

# HOMOGENIZATION OF FRESHWATER FAUNAS

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■ **Abstract** Biotic homogenization is the increased similarity of biotas over time caused by the replacement of native species with nonindigenous species, usually as a result of introductions by humans. Homogenization is the outcome of three interacting processes: introductions of nonnative species, extirpation of native species, and habitat alterations that facilitate these two processes. A central aspect of the homogenization process is the ability of species to overcome natural biogeographic barriers either through intentional transport by humans or through colonization routes created by human activities. Habitat homogenization through reservoir construction contributes to biotic homogenization as local riverine faunas are replaced with cosmopolitan lentic species. The homogenization process has generally increased biodiversity in most freshwater faunas, as the establishment of new species has outpaced the extinction of native species. There are important exceptions, however, where the establishment of nonindigenous species has had devastating impacts on endemic species. The homogenization process appears likely to continue, although it could be slowed through reductions in the rate of invasions and extirpations and by rehabilitating aquatic habitats so as to favor native species.

## INTRODUCTION

Biotic homogenization is the increased similarity of biotas over time caused by the replacement of native species with nonindigenous species, usually as a result of introductions by humans. It is an accelerating phenomenon that is a consequence of human domination of Earth's ecosystems (Vitousek et al. 1997, McKinney & Lockwood 2001). Biologists are concerned about homogenization because it often results in a decline in biodiversity (McKinney & Lockwood 1999). Even when biodiversity is enhanced through species introductions, the enhancement often includes taxa that are already widespread, tolerant of degraded habitats, and considered a nuisance by humans (Angermeier 1994, Pimentel et al. 2000, Scott & Helfman 2001).

Homogenization is a complicated process because it integrates many aspects of the biodiversity crisis such as species introductions, extirpations, and habitat alteration. The introduction of cosmopolitan species will, by itself, increase

homogenization, but this effect will be magnified if the introduced species also cause extinction of endemic species that make the aquatic system unique. An unfortunate example is the loss of almost 200 species of endemic cichlids following introduction of the predatory Nile perch *Lates nilotica* into Lake Victoria in Africa (Kaufman 1992). Habitat alteration may directly cause the extirpation of native species that cannot tolerate the new abiotic conditions. A well known example is the loss of mussel species following reservoir creation on rivers in the southeastern United States (Williams et al. 1993). But sometimes the effect of habitat alteration in causing extirpations is indirect. For example, Baltz & Moyle (1993) reported that altered abiotic conditions allow nonnative fishes to become established in California streams, and these new species then eliminate native species through competition or predation.

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 all levels of biological organization. For example, habitat homogenization has resulted in similar habitats across North America such as urban business districts, golf courses, canals, and warmwater reservoirs. 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. Blair (2001) reported that bird and butterfly assemblages from urban areas in California and Ohio were more similar to each other than they were to the native assemblages they replaced. The same phenomenon occurs in urban lakes across North America that tend to be dominated by a suite of organisms tolerant of degraded water quality, such as aquatic oligochaetes, common carp *Cyprinus carpio*, and goldfish *Carassius auratus*. Below the species level, genetic homogenization is of concern for taxa subject to artificial propagation and widespread stocking, such as many species of salmonids.

In the following sections I discuss how biotic homogenization is measured and examine three interacting mechanisms that result in homogenization: introductions, extirpations, and habitat alterations. Next, I discuss the consequences of homogenization on aquatic systems such as the replacement of unique regional biotas with cosmopolitan species, and the loss of genetic diversity for some widely cultivated species. I end with future scenarios of biotic homogenization and how the process may be slowed, although it is not likely to be stopped altogether. My review is focused on North America because much of the work on homogenization of aquatic biotas has been done there, but homogenization is a global phenomenon (Arthington 1991, Holcik 1991, Ogutu-Ohwayo & Hecky 1991, Contreras-Balderas 1999, Lodge et al. 2000a).

## HOW HOMOGENIZATION IS MEASURED

Homogenization is defined as an increase in the similarity of biotas over time, and an obvious way to measure this increase is through similarity indices. A widely used index is Jaccard's coefficient of similarity, calculated as percent

similarity =  $[a/(a + b + c)] \times 100$  where  $a$  = number of species present in both biotas,  $b$  = number of species present only in the first biota and  $c$  = number of species present only in the second biota (Radomski & Goeman 1995, Marchetti et al. 2001). Values can range from 0% (biotas have no species in common) to 100% (biotas have identical species composition). A common approach for assessing temporal changes in homogenization is to calculate the similarity between a pair of biotas at two times, typically pre- and post-alteration by humans. If similarity has increased, then the biotas have become more homogeneous. Rahel (2000) used this approach to quantify the change in similarity of fish faunas among the 48 coterminous United States from pre-European settlement to the present.

Ecologists distinguish between  $\alpha$  diversity (the number of species in a specific habitat) and  $\beta$  diversity (the turnover of species across habitats). A decrease in  $\beta$  diversity indicates that homogenization has occurred. Spatial turnover or  $\beta$  diversity can be measured by counting the number of species lost or gained as one moves from one site to another site along a spatial continuum (Russell 1999). The resultant value is then scaled to the size of the combined species pool at both sites. One formula for measuring  $\beta$  diversity is  $T = (G + L)/\alpha$  where  $T$  is spatial turnover,  $G$  is the number of species found in the first site but not in the second,  $L$  is the number of species found in the second site but not the first, and  $\alpha$  is the total number of species found within both. Duncan & Lockwood (2001) used this approach to examine the change in spatial turnover of fish, amphibian, and mussel species across zoogeographic zones in Tennessee. Other measures of species turnover along spatial gradients are discussed by Sheldon (1988) and Russell (1999).

Cluster analysis and ordinations are multivariate approaches used to assess similarity among a group of sampling sites. In a cluster analysis, sites with similar faunal assemblages are sorted into hierarchical groups showing a progressive increase in their similarity. This approach allows one to see relationships among all sites, not just one pair at a time. Blair (2001) used cluster analysis to show that the physical habitat and biotic communities of urban areas in California and Ohio were more similar than the original ecosystems present in these areas. Thus, these areas have experienced homogenization of both habitats and biota. In an ordination, sites are projected onto a reduced set of axes that represent gradients of community composition. Sites close together in the ordination plot are more similar in their faunal composition than sites located far apart. Jackson (2002) used this approach to examine homogenization of fish faunas in lakes following the addition of a piscivore.

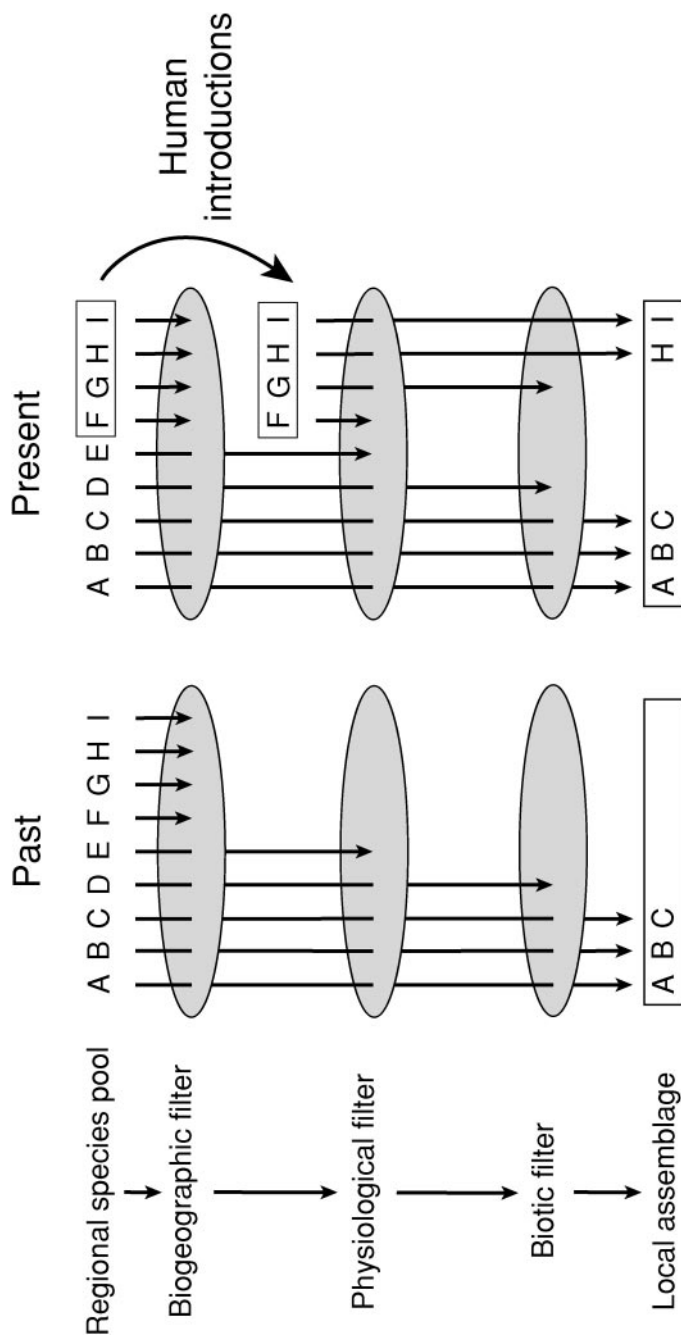
## CAUSES OF BIOTIC HOMOGENIZATION

Biotic homogenization is the outcome of three interacting processes: introductions of nonnative species, extirpation of native species, and habitat alterations that facilitate these two processes. Although invasions have always been a part of nature, they now occur at an accelerated rate as a result of human activities (Vermeij 1991,

