conservation **feature**

# Native Invasions, Homogenization, and the Mismeasure of Integrity of Fish Assemblages

**ABSTRACT**

Human activities, particularly habitat destruction and species introductions, are resulting in increased homogenization of once unique biogeographic regions. In the southeastern United States, extensive endemism occurs among highland fish species that have specialized ecologies, are adapted to cool, clear, nutrient-poor conditions, and are sediment-intolerant. Highland streams flow into lower elevation systems, which are often inhabited by more widespread, generalist fish species adapted to warmer, more turbid, fine-sediment-rich, and nutrient-rich conditions. Common land use practices, such as deforestation, degrade stream habitats and reduce habitat diversity, which is often correlated with taxonomic and ecological diversity. Habitat homogenization can thus cause assemblage homogenization via loss of native species and addition of nonindigenous species. However, midpoints in the homogenization process may be characterized by constant or even increased species diversity because generalist, sediment-tolerant, "native" species invade from downstream areas. Perusal of a species list for a river system would not reveal such invasions because lists seldom discriminate between upstream and downstream assemblages in a drainage. Traditional metrics often used in biological assessment, such as species richness ($\alpha$ diversity) and evenness, should not include invasive species, whether native or exotic. Greater attention should be paid to the actual species present and their ecological requirements, and to changes in overlap in species occurrence among regions. Aquatic ecosystem integrity can degrade despite apparent increases in species diversity.

**Mark C. Scott**
**Gene S. Helfman**

Mark C. Scott is a Ph.D. candidate and Gene S. Helfman is a professor of ecology at the Institute of Ecology, University of Georgia, Athens, GA 30602. Scott can be contacted at mscott@sparc.ecology.uga.edu. Helfman can be reached at helfman@sparc.ecology.uga.edu.

*As cosmopolitan species invade more and more regions, regional biotas are homogenized and lose their distinctness—a "mongrelization" of the global landscape. This process of homogenization is one of the most prominent forms of biotic impoverishment worldwide.*

—Meffe and Carroll (1997: 298)

Increasing attention is being given to the homogenization of the world's faunas and floras (Vitousek et al. 1997; Bright 1998). This growing concern reflects the realization that a small number of plant and animal species are being spread through human activities and are replacing regionally unique organisms in a "world-wide pooling of faunas and floras" (Leopold 1949: 217). The result is an overall loss of diversity and destruction of the distinct components that define biogeographic regions (Mooney 1998). Transported invasive species are often characterized as weedy, tolerant, generalist, and cosmopolitan. The process by which they invade frequently involves habitat destruction prior to human introduction (Moyle and Leidy 1992). A common endpoint is replacement of unique, endemic, often specialized, native species by widespread, nonindigenous generalists. Hence at the level of both habitats and species, unique elements are displaced and eventually replaced by common, widespread elements.

Concern over homogenization has focused primarily on terrestrial systems, particularly plants and birds (e. g., Office of Technology Assessment 1993; Lockwood et al. 2000). In North America, native birds have disappeared and have been widely replaced by European species such as starlings and English sparrows. Among plants, Scotch broom, purple loosestrife, and kudzu are well documented invaders. Aquatic systems have received less attention, with the exception of the widespread impacts of nuisance species such as Asian clam, zebra mussel, hydrilla, and water hyacinth. Less publicized but no less alarming is replacement and homogenization among marine invertebrates and algae (e. g., Carlton 1996).

Homogenization of fish assemblages has received comparatively little treatment (Sheldon 1988; Radomski and Goeman 1995). Most recently, Rahel (2000) analyzed homogenization in North American fish assemblages, concluding that homogenization among state faunas is extensive and that it occurs primarily as the result of deliberate introductions of a small group of relatively cosmopolitan species that are useful to humans. These papers, as well as most treatments of introductions, invasions, and homogenization, emphasize species that have been introduced deliberately or accidentally by humans. Concern over homogenization has focused on human-caused habitat degradation and its role in setting the stage for invasion, with humans actively transporting and introducing nonindigenous (foreign, alien, exotic, or transplanted) species.

Our work with stream fishes in the southern Appalachian region suggests that the process of homogenization includes intermediate steps that also involve habitat degradation and replacement of endemic species. However, this replacement initially involves invasion by *native* species, a process that may lead at first to no change or even an increase in species richness (e.g., Meffe and Carroll 1997). Because of stable or increased native diversity, which is usually viewed as a positive indicator of ecosystem integrity, biotic degradation is less likely to be noticed and warning signs of the eventual demise of unique elements in the fauna may be overlooked.

## Diversity of the southeastern United States ichthyofauna

Species richness is measured in several ways, the most common being α and β diversity: α diversity is the number of species in a defined, localized region, and β diversity is the turnover in species occurrence across habitats within a region (Meffe and Carroll 1997). Both the α and β diversity of the southeastern United States are exceptionally high. The α fish diversity of the region is estimated at 609 species (Warren et al. 2000), which is considered the richest fish diversity of any temperate freshwater region (e.g., Lydeard and Mayden 1995). Contributing to high diversity among fishes and other aquatic taxa is a high degree of habitat diversity at both regional and local scales (Warren et al. 1997; Angermeier and Winston 1999). At least 51 major river drainages occur across the southern landscape. These rivers were not exposed to Pleistocene glaciation and therefore have a long history of isolation and relative stability, allowing sufficient time for distinct faunas to evolve (Swift et al. 1986; Warren et al. 2000). Local endemism contributes to the high β diversity of the area. Overall, 28% of southern fishes occur in only 1 drainage, and 37 of the 51 identified drainages have at least 1 unique taxon (Warren et al. 2000). Darters (Percidae) and minnows (Cyprinidae) make up the majority (69%) of endemic species. Of the 223 recognized (described and under description) species and subspecies of southeastern darters in the genera *Ammocrypta*, *Etheostoma*, and *Percina*, 108 (48%) occupy only a single river drainage, and an additional 24 (11%) occur in only 2 drainages (Warren et al. 2000, discounting areas of intergradation). Among 198 cyprinid taxa, 31 (16%) are restricted to a single drainage and 22 (11%) are restricted to 2 drainages. Almost 60% of southeastern darter taxa and more than 25% of minnow taxa are restricted to 1 or 2 drainage systems (Warren et al. 2000).

