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# Landscape determinants of nonindigenous fish invasions *

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**Abstract**

Much has been written about the influence of exotic or nonindigenous species on natural habitats and communities of organisms, but little is known of the physical or biological conditions that lead to successful invasion of native habitats and communities by exotics. We studied invasivity factors in headwater streams of the Susquehanna River West Branch, which drains portions of the northern Appalachian Plateau. A replicated (two major tributaries) $3 \times 3$ factorial design was used to determine landscape effects of size (stream order) and quality (land use) on abiotic (physical and chemical) and biotic (fish community structure and function) stream attributes. Seven (21%) of thirty-four fish species (brown trout, common carp, mimic shiner, bluegill, smallmouth bass, fantail darter, and banded darter) collected in the eighteen streams sampled were nonindigenous to the basin. Watershed size (stream orders 1, 3, and 5) significantly affected stream geomorphologic and habitat variables (gradient, width, depth, current velocity, diel water temperature, bank overhang, canopy cover, and woody debris density) but not water-quality variables, while land use in watersheds (conservation, mining, and agriculture) significantly affected measured water-quality variables (alkalinity and concentrations of manganese, calcium, chloride, nitrate, and total dissolved solids) but not stream physical or habitat quality. Both watershed size and land use affected fish-community variables such as presence of particular species, species density, species diversity, tolerance diversity, and mean fish size, but in both cases the effect was transparent to native-origin status of fish species. No relationships were found between occurrence of nonindigenous species in watersheds and trophic structure or functional diversity. Therefore, the hypothesis that reduced species diversity increases vulnerability to nonindigenous species was not supported. However, the spatial variation associated with both water-quality and habitat-quality factors was greater in streams with mixed (those with nonindigenous species) than with exclusively native assemblages. These findings suggest that the mechanism for successful invasion by nonindigenous or exotic species is through change in water or habitat quality associated with human or natural disturbances, such as agriculture and mining activities in watersheds. Biotic factors appear to play no or a lesser role in the invasibility of northern Appalachian lotic systems.

## Introduction

Biodiversity in North America is threatened directly or indirectly by human disturbances such as land-use practices (deforestation, agriculture, mining, and urbanization), overharvest of native species, and alien species introductions (Ehrlich and Wilson 1991). Aquatic biodiversity is particularly at risk because watersheds often concentrate the effects of large numbers of people (Wilcove 1993). Over a third of North American freshwater fishes are now rare, at risk of extinction, or extinct (Master 1990; Master et al. 1998). The extinction rate for this group has doubled in the past century (Miller et al. 1989; Wilcove et al. 1992) and is predicted to increase six-fold in the next (Ricciardi and Rasmussen 1999). Most extinctions (74%) involved physical habitat alteration, followed by exotic species (68%), chemical changes or pollution (38%), overharvesting (15%), or some combination of these factors (Miller et al. 1989).

The mechanisms by which exotic or introduced species have caused declines or losses are not always clear. The stocking of alien species (Moyle et al. 1986) and unintentional transfers (Welcomme 1984; Allan and Flecker 1993) have lead to native species declines through a number of abiotic and biotic processes. Ross (1991) found native faunas especially vulnerable to exotic species after human disturbance or when initially depauperate. Biotic interactions, including competition and predation, were important in structuring such assemblages. Baltz and Moyle (1993) found predation to be the most important biotic process limiting exotic species invasions in California stream fishes. Scoppettone (1993) identified predation on native fish larvae as likely the mechanism of native fish decline in a Colorado River tributary. Competition for space was implicated in the success of exotic salmonids in northwest coastal streams (Volpe et al. 2001). Introduced diseases and parasites have also adversely affected native fish faunas (Courtenay and Moyle 1992; LoVullo and Stauffer 1993). Communities with low species richness are thought to be more invasible (Vermeij 1991). Reduced species diversity may increase invasibility by increasing available limiting resources, whether biotic or abiotic (Stachowicz et al. 1999; Tilman 1999). Among abiotic factors, the effect of temperature on competitive ability has been identified as a determinant of native species displacement in western streams (Taniguchi et al. 1998). In many lotic systems, especially California streams, abiotic factors such as the match between an invading fish's spawning requirements and the hydrologic regime are critical to its success (Baltz and Moyle 1993; Moyle and Light 1996; Brown and Moyle 1997).