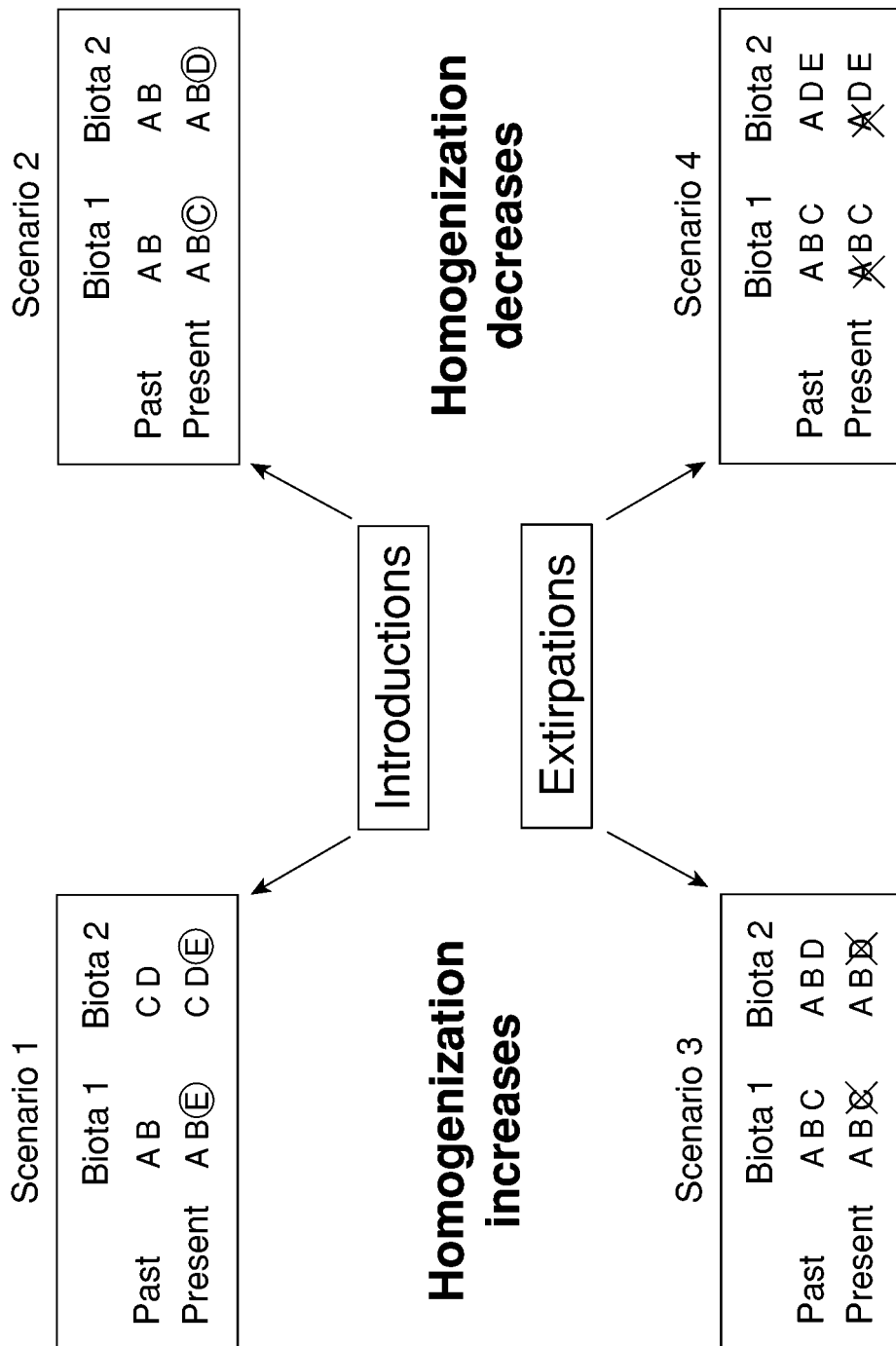
Benson & Boydstun 1999, Fuller et al. 1999). Ecologists often describe the species assemblage of a local area as the result of filters that reduce the regional species pool to a subset of species that have had the opportunity to colonize the habitat, are physiologically adapted to the abiotic conditions, and have the ecological characteristics needed to interact successfully with the other species present. In such a model of community assembly, the first filter is represented by glacial events and biogeographic barriers that prevent many species from colonizing a region (Figure 1). Some of these species are physiologically and ecologically suited to the region but have not had the opportunity to realize this potential. A major effect of humans is to move species across barriers to colonization and thus to eliminate the biogeographic filter as a factor in determining the species composition of local assemblages (Figure 1). Bypassing of the biogeographic filter can occur when species are transplanted across basin divides within a region (Brown & Moyle 1997) or when species are transported to new continents or oceans (Baltz 1991, Ricciardi & MacIsaac 2000). In some cases, humans may not actively transport species but may create colonization routes that did not exist naturally. For example, shipping canals near Chicago, Illinois that link the Great Lakes with the Mississippi River have allowed the exchange of 15 species of fish and invertebrates formerly confined to just one of the basins (Kolar & Lodge 2000).

Introductions can either increase or decrease the similarity among biotas. Increased similarity occurs when the same group of species is introduced into two biotas that originally had few species in common (Scenario 1 in Figure 2). The widespread introduction of a group of common sport fish such as largemouth bass *Micropterus salmoides* and rainbow trout *Oncorhynchus mykiss* across the United States is a good example of this phenomenon (Rahel 2000). By contrast, decreased similarity occurs when different species are introduced into initially similar biotas (Scenario 2 in Figure 2). Marchetti et al. (2001) provided an example of this phenomenon for watersheds in California. Within a given ecoregion, watershed fish faunas that were initially similar because of zoogeographic and historical reasons have diverged as a result of haphazard introductions among different watersheds.

Extirpations also can increase or decrease the similarity of biotas. An increase in similarity occurs when each biota loses its unique species but retains widespread species (Scenario 3 in Figure 2). Duncan & Lockwood (2001) argue that this scenario will result in the future homogenization of amphibian, fish, and mussel faunas in Tennessee. Their rationale is that different ecoregions currently have a large number of unique species that are localized with small population sizes and thus highly vulnerable to extinction. As these species become extinct in the future, only relatively widespread and abundant species will remain. Hence the ecoregions will become more similar, even without introductions of new, cosmopolitan species. A decrease in similarity due to extirpation would happen if two biotas lose the species they have in common and retain their unique species (Scenario 4 in Figure 2). It is difficult to imagine this phenomenon occurring on a large scale because widespread species tend to be abundant and have many populations that facilitate recolonization if local extinction occurs. Thus, widespread species



**Figure 1** The species present at a local scale are the result of several filters. At the regional scale there is a pool of species present as a result of continental movement patterns and evolutionary events. Biogeographic filters such as glaciation and geographic barriers prevent some species from colonizing certain water bodies or drainage systems. Species that make it through this filter must be able to tolerate the abiotic conditions (physiological filter) and then interact successfully with the other species present (biotic filter). In the past, species such as A, B, and C that made it through all three filters comprised the local assemblage. Humans act to circumvent biogeographic filters by introducing species into areas they would not be able to colonize on their own. Introduced species such as H and I that subsequently pass through the physiological and biotic filters then become members of the local assemblage.