In highland regions, many of these endemics occur in relatively small, clear, cool, high-gradient streams. Many are benthic-dependent, imperiled species of darters (Etnier and Starnes 1993; Jenkins and Burkhead 1994; Burkhead et al. 1997). Highland streams typically contain a large variety of habitats (riffles, runs, torrents, chutes, waterfalls, woody debris, small and large pools), are naturally shaded by extensive riparian vegetation, flow over cobble or gravel substrates, and are characterized by low primary and moderate secondary production. In contrast, the larger rivers into which creeks and small rivers flow are often more turbid, warmer, more nutrient rich, less shaded, and have higher total productivity. They also contain a different mix of habitat types dominated by long runs and deep pools that are more depositional, with sandier or silt-laden bottoms (Wallace et al. 1992; Allan 1995; Grubaugh et al. 1997).

The fish faunas of highland and lowland regions differ taxonomically and ecologically. In the eastern United States, highlands are the chief domain of the regional endemics, many of which are imperiled (Warren and Burr 1994; Warren et al. 1997, 2000). Lower elevation streams and rivers across the Southeast typically share many species; although endemics occur in lower drainages, β diversity appears to be lower relative to highland regions. For example, 2 basins draining the southern Appalachian highlands (upper Tennessee and Coosa-Tallapoosa systems) contain 31 unique taxa (Warren et al 1997). In contrast, the coastal plain drainages of the Atlantic Slope from the Tar-Neuse to the Ogeechee-Altamaha contain only 13 unique taxa, and 7 unique taxa occur in the coastal plain tributaries draining to the Mississippi River in western Tennessee and Mississippi. The Gulf drainages are somewhat richer in endemic forms than other southeastern lowlands, with 20 unique species occurring in 7 drainages from the Suwannee-Aucilla-Ochlockonee rivers to the Pearl River system (Warren et al. 1997). Mayden (1987) analyzed the freshwater ichthyofauna of eastern North America and categorized many species as either restricted highland endemics versus more widespread, cosmopolitan, and often lowland dwellers (Figure 1). Most highland species can be characterized as relative feeding, breeding, and habitat specialists dependent on drifting or rock-associated aquatic insects for food and on clean, rocky bottoms for spawning. Widespread species are relative generalists, feeding on insects as well as zooplankton, detritus, or plant resources, and spawning in a greater variety of habitats. Larger piscivores increase in number and diversity in downstream