Though stream size (and its covariates stream order, discharge, and drainage area) has an obvious effect on fish species richness (Newall and Magnuson 1999; Jackson et al. 2001), its relation to exotic invasivity is not known. Zalewski and Naiman (1985) suggested that streams dominated by 'abiotic regulation' exhibit highly fluctuating reproductive success and inefficient introduction of new fish species due to catastrophic mortality. The river continuum concept (Vannote et al. 1980) suggests longitudinal variation in both faunal energy sources and trophic complexity. However, experimental studies using test panels or plots in natural environments suggest that species-rich communities more completely and efficiently use available limiting resources, thus better resisting invasion by exotic species (Stachowicz et al. 1999; Tilman 1999). Landscape factors and land use within watersheds are increasingly understood to play important roles in aquatic impoverishment and ichthyofaunal losses (Larsen et al. 1986; Frissell 1993; Angermeier 1995; Richards et al. 1996; Wallace et al. 1997). Of principal concern in northern Appalachia are the effects of agriculture (Brenner et al. 1991; Richards et al. 1993; Wohl and Carline 1996) and stream acidification due to precipitation or mine-drainage (CEQ 1981; Pinder and Morgan 1995; Starnes and Gasper 1995; Heard et al. 1997). Little is known of the relationship between land-use change in watersheds and exotic species invasivity.

Due to the growing importance of nonindigenous species in freshwater ecosystems and the paucity of information on colonization mechanisms in freshwater streams of varying sizes, we studied the upper reaches of a major river draining eastern slopes of the Appalachian Mountains to address these concerns. Nonindigenous fishes currently inhabiting some of these streams include two salmonids (brown trout, *Salmo trutta*, and rainbow trout, *Oncorhynchus mykiss*), three cyprinids (goldfish, *Carassius auratus*; common carp, *Cyprinus carpio*; and mimic shiner, *Notropis volucellus*), two centrarchids (bluegill, *Lepomis macrochirus*, and smallmouth bass, *Micropterus dolomieu*), two darters (fantail, *Etheostoma flabellare*, and banded, *Etheostoma zonale*), and walleye (*Stizostedeon vitreum*). Species such as smallmouth bass, though popular as a sportfish and economically significant for some communities, have been shown to cause food-web shifts with severe consequences for native species and ecosystems (Vander Zanden et al. 1999; Whittier and Kincaid 1999; Findlay et al. 2000; MacRae and Jackson 2001).

Our objectives in this study were to determine (1) landscape effects of both scale (stream order or watershed size) and quality (land use) on habitat quality, water quality, and fish community structure, (2) differential effects of landscape factors on native and nonindigenous fishes, and (3) the relative importance of biotic and abiotic factors to the potential for nonindigenous fishes to invade northcentral Appalachian streams. We further sought to test the following specific hypotheses relating to nonindigenous fish invasions in northcentral Appalachian streams:

$H_1$: Type of land use in watershed (forest conservation, mining, or agriculture) affects fish communities and their ability to resist invasion by nonindigenous fishes,

$H_2$: Biotic factors are more important than abiotic to the invasion potential of nonindigenous fishes in northcentral Appalachian streams, and

$H_3$: Low-order (headwater) streams are more susceptible to invasion by nonindigenous species than high-order streams due to reduced species diversity and potentially increased available limiting resources.

Hypotheses were tested both directly and indirectly through analysis of spatial variation in land use, stream size, habitat quality, water quality, and fish community relations. Temporal variability (dynamics of the invasion process, such as rates of invasion success and failure) was not used to achieve objectives in this study. In addition, sociological and historical factors related to non-native introductions, such as stocking and bait-fish releases, while potentially important, are beyond the scope of this study (Lodge 1993). We assume that these invasion factors led to success (incorporation of a ‘permanent’ breeding population into the existing native community of fishes) only in proportion to what natural (abiotic and biotic) and anthropogenic stream conditions would allow. Our general approach was to determine effects of stream size and land use on either abiotic (water and habitat-quality variables) or biotic (fish community composition, diversity indices, and trophic structure) components of stream ecosystems, then to test for differential response by native and nonindigenous species.