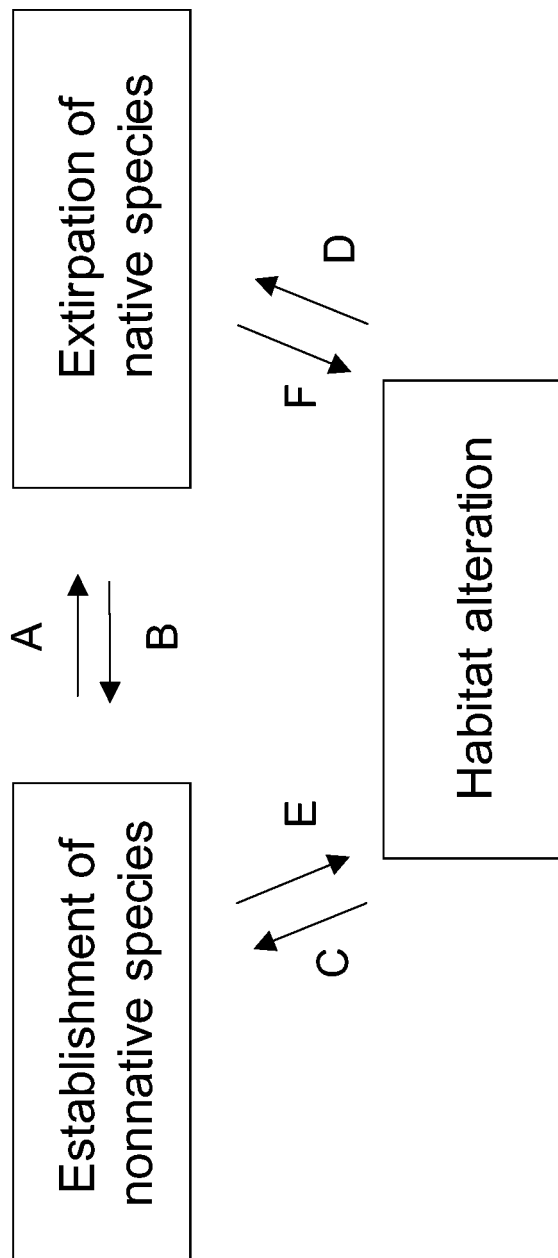


generally are not vulnerable to extinction. However, at a local scale, it is possible for two water bodies to lose some species they originally had in common and thus experience a decrease in their similarity. This scenario might be important for rehabilitation efforts involving degraded urban water bodies that currently share the same group of nonnative, pollution-tolerant species. As habitat conditions improve, cosmopolitan species such as common carp, goldfish, and bullheads may be replaced by more distinctive species native to the region (Kanehl et al. 1997).

Introductions and extirpations can facilitate each other and habitat alterations can strongly influence both (Figure 3). For example, the introduction of a predator or strong competitor can eliminate native species even when habitat remains relatively intact (Path A in Figure 3). Examples include the replacement of native trout by introduced trout in many pristine habitats in western North America (Harig et al. 2000), loss of amphibians in high elevation lakes to predation from introduced fish (Bradford et al. 1993), and replacement of native crayfish by introduced crayfish in undisturbed habitats in the midwestern United States (Lodge et al. 2000a). Conversely, loss of a native species may allow nonnatives to invade as resources and living space are freed up (Path B in Figure 3). An example is the changed fish assemblage in Lake Michigan. Overfishing and predation by sea lampreys *Petromyzon marinus* devastated the native top predators in the system, especially lake trout *Salvelinus namaycush*. The absence of predators provided an opportunity for introduction of nonnative predators such as Pacific salmon and steelhead trout *Oncorhynchus mykiss* that would use nuisance prey fish populations such as alewife *Alosa pseudoharengus* (Jude & Leach 1999). The predators were intentionally introduced by management agencies, but their success was due partly to the loss of native piscivores from the system. In a similar vein, loss of native crayfish populations in Europe as a result of introduced diseases has facilitated invasion by species introduced from North America (Lodge et al. 2000a).

Habitat alterations can lead to establishment of nonnative species (Path C in Figure 3) or extirpation of native species (Path D in Figure 3). As an example of Path C, flow regulation favors nonnative over native fishes in California streams (Marchetti & Moyle 2001). Under natural flow regimes, high flows in winter and spring prevent the establishment of nonnative species. But when flows are stabilized by dams, nonnatives dominate and displace natives through competition and predation. The role of habitat alteration in causing extirpations (Path D) is

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**Figure 2** Introductions and extirpations can either decrease or increase the similarity of biotas. Introduced species are indicated by circles and extirpated species are indicated by being crossed out. Introductions increase homogenization when the same cosmopolitan species are introduced to sites with initially distinct biotas (Scenario 1) or decrease homogenization if disparate species are introduced into sites with initially similar biotas (Scenario 2). Extirpations increase homogenization when disparate species are eliminated from biotas (Scenario 3) and decrease homogenization when common species are eliminated (Scenario 4).



**Figure 3** At the center of the homogenization process are species introductions and extirpations both of which can be influenced by habitat alterations. Introductions may lead directly to extirpations and extirpations may allow new species to colonize even in the absence of habitat disturbance (Paths A and B). Habitat alterations may accelerate this process by facilitating the establishment of new species (Path C) or the elimination of current species (Path D). The establishment of new species or the loss of current species both can result in habitat alterations (Paths E and F). Interactions involve situations where habitat alteration favors the establishment of a new species that, in turn, causes the extirpation of existing species (Path CA) or where the establishment of a nonnative species alters the habitat and causes the extirpation of native species (Path ED).



clearly documented for freshwater mussels. The extirpation of many populations in the southeastern United States is attributed to reservoir construction that eliminated the riffle-habitats required by many species (Williams et al. 1993, Bogan 1993).

An interesting situation is when establishment of nonnative species leads to a major alteration of the habitat (Path E in Figure 3). Establishment of the zebra mussel *Dreissena polymorpha* in the Great Lakes has substantially altered water clarity, primary productivity, and benthic substrates (Dermott & Kerec 1997). Because of their tremendous capacity for filtering algae and detritus from the water, energy is shifted away from the pelagic zone to the benthic zone. The result is less energy for pelagic organisms including larval fish. Because of their high numbers, zebra mussels replace complex benthic substrates with a more uniform carpet of mussel shells. This change has negative consequences for other benthic fauna, especially native mussels (Nalepa et al. 1996). The establishment of the Asian clam *Potamocorbula amurensis* in San Francisco Bay also has redirected energy pathways to the benthic zone with negative consequences for many pelagic species in this ecosystem (Grosholz 2002).

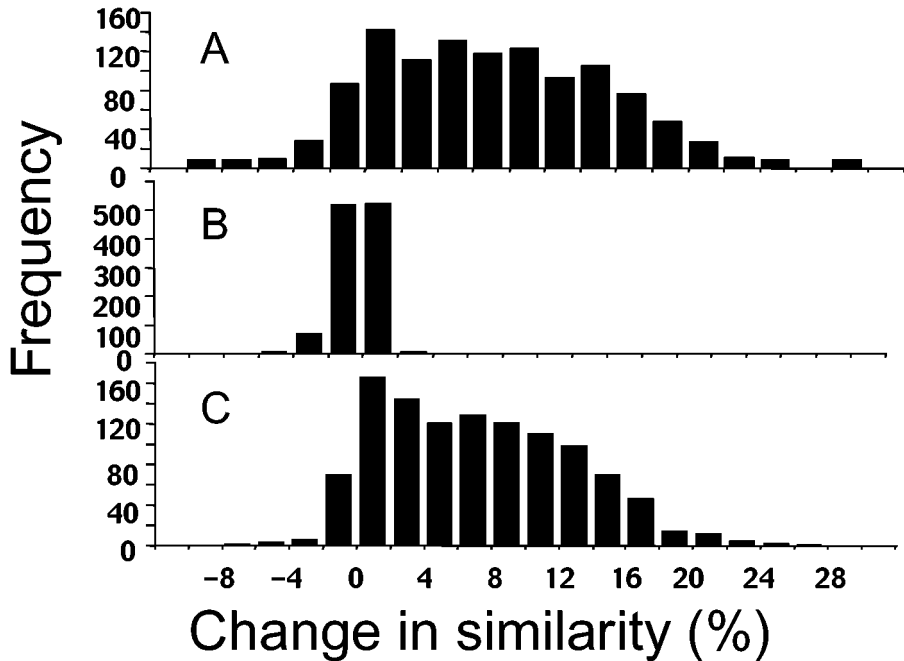
Sometimes extirpation of a native species can lead to major habitat alterations (Path F in Figure 3). An example is extirpation of the sea otter *Enhydra lutris* off the Pacific coast of North America (Estes & Palmisano 1974). Loss of otters resulted in loss of kelp forests in the near shore region. This was a major habitat alteration because the kelp forests reduced the effects of waves and provided structure for an entire fish assemblage. The otters preyed on the sea urchins and the loss of otters through overhunting allowed sea urchin populations to expand and decimate the kelp forests. Cessation of hunting allowed sea otter populations to recover, which led to a reduction in sea urchin populations and, subsequently, expansion of kelp forests. Recently, sea otter populations have declined again in some areas because of increased predation by killer whales *Orcinus orca*. The result has been another cascade of trophic interactions ultimately leading to reduction of kelp beds. (Estes et al. 1998). Beaver *Castor canadensis* provide another example where extirpation of a species causes significant habitat alteration. Beaver create small impoundments that provide habitat for a different assemblage of fishes than normally occurs in free-flowing stream reaches (Snodgrass & Meffe 1998, Schlosser & Kallemeyn 2000). Loss of beaver results in a reversion to flowing water habitat and loss of many pond-dependent taxa. Ecologists refer to species such as sea otters and beavers as ecosystem engineers because of their dominant role in determining the structure of the habitats they inhabit (Jones et al. 1994).

Introductions, extirpations and habitat alterations often will interact in complex ways. For example, habitat alteration in the California streams discussed above leads to establishment of nonnative fish species that then extirpate native species. This process corresponds to a combination of Paths C and A (Path CA in Figure 3). Loss of sea otters or beavers leads to loss of many other species that depend on habitat conditions maintained by these ecosystem engineers. This process would correspond to community changes along Path FD in Figure 3. Introduction of zebra mussels causes major habitat changes that have negative effects on many

native species; hence this case would exemplify Path ED in Figure 3. A particularly insidious mechanism altering biotas is represented by Path EC in Figure 3 where the introduction of a nonnative species alters the environment to favor introductions of additional nonnative species. Simberloff & Von Holle (1999) referred to this positive feedback loop as "invasional meltdown." A recent series of invasions by euryhaline organisms from the Black and Caspian seas might be the start of an invasional meltdown in the North American Great Lakes. Ricciardi (2001) reported that establishment of large zebra mussel populations likely facilitated the rapid invasion of the round goby *Neogobius melanostomus*, a major predator of the mussel in the Caspian Sea basin. Additionally, *Echinogammarus*, a deposit-feeder associated with zebra mussels in Europe, has replaced other amphipods in zebra mussel beds in Lake Erie and Lake Ontario. And a hydroid from the Black and Caspian seas, *Cordylophora caspia*, that feeds on zebra mussel larvae and uses mussel shells as a substrate has produced luxuriant colonies on newly formed mussel beds in Lake Michigan. It seems likely that zebra mussels have altered the benthic environment of the Great Lakes so as to facilitate invasions by additional exotic species.

## EVIDENCE OF BIOTIC HOMOGENIZATION IN AQUATIC SYSTEMS

Rahel (2000) reported that fish faunas across the United States have become increasingly homogenized, largely as the result of introductions of sport and food fishes. Jaccard's coefficient was used to calculate the similarity between each pair of states based on species presence and absence data. Similarity was calculated for two time periods, past and present, with the latter accounting for species extirpations and introductions that have occurred since European settlement. When the change in similarity (present minus past similarity) was determined for all 1,128 possible pairwise combinations of the 48 coterminous states, it was clear that fish faunas had become more similar (Figure 4a). Also, pairs of states averaged 15.4 more species in common now than they did in the past. The 89 pairs of states that historically had zero similarity (no species in common) now have an average similarity of 12.2% and an average of 25 species in common. The cause of homogenization was examined by calculating the change in similarity assuming only extirpations had occurred (i.e., omitting all introduced species from current state fish faunas) or that only introductions had occurred (i.e., assuming no species had been extirpated). Extirpations accounted for little of the observed change in similarity between past and present fish faunas (Figure 4b). By contrast, introductions produced big increases in similarity and were clearly the key factor homogenizing fish faunas (Figure 4c). Most of the introductions were of species intentionally introduced for sport or aquaculture purposes by management agencies. This example parallels the situation for birds, where most introductions result from intentional transport by humans (Lockwood et al. 2000).



**Figure 4** Changes in similarity of fish faunas among 1128 pairwise combinations of the 48 coterminous United States. (A) Change in similarity based on combined effects of species extirpations and introductions. Distribution is skewed toward positive values indicating fish faunas have become more similar by an average of 7.2%. (B) Change in similarity based on species extirpations only. Extirpations have caused a negligible change in the similarity among state fish faunas. (C) Change in similarity based on introductions only. Distribution resembles that in A, indicating most of the increased similarity in fish faunas is due to introduction of a group of cosmopolitan species. (From Rahel 2000).

Radomski & Goeman (1995) found an increase in homogenization of fish assemblages among lakes in Minnesota. They quantified the similarity of past and present fish assemblages among pairs of lakes using Jaccard's coefficient of similarity and presence and absence data from fisheries surveys. Changes in similarity were contrasted between a group of lakes subject to extensive stocking and a group with little stocking activity. Fish assemblages had become more similar among the stocked lakes but not the unstocked lakes, again implicating the role of intentional introductions in homogenizing fish faunas. Most of the stocked lakes increased their richness by one to three species. As a result of stocking activities, six species had become significantly more widespread including five game fish species and common carp. One species was less widespread, the bowfin *Amia calva*, which is piscivorous and a likely competitor with the introduced game fish species.

Marchetti et al. (2001) studied homogenization of California fish assemblages, using Jaccard's coefficient to measure the similarity of past (pre-1850) and current assemblages. A unique aspect of this study was examination of changes in similarity at three spatial scales. At the largest scale, there was an increase in the similarity of fish faunas across the six zoogeographic provinces of California. This increase was largely due to all six provinces' having gained a similar set of species not native to California. At the middle spatial scale, similarity either decreased or showed no clear pattern for fish assemblages in watersheds within each of the zoogeographic provinces. This result was attributed to the haphazard nature of introductions within individual watersheds that diversified the historically uniform within-province faunas. At the finest spatial scale, within-province comparisons were made among the fish faunas of reservoirs and the river reaches they replaced. For one province, the reservoir fish faunas were more similar today than the corresponding river reaches were in the past. No pattern was evident for the other province for which adequate data were available. To explore the relationship between habitat alteration and faunal change, Marchetti et al. (2001) examined the effects of environmental variables on the change in composition between each watershed's original (pre-1850) and current fish fauna. The degree of change between historical and current fish faunas was quantified using Jaccard's coefficient of similarity and species presence/absence data. A low similarity indicated extensive faunal change within the watershed. Extent of water development, degree of urban development, watershed area and mean elevation were positively associated with the degree of faunal change in a watershed. Only mean rainfall was negatively associated with the degree of faunal change. These results supported the idea that habitat alterations drove alteration of fish faunas at the watershed scale.

Duncan & Lockwood (2001) examined homogenization of amphibian, fish, and mussel faunas by quantifying the spatial turnover of species (beta diversity) across ecoregions in Tennessee. They first estimated spatial turnover for pre-settlement faunas prior to extirpations or introductions. This analysis provided a baseline for spatial turnover prior to significant human disturbance. Then they estimated turnover when introduced species were included but extirpated species as well as those classified as threatened, endangered, or vulnerable were omitted from the data set. The idea was to simulate spatial turnover in the future following species losses. Under the future scenarios, regional differences in species composition (spatial turnover) declined an average of 16% for fish, 21% for mussels, and 30% for amphibians. This represents a significant homogenization of aquatic faunas among ecoregions in Tennessee. In contrast to the studies discussed previously (Radomski & Goeman 1995, Rahel 2000, Marchetti et al. 2001), the future homogenization of aquatic faunas in Tennessee was predicted to result from extirpations rather than introductions. This prediction was based on the assumptions that no new species would invade and all threatened, endangered, and vulnerable species would be extirpated. Whereas these assumptions may be somewhat extreme, they do indicate that in regions with diverse faunas characterized by many endemic species with limited geographic ranges, extirpation rather than introductions will be the major homogenizing factor (Warren et al. 2000).

Scott & Helfman (2001) discussed the influence of native species invasions on the homogenization of fish faunas in the southeastern United States where headwater streams have many endemic fishes adapted to cool, clear, nutrient-poor conditions, and low sediment loads. As these streams flow into lower elevations, they are inhabited by widespread, generalist fish species adapted to warm, turbid, sediment-rich, and nutrient-rich conditions. Headwater species occur, on average, in only 3.3 drainages, whereas downstream species occur in an average of 29.5 drainages. Land use practices such as deforestation degrade stream habitats and reduce habitat diversity. As a result of this habitat homogenization, endemic headwater species are lost and the streams are invaded by generalist, downstream species. Even though the invaders are native to the drainage, they are not native to the headwater reaches. Although this process was not quantified, it seems plausible that replacement of unique headwater species with widespread downstream species will homogenize fish faunas across the region. Scott & Helfman (2001) cautioned that assessments of the integrity or conservation value of aquatic habitats should consider the effects of native invasions, as well as invasions by exotic species.

Jackson (2002) found that Ontario lakes containing bass (*Micropterus* spp.) were grouped together more closely in an ordination plot than lakes without bass. Thus, as a group, lakes with bass had more similar fish assemblages than lakes without bass. Bass were not native to the region, and all lakes were assumed to have had the same initial suite of species. The implication, therefore, was that bass had homogenized the fish assemblages by eliminating a diverse group of small-bodied prey species.

To date, much of the effort in quantifying faunal homogenization in freshwaters has focused on fish. Two other taxa that appear vulnerable to large-scale homogenization in North America are crayfish and freshwater mussels. In both cases, extirpation of many endemic species and their replacement by a few generalist species is considered likely. Lodge et al. (2000a) reviewed the status of crayfish and concluded that "the most important threat to native North American crayfish biodiversity is nonindigenous crayfishes (many from within North America)." Two species in particular, the signal crayfish (*Pacifastacus leniusculus*) and the rusty crayfish (*Orconectes rusticus*), have proven to be aggressive invaders that have contributed to the extinction of one crayfish species, the endangerment of another, and the loss of many populations of other species. There is concern that introduction of the rusty crayfish into the southeastern United States would be devastating to the many endemic crayfish found there (Taylor et al. 1996). Many of these species have small native ranges and thus are highly vulnerable to extirpation by competitively superior species such as the rusty crayfish (Hill & Lodge 1999).

Freshwater mussels in the families Margaritiferidae and Unionidae are world-wide in distribution but reach their greatest diversity in North America with 281 species and 16 subspecies (Williams et al. 1993). They are the most imperiled freshwater fauna with 12% of the taxa listed as probably extinct and 60% considered endangered, threatened, or of special concern (Ricciardi et al. 1998). During the twentieth century, the most important source of imperilment was destruction

of habitat by damming, dredging, and channelization of rivers, especially in the southeastern United States. Dams were particularly harmful because of the change from riverine to reservoir habitat and the disruption of the reproductive cycle by eliminating host fish species needed to harbor the larval stages (Bogan 1993). Over-exploitation by commercial harvest also has been a concern (Anthony & Downing 2001). In the 1990s, a significant new threat was added with the establishment of the Eurasian zebra mussel, a suspension feeding organism that smothers the shells of other mollusks and competes with them for food (Nalepa et al. 1996). This species has rapidly spread throughout the Great Lakes and the Mississippi River basin, often reaching densities in excess of 3000 individuals  $m^{-2}$  and extirpating native mussel species within 4–8 years. Ricciardi et al. (1998) projected that if the current rate of spread continues, the zebra mussel will accelerate the regional extinction rates of North American freshwater mussels by ten-fold and will threaten the existence of over 60 endemic species in the Mississippi River basin. The replacement of so many native mussel species by a single nonnative species would constitute an extreme case of biotic homogenization.

Another example of biotic homogenization is the establishment of over 145 nonnative species in the North American Great Lakes (Mills et al. 1993). Especially noteworthy is that since 1985, 70% of the invading species are native to fresh and brackish waters of the Ponto-Caspian region (Black, Caspian, and Azov seas) (Ricciardi & MacIsaac 2000). Some of these species have achieved high abundance and now play a major role in Great Lake food webs. Examples include ruffe *Gymnocephalus cemuus*, round goby *Neogobius melanostomus*, tubenose goby *Proterorhinus marmoratus*, zebra mussel, quagga mussel *Dreissena bugensis*, and the amphipod *Echinogammarus ischnus*. Most of the invasions result from ship ballast water release. This invasion is decidedly one-sided, as few North American species have invaded the Ponto-Caspian region. Still, it illustrates a situation where the introduction of diverse taxonomic groups is contributing to an increasing similarity between major water bodies located half a world apart.

## CONSEQUENCES OF BIOTIC HOMOGENIZATION

Biotic homogenization results in the paradox of gaining species but losing diversity. This is because local richness often increases with the introduction of cosmopolitan species while, at the same time, regional and global diversity decrease as endemic species are driven to extinction. Consider Clear Lake, California, which originally contained 12 native fish taxa, including three endemic to the lake (Hunter 1996). As a result of efforts to increase the fish diversity in the lake, 16 species have been introduced and become established. Most are common sport fishes such as sunfishes, basses, and catfishes, and their establishment has made the fish fauna in Clear Lake more similar to fish faunas across the United States. But these introductions along with habitat alterations caused the global extinction of two native species, the Clear Lake splittail *Pogonichthys ciscooides* and the thicktail chub *Gila crassicauda*. Thus, although Clear Lake has gained 16 species, the earth's fish fauna has declined by two species. The gain in species and loss of

diversity is evident at the scale of the United States where 39 species have been added to the fish fauna, all of which were already common in other parts of the world, and 19 species found nowhere else in the world have become extinct (Miller et al. 1989, Rahel 2000).

Because biotic homogenization is the combined result of introductions and extirpations, the negative consequences of both processes also apply to the process of homogenization (Tilman 1999, Mack et al. 2000). Concerns about introductions typically center on species that become pests or reduce the abundance of more desirable species. Most introduced species do not have major, detectable effects on native species, and in some cases they provide economic benefits related to sport fishing or aquaculture (Horak 1995). Mills et al. (1993) estimated that only 10% of the 139 introduced species in the North American Great Lakes have had demonstrably substantial impacts. In a review of the literature on invasive species, Lodge (1993) noted that between 2 and 40% of introduced species had an impact large enough to be detected. But the minority of introduced species that prove harmful can have major ecological and economic impacts (Pimental et al. 2000). Zebra mussels, for example, have had negative economic effects by clogging water intake structures, and they appear poised to have major ecological effects by causing the extinction of native mussel species in North America (Ricciardi et al. 1998). Common carp reduce the abundance of native fish species, and there is a long history of expensive and generally unsuccessful efforts to control them (Cooper 1987). Nile perch have contributed to the global extinction of hundreds of endemic cichlid species in the Great Lakes of Africa (Kaufman 1992). Most natural resource managers today are aware of the dangers of introducing nonnative species, and the rate of official introductions has declined (Townsend & Winterbourn 1992, Rahel 1997). However, unofficial and often illegal introductions continue to be a problem. There have been 210 instances of illegal fish species introductions within the state of Montana (Vashro 1995). And in the Pacific northwest of the United States, illegal introductions of northern pike *Esox lucius* and walleye *Stizostedion vitreum* are a concern (McMahon & Bennett 1996).

The consequences of species extinctions include lost opportunities for human use and potential negative effects on ecosystem services (Tilman 1999). Even the loss of seemingly unimportant species can be detrimental because such species may play a hidden role in supporting other species and because biodiversity provides insurance that ecosystem functions will be maintained in the face of environmental change (Yachi & Loreau 1999). As Hector et al. (2001) noted, we are far from being able to identify which subset of species is most important for the long-term health of ecosystems and whose conservation would preclude the need for other species. From a homogenization viewpoint, introductions are especially important when they cause extirpations of native species either through direct interactions (Path A in Figure 3) or by making habitats unsuitable for native species (Path ED in Figure 3).

An interesting question is whether aquatic biotas are more vulnerable to homogenization than terrestrial biotas. This question has three components: Are aquatic habitats more invisable than other habitats, are extinctions more likely for aquatic

than terrestrial organisms, and are aquatic habitats more altered by human activities than terrestrial habitats? Moyle (1999) noted that many freshwater and estuarine ecosystems have been extensively invaded by nonnative species, but he did not attribute this pattern to aquatic systems being innately more invasible. Rather, Moyle felt the high frequency of successful invasions indicated (a) most aquatic environments have been altered by human activity, (b) there has been a high frequency of introductions into aquatic systems, both intentionally (sport fish) and as by-product introductions (e.g., canal building, ballast water discharge, aquaculture operations) and (c) people have been highly successful introducing aquatic organisms in matching the organism to the local environment. There does appear to be a difference in extinction rates for aquatic taxa compared to terrestrial taxa. Ricciardi & Rasmussen (1999) reported that extinction rates for North American freshwater fauna (fish, crayfish, mussels, gastropods, and amphibians) were five times higher than extinction rates for terrestrial and marine fauna (birds, reptiles, land mammals, and marine mammals). Extinction rates for all taxa were projected to increase, but rates for aquatic fauna would remain higher. The high extinction rate of aquatic organisms has been attributed to the extensive deterioration of aquatic ecosystems (Richter et al. 1997, Ricciardi & Rasmussen 1999, Pringle et al. 2000). Moyle (1999) indicated that freshwater and estuarine habitats are among the most altered ecosystems on Earth because they are the ultimate sumps for watershed pollutants, their water is increasingly diverted for human use through dams and reservoirs that alter flow regimes and fragment drainages, they are the focus of most human activity, especially large cities and agriculture that degrade water quality, and their biota is subject to intense exploitation.

Homogenization of terrestrial faunas is in large part driven by human habitat alteration. This is because the biodiversity of a region is strongly linked to the diversity of habitats, and human activities tend to replace diverse natural habitats with already common agricultural and urban landscapes (Blair 2001, McKinney & Lockwood 2001). Thus, homogenization of terrestrial faunas is a consequence of spatial homogenization followed by range expansions of species adapted to human-created habitats. McKinney & Lockwood (1999) referred to this process as a few winners replacing many losers. Habitat homogenization also plays a role in homogenizing aquatic biotas. The effects of urbanization are similar in streams across North America and include flashier hydrographs, increased nutrients and toxicants, absence of woody debris, and warmer temperatures (Paul & Meyer 2001). As a result, urban streams tend to be dominated by the same suite of pollution tolerant taxa. Also, diverse riverine habitats have been replaced by reservoirs dominated by the same suite of introduced game fishes (Marchetti et al. 2001). Thus the physical convergence of habitats (abiotic homogenization) has facilitated an increase in faunal similarity (biotic homogenization) in many aquatic systems. However, habitat alteration is not always the major cause of biotic homogenization in aquatic systems. Even relatively undisturbed aquatic habitats can harbor many nonnative species as a result of human introductions (Drake & Naiman 2000, Findlay et al. 2000, Lodge et al. 2000a).



Loss of genetic diversity is another aspect of biotic homogenization. Genetic homogenization reduces the ability of species to adapt to changing environmental conditions or new diseases (Allendorf et al. 2001). In many species, there is a large spatial component to genetic variation that is lost when one or a few hatchery stocks are used to replace extirpated populations or supplement declining populations (Allendorf & Leary 1988, Nehlsen et al. 1991). Genetic homogenization is especially a problem for cultured species that are widely distributed into the natural environment through intentional stocking or escapes from aquaculture facilities (Hindar et al. 1991, Beveridge et al. 1994). Also, introduction of genotypes outside of their native range can disrupt native gene pools (Philipp et al. 1993, Bulak et al. 1995). Allendorf et al. (2001) cautioned against the genetic homogenization of trout populations that would occur if a single strain resistant to whirling disease was developed and adopted for widespread stocking throughout North America. In addition to genetic homogenization at the intraspecific level, a similar process can reduce biotic diversity at the species level. Hybridization with introduced species is thought to have been a major factor in the extinction of several fish species in North America and hybridization with introduced rainbow trout currently threatens several native trout species in the southwestern United States (Miller et al. 1989, Rhymer & Simberloff 1996).

## FUTURE TRENDS IN BIOTIC HOMOGENIZATION

The increase in similarity among aquatic ecosystems will continue because the three main drivers of homogenization—species introductions, species extirpations, and habitat alteration—are likely to continue (Vitousek et al. 1997, Ricciardi & Rasmussen 1999, Fuller et al. 1999). An important issue is whether the primary consequence of homogenization will be the addition of new species with relatively minor effects on ecosystems, or mass extinctions of current species and substantial alteration of ecosystems. To date, most studies have shown an increase in biodiversity because the introduction of new species has outpaced extirpation of native species (Hobbs & Mooney 1998, Gido & Brown 1999, Rahel 2000). Additionally, most invaders become integrated without major negative effects (e.g., extirpations) on the communities being invaded. Moyle & Light (1996) felt this was true for most fish assemblages, although they noted important exceptions when the invading species was an effective piscivore such as bass or Nile perch (Kaufman 1992, Jackson 2002). Gido & Brown (1999) found that, in 80% of the drainages across North America, the number of introduced species exceeded the number of extirpated species, indicating a net increase in species richness due to species introductions. Rahel (2000) reported 4.6 introductions for every extirpation among fish faunas of the 48 coterminous United States, again supporting the view that most introductions do not result in extirpations. Griffiths (1997) found that local fish species richness was proportional to regional species richness in North American lakes. He noted that lakes do not appear to be species-saturated, suggesting that new species could be added without eliminating existing species.

Some of the increased biodiversity from homogenization may prove to be transient. Most introductions are relatively recent, and there simply may not have been enough time for the extinction process to complete its course. McKinney (2002) argued this would be the scenario for fish assemblages across the United States because extirpations would outpace introductions in the future. Scott & Helfman (2001) presented a similar scenario for upland streams in the southeastern United States, where biodiversity would initially increase because of invasions by native, downstream species but would eventually decline as endemic upland species were extirpated. These scenarios resemble the process of faunal relaxation that is hypothesized to occur when islands are created from formerly contiguous habitat (Brooks et al. 1999). The islands initially contain more species than predicted by species-areas curves but then slowly lose species until they reach a number more in line with other islands of similar size. We may have inflated the species richness in some habitats through introductions, and the result could be a return to lower levels of richness, albeit with a biota containing many nonindigenous species. Continued habitat alteration also may cause extinctions to outpace introductions as the extinction debt is paid off (Tilman et al. 1994). This seems to be the case for plants on Staten Island, New York. Robinson et al. (1994) documented a net gain of several hundred plant species through 1930, but most of this gain was erased by 1991 by the extinction of hundreds of native species attributable, in part, to habitat loss from urbanization.

Even if most introduced species are relatively harmless, a minority have disastrous effects, and we often lack the ecological knowledge to forecast whether a species will be relatively benign or will cause major environmental harm (Moyle et al. 1986). An important research agenda for conservation biology is determining whether future biodiversity will decrease or increase and how invasion/extinction processes are influenced by the initial species composition of communities, characteristics of the invading species, and the degree of habitat alteration (Moyle & Light 1996, Kolar & Lodge 2001).

## WHAT CAN BE DONE TO REDUCE THE RATE OF BIOTIC HOMOGENIZATION?

What can be done to reduce the rate of biotic homogenization in freshwater habitats? Solutions involve controlling the three factors promoting homogenization: introductions, extinctions, and habitat homogenization. Agency-sponsored introductions have declined in recent years as natural resource managers have gained an awareness of the problems nonnative species can cause (Rahel 1997, Moyle 1999). Sterile hybrids are increasingly used for aquaculture or stocking, which should reduce the risk of nonnative species becoming established (Hindar et al. 1991). We are beginning to take steps to curb inadvertent introductions such as those associated with ballast water release or the pet industry, although regulatory statutes remain weak and enforcement is problematic (Locke et al. 1993, Dextrase & Coscarelli 1999). Most states and provinces regulate the use of crayfish or fish as

bait, and there is an increased awareness of problems caused by bait bucket releases (Litvak & Mandrak 1999, Lodge et al. 2000b). However, illegal introductions remain a problem, and public education about the harmful effects of introduced species (Vashro 1995) or rewards for the identification of violators could help (Kaeding et al. 1996). The U.S. Geological Survey maintains a web site that offers ideas on how to dispose of unwanted pet fish humanely instead of releasing them into local waters (<http://nas.er.usgs.gov/fishes/>).

In addition to preventing new introductions, resource managers also are working to remove naturalized populations of nonnative species prior to reestablishing native species (Bradford et al. 1993, Thompson & Rahel 1996, Young & Harig 2001). In big river systems or large lakes, elimination of nonnatives may not be possible, but controlling their abundance helps in recovery efforts for native species (Tyus & Saunders 2000).

Preventing species extinctions is an ongoing effort (Rahel et al. 1999, Abell et al. 2000). Unfortunately, no fish species have been removed from the U.S. endangered species list because of successful recovery, although several have been removed because they became extinct (Williams et al. 1989, Young & Harig 2001). Because people often do not discriminate between native and nonnative diversity (Brown et al. 1979), resource managers must find ways to promote the appreciation of native taxa. This may be easier to accomplish with bird and mammal species that have more charisma with the public than do most aquatic taxa (Meffe & Carroll 1997). Still, efforts could be made to capitalize on regionally unique organisms. One example is the Cutt-Slam Program of the Wyoming Game and Fish Department. The program is designed to have anglers learn about the four subspecies of cutthroat trout that occur in Wyoming and to develop more appreciation and support for conservation efforts. When an angler catches all four subspecies, s/he is awarded a certificate featuring color pictures of all four subspecies. The program also promotes catch-and-release fishing to prevent mortality of the fish. Such programs encourage the public to discriminate between native and introduced fishes and to appreciate biodiversity even at the subspecies level. Partnering with the fishing public could be an important tool for preservation of native species because anglers can be an important political force.

The third approach for reducing biotic homogenization is to minimize habitat alteration and homogenization. Habitat preservation and rehabilitation is a cornerstone of most species recovery efforts and there is an increasing recognition of the need to deal with habitat issues at larger spatial scales than we have in the past (Angermeier & Schlosser 1995, Poff et al. 1997). For example, the natural-flow paradigm has been proposed as a landscape-level approach for restoring native assemblages in streams and rivers. The idea is that restoring natural flow regimes will favor native species that are better adapted to these conditions than introduced species (Minckley & Meffe 1987, Marchetti & Moyle 2001, Valdez et al. 2001). Removing dams and their associated reservoirs is another ecosystem-level approach to restoring native biodiversity (Fahlund 2000). Removal of a dam from the Milwaukee River in Wisconsin resulted in a switch from a fish assemblage dominated by pollution-tolerant nonnative species that are common in urban

environments across North America to a fish assemblage characterized by regionally distinctive darter and sucker species (Kanehl et al. 1997). Cleaning up pollution also can reverse the effects of biotic homogenization. For example, a reversal of eutrophication in Lake Erie has resulted in a decline in pollution-tolerant exotic species such as common carp and goldfish; recovery of native species such as burbot *Lota lota*, lake whitefish *Coregonus clupeaformis*, and several minnow species and the reappearance of nine aquatic plants species thought to have been extirpated (Stuckey & Moore 1995, Ludsins et al. 2001). Thus habitat rehabilitation through restoration of natural flows, removal of dams, and elimination of pollution can reverse biotic homogenization. Of course, there can never be a complete reversal of biotic homogenization if endemic taxa, such as the blue pike *Stizostedion vitreum glaucum* in Lake Erie, have become globally extinct or nonnatives such as the round goby have established widespread reproducing populations.

## CONCLUSION

Despite progress in dealing with the above issues, it is apparent that during the next 100 years the earth will lose many more species through human-related extinctions than it will gain through the evolutionary creation of new ones. Thus on a global scale, species richness will continue to decline (McKinney & Lockwood 1999). Continued introductions of cosmopolitan species both intentionally and inadvertently likely will continue and may even accelerate with climate change (Leach 1999). The prognosis then is for the continued homogenization of aquatic systems. With greater awareness of the problems, however, and more attention to reducing the rate of both extirpations and introductions, there is hope that the rate of biotic homogenization in freshwater systems can be lessened.

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## LITERATURE CITED

- Abell RA, Olson DM, Dinerstein E, Hurley PT, Diggs JT, et al. 2000. *Freshwater Ecoregions of North America: A Conservation Assessment*. Washington, DC: Island. 319 pp.
- Allendorf FW, Leary RF. 1988. Conservation and distribution of genetic variation in a polytypic species: the cutthroat trout. *Conserv. Biol.* 2:170–84.
- Allendorf FW, Spruell P, Utter FM. 2001. Whirling disease and wild trout: Darwinian fisheries management. *Fisheries* 26(5):27–29.

- Angermeier PL. 1994. Does biodiversity include artificial diversity? *Conserv. Biol.* 8: 600–2
- Angermeier PL, Schlosser IJ. 1995. Conserving aquatic biodiversity: beyond species and populations. *Am. Fish. Soc. Symp.* 17:402–14
- Anthony JL, Downing JA. 2001. Exploitation trajectory of a declining fauna: a century of freshwater mussel fisheries in North America. *Can. J. Fish. Aquat. Sci.* 58:2071–90
- Arthington AH. 1991. Ecological and genetic impacts of introduced and translocated freshwater fishes in Australia. *Can. J. Fish. Aquat. Sci.* 48(Suppl. 1):33–43
- Baltz DM. 1991. Introduced fishes in marine ecosystems and seas. *Biol. Conserv.* 56:151–78
- Baltz DM, Moyle PB. 1993. Invasion resistance to introduced species by a native assemblage of California stream fishes. *Ecol. Appl.* 3:246–55
- Benson AJ, Boydston CP. 1999. Documenting over a century of aquatic introductions in the U.S. See Claudi & Leach 1999, pp. 1–31
- Beveridge MCM, Lindsay GR, Kelly LA. 1994. Aquaculture and biodiversity. *Ambio* 23: 497–502
- Blair BB. 2001. Birds and butterflies along urban gradients in two ecoregions of the United States: Is urbanization creating a homogeneous fauna? See Lockwood & McKinney 2001, pp. 33–56
- Bogan AE. 1993. Freshwater bivalve extinctions (Mollusca:Unionoida): a search for causes. *Am. Zool.* 33:599–609
- Bradford DF, Tabatabai F, Graber DM. 1993. Isolation of remaining populations of the native frog, *Rana muscosa*, by introduced fishes in Sequoia and Kings Canyon National Parks, California. *Conserv. Biol.* 7:882–88
- Brooks TM, Pimm SL, Oyugi JO. 1999. Time lag between deforestation and bird extinction in tropical forest fragments. *Conserv. Biol.* 13:1140–50
- Brown TC, Dawson C, Miller R. 1979. Interests and attitudes of metropolitan New York residents about wildlife. *N. Am. Wildl. Nat. Res. Conf.* 44:289–97
- Brown LR, Moyle PB. 1997. Invading species in the Eel River, California: successes, failures, and relationships with resident species. *Environ. Biol. Fish.* 49:271–91
- Bulak J, Leitner J, Hilbisch T, Dunham RA. 1995. Distribution of largemouth bass genotypes in South Carolina: initial implications. *Am. Fish. Soc. Symp.* 15:226–35
- Claudi R, Leach JH, eds. 1999. *Nonindigenous Freshwater Organisms*. Boca Raton, FL: Lewis
- Contreras-Balderas S. 1999. Annotated checklist of introduced invasive fishes in Mexico, with examples of some recent introductions. See Claudi & Leach 1999, pp. 33–54
- Cooper EL, ed. 1987. *Carp in North America*. Bethesda, MD: Am. Fish. Soc.
- Dermott R, Kerec D. 1997. Changes to the deep-water benthos of eastern Lake Erie since the invasion of *Dreissena*: 1979–1993. *Can. J. Fish. Aquat. Sci.* 54:922–30
- Dextrase AJ, Coscarelli MA. 1999. Intentional introductions of nonindigenous freshwater organisms in North America. See Claudi & Leach 1999, pp. 61–98
- Drake DC, Naiman RJ. 2000. An evaluation of restoration efforts in fishless lakes stocked with exotic trout. *Conserv. Biol.* 14:1807–20
- Duncan JR, Lockwood JL. 2001. Spatial homogenization of the aquatic fauna of Tennessee: extinction and invasion following land use change and habitat alteration. See Lockwood & McKinney 2001, pp. 245–57
- Estes JA, Palmisano JF. 1974. Sea otters: their role in structuring nearshore communities. *Science* 185:1058–60
- Estes JA, Tinker MT, Williams TM, Doak DF. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–76
- Fahlund A. 2000. Reoperation and decommission of hydropower dams: an opportunity for river rehabilitation. See Abell et al. 2000, pp. 117–19
- Findlay CS, Bert DG, Zheng L. 2000. Effect of introduced piscivores on native minnow communities in Adirondack lakes. *Can. J. Fish. Aquat. Sci.* 57:570–80

- Fuller PL, Nico LG, Williams JD. 1999. Non-indigenous fishes introduced into inland waters of the United States. *Am. Fish. Soc. Spec. Publ.* 27
- Gido KB, Brown JH. 1999. Invasion of North American drainages by alien fish species. *Freshw. Biol.* 42:387–99
- Griffiths D. 1997. Local and regional species richness in North American lacustrine fish. *J. Anim. Ecol.* 66:49–56
- Grosholz E. 2002. Ecological and evolutionary consequences of coastal invasions. *Trends Ecol. Evol.* 17:22–27
- Harig AL, Fausch KD, Young MK. 2000. Factors influencing success of greenback cutthroat trout translocations. *N. Am. J. Fish. Manag.* 20:994–1004
- Hector A, Joshi J, Lawler SP, Spehn EM, Wilby A. 2001. Conservation implications of the link between biodiversity and ecosystem functioning. *Oecologia* 129:624–28
- Hill AM, Lodge DM. 1999. Replacement of resident crayfishes by an exotic crayfish: the roles of competition and predation. *Ecol. Appl.* 9:678–90
- Hindar K, Ryman N, Utter F. 1991. Genetic effects of cultured fish on natural fish populations. *Can. J. Fish. Aquat. Sci.* 48:945–57
- Hobbs RJ, Mooney HA. 1998. Broadening the extinction debate: population deletions and additions in California and western Australia. *Conserv. Biol.* 12:271–83
- Holcik J. 1991. Fish introductions in Europe with particular reference to its central and eastern part. *Can. J. Fish. Aquat. Sci.* 48(Suppl. 1):13–23
- Horak D. 1995. Native and nonnative fish species used in state fisheries management programs in the United States. *Am. Fish. Soc. Symp.* 15:61–67
- Hunter ML Jr. 1996. *Fundamentals of Conservation Biology*. Cambridge, MA: Blackwell Sci. 482 pp.
- Jackson DA. 2002. Ecological effects of *Microphterus* introductions: the dark side of black bass. In *Proc. Black Bass 2000 Symp.* ed. DP Philipp, M Ridgeway. Bethesda, MD: Am. Fish. Soc. In press
- Jones CG, Lawton JH, Shachak M. 1994. Organisms as ecosystem engineers. *Oikos* 69:373–86
- Jude DJ, Leach J. 1999. Great Lakes Fisheries. In *Inland Fisheries Management in North America*, ed. CC Kohler, WA Hubert, pp. 623–64. Bethesda, MD: Am. Fish. Soc. 2<sup>nd</sup> ed.
- Kaeding LR, Boltz GD, Carty DG. 1996. Lake trout discovered in Yellowstone Lake threaten native cutthroat trout. *Fisheries* 21(3):16–20
- Kanehl PD, Lyons J, Nelson JE. 1997. Changes in the habitat and fish community of the Milwaukee River, Wisconsin, following removal of the Woolen Mills dam. *N. Am. J. Fish. Manag.* 17:387–400
- Kaufman L. 1992. Catastrophic change in species-rich freshwater ecosystems: the lessons of Lake Victoria. *BioScience* 42:846–58
- Kolar CS, Lodge DM. 2000. Freshwater non-indigenous species: interactions with other global changes. In *Invasive Species in a Changing World*, ed. HA Mooney, RJ Hobbs, pp. 3–30. Washington, DC: Island
- Kolar CS, Lodge DM. 2001. Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* 16:199–204
- Leach JH. 1999. Climate change and the future distribution of aquatic organisms in North America. See Claudi & Leach 1999, pp. 399–400
- Litvak MK, Mandrak NE. 1999. Baitfish trade as a vector of aquatic introductions. See Claudi & Leach 1999, pp. 163–180
- Locke A, Reid DM, van Leeuwen HC, Sprules WG, Carlton JT. 1993. Ballast water exchange as a means of controlling dispersal of freshwater organisms by ships. *Can. J. Fish. Aquat. Sci.* 50:2086–93
- Lockwood JL, Brooks TM, McKinney ML. 2000. Taxonomic homogenization of the global avifauna. *Anim. Conserv.* 3:27–35
- Lockwood JL, McKinney ML, eds. 2001. *Biotic Homogenization*. New York: Kluwer
- Lodge DM. 1993. Biological invasions: lessons for ecology. *Trends Ecol. Evol.* 8:133–37

- Lodge DM, Taylor CA, Holdich DM, Skurdal J. 2000a. Nonindigenous crayfishes threaten North American freshwater biodiversity: lessons from Europe. *Fisheries* 25(8):7–20
- Lodge DM, Taylor CA, Holdich DM, Skurdal J. 2000b. Reducing impacts of exotic crayfishes: new policies needed. *Fisheries* 25(8):21–23
- Ludsin SA, Kershner MW, Blocksom KA, Knight RL, Stein RA. 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. *Ecol. Appl.* 11:731–46
- Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10:689–710
- Marchetti MP, Light T, Feliciano J, Armstrong T, Hogan Z, et al. 2001. Homogenization of California's fish fauna through abiotic change. See Lockwood & McKinney 2001, pp. 259–78
- Marchetti MP, Moyle PB. 2001. Effects of flow regime on fish assemblages in a regulated California stream. *Ecol. Appl.* 11:530–39
- McKinney ML. 2002. Do human activities raise species richness? Contrasting patterns in United States plants and fishes. *Glob. Ecol. Biogeogr. Lett.* 11:343–48
- McKinney ML, Lockwood JL. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14:450–53
- McKinney ML, Lockwood JL. 2001. Biotic homogenization: a sequential and selective process. See Lockwood & McKinney 2001, pp. 1–17
- McMahon TE, Bennett DH. 1996. Walleye and northern pike: boost or bane to northwest fisheries? *Fisheries* 21(8):6–13
- Meffe GK, Carroll CR. 1997. The species in conservation. In *Principles of Conservation Biology*, ed. GK Meffe, CR Carroll, pp. 57–86. Sunderland, MA: Sinauer
- Miller RR, Williams JD, Williams JE. 1989. Extinctions of North American fishes during the past century. *Fisheries* 14(6):22–38
- Mills EL, Leach JH, Carlton JT, Secor CL. 1993. Exotic species in the Great Lakes: A history of biotic crisis and anthropogenic introductions. *J. Great Lakes Res.* 19:1–54
- Minckley WL, Meffe GK. 1987. Differential selection by flooding in stream fish communities of the arid American Southwest. In *Community and Evolutionary Ecology of North American Stream Fishes*, ed. WJ Matthews, DC Heins, pp. 93–104. Norman, OK: Univ. Okla. Press
- Moyle PB. 1999. Effects of invading species on freshwater and estuarine ecosystems. In *Invasive Species and Biodiversity Management*, ed. T Sandlund, PJ Schei, A Viken, pp. 177–91. Dordrecht, The Netherlands: Kluwer
- Moyle PB, Li HW, Barton BW. 1986. The Frankenstein effect: impact of introduced fishes on native fishes of North America. In *The Role of Fish Culture in Fisheries Management*, ed. R Stroud, pp. 415–26. Bethesda MD: Am. Fish. Soc.
- Moyle PB, Light T. 1996. Biological invasions of fresh water: empirical rules and assembly theory. *Biol. Conserv.* 78:149–61
- Nalepa TF, Hartson DJ, Gostenik GW, Fanslow DL, Lang GA. 1996. Changes in the freshwater mussel community of Lake St. Clair: from Unionoida to *Dreissena polymorpha* in eight years. *J. Great Lakes Res.* 22:354–69
- Nehlsen W, Williams JE, Lichatowich JA. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho and Washington. *Fisheries* 16(2):4–21
- Ogutu-Ohwayo R, Hecky RE. 1991. Fish introductions in Africa and some of their implications. *Can. J. Fish. Aquat. Sci.* 48(Suppl. 1): 8–12
- Paul MJ, Meyer JL. 2001. Streams in the urban landscape. *Annu. Rev. Ecol. Syst.* 32:333–65
- Philipp DP, Epifanio JM, Jennings MJ. 1993. Conservation genetics and current stocking practices: Are they compatible? *Fisheries* 18(12):14–16
- Pimental D, Lach L, Zuniga R, Morrison D. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50:53–65

- Poff NL, Allan JD, Bain MB, Karr JR, Prestegard KL, et al. 1997. The natural flow regime: a paradigm for river conservation and restoration. *BioScience* 47:769–84
- Pringle CM, Freeman MC, Freeman BJ. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the new world: tropical-temperate comparisons. *BioScience* 50:807–23
- Radomski PJ, Goeman TJ. 1995. The homogenizing of Minnesota lake fish assemblages. *Fisheries* 20(7):20–23
- Rahel FJ. 1997. From Johnny Appleseed to Dr. Frankenstein: changing values and the legacy of fisheries management. *Fisheries* 22(8):8–9
- Rahel FJ. 2000. Homogenization of fish faunas across the United States. *Science* 288:854–56
- Rahel FJ, Muth RT, Carlson CA. 1999. Endangered species management. In *Inland Fisheries Management in North America*, ed. CC Kohler, WA Hubert, pp. 345–74. Bethesda, MD: Am. Fish. Soc.
- Rhymer JM, Simberloff D. 1996. Extinction by hybridization and introgression. *Annu. Rev. Ecol. Syst.* 27:83–109
- Ricciardi A. 2001. Facilitative interactions among aquatic invaders: Is an “invasional meltdown” occurring in the Great Lakes? *Can. J. Fish. Aquat. Sci.* 58:2513–25
- Ricciardi A, MacIsaac HJ. 2000. Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends Ecol. Evol.* 15:62–65
- Ricciardi A, Neves RJ, Rasmussen JB. 1998. Impending extinctions of North American freshwater mussels (Unionoida) following the zebra mussel (*Dreissena polymorpha*) invasion. *J. Anim. Ecol.* 67:613–19
- Ricciardi A, Rasmussen JB. 1999. Extinction rates of North American freshwater fauna. *Conserv. Biol.* 13:1220–22
- Richter BD, Braun DP, Mendelson MA, Master LL. 1997. Threats to imperiled freshwater fauna. *Conserv. Biol.* 11:1081–93
- Robinson GR, Yurlina ME, Handel SN. 1994. A century of change in the Staten Island flora: ecological correlates of species losses and invasions. *Bull. Torrey Bot. Club* 121:119–29
- Russell GJ. 1999. Turnover dynamics across ecological and geological scales. In *Biodiversity Dynamics: Turnover of Populations, Taxa, and Communities*, ed. ML McKinney, JA Drake, pp. 377–404. New York: Columbia Univ. Press
- Schlosser IJ, Kallemeyn LW. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology* 81:1371–82
- Scott MC, Helfman GS. 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26(11):6–15
- Sheldon AL. 1988. Conservation of stream fishes: patterns of diversity, rarity, and risk. *Conserv. Biol.* 2:149–56
- Simberloff D, Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* 1:21–32
- Snodgrass JW, Meffe GK. 1998. Influence of beavers on stream fish assemblages: effects of pond age and watershed position. *Ecology* 79:928–42
- Stuckey RL, Moore DL. 1995. Return and increase in abundance of aquatic flowering plants in Put-In-Bay Harbor, Lake Erie, Ohio. *Ohio J. Sci.* 95:261–66
- Taylor CA, Warren ML Jr, Fitzpatrick JF Jr, Hobbs HH III, Jezerinac RF, et al. 1996. Conservation status of crayfishes of the United States and Canada. *Fisheries* 21(4):25–38
- Thompson PD, Rahel FJ. 1996. Evaluation of depletion-removal electrofishing of brook trout in small Rocky Mountain streams. *N. Am. J. Fish. Manag.* 16:332–39
- Tilman D. 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80:1455–74
- Tilman D, May RM, Lehman CL, Nowak MA. 1994. Habitat destruction and the extinction debt. *Nature* 371:65–66
- Townsend CR, Winterbourn MJ. 1992. Assessment of the environmental risk posed by



- an exotic fish: the proposed introduction of channel catfish (*Ictalurus punctatus*) to New Zealand. *Conserv. Biol.* 6:273–82
- Tyus HM, Saunders JF III. 2000. Nonnative fish control and endangered fish recovery: lessons for the Colorado River. *Fisheries* 25(9):17–24
- Valdez RA, Hoffnagle TL, McIvor CC, McKinney T, Leibfried WC. 2001. Effects of a test flood on fishes of the Colorado River in Grand Canyon, Arizona. *Ecol. Appl.* 11:686–700
- Vashro J. 1995. The “bucket brigade” is ruining our fisheries. *Montana Outdoors* 26(5):34–37
- Vermeij GJ. 1991. When biotas meet: understanding biotic interchange. *Science* 253:1099–1104
- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth’s ecosystems. *Science* 277:494–499
- Warren ML Jr, Burr BM, Walsh SJ, Bart HL Jr, Cashner RC, et al. 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. *Fisheries* 25(10):7–31
- Williams JD, Warren ML Jr, Cummings KS, Harris JL, Neves RJ. 1993. Conservation status of freshwater mussels of the United States and Canada. *Fisheries* 18(9):6–22
- Williams JE, Johnson JE, Hendrickson DA, Contreras-Balderas S, Williams JD, et al. 1989. Fishes of North America endangered, threatened, or of special concern: 1989. *Fisheries* 14(6):2–20
- Yachi S, Loreau M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. USA* 96:1463–68
- Young MK, Harig AL. 2001. A critique of the recovery of greenback cutthroat trout. *Conserv. Biol.* 15:1575–84

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## ERRATA

An online log of corrections to *Annual Review of Ecology and Systematics* chapters may be found at <http://ecolsys.annualreviews.org/errata.shtml>