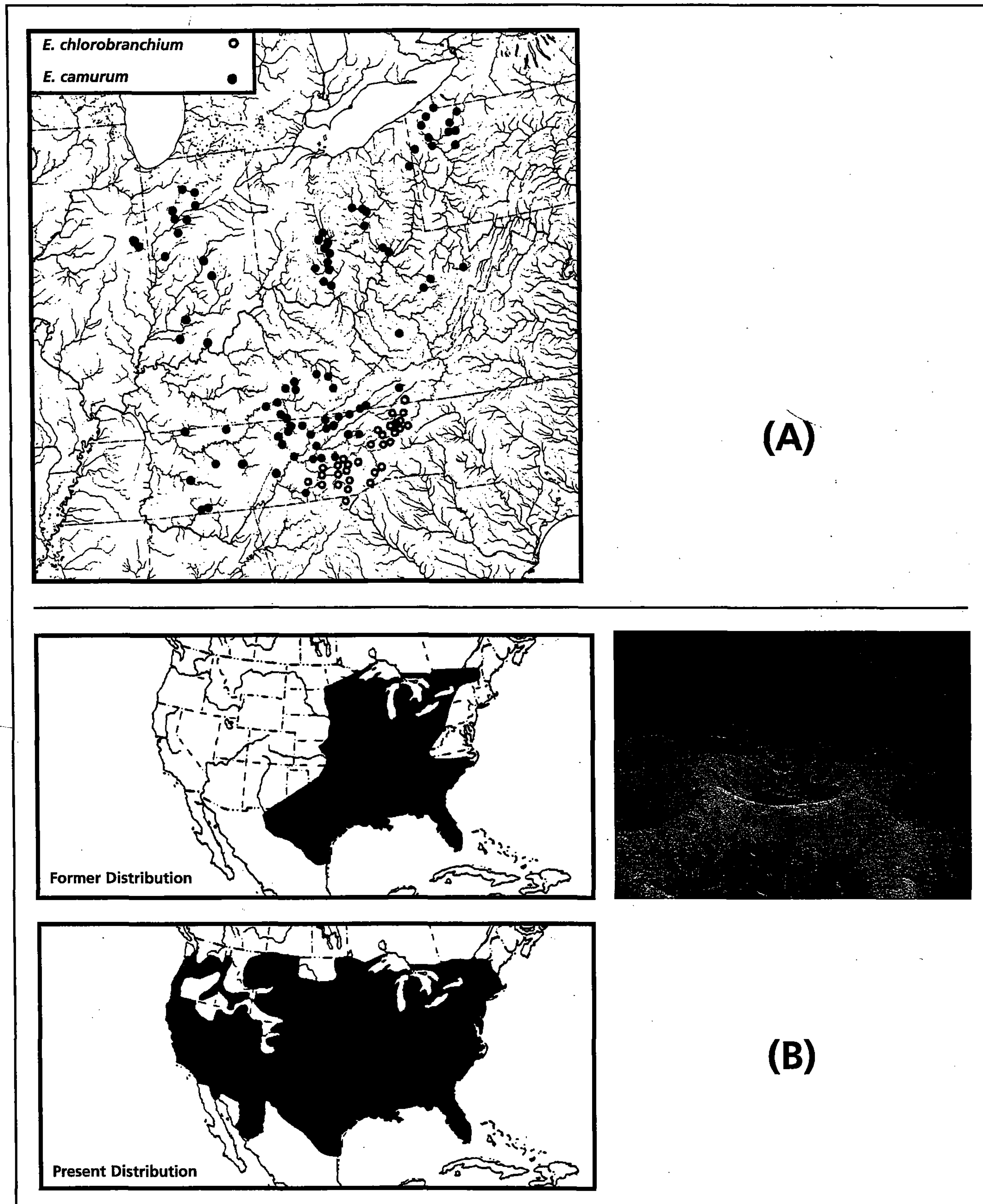



**Figure 1.** Representative highland endemic and relatively cosmopolitan species (as classified by Mayden 1987), and their respective distributions. (A) greenfin darter (*Etheostoma chlorobranchium*). This species (open circles on map) is restricted to creeks and small rivers of the upper Tennessee drainage of primarily North Carolina and Tennessee, where it occurs in riffle habitats; photo by J. DeVivo; (B) bluegill sunfish (*Lepomis macrochirus*). This species is native to much of eastern North America, where it occurs in a variety of stream, river, pond, and lake habitats. It has been successfully introduced over a much wider area; photo by G. Helfman. Distributional maps reproduced from Lee et al., 1980, *Atlas of North American Freshwater Fishes* (courtesy NC Museum of Natural Sciences).

areas (Schlosser 1982; Matthews 1998). Although α diversity increases downstream in most riverine systems, upstream and downstream areas in relatively undisturbed rivers generally have distinct components in their resident fish assemblages (Matthews 1998; Angermeier and Winston 1999).

## Land use, stream habitats, and effects on fishes

Habitat degradation in southeastern streams results often from poor land use practices, chiefly removal of forest to facilitate crop planting, cattle grazing, silviculture, and residential and urban development. The strongest effects are experienced when riparian vegetation is removed. These practices increase erosion and sediment transport into streams and decrease shading of riparian zones, which in turn elevates stream temperatures, increases turbidity, and increases nutrient inputs from direct application of fertilizer and from wastes generated by high densities of humans and livestock. Removal of riparian vegetation also leads to changes in stream morphology as streams typically widen and become shallower (Waters 1995; Roth et al. 1996).

Importantly, riparian deforestation has been linked to reduced diversity of stream habitats. Streams subjected to extensive riparian or upland deforestation demonstrate loss of riffle and shallow pool areas, increased sediment transport and deposition, and increased embeddedness of riffles (Jones et al. 1999; Meyer et al. 1999). The entire process can be summarized as one of habitat homogenization: cool, allochthonous-dominated, upland streams with high habitat diversity are progressively transformed into warmer streams with fewer habitat types, more fine sediments in both the water column and on the stream bed, more nutrients, and higher productivity. Without a change in slope, aspect, or altitude, deforestation transforms upland streams functionally into lower elevation streams (see also Marchetti et al. 2001).

Not surprisingly, altered physical conditions affect the composition of fish assemblages (Berkman and Rabeni 1987; Harding et al. 1998; Jones et al. 1999). Most fish species endemic to southern Appalachian highlands are characterized as preferring relatively cold water (Etnier and Starnes 1993; Jenkins and Burkhead 1994); they would be expected to suffer following deforestation-caused elevation of stream temperatures. In addition, homogenization of habitats appears to promote the loss of stream specialists (Boet et al. 1999). Sediment-intolerant species that are dependent on benthic resources for feeding and that deposit eggs in the interstices between rocks decrease in relative abundance. This group includes many darters, sculpins, and some benthic-spawning minnows, such as the spotfin chub (*Erimonax monacha*), federally listed as threatened. Fishes that increase in relative abundance are generally sediment-tolerant species that often feed in the water column. If they spawn on the bottom, they typically keep their nests clean of sediment (e.g., sunfishes, nest-guarding *Nocomis* chubs). Faunal replacement and homogenization occur when highland endemics with narrow geographic ranges are replaced by species that are relatively widespread in distribution and that often inhabit lower elevation areas.

The impact of land use practices on fish assemblages and homogenization has been evident in our analyses of fish diversity as a function of land disturbing activities (Scott and Helfman, unpublished manuscript). We sampled fishes using backpack shockers at 36 3rd-to-5th-order stream sites in the Little Tennessee and French Broad rivers of the upper Tennessee River system, between 1995 and 1998 (see Jones et al. 1999; Scott unpublished manuscript for methodological details). We then correlated species diversity with intensity of land use based on geographic information system (GIS) coverages for 1993. Land use intensity was calculated as the sum of (1) the percent of each watershed at each site that had been deforested, plus (2) the density of buildings in the watershed (number of buildings per ha) normalized to the maximum value, plus (3) the density of roads in the watershed (km of roads per ha) normalized to the maximum value. All land use measures were weighted equally.

If all species at all 36 sites are considered, no statistical relationship is evident between diversity, measured as richness or evenness, and intensity of land use (richness, $r = 0.10$, $P = 0.8$; Shannon-Wiener H', $r = 0.22$, $P = 0.2$). However, if the fauna is separated into highland endemics and relatively cosmopolitan species (Table 1), a very different pattern emerges (Figure 2). The relative abundance of highland endemics decreases and that of cosmopolitan species increases as a function of increasing human impact. The nearly reciprocal values for the two groups at any point along the scale of land use intensity explains why no relationship exists when the two ecological groups are lumped together. In essence, two fish faunas are involved that have almost opposite responses to the suite of habitat characteristics that accompany human activity.