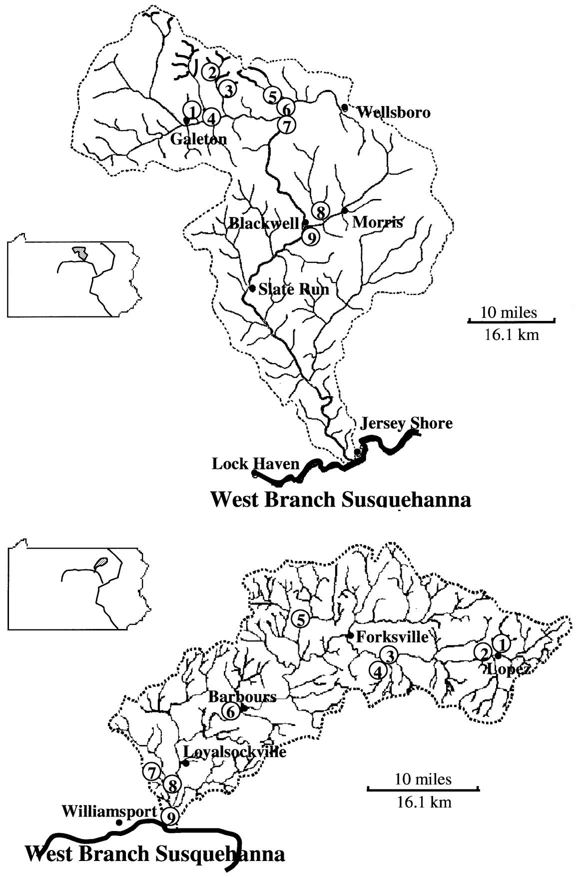


*Figure 1.* Map of Pine Creek and Loyalsock Creek watersheds. Sample sites are shown and abbreviated with nominal land-use categories (HQ, MD, and AG are forested, mine-influenced, and agriculturally influenced streams, while 1, 3, and 5 are nominal stream orders) as follows: (1) HQ1, (2) MD1, (3) AG1, (4) HQ3, (5) MD3, (6) AG3, (7) HQ5, (8) MD5, and (9) AG5.

## Methods

### *Study site*

We studied 5th- and 6th-order drainages that are freestone (sensu Waters 2000) tributaries of the Susquehanna River West Branch in the northern Appalachian Plateau and northcentral Appalachian ecoregions (Omernik 1995) of Pennsylvania at elevations of 152–549 m. Pine Creek (41°15–45′ N, 77°15–45′ W), with a mainstem length of 137 km, drains 2540 km$^2$, while Loyalsock Creek (41°15–30′ N, 76°15′–77°00′ W), 100 km long, drains 1279 km$^2$ (Figure 1). Both streams maintain notable coldwater trout fisheries and drain significant forested (both public and privately owned), mine-impacted, and agricultural landscapes. Pine Creek is a proposed national and legislated state Wild and Scenic River, while 69 km of Loyalsock Creek are registered on the Nationwide Rivers Inventory program of the National Park Service with some federal protection. Further details of the geology, hydrology, and biology of the streams are available (DER 1989; Hughey 1991, 1992).

*Study design*

We sampled stream segments appropriate for testing the effect of two independent variables, stream order and land use, on all water-chemistry, habitat quality, and fish-community variables in a $3 \times 3$ block design. Replicated in each basin (Pine and Loyalsock Creeks), the total number of stream segments sampled was 18. Three stream sizes (1st or 2nd, 3rd or 4th, and 5th or 6th order; nominally hereafter 1st, 3rd, and 5th order or headwaters, midreaches, and riverine) and three land-use categories (forest conservation, mine-influenced, and agricultural) guided our choice of stream segments to sample. We used USGS 1 : 24,000-scale topographic maps and state lists of streams with special protection and usage (Commonwealth of Pennsylvania 1992) to compile candidate streams for each land-use category without numeric criteria. Candidates were further pared in discussion with state environmental and fishery managers. Streams were field checked for suitability and accessibility. Maptech®[1] (Maptech, Inc., Greenland, New Hampshire) software was used to quantify principal land uses for each selected watershed, using the routing function, in order to gauge how well actual land use above selected stream segments matched nominal land-use categories (Table 1). Analyses of variance showed significant or nearly significant effects of nominal land-use category for all three actual land uses (ideally significant in all cases) and significant effects of stream order only in the case of actual mining land use (ideally no significant effects). Though interaction between stream order and land use occurred and mine-influenced and agricultural land uses represented less than half the area of their nominal categories, we assumed these land uses have the potential to substantially influence stream abiotic and biotic conditions.

Segment lengths of at least 100 m with at least two repeating geomorphic channel units (riffle-pool sequences) were identified for sampling; such criteria are generally recognized to yield representative ichthyofaunal samples (Karr 1981; Leonard and Orth 1986; Maret et al. 1997). Given the magnitude of 5th order streams relative to 1st order, species sampling efficiency was probably influenced by stream order with this protocol, a source of error partially offset by the much larger areas (3 times) and number of individual fish (nearly 2 times) sampled in 5th versus 1st order streams. Sampling was conducted in June and July 1995.

*Table 1.* Percentage of watersheds, classified by stream order and land use, whose areas were found to be forested (Forest), mine-influenced (Mine), or agriculturally influenced (Agriculture) on USGS 7.5-min topographic maps.

| Designated stream order | Designated land use category | Actual land use (% of surface area) | | | |
|---|---|---|---|---|---|
| | | Forest[a] | Mine[b] | Agriculture[c] | Total |
| 1 | HQ | 98.6 | 0.0 | 0.6 | 99.2 |
| | MD | 48.1 | 6.8 | 45.0 | 99.9 |
| | AG | 36.6 | 0.0 | 63.4 | 100.0 |
| | $\bar{\chi}$ | 61.2 | 2.3 | 36.3 | |
| 3 | HQ | 76.4 | 0.2 | 23.4 | 100.0 |
| | MD | 68.6 | 0.8 | 30.7 | 100.1 |
| | AG | 68.1 | 0.0 | 31.8 | 99.9 |
| | $\bar{\chi}$ | 71.1 | 0.3 | 28.7 | |
| 5 | HQ | 76.1 | 0.2 | 23.8 | 100.1 |
| | MD | 79.0 | 0.7 | 20.3 | 100.0 |
| | AG | 73.8 | 0.1 | 26.1 | 100.0 |
| | $\bar{\chi}$ | 76.3 | 0.3 | 23.9 | |
| Mean | HQ | 83.7 | 0.1 | 15.9 | 99.7 |
| | MD | 65.3 | 2.8 | 32.0 | 100.1 |
| | AG | 59.5 | 0.1 | 40.4 | 100.0 |
| | $\bar{\chi}$ | 69.5 | 1.0 | 29.4 | |

Designated or nominal land-use categories are forested-conservation (HQ), mine-influenced (MD), and agriculturally influenced (AG). Numeric entries are the means of replicate observations from Pine and Loyalsock creeks.

[a] *Forest ANOVA*: Stream order (SO): $F_{2,9} = 2.01$, $P = 0.190$; Land use (LU): $F_{2,9} = 3.77$, $P = 0.065$; SO × LU: $F_{4,9} = 2.58$, $P = 0.109$.

[b] *Mine ANOVA*: Stream order (SO): $F_{2,9} = 5.16$, $P = 0.032$; Land use (LU): $F_{2,9} = 43.63$, $P = 0.0001$; SO × LU: $F_{4,9} = 13.15$, $P = 0.001$.

[c] *Agriculture ANOVA*: Stream order (SO): $F_{2,9} = 0.08$, $P = 0.926$; Land use (LU): $F_{2,9} = 6.04$, $P = 0.022$; SO × LU: $F_{4,9} = 4.02$, $P = 0.039$.

*Field sampling and laboratory analysis*

*Water quality.* Water pH, dissolved oxygen (DO), and total dissolved solids (TDS) were measured on-site using a Checkmate®[1] modular testing system (Corning, Inc., Corning, New York). Water samples were collected into 1-l Nalgene®[1] polyethylene bottles, iced en route to laboratory facilities in Wellsboro, Pennsylvania, then refrigerated at 2.2 °C until analysis. We measured alkalinity within 24 h of sample collection according to APHA (1985) titration method 403. Calcium, magnesium, manganese, and iron were measured by atomic absorption spectrophotometry (Instrumentation Laboratory model 551, Levington, Massachusetts) by aspiration directly into an air–acetylene flame. Sulfate, nitrate, chloride, and phosphate were measured by ion chromatography according to the methods of APHA (1989) using a Dionex®[1] model DX300 system (Dionex Corporation, Sunnyvale, California).

*Fish communities.* Fish communities were sampled by stream order sequentially (all 1st, all 3rd, then all 5th order streams, rather than all forested, then all mined, then all agricultural streams) to minimize potential sampling bias with land use over the 2-month sampling period. Reduced discharge, the most likely temporal source of bias associated with stream order, was minimized by sampling low-order streams earliest in the season. A sampling team of four people (shocker, two netters, and fish length/data recorder) collected fish from the entire segment using electrofishing techniques. A backpack electrofisher (Smith–Root[1] model 12, Vancouver, Washington) set to deliver direct current in gaited bursts was used at voltages ranging from 600 to 900 depending on stream conductivity. Segments were fished in an upstream direction in single passes without blocking nets (except for 5th order pools), whose usefulness in species richness estimates of streams is negligible under most circumstances (Simonson and Lyons 1995). Only fish >2.5 cm total length (TL) were collected and fish of uncertain identity were retained in 15% buffered formalin solution. Upon capture and identification, sampled fish were measured to the nearest mm of TL and immediately returned to the stream behind the capture zone.

*Habitat assessment.* Habitat quality was assessed after fish community sampling. We measured or scored the following geomorphic or physical habitat variables at transects 10 m apart for the length of each segment: habitat type; stream width; stream depth, current velocity, substrate type, and relative surface turbulence at each of three equidistant points across the transect; percent bank overhang; percent emergent vegetation zone; and woody debris density. Water velocity was measured at mid-depth with a current meter (Marsh–McBirney®[1] model 201D, Gaithersburg, Maryland). Substrate type was scored (1, particulate organic matter, to 7, bedrock) on a modified Wentworth ranked scale (Orth et al. 1981). Relative surface turbulence was scored 0, 1, or 2 (0 = glassy, 1 = moderate visual aberration, 2 = surface turbulence or 'white water'). We calculated woody debris density ($D$) as:

$$D = \sum_{i=1}^{n} A_i / w_s d_{\bar{x}}$$

where $A_i$ is the cross-sectional area, derived from measured stem diameter, of each woody stem crossing the transect line underwater; $w_s$ is the wetted stream width, and $d_{\bar{x}}$ is the mean stream depth. In addition, stream segment gradient was determined as the mean of three or more clinometer measurements along the entire segment, each of which was recorded as the average of three successive readings. We measured percent canopy cover with a spherical densiometer at three equidistant points along the segment length and calculated the average. Water temperature was recorded hourly with instream data loggers (Optic Stow Away Temp logger, Onset Computer Corporation, Bourne, Massachusetts) over a single 24-h period simultaneously for all 18 streams and the mean calculated for each stream.

*Data analysis.* We used SAS (1987) to perform our statistical testing with significance at the $P \leq 0.05$ level. The study design itself was tested to ensure the 18 stream segments were assigned to appropriate land-use categories. Effects of stream order (SO) and land use (LU) on water quality, habitat quality, and fish assemblages were determined followed by an analysis of the effects of water quality and habitat quality on the fish assemblages. Finally, we examined how changes in water quality and habitat quality among the three land-use categories may account for the presence of nonindigenous species.

Stream assignments were tested (i.e., 'were the streams correctly categorized by land use?', not 'what were the effects of land use?') by two-way analysis of variance (ANOVA) using two replicates in a 3 × 3 block design with SO and LU as class variables. The test variable was the arcsine-transformed proportion of each drainage basin calculated to be forested-conservation (HQ), mine-influenced (MD), or agriculturally influenced (AG). Using digital topographical maps, drainage basin and sub-basin areas were determined using the route function by outlining the entire drainage as well as forested, strip-mined, and agricultural areas. Proportions of each land-use category were obtained by dividing each land-use area by the entire drainage area. Each drainage basin of the 18 stream segments was considered to be the area upstream of the furthest downstream sampling point.

Cluster analysis was used in a preliminary examination of abiotic and biotic variables to determine relationship to the three types of land use and levels of stream order. We used a variable cluster analysis to look for hydrogeochemical linkages in water quality data. Here water-quality variables were clustered, with each site an observation. Fish assemblages were analyzed with average linkage cluster analysis using presence/absence data and Jaccard's similarity coefficients (in this case sites were clustered). With this technique clusters that developed early in the analysis represented the most similar fish communities (least root mean square distance). Giving equal importance to rare and common species in presence/absence analyses was considered justified due to the sampling of only single sites on each stream. Effects of SO and LU on each of 22 abiotic metrics (11 water quality and habitat quality each) were tested using two-way ANOVA. Data were first analyzed as a $3 \times 3$ factorial of stream order and land use replicated across two drainages (total $n = 18$) using the general linear models procedure of the Statistical Analysis System (SAS 1988). If no significant ($P > 0.05$) interaction was detected between stream order and land use using this analysis, stream order and land use were analyzed as independent variables blocked within drainage. Differences in treatment means were detected using the Waller/Duncan multiple range test (SAS 1988). Fisher's exact tests were then used to examine the effects of SO and LU on the presence and absence of each fish species in $2 \times 3$ contingency tables.

The Shannon–Wiener diversity index (Shannon and Weaver 1949) was used to calculate species ($H_s$), trophic or functional ($H_f$), and tolerance ($H_t$) diversity as response variables to landscape factors. Trophic and tolerance diversities were calculated using generally accepted trophic and tolerance designations for each species (e.g. Halliwell et al. 1999). Where clearly conflicting designations were found from multiple sources in the literature, species were assigned to the class 'other'. ANOVA was used to test the effects of SO and LU on each of the three diversity metrics plus fish density (individuals/$m^2$) and a biomass surrogate (sum of total lengths/$m^2$). We also examined the effect of removing nonindigenous fishes from all samples on changes in both functional diversity ($H_f$) and the number of trophic levels represented by remaining native fishes using ANOVA (for $H_f$) and the Wilcoxon rank sum test (for number of trophic levels).

Principal components analysis was used with water and habitat quality data to compare the distribution of streams containing nonindigenous species to those with exclusively native species in relation to variation in environmental factors. With this technique sites were oriented in environmental-factor space.

## Results

### *Stream characterization*

*Abiotic attributes.* The 18 stream segments sampled ranged in length from 80 (5th order) to 200 (1st and 3rd order) m and in area from 328 (1st order) to 2622 (5th order) $m^2$. Sampled areas for 1st, 3rd, and 5th order streams averaged 682, 1651, and 2056 $m^2$, respectively.

Water-quality variables ranged as follows: pH = 5.2–8.3, alkalinity = 2–85 mg/l, sulfate = 3.8–35.7 mg/l, calcium = 1.5–19.5 mg/l, magnesium = 0.5–3.8 mg/l, manganese = 0.001–0.139 mg/l, nitrate = 1.4–11.5 mg/l, chloride = 0.3–15.2 mg/l, and iron = 0.004–0.054 mg/l. These chemical variables separated into two distinct groups in variable cluster analysis among the 18 streams, with cluster 1 consisting of pH, alkalinity, sulfate, calcium, and magnesium and cluster 2 of nitrate, chloride, and iron.

Mean stream values for the 11 geomorphic or physical habitat variables ranged as follows: segment gradient = 0.6 (5th order) to 4.3 (1st order) degrees, stream width = 1.7 (1st order) to 25.3 (5th order) m, stream depth = 0.1–0.4 m, current velocity = 0.1–0.6 m/s, diel water temperature = 14.3–23.8 °C, substrate particle size = gravel/rubble-cobble/boulder, surface turbulence = 0.3–1.0 (ranks 0, 1, 2), bank overhang = 0.5–9.7%, canopy cover = 6.4–97%, instream vegetation zone = 0–3.1%, and woody debris density = 0–5.0% (Figure 2). Most habitat variables showed relationship to stream order but not land use.

*Fish community attributes.* We collected 34 fish species representing eight families from the 18 stream segments sampled (Table 2). Seven of these (brown trout, common carp, mimic shiner, bluegill, smallmouth bass, fantail darter, and banded darter), or 21% of species, were nonindigenous to the Susquehanna River basin (Cooper 1983). Species with the highest frequencies of occurrence by stream were blacknose dace (*Rhinichthys atratulus*) (13 of 18 streams); white sucker (*Catostomus commersoni*) (12); longnose dace (*Rhinichthys cataractae*), fallfish (*Semotilus corporalis*), and slimy sculpin (*Cottus cognatus*) (11); and brook trout (*Salvelinus fontinalis*) (10). Seven species (chain pickerel (*Esox niger*), common carp, golden shiner (*Notemigonus crysoleucas*),

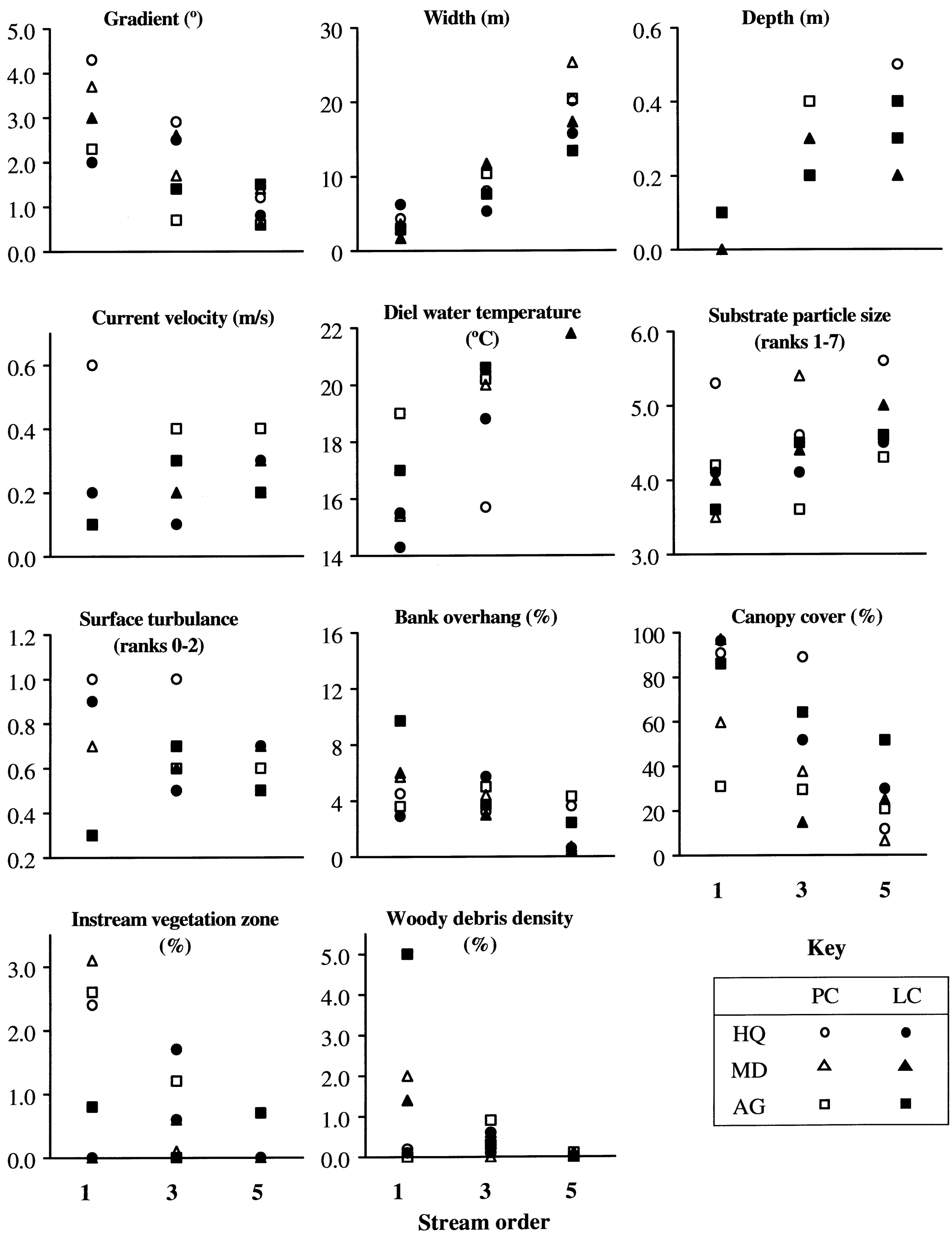


*Figure 2.* Habitat quality at sampled sites in Pine (PC) and Loyalsock (LC) Creeks. Abbreviated as in Figure 1.

spottail shiner (*Notropis hudsonius*), fathead minnow (*Pimephales promelas*), pearl dace (*Margariscus margarita*), and fantail darter) were each found in only one stream.

Streams with the highest species richness were 5th order forested (21 and 19 species) and 3rd order agricultural land use (19 species). Streams with the lowest species richness were 1st order mine-influenced

*Table 2.* List (taxonomic order (AFS 1991)) of fish species found in 18 sampled stream segments with standard (e.g. Halliwell et al. 1999) functional and tolerance group designations.

| Species | Scientific name | Functional group[a] | Tolerance group[b] |
|---|---|---|---|
| Brown trout[c] | *Salmo trutta* | P | I |
| Brook trout | *Salvelinus fontinalis* | P | I |
| Chain pickerel | *Esox niger* | P | I |
| Central stoneroller | *Campostoma anomalum* | H | T |
| Common carp[c] | *Cyprinus carpio* | O | T |
| Cutlips minnow | *Exoglossum maxillingua* | I | I |
| River chub | *Nocomis micropogon* | I | I |
| Golden shiner | *Notemigonus crysoleucas* | O | T |
| Common shiner | *Luxilus cornutus* | O | U |
| Spottail shiner | *Notropis hudsonius* | I | I |
| Rosyface shiner | *Notropis rubellus* | I | I |
| Mimic shiner[c] | *Notropis volucellus* | I | U |
| Bluntnose minnow | *Pimephales notatus* | O | T |
| Fathead minnow | *Pimephales promelas* | O | T |
| Blacknose dace | *Rhinichthys atratulus* | I | U |
| Longnose dace | *Rhinichthys cataractae* | I | I |
| Creek chub | *Semotilus atromaculatus* | O | T |
| Fallfish | *Semotilus corporalis* | O | T |
| Pearl dace | *Margariscus margarita* | I | U |
| White sucker | *Catostomus commersoni* | O | T |
| Northern hogsucker | *Hypentelium nigricans* | I | I |
| Yellow bullhead | *Ameiurus natalis* | I | T |
| Brown bullhead | *Ameiurus nebulosus* | I | T |
| Margined madtom | *Noturus insignis* | I | I |
| Rock bass | *Ambloplites rupestris* | P | I |
| Pumpkinseed | *Lepomis gibbosus* | I | I |
| Bluegill[c] | *Lepomis macrochirus* | I | T |
| Smallmouth bass[c] | *Micropterus dolomieu* | P | I |
| Fantail darter[c] | *Etheostoma flabellare* | I | U |
| Tesselated darter | *Etheostoma olmstedi* | I | U |
| Banded darter[c] | *Etheostoma zonale* | I | I |
| Shield darter | *Percina peltata* | I | I |
| Mottled sculpin | *Cottus bairdi* | I | I |
| Slimy sculpin | *Cottus cognatus* | I | I |

[a]P = predator, I = insectivore, O = omnivore, H = herbivore.
[b]I = intolerant, T = tolerant, U = undetermined.
[c]Species nonindigenous to the Susquehanna River basin.

(3 species), 1st order forested (3 species), and 3rd order forested (4 species). The mean number of species per stream was 5, 11, and 16 for 1st, 3rd, and 5th order streams, respectively, while the mean number of streams in which each species was found was six (one third of sampled streams). Cluster analysis revealed two groups of assemblages among the 18 stream samples (Figure 3). Group 1 (four assemblages) consisted of non-agriculturally influenced headwater streams where only trout and sculpin (3 or 4 species) were present. Group 2 (five assemblages) consisted of nearly all the 5th order streams with relatively high fish species richness (13–21 species).

### *Landscape influences on stream characteristics*

*Stream order.* Of the 11 water-chemistry variables measured in each of the 18 streams, none were significantly affected by stream order (Table 3). On the other hand, eight of eleven habitat-quality variables were significantly related to stream order (Table 4). First order streams had the highest gradients, bank overhang, canopy cover, instream vegetation zone, and woody debris density, while 5th order streams had the highest widths, depths, current velocities, and diel temperature means (Figure 2).

Fisher's exact test comparisons showed significant direct effects of stream order on the presence of the following 12 of 34 fish species: brook trout, central stoneroller (*Campostoma anomalum*), cutlips minnow (*Exoglossum maxