocations tend to cause homogenization among faunas (McKinney 2004; Leprieur et al. 2008). The reason is that exotic species are often introduced into a small number of sites, making those sites unique compared to the majority of sites. However, the differentiating effect of exotic species is reduced as the species spread and become shared among more sites. In fact, an exotic species will tend to decrease pairwise similarity among a set of sites until half of the sites are occupied, after which the continued spread of the species will increase pairwise similarity, at least at the level of species

occurrence data (Rooney et al. 2007). To the extent that translocated species already occur at many of the sites, their introduction to new sites is likely to reduce the distinctness among sites, thus contributing to homogenization.

Leprieur et al. (2008) noted that among 25 river basins across Europe, there was a general trend for introductions of exotic species to cause differentiation, but for translocations of species to cause homogenization (Figure 4). This was because most translocated fish species in Europe are native to eastern basins and were widely introduced into less speciose drainages of southern and Western Europe, thus contributing a large cosmopolitan element to the overall fish faunas of European basins. By contrast, exotic species tended to be introduced only into subsets of basins, thus enhancing the regional distinctiveness of fish faunas. Such exotic species include black bullhead *Ameiurus melas* and pumpkinseed *Lepomis gibbosus*, which have been introduced mainly in Western Europe; Amur sleeper *Percottus glenii* and black carp *Mylopharyngodon piceus,* which have been introduced mainly in eastern Europe; and western mosquitofish *Gambusia affinis* and eastern mosquitofish *G. holbrooki,* which have been

introduced mainly in southern Europe. McKinney (2005) also reported that translocated species caused homogenization while exotic species tended to cause differentiation among the fish faunas of 12 randomly selected states in the United States.

Biotic Homogenization Caused by Habitat Homogenization and Degradation

The degradation and homogenization of habitats is thought to be a major cause of biotic homogenization (McKinney 2006). Environmental homogenization can increase the speed of species invasions and thus accelerate the homogenization process (García-Ramos and Rodríguez 2002). In aquatic systems, dams homogenize stream flow regimes by reducing variation in the timing, magnitude, duration, and frequency of flooding and desiccation (Poff et al. 2007). A constancy of flow regime can favor widespread nonnative species at the expense of endemic native species (Marchetti and Moyle 2001). Another common form of habitat homogenization is replacement of diverse stream habitats (pools, riffles, runs, and side channels) with the standing water habitat of reservoirs. Often, native rheophyllic species are replaced by a few widespread sport fishes that thrive in the standing water habitat of reservoirs (Marchetti et al. 2001; Taylor et al. 2001). This was clearly demonstrated in a comparison of fish assemblages among streams and reservoirs in the Great Plains of the United States (Gido et al. 2009). The average similarity based on Jaccard's index among stream sites was 24.6%, whereas the average similarity among reservoirs was 44.9% (Gido et al. 2009). Despite being located in the same drainages as the stream sites, reservoir fish faunas were more homogeneous because they were dominated by a suite of lentic-adapted species introduced for sport fishing. By contrast, the stream sites retained a diverse suite
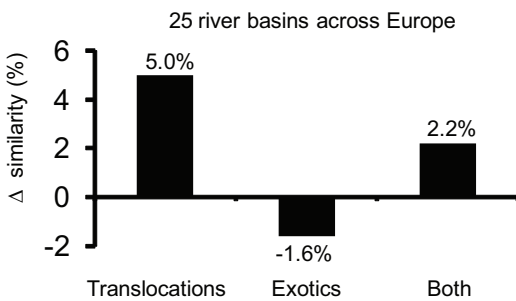

Figure 4. Change in similarity between historic and current fish faunas for 25 river basins across Europe. Shown is the average change in similarity that would have occurred if only species translocations had occurred, if only exotic species introductions had occurred, and the combined effect of both processes. (Data from Leprieur et al. 2008).

of rheophyllic species that varied geographically due to historic, biogeographic factors. A situation where reservoir development contributed to biotic differentiation was reported among 44 watersheds in California (Marchetti et al. 2006). In this case, the introduction of fishes to reservoirs was idiosyncratic, with the result that reservoirs were not dominated by the same set of nonnative fishes. However, Marchetti et al. noted that this result was scale-dependent, as homogenization was noted at local scales (i.e., within a single drainage) and at very large scales (i.e., between zoogeographic provinces).

Habitat degradation is another factor contributing to biotic homogenization. The percent of a watershed in urban land use; the number of canals, dams, or reservoirs; and the sediment load in streams are often correlated with the amount of biotic homogenization (Marchetti et al. 2001; Walters et al. 2003; Olden et al. 2008). In the southeastern United States, high amounts of sediment favor a few cosmopolitan, tolerant fish species at the expense of endemic species that require clean gravels for foraging and reproduction (Walters et al. 2003; Scott 2006). In urban streams, a flashier hydrograph, elevated concentrations of nutrients and contaminants, and altered channel morphology eliminate most fish species except for a few tolerant forms (Boët et al. 1999; Walsh et al. 2005). Often, habitat degradation facilitates invasions by a suite of nonnative species, further contributing to biotic homogenization. Across North America, dominant species in urban waters include exotic species such as common carp and goldfish, as well as translocated species such as green sunfish *Lepomis cyanellus* and bullheads.

Why Should We Care about Changes in Biotic Similarity?

Homogenization or differentiation can be harbingers of conservation failures. Changes in biotic similarity are caused by a combination of species introductions and extirpations, both of which are facilitated by habitat alterations. The negative consequences of introductions and habitat alterations on native biodiversity are well known (Chapin et al. 2000). In many cases, homogenization is caused by introductions of nonnative species rather than extirpations of native species. Because of time lags in extirpations, introduced species can initially increase local species richness without causing immediate loss of native species (Sax et al. 2002). Ultimately, however, the negative effects become manifest, with the eventual decline or loss of some native species (Ruesink 2003). For example, hybridization with introduced species can lead to the eventual loss of endemic species but may occur over many years (Rhymer and Simberloff 1996).

Biotic differentiation is often the result of exotic species being introduced idiosyncratically in a few locations (Marchetti et al. 2001; Leprieur et al. 2008). But differentiation is likely to be a short-term phenomenon as nonnative species spread and increase the geographic extent over which negative effects are likely to occur (Marchetti et al. 2006). Such an expansion was documented in the Iberian Peninsula where the number of basins occupied by various nonnative fish species was positively correlated with elapsed time since the initial introduction (Clavero and García-Berthou 2006). And secondary spread of nonnative species accounted for 34% of the unauthorized fish introductions reported in Wyoming (Rahel 2004). Fish communities in arid basins of the southwestern United States have shown an exponential increase in the number of reaches with nonnative fishes and are predicted to converge toward dominance by nonnative species, albeit with a time-lag reflecting differences in the time course of introductions (Unmack and Fagan 2004). Thus, given enough time, both

homogenization and differentiation may converge on the same result, a few winners replacing many losers and the impoverishment of global biodiversity (McKinney and Lockwood 1999; Scott 2006).

In addition to the loss of species diversity, taxonomic homogenization can have other negative ecological and evolutionary consequences. There is evidence that specialist species are more likely to be negatively affected by habitat degradation than generalist species (Scott 2006; Devictor et al. 2008). The replacement of ecological specialists by widespread generalists results in the functional homogenization of communities. Functional homogenization is of concern because it can alter important ecosystem processes and reduce the ability of communities to adapt to novel environmental conditions such as those associated with climate change (Chapin et al. 2000; Olden et al. 2004). Furthermore, the loss of spatial uniqueness reduces the raw material of evolution by reducing spatial diversity in species composition and genetic make-up (Olden et al. 2004; Williamson and May 2005).

Biotic homogenization often goes hand in hand with cultural homogenization. Olden et al. (2005) suggested that the increasingly global uniformity in the Earth's biota may be linked to a loss of traditional values and have important consequences for conservation-oriented advocacy and ecotourism. In essence, biological diversity, especially its endemic features, contributes to our sense of place and our attachment to a particular geographic area. This attachment is a critical component of our psychological well-being and forms an important basis for conservation advocacy. Indeed, the need to "save our wildlife heritage" is a common theme in pleas for public support of conservation actions. There are concerns that biotic homogenization could reduce our sense of place and thus weaken an important basis

for support of conservation efforts. Ecotourism might also suffer economic repercussions from biotic homogenization. There will be less incentive for tourists to travel great distances to view biotas that are becoming increasingly similar across the Earth.

Can We Slow or Reverse the Homogenization Process?

Reducing the rate by which spatial patterns in biodiversity are being altered will require controlling the three driving factors: introductions, extinctions, and habitat homogenization. Historically, many introductions of nonnative fish species were done by management agencies to promote sportfishing. Agency-sponsored introductions have declined in recent years as natural resource managers have gained an awareness of the problems nonnative species can cause (Rahel 2004). Unfortunately, illegal introductions remain a problem and public education about the harmful effects of introduced species is needed. In some cases, it may be possible to eliminate populations of nonnative species to facilitate the reestablishment of native species (Lintermans 2000; Vredenburg 2004). Elimination of nonnatives may not be possible in large rivers or lakes, but controlling the abundance of such species can help in recovery efforts for native species (Tyus and Saunders 2000).

Preventing species extinctions is crucial to minimizing changes in spatial patterns of biodiversity. Unfortunately, widespread declines in the distributions of native fishes are still occurring. An assessment of the conservation status of North America's fishes concluded that 39% of the continent's species are imperiled and 61 taxa (including subspecies) have become extinct (Jelks et al. 2008). Despite extensive recovery efforts for endangered fishes, success has been limited. Of 364 taxa listed as being of

conservation concern in 1989, only 8 had recovered enough to be removed from the list by 2008 (Jelks et al. 2008). Efforts at preventing the loss of native taxa will have to be increased if further homogenization of the Earth's biota is to be slowed.

The third approach for reducing biotic homogenization is to minimize habitat alteration and homogenization. Habitat preservation and rehabilitation has long been a cornerstone for recovery efforts of imperiled species. Habitat alteration not only affects imperiled species directly through habitat loss, but also indirectly by facilitating establishment of nonnative species (Marchetti et al. 2004). Consequently, there is much interest in habitat restoration efforts that help native species while simultaneously controlling nonnative species. Habitat improvements at the outflow of a desert spring in the Mojave Desert converted a marsh to flowing water habitat and changed the fish composition from predominantly nonnative sailfin molly *Poecilia latipinna* and western mosquitofish to predominantly native Amargosa pupfish *Cyprinodon nevadensis* (Scoppettone et al. 2005). The natural-flow paradigm has been proposed as a landscape-level approach for restoring native assemblages in streams and rivers (Poff et al. 2007). The idea is that restoring natural flow regimes will favor native species that are better adapted to these conditions than introduced species (Marchetti and Moyle 2001; Moyle and Mount 2007). Removing dams and their associated reservoirs is another approach for restoring native biodiversity. Dam removal can facilitate recovery of native riverine species, many of which are regionally endemic, while reducing the abundance of nonnative species that are widespread in impoundments across North America (Kanehl et al. 1997; Johnson et al. 2008). There is a need to develop quantitative models that link land use change and water develop-

ment activities to environmental changes that, in turn, predict the homogenization process. Examples of such models include relating the degree of homogenization to the proportion of a watershed that has undergone anthropogenic modification (Marchetti et al. 2006) or to changes in flow regimes, land use, or human infrastructures (Olden et al. 2008).

Reversing biotic homogenization will involve reversing species extirpations, species introductions, and habitat homogenization. One way to restore historic patterns in biodiversity is to restore habitat conditions to a more pristine state. Restoration of water quality in urban streams can restore native fish assemblages. Because urban streams are often dominated by a few cosmopolitan and pollution-tolerant fish species, habitat improvements that allow recovery of regionally endemic species will reverse the homogenization process. Consider the case of the Scioto River in Columbus, Ohio and the Cuyahoga River in Cleveland, Ohio (Table 2). Prior to habitat improvements, both rivers suffered from the urban river syndrome (Walsh et al. 2005) and had fish assemblages dominated by a few, pollution-tolerant taxa (Table 2). Following improvements in water quality and habitat conditions, additional species reappeared and the fish faunas became less similar. Assemblage similarity based on relative abundance data declined from 61% to 14%. Thus, habitat rehabilitation led to a reversal of the homogenization process.

Introduced predators can have dramatic effects on fish biodiversity by eliminating or reducing the abundance of numerous prey species. For example, nonnative smallmouth bass *Micropterus dolomieu* were found to homogenize fish assemblages in small North American lakes by eliminating or reducing the abundance of small-bodied prey species (MacRae and Jackson 2001). Experimentally reducing the population of smallmouth bass in an

Table 2. A comparison of fish assemblages in the Scioto River and Cuyahoga River before and after habitat and water quality improvements. Shown are the total number of species collected by electro-fishing and the proportional abundance of all species that constituted ≥1% of the total number of individuals captured. The similarity of the assemblages was calculated as percent similarity = $\sum$ minimum (p_{i1}, p_{i2}) where p_{i1} is the proportion of the ith species in site 1 and p_{i2} is the proportion of the *i*th species in site 2. The Scioto River was sampled at river mile 126.4 in 1979 and 2005. The Cuyahoga River was sampled at river mile 15.9 in 1984 and 2000. Data provided by Dennis Mishne and Steven Tuckerman of the Ohio Environmental Protection Agency.

Pre-recovery fish assemblages (percent similarity = 61%)

Scioto River (11 species)		Cuyahoga River (8 species)	
Gizzard shad *Dorosoma cepedianum*	47%	Gizzard shad	51%
Sunfishes *Lepomis* spp.	19%	Sunfishes	19%
Common carp *Cyprinus carpio*	17%	Common carp	13%
River carpsucker *Carpiodes carpio*	6%	White sucker *Catostomus commersonii*	15%
Northern hog sucker *Hypentelium nigricans*	5%	Creek chub *Semotilus atromaculatus*	2%
Smallmouth buffalo *Ictiobus bubalus*	2%	Brown bullhead *Ameiurus nebulosus*	2%
		Freshwater drum *Aplodinotus grunniens*	2%

Post-recovery fish assemblages (percent similarity = 14%)

Scioto River (40 species)		Cuyahoga River (25 species)	
Emerald shiner *Notropis atherinoides*	47%	Spotfin shiner *Notropis spilopterus*	19%
Sunfishes	17%	Northern hog sucker	17%
River carpsucker	7%	Bluntnose minnow *Pimephales notatus*	12%
Gizzard shad	4%	Central stoneroller *Campostoma anomalum*	8%
Smallmouth buffalo	3%	Common shiner *Luxilus cornutus*	8%
Gravel chub *Hybopsis x-punctata*	3%	Smallmouth bass *Micropterus dolomieu*	7%
Northern hog sucker	2%	White sucker	6%
Spotted bass *Micropterus punctulatus*	2%	Common carp	6%
Common carp	2%	Sand shiner *Notropis stramineus*	5%
Smallmouth bass	1%	Sunfish	2%
Spotfin shiner	1%	Gizzard shad	2%
Channel catfish *Ictalurus punctatus*	1%	Greenside darter *Etheostoma blennioides*	1%
Central stoneroller	1%		
Sauger *Sander canadensis*	1%		

Adirondack lake allowed populations of native littoral species to recover, indicating that homogenization could be reversed (Weidel et al. 2007). Removing nonnative fishes by netting or electrofishing is time-consuming and expensive and must be repeated often to be effective (Weidel et al. 2007; Peterson et al. 2008). In some situations, however, it may be possible to use human fishers to achieve on-going control of nonnative predators. For example, in Lake Victoria, intensive exploitation of Nile perch *Lates niloticus*, a nonnative piscivore, has allowed a resurgence by many native species that were in decline or even thought to have gone extinct (Balirwa et al. 2003). In a similar vein, sustained exploitation of nonnative flathead catfish *Pylodictis olivaris* by recreational or commercial fishers in a North Carolina river may allow recovery of native fishes whose biomass was suppressed by up to 50% through predation and competition (Pine et al. 2007). The continual suppression of apex predators needed to maintain native biodiversity may be done more effectively through angler exploitation rather than through mechanical removal by agency biologists.

Future Changes in Spatial Patterns of Biodiversity

Homogenization of fish assemblages seems likely to continue. Even the differentiation of fish assemblages that has been observed at inter-mediate spatial scales seems to be a short-term phenomenon that will be replaced by homogenization as nonnative species continue to spread across the landscape. New patterns of global commerce may allow biotic exchanges between areas that had little opportunity for exchange in the past. The construction of reservoirs, which are hotspots for invasive species, seems likely to continue (Johnson et al. 2008). Continuing declines in populations of native species seems a likely scenario as the human footprint continues to grow across the Earth.

Perhaps the best hope for slowing or even reversing the homogenization process lies in habitat restoration. Recreating historical flow regimes, improving water quality in urban rivers, or removing obsolete dams to recover flow-ing water habitats are ways to control nonnative species while simultaneously restoring native species. Continued education of the public about the dangers of introducing nonnative species may help slow the homogenization process, as will increasing the restrictions on the use of live bait (Rahel 2004). We owe it to future generations to continue to work towards preserving a sense of place for our aquatic environments.

Acknowledgments

References

Angermeier, P. L. 1994. Does biodiversity include artificial diversity? Conservation Biology 8:600–602.

Angermeier, P. L. 2000. The natural imperative for biological conservation. Conservation Biology 14:373–381.

Balirwa, J. S., C. A. Chapin, L. J. Chapman, I. G. Cowx, K. Geheb, L. Kaufman, R. H. Lowe-McConnell, O. Seehausen, J. H. Wanink, R. L Welcomme, and F. Witte. 2003. Biodiversity and fishery sustainability in the Lake Victoria basin: an unexpected marriage? BioScience 53:703–716.

Boët P., J. Belliard, R. Berrebi-dit-Thomas, and E. Tales. 1999. Multiple human impacts by the city of Paris on fish communities in the Seine River basin, France. Hydrobiologia 410:59–68.

Casatti, L., C. P. Ferreira, and F. R. Carvalho. 2009. Grass-dominated stream sites exhibit low fish species diversity and guppies dominance: an assessment on two tropical pasture river basins. Hydrobiologia 632:273–283.

Cassey, P., J. L. Lockwood, T. M. Blackburn, and J. D. Olden. 2007. Spatial scale and evolutionary history determine the degree of taxonomic homogenization across island bird assemblages. Diversity and Distributions 13:458–466.

Chapin, F. S., III, E. S. Zavaleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, H. L. Reynolds, D. U. Hooper, S. Lavorel, O. E. Sala, S. E. Hobbie, M. C. Mack, and S. Díaz. 2000. Consequences of changing biodiversity. Nature(London) 405:234–242.

Chizinski, C. J., C. L. Higgins, C. E. Shavlik, and K. L. Pope. 2006. Multiple hypotheses testing of fish incidence patterns in an urbanized ecosystem. Aquatic Ecology 40:97–109.

Clavero, M., and E. García-Berthou. 2006. Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. Ecological Applications 16:2313–2324.

Copp, G. H. 2005. Pathways of ornamental and aquarium fish introductions into urban ponds of Epping Forest (London, England): the human vector. Journal of Applied Ichthyology 21:263–274.

Devictor, V., R. Julliard, J. Clavel, F. Jiguet, A. Lee, and D. Couvet. 2008. Functional biotic homogenization of bird communities in disturbed landscapes. Global Ecology and Biogeography 17:252–261.

Duncan, J. R., and J. L. Lockwood. 2001. Spatial homogenization of the aquatic fauna of Tennessee: extinction and invasion following land use change and habitat alteration. Pages 245–257 in J. L. Lockwood and M. L. McKinney, editors. Biotic homogenization. Kluwer Academic/Plenum Publishers, New York.

Eberle, M. E. 2007. Homogenization of fish faunas and concurrent anthropogenic impacts on plains streams in western Kansas: 1854–2003. Fort Hays State University, Fort Hays Studies, Fourth Series, No. 4, Hays, Kansas.

García-Ramos, G., and D. Rodríguez. 2002. Evolutionary speed of species invasions. Evolution 56:661–668.

Gido, K. B., C. S. Guy, T. R. Strakosh, R. J. Bernot, K. J. Hase, and M. A. Shaw. 2002. Long-term changes in the fish assemblages of the Big Blue River basin 40 years after the construction of Tuttle Creek Reservoir. Transactions of the Kansas Academy of Sciences 105:193–208.

Gido, K. B., J. F. Schaefer, and J. A. Falke. 2009. Convergence of littoral zone fish communities in reservoirs. Freshwater Biology 54:1163–1177.

Habit, E., M. C. Belk, R. C. Tuckfield, and O. Parra. 2006. Response of the fish community to human-induced changes in the BioBio River in Chile. Freshwater Biology 51:1–11.

Hoagstrom, C. W., S. S. Wall, J. G. Kral, B. G. Blackwell, and C. R. Berry, Jr. 2007. Zoogeographic patterns and faunal change of South Dakota fishes. Western North American Naturalist 67:161–184.

Jelks, H. L., S. J. Walsh, N. M. Burkhead, S. Contreras-Balderas, E. Díaz-Pardo, D. A. Hendrickson, J. Lyons, N. E. Mandrak, F. McCormick, J. S. Nelson, S. P. Platania, B. A. Porter, C. B. Renaud, J. J. Schmitter-Soto, E. B. Taylor, and M. L. Warren, Jr. 2008. Conservation status of imperiled North American freshwater and diadromous fishes. Fisheries 33(8):372–407.

Johnson, P. T. J., J. D. Olden, and M. J. Vander Zanden. 2008. Dam invaders, impoundments facilitate biological invasions into freshwaters. Frontiers in Ecology and the Environment 6:357–363.

Kanehl, P. D., J. Lyons, and J. E. Nelson. 1997. Changes in the habitat and fish community of the Milwaukee River, Wisconsin, following removal of the Woolen Mills dam. North American Journal of Fisheries Management 17:387–400.

Leprieur, F., O. Beauchard, B. Hugueny, G. Grenouillet, and S. Brosse. 2008. Null model of biotic homogenization: a test with the European freshwater fish fauna. Diversity and Distributions 14:291–300.

Lintermans, M. 2000. Recolonization by the mountain galaxias *Galaxias olidus* of a montane stream after the eradication of rainbow trout *Oncorhynchus mykiss*. Marine and Freshwater Research 51:799–804.

MacRae, P. S. D., and D. A. Jackson. 2001. The influence of smallmouth bass (*Micropterus dolomieu*) predation and habitat complexity on the structure of littoral zone fish assemblages. Canadian Journal of Fisheries and Aquatic Sciences 58:342–351.

Marchetti, M. P., and P. B. Moyle. 2001. Effects of flow regime on fish assemblages in a regulated California stream. Ecological Applications 11:530–539.

Marchetti, M. P., T. Light, J. Feliciano, T. Armstrong, Z. Hogan, J. Viers, and P. B. Moyle. 2001. Homogenization of California's fish fauna through abiotic change. Pages 259–278 *in* J. L. Lockwood and M. L. McKinney, editors. Biotic homogenization. Kluwer Academic/Plenum Publishers, New York.

Marchetti, M. P., T. Light, P. B. Moyle, and J. H. Viers. 2004. Fish invasions in California watersheds: testing hypotheses using landscape patterns. Ecological Applications 14:1507–1525.

Marchetti, M. P., J. L. Lockwood, and T. Light. 2006. Effects of urbanization on California's fish diversity: differentiation, homogenization and the influence of spatial scale. Biological Conservation 127:310–318.

McKinney, M. L. 2004. Do exotics homogenize or differentiate communities? Roles of sampling and exotic species richness. Biological Invasions 6:495–504.

McKinney, M. L. 2005. Species introduced from nearby sources have a more homogenizing effect than species from distant sources: evidence from plants and fishes in the USA. Diversity and Distributions 11:367–374.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. Biological Conservation 127:247–260.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology and Evolution 14:450–453.

Moyle, P. B., and J. F. Mount. 2007. Homogenous rivers, homogenous faunas. Proceedings of the National Academy of Sciences of the United States of America 104:5711–5712.

Olden, J. D. 2006. Biotic homogenization: a new research agenda for conservation biogeography. Journal of Biogeography 33:2027–2039.

Olden, J. D., and N. L. Poff. 2003. Toward a mecha-

nistic understanding and prediction of biotic homogenization. The American Naturalist 162:442–460.

Olden, J. D., N. L. Poff, M. R. Douglis, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology and Evolution 19:18–24.

Olden, J. D., M. E. Douglas, and M. R. Douglas. 2005. The human dimensions of biotic homogenization. Conservation Biology 19:2036–2038.

Olden, J. D., and T. P. Rooney. 2006. On defining and quantifying biotic homogenization. Global Ecology and Biogeography 15:113–120.

Olden, J. D., M. J. Kennard, and B. J. Pusey. 2008. Species invasions and the changing biogeography of Australian freshwater fishes. Global Ecology and Biogeography 17:25–37.

Peterson, D. P., K. D. Fausch, J. Watmough, and R. A. Cunjak. 2008. When eradication is not an option: modelling strategies for electrofishing suppression of nonnative brook trout to foster persistence of sympatric native cutthroat trout in small streams. North American Journal of Fisheries Management 28:1847–1867.

Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. BioScience 50:53–65.

Pine, W. E., III, T. J. Kwak, and J. A. Rice. 2007. Modeling management scenarios and the effects of an introduced apex predator on a coastal riverine fish community. Transactions of the American Fisheries Society 136:105–120.

Poff, N. L., J. D. Olden, D. M. Merritt, and D. M. Pepin. 2007. Homogenization of regional river dynamics by dams and global biodiversity implications. Proceedings of the National Academy of Sciences of the United States of America 104:5732–5737.

Quinn, J. W., and T. J. Kwak. 2003. Fish assemblage changes in an Ozark River after impoundment: a long-term perspective. Transactions of the American Fisheries Society 132:110–119.

Rahel, F. J. 2000. Homogenization of fish faunas across the United States. Science 288:854–856.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology Evolution, and Systematics 33:291–315.

Rahel, F. J. 2004. Unauthorized fish introductions: fisheries management of the people, for the people, or by the people? Pages 431–444 *in* M. J. Nickum, P. M. Mazik, J. G. Nickum, and D. D.

MacKinlay, editors. Propagated fishes in resource management. American Fisheries Society, Symposium 44, Bethesda, Maryland.

Rahel, F. J. 2007. Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all. Freshwater Biology 52:696–710.

Radomski, P. J., and T. J. Goeman. 1995. The homogenizing of Minnesota Lake fish assemblages. Fisheries 20(1):20–23.

Rhymer, J. M., and D. Simberloff. 1996. Extinction by hybridization and introgression. Annual Review of Ecology and Systematics 27:83–109.

Rooney, T. P., J. D. Olden, M. K. Leach, and D. A. Rogers. 2007. Biotic homogenization and conservation prioritization. Biological Conservation 134:447–450.

Ruesink, J. L. 2003. One fish, two fish, old fish, new fish: which invasions matter? Pages 161–178 *in* P. Kareiva and S. A. Levin, editors. The importance of species: perspectives on expendability and triage. Princeton University Press, Princeton, New Jersey.

Sax, D. F., S. D. Gaines, and J. H. Brown. 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. American Naturalist 160:766–783.

Scoppettone, G. G., P. H. Rissler, C. Gourley, and C. Martinez. 2005. Habitat restoration as a means of controlling non-native fish in a Mojave Desert oasis. Restoration Ecology 13:247–256.

Scott, M. C. 2006. Winners and losers among stream fishes in relation to land use legacies and urban development in the southeastern US. Biological Conservation 127:301–309.

Scott, M. C., and G. S. Helfman. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. Fisheries 26(11):6–15.

Taylor, C. A., J. H. Knouft, and T. M. Hiland. 2001. Consequences of stream impoundment on fish communities in a small North American drainage. Regulated Rivers Research and Management 17:687–698.

Taylor, E. B. 2004. An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 61:68–79.

Tyus, H. M., and J. F. Saunders, III. 2000. Nonnative fish control and endangered fish recovery: lessons for the Colorado River. Fisheries 25(9):17–24.

Unmack, P. J., and W. F. Fagan. 2004. Convergence of differentially invaded systems toward invader-dominance: time-lagged invasions as a predictor in desert fish communities. Biological Invasions 6:233–243.

Vredenburg, V. T. 2004. Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. Proceedings of the National Academy of Sciences of the USA 101:7646–7650.

Walsh, C. J., A. H. Roy, J. W. Feminella, P. D. Cottingham, P. M. Groffman, and R. P. Morgan, II. 2005. The urban stream syndrome, current knowledge and the search for a cure. Journal of the North American Benthological Society 24:706–723.

Walters, D. M., D. S. Leigh, and A. B. Bearden. 2003. Urbanization, sedimentation, and the homogenization of fish assemblages in the Etowah River basin, USA. Hydrobiologia 494:5–10.

Weidel, B. C., D. C. Josephson, and C. E. Kraft. 2007. Littoral fish community response to smallmouth bass removal from an Adirondack lake. Transactions of the American Fisheries Society 136:778–789.

Williamson, K. S., and B. May. 2005. Homogenization of fall-run Chinook salmon gene pools in the central valley of California, USA.