**Table 1.** Endemic, highland versus relatively cosmopolitan, often lower elevation species of southeastern fishes found in small (3rd to 5th order) streams of the Little Tennessee and French Broad river basins. Designations are based on Mayden (1987). Value in parentheses is the number of river drainages in which each species occurs throughout the Southeast as a measure of distributional extent of highland versus widely-distributed species (based on Warren et al. 2000).

**ENDEMIC HIGHLAND SPECIES**
($\bar{x}$ = 3.3 drainages/species)

CYPRINIDAE
*Clinostomus funduloides* ssp., smoky dace (1)
*Erimystax insignis eristigma,* mountain blotched chub (1)
*Luxilus coccogenis,* warpaint shiner (5)
*Notropis leuciodus,* Tennessee shiner (9)
*N. rubricroceus,* saffron shiner (4)
*N. spectrunculus,* mirror shiner (3)
*Phenacobius crassilabrum,* fatlips minnow (1)

SALMONIDAE
*Salvelinus fontinalis,* brook trout (14)[a]

COTTIDAE
*Cottus bairdi* ssp., smoky sculpin (5)

PERCIDAE
*Etheostoma blennioides gutselli,* Tuckasegee darter (1)
*E. chlorobranchium,* greenfin darter (1)
*E. rufilineatum,* redline darter (3)
*E. swannanoa,* Swannanoa darter (1)
*E. vulneratum,* wounded darter (1)
*Percina evides* ssp., Appalachian gilt darter (1)
*P. squamata,* olive darter (2)

**WIDELY DISTRIBUTED SPECIES**
($\bar{x}$ = 29.5 drainages/species)

CYPRINIDAE
*Hybopsis amblops,* bigeye chub (12)
*Nocomis micropogon,* river chub (11)
*Notemigonus crysoleucas,* golden shiner (51)
*Notropis lutipinnis,* yellowfin shiner (6)
*N. photogenis,* silver shiner (8)
*Carassius auratus,* goldfish[b]
*Rhinichthys atratulus,* blacknose dace (15)[c]
*Semotilus atromaculatus,* creek chub (42)

CATOSTOMIDAE
*Catostomus commersoni,* white sucker (24)
*Hypentelium nigricans,* northern hog sucker (35)
*Moxostoma duquesnei,* black redhorse (22)
*M. erythrurum,* golden redhorse (27)

ICTALURIDAE
*Ameiurus melas,* black bullhead (36)
*A. natalis,* yellow bullhead (51)

POECILIIDAE
*Gambusia affinis,* western mosquitofish (34)

CENTRARCHIDAE
*Ambloplites rupestris,* rock bass (20)
*Lepomis auritus,* redbreast sunfish (37)
*Lepomis cyanellus,* green sunfish (47)
*Lepomis macrochirus,* bluegill sunfish (51)
*Micropterus salmoides,* largemouth bass (51)

PERCIDAE
*Etheostoma zonale,* banded darter (17)
*Perca flavescens,* yellow perch (23)

[a] widely introduced as a game fish; native distribution enigmatic
[b] nonindigenous
[c] often found in highlands, particularly where fine sediment is abundant (W. McLarney, Little Tennessee Waershed Association, Franklin, TN, pers. comm.)

Changes in assemblage structure following disturbance do not necessarily require active invasion. Habitat change induced by anthropogenic activities may simply increase the suitability of highland regions for cosmopolitan species that are indigenous to the highlands but that are normally present in low numbers (e. g., blacknose dace [*Rhinichthys atratulus*] and creek chub [*Semotilus atromaculatus*] occur in our forested reference samples, unpublished data). At the same time, habitat suitability for endemic highland species is decreased and their populations undergo a concomitant decline. The result is a marked shift in assemblage structure as relatively "weedy" species thrive and more sensitive endemics become rare. The relative influences of dispersal versus in situ replacement on assemblage structure and homogenization can only be determined if we have knowledge of the distribution and abundance of species prior to disturbance.

Four observations emerge from our analyses. First, land disturbing activities, particularly deforestation, lead to a homogenization of stream habitats (Scott et al. unpublished). Second, invasion of highland regions is not necessarily by exotic species introduced by humans but instead may be by native species that normally occur in downstream regions. Third, at least initially, highland stream conditions change sufficiently to facilitate the establishment of widespread native invaders while remaining hospitable to upland endemics, but supporting them in reduced numbers (Jones et al. 1999). The result is that native invasions first lead to no change in diversity and perhaps even an increase in diversity. Increased species richness has been found in a variety of aquatic systems subject to invasions (Courtenay and Moyle 1996; Gido and Brown 1999; Rahel 2000). Fourth, measuring native diversity alone, without accounting for a possible disruption of natural distribution patterns as may occur following upstream migrations by native invaders, is an unreliable and potentially misleading indicator of the integrity of a fish assemblage. Methods for assessing the integrity or conservation value of aquatic habitats—such as the Index of Biotic Integrity (IBI, Karr et al. 1986) and Index of Centers of Diversity (ICD, Winston and Angermeier 1995)—recognize the importance of discounting nonindigenous species, but they do not directly account for native invasions. Separation of a fauna into tolerant and intolerant species, as is often done in an IBI, is a potential but indirect means of correcting for native invasions.

## Mechanisms, trends, and future scenarios

Several factors may promote invasion by and establishment of cosmopolitan invaders in upland areas, especially biological differences in foraging and spawning interacting with sediment inputs. Many highland endemics are benthic feeders that spawn on clean, rocky bottoms and whose evolutionary histories may not prepare them for dealing with excess sedimentation. Land-disturbing activities often result in increased erosion and run-off, and removal of riparian vegetation additionally causes continued mobilization of sediments stored in a stream's banks. Replacement/invader species from downstream regions are generally more tolerant of turbid or silty conditions (Berkman and Rabeni 1987; Meyer et al. 1999; Jones et al. 1999). Deforestation would therefore set the stage for invasion because of increased sediment inputs and elevated temperatures, and reversion to pre-disturbance conditions appears to be difficult if habitats do not improve overtime (Harding et al. 1998).

Two trends raise concern for the future of regional endemism among southeastern fishes and other taxa. These trends involve the impact of homogenization-via-native-invasion as a function of urbanization, and the apparent time course and endpoints of homogenization where it has already taken place. Although logging and agriculture will contribute to the process, urbanization is the major land use change predicted for many upland locales throughout the southern Appalachians (Wear and Bolstad 1998). A commonly observed practice during urbanization is the removal of riparian vegetation as development increases along stream and river courses. Our evidence suggests that deforestation of riparian and upland regions and its attendant cumulative impacts on habitats in receiving aquatic ecosystems is a major contributor to homogenization.

Because local endemics by definition have small geographic ranges, they are more extinction prone (Meffe and Carroll 1997). This in itself accelerates the process of homogenization: diversity is lost as extinction-prone taxa are eliminated because their habitats are altered. Their former habitats are, however, still inhabitable by fishes, but only by more disturbance-tolerant taxa, including species already present but rare. Invasion is most likely by wide-ranging species (McKinney 1997), or by the weedy species that are most frequently transported by humans. At extremes of habitat destruction and human introduction, a common set of introduced species is likely to occupy a wide range of conditions and locales. This scenario is evident in many places in the southwestern United States, and also in much of western Europe where the same list of 14 introduced species can be found in many countries, and where they often dominate the fauna (Lever 1996; Marchetti et al. 2001). An important aspect of this scenario of disturbance, introduction, and replacement is that it appears to include invasion by native species in its initial stages (Figure 3), suggesting that such invasion should be recognized as an early warning sign of the homogenization process.

## Conclusions

*We are...selecting for a world full of plant and animal weeds that are best adapted for human-created environments.*

—Bruton (1995:11)

First, we concur with authors who emphasize the problematic value of using diversity as a measure of system integrity (e. g., Angermeier 1994; Bianco 1995; Moyle and Marchetti 1999). Previous authors have emphasized the inaccuracy contributed by including nonindigenous species. We add to this concern the observation that native invaders further inflate diversity scores and mislead conservation practitioners. Native invaders are likely to be overlooked because they typically occur on species lists for an area, which misrepresents which species belong where. Few such lists discriminate between upstream and downstream assemblages. Such lists thus provide an inaccurate picture of the assemblages to be expected in different stream reaches. If a stream survey mistakenly includes invading cosmopolitan species as a component of local diversity because of their "native" status, their potential invasive impact is likely to be underestimated. To paraphrase Fuller et al. (1999:12), we should not assume that "introduction of a species into an adjacent watershed [or upstream region] poses a less serious threat than establishment of a foreign species in the same system."

Second, our findings emphasize the need for ecological and behavioral knowledge of the species in an assemblage. Because of the wealth of infor-

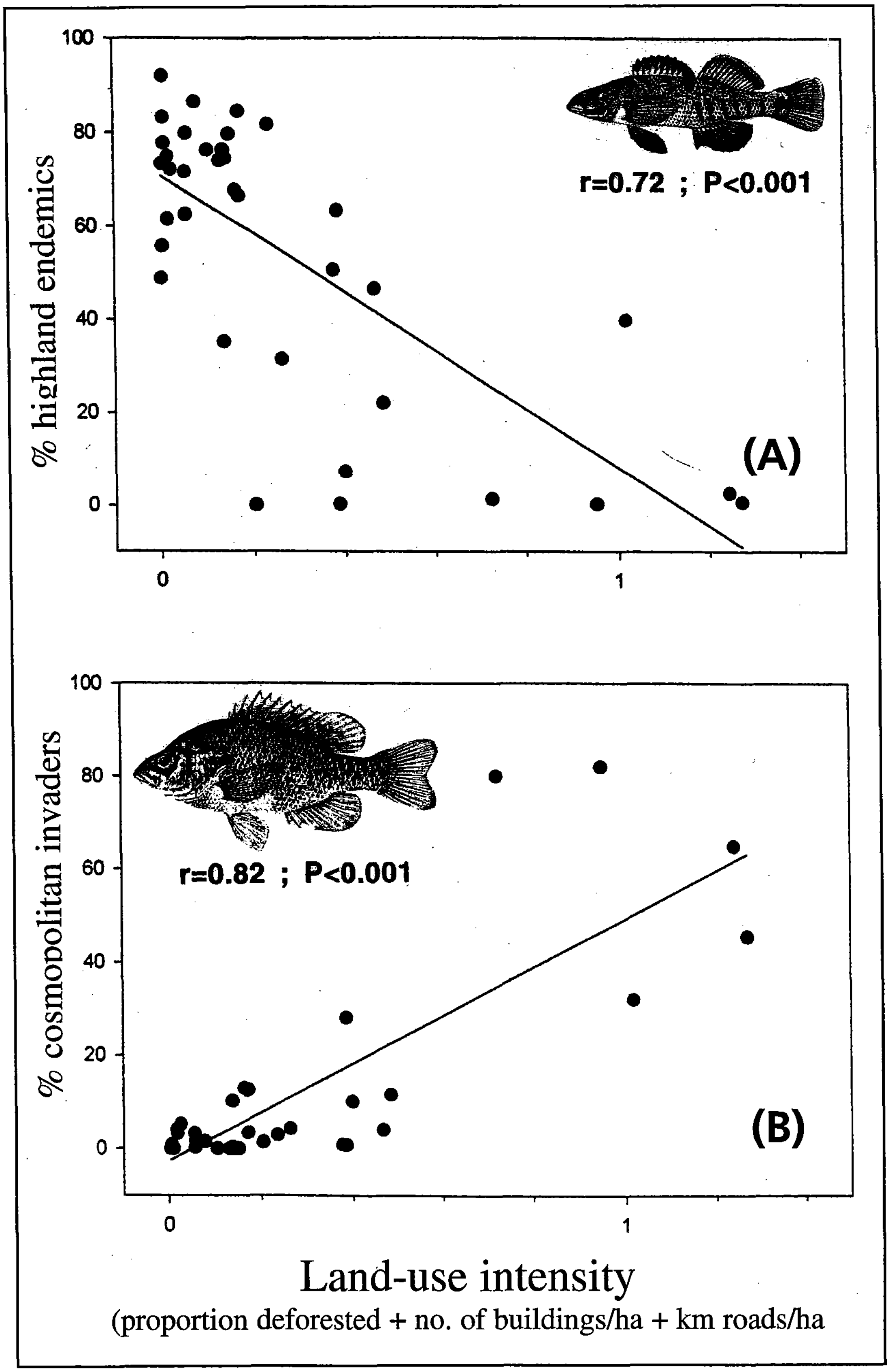



**Figure 2.** Relative abundance of (A) highland endemic versus (B) cosmopolitan fish species as a function of land use intensity at 36 sites in the Little Tennessee and French Broad river basins. Highland endemics decrease and cosmopolitan species increase with increasing land use intensity. Land use intensity was calculated as the sum of the deforested proportion + number of buildings per ha + km of roads per ha in each watershed. Line drawings from Tomelleri and Eberle (1990); used with permission.

mation available on the taxonomy, biogeography, ecology, and behavior of southeastern fishes, we were able to classify species not only into taxonomic and zoogeographic categories but also into feeding and breeding guilds. This sensitized us to possible interactions among habitat, sediment, feeding, and breeding. Without knowledge of important life history and biological attributes, we would have had to rely primarily on measures of diversity and abundance and would not have detected the changes that appear to be taking place within our study area. Because of the multidisciplinary nature of any conservation-oriented investigation, studies of basic biology, ecology, and behavior must be encouraged and supported.

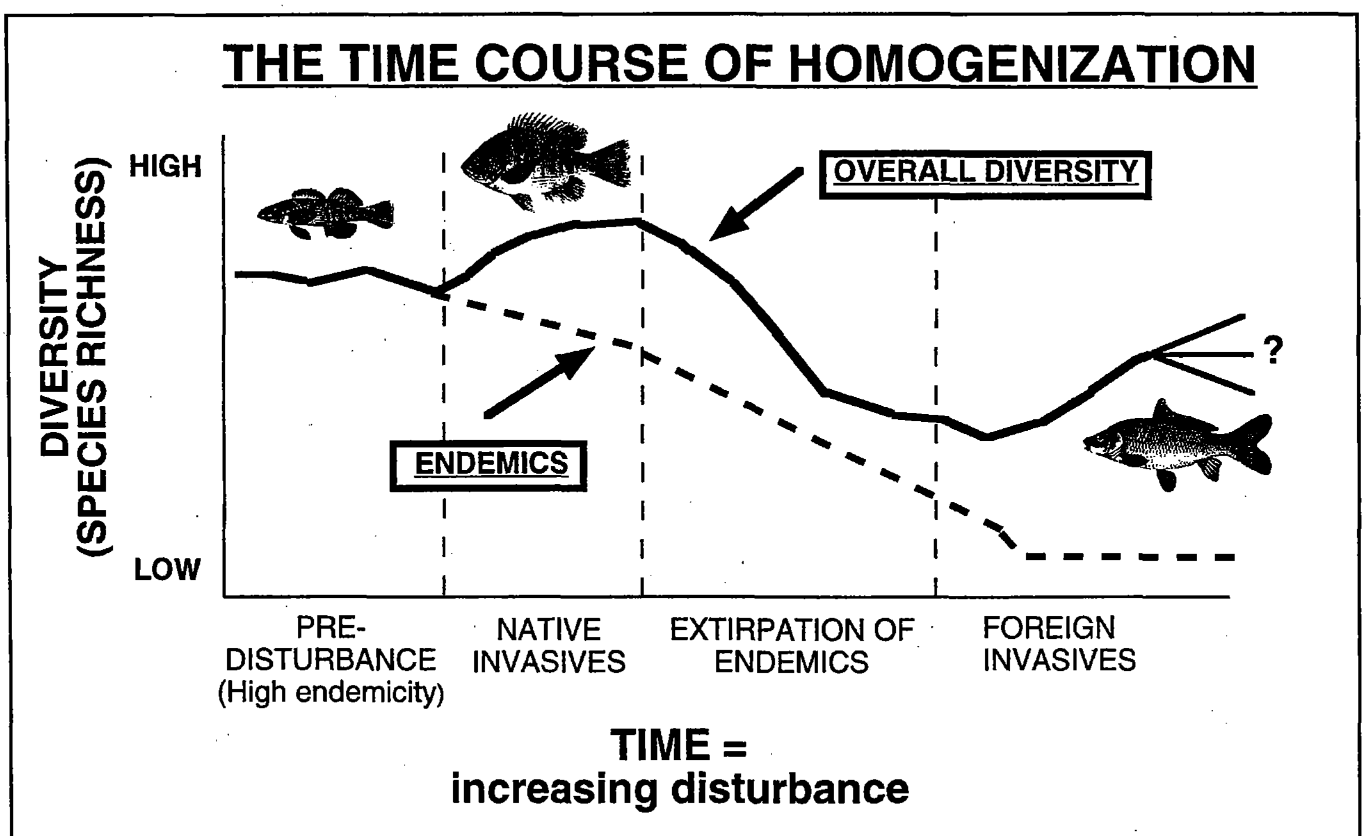
Finally, homogenization can result first from a loss of β diversity before any loss in α diversity occurs (e. g., Radomski and Goeman 1995). Measuring α diversity alone tells us little about the integrity of assemblages and regions, whereas decreases in β diversity (e.g., increases in species overlap between regions) indicate that homogenization is occurring. Calculations of β diversity, such as those provided in Hocutt and Wiley (1986) and Sheldon (1988), provide a baseline against which future changes in fish faunas can be tracked. More attention should therefore be paid to β diversity because of its value as an indicator of deteriorating conditions, especially as a metric of growing homogenization.



## Acknowledgments

We thank W. Matthews and J. Meyer for providing important background literature, P. Bolstad and N. Gardiner for GIS assistance, and P. Angermeier, M. Freeman, K. Leftwich, W. McLarney, J. Meyer, T. Reinert, D. Walters, M. Warren, and an anonymous reviewer for commenting on earlier drafts of the manuscript. This research was supported by NSF Grant DEB-9632854 to the University of Georgia Coweeta Long Term Ecological Research Program.

**Figure 3.** Postulated time course over which homogenization occurs in highland streams with increasing watershed disturbance. Diversity is high initially with a strong contribution from regional, specialist, endemic species. After initial disturbance, such as moderate deforestation in the southern Appalachian region, losses among endemic species are balanced or may be outweighed by invasion of native, generalized, cosmopolitan species. Some invaders migrate from downstream regions into the increasingly homogenized highland habitats. With continued disturbance, upland streams become uninhabitable by highland endemics and even by some cosmopolitan species, but all may eventually be replaced by widespread, introduced exotics. Deliberate introduction of exotic predators at any point can accelerate the loss of native species. Fish drawings from Tomelleri and Eberle (1990); used with permission.



## References


**Allan, J. D.** 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London.

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

**Angermeier, P. L.,** and **M. R. Winston.** 1999. Characterizing fish community diversity across Virginia landscapes: prerequisite for conservation. Ecological Applications 9:335-349.

**Berkman, H. E.,** and **C. F. Rabeni.** 1987. Effect of siltation on stream fish communities. Environmental Biology of Fishes 18:285-294.

**Bianco, P. G.** 1995. Alien introductions, chief elements of native freshwater fish degradation and use of indices and coefficients as an example to quantify the situation existing in Italy. Pages 175-198 *in* D. P. Philipp et al., eds. Protection of aquatic biodiversity. Proceedings of the World Fisheries Congress, Theme 3. Oxford & IBH Publishing Co, New Delhi.

**Boet, 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.

**Bright, C.** 1998. Life out of bounds: bioinvasion in a borderless world. W. W. Norton., New York.

**Bruton, M. N.** 1995. Have fishes had their chips? The dilemma of threatened fishes. Environmental Biology of Fishes 43:1-27.

**Burkhead, N. M., S. J. Walsh, B. J. Freeman,** and **J. S. Williams.** 1997. Status and restoration of the Etowah River, an imperiled southern Appalachian ecosystem. Pages 375-444 *in* G. W. Benz and D. E. Collins, eds. Aquatic fauna in peril: the southeastern perspective. Southeast Aquatic Research Institute Special Publication 1. Lenz Design and Communications, Decatur, GA.

**Carlton, J. T.** 1996. Pattern, process, and prediction in marine invasion ecology. Biological Conservation 78:97-106.

**Courtenay, W. R., Jr.,** and **P. B. Moyle.** 1996. Biodiversity, fishes, and the introduction paradigm. Pages 239-252 *in* R. C. Szaro and D. W. Johnston, eds. Biodiversity in managed landscapes: theory and practice. Oxford University Press, New York.

**Etnier, D. A.,** and **W. C. Starnes.** 1993. The fishes of Tennessee. University of Tennesee Press, Knoxville.

**Fuller, P. L., L. G. Nico,** and **J. D. Williams.** 1999. Nonindigenous fishes introduced into inland waters of the United States. American Fisheries Society Special Publication 27.

**Gido, K. B.,** and **J. H. Brown.** 1999. Invasion of North American drainages by alien fish species. Freshwater Biology 42:387-399.

**Grubaugh, J. W., J. B. Wallace,** and **E. S. Houston.** 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. Freshwater Biology 37:581-596.

**Harding, J. S. , E. F. Benfield, P. V. Bolstad, G. S. Helfman,** and **E. B. D. Jones III.** 1998. Stream biodiversity: the ghost of land-use past. Proceedings of the National Academy of Sciences, United States 95:14843-14847.

**Hocutt, C. H.,** and **E. O. Wiley, eds.** 1986. The zoogeography of North American freshwater fishes. J. Wiley and Sons, New York.

**Jenkins, R. E.,** and **N. M. Burkhead.** 1994. Freshwater fishes of Virginia. American Fisheries Society, Bethesda, MD.

**Jones, E. B. D., III, G. S. Helfman, J. O. Harper,** and **P. V. Bolstad.** 1999. The effects of riparian deforestation on fish assemblages in southern Appalachian streams. Conservation Biology 13:1454-1465.

**Karr, J. R., K. D. Fausch, P. L. Angermeier, P. R. Yant,** and **I. J. Schlosser.** 1986. Assessing biological integrity in running waters: a method and its rationale. Illinois Natural History Survey, Special Publication 5, Champaign.

**Lee, D. S., C. R. Gilbert, C. H. Hocutt, R. E. Jenkins, D. E. McAllister,** and **J. R. Stauffer Jr.** 1980. Atlas of North American freshwater fishes. North Carolina Biological Survey, North Carolina State Museum of Natural History, Publication Number 1980-12.

**Leopold, A.** 1949. A Sand County almanac and sketches here and there. Oxford University Press, New York.

**Lever, C.** 1996. Naturalized fishes of the world. Academic Press, San Diego, CA.

**Lockwood, J. L., T. M. Brooks,** and **M. L. McKinney.** 2000. Taxonomic homogenization of the global avifauna. Animal Conservation 3:27-35

**Lydeard, C.,** and **R. L. Mayden.** 1995. A diverse and endangered aquatic ecosystem of the southeast United States. Conservation Biology 9:800-805.

**Marchetti, M. P., T. Light, J. Felicano, T. Armstrong, Z. Hogan,** 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, eds. Biological homogenization. Kluwer Plenum/Academic Press, New York.

**Matthews, W. J.** 1998. Patterns in freshwater fish ecology. Chapman and Hall, New York.

**Mayden, R. L.** 1987. Historical ecology and North American highland fishes: a research program in community ecology. Pages 210-222 *in* W.J. Matthews and D. C. Heins, eds. Community and evolutionary ecology of North American stream fishes. University of Oklahoma Press, Norman.

**McKinney, M. L.** 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495-516.

**Meffe, G. K.,** and **C. R. Carroll.** 1997. Principles of conservation biology, second edition. Sinauer Associates, Inc., Sunderland, MA.

**Meyer, J. L., A. Sutherland, K. Barnes, D. Walters,** and **B. Freeman.** 1999. A scientific basis for erosion and sedimentation standards in the Blue Ridge physiographic province. Pages 321-324 *in* K. J. Hatcher, ed. Proceedings 1999 Georgia Water Resources Conference. University of Georgia, Athens.

**Mooney, H. A.** 1998. The globalization of ecological thought. Excellence in ecological thought 5. Ecology Institute, Luhe, Germany.

**Moyle, P. B.,** and **R. A. Leidy.** 1992. Loss of biodiversity in aquatic ecosystems: evidence from fish faunas. Pages 127-169 *in* P. L. Fiedler and S. K. Jain , eds. Conservation biology: the theory and practice of nature conservation, preservation and management. Chapman and Hall, New York.

**Moyle, P. B.,** and **M. P. Marchetti.** 1999. Application of indices of biotic integrity to California streams and watersheds. Pages 367-380 *in* T. P. Simon, ed. Assessing the sustainability and biological integrity of water resources using fish communities. CRC Press, Boca Raton, FL.

**Office of Technology Assessment, U. S. Congress.** 1993. Harmful non-indigenous species in the United States. U.S. Government Printing Office, OTA-F-565, Washington, D.C. (see www.invasivespecies.gov).

**Radomski, P. J., and T. J. Goeman.** 1995. The homogenizing of Minnesota lake fish assemblages. Fisheries 20(7):20-23.

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

**Roth, N. E., J. D. Allan, and D. L. Erickson.** 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11:141-156.

**Schlosser, I. J.** 1982. Fish community structure and function along two habitat gradients in a headwater stream. Ecological Monographs 52:395-414.

**Sheldon, A. L.** 1988. Conservation of stream fishes: patterns of diversity, rarity, and risk. Conservation Biology 2:149-156.

**Swift, C. C., C. R. Gilbert, S. A. Bortone, G. H. Burgess, and R. W. Yerger.** 1986. Zoogeography of the freshwater fishes of the southeastern United States: Savannah River to Lake Pontchartrain. Pages 213-265 *in* C. H. Hocutt and E. O. Wiley, eds. The zoogeography of North American freshwater fishes. John Wiley and Sons, New York.

**Tomelleri, J. R., and M. E. Eberle.** 1990. Fishes of the central United States. University Press of Kansas, Lawrence.

**Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo.** 1997. Human domination of Earth's ecosystems. Science 277:494-499.

**Wallace, J. B., J. R. Webster, and R. L. Lowe.** 1992. High-gradient streams of the Appalachians. Pages 133-191 *in* C.T. Hackney, S.M. Adams, and W.H. Martin, eds. Biodiversity of the southeastern United States: aquatic communities. John Wiley & Sons, New York.

**Warren, M. L., and B. M. Burr.** 1994. Status of freshwater fishes of the United States: overview of an imperiled fauna. Fisheries 19(1):6-18.

**Warren, M. L., P. L. Angermeier, B. M. Burr, and W. R. Haag.** 1997. Decline of a diverse fish fauna: patterns of imperilment and protection in the southeastern United States. Pages 105-164 *in* G. W. Benz and D. E. Collins, eds. Aquatic fauna in peril: the southeastern perspective. Southeast Aquatic Research Institute Special Publication 1. Lenz Design and Communications, Decatur, GA.

**Warren, M. L., and 11 others.** 2000. Diversity, distribution, and conservation status of the native freshwater fishes of the southern United States. Fisheries 25(10):7-31.

**Waters, T. F.** 1995. Sediment in streams: sources, biological effects and control. American Fisheries Society, Bethesda, MD.

**Wear, D. N., and P. V. Bolstad.** 1998. Land-use changes in southern Appalachian landscapes: spatial analysis and forecast evaluation. Ecosystems 1:575-594.

**Winston, M. R., and P. L. Angermeier.** 1995. Assessing conservation value using centers of population density. Conservation Biology 9:1518-1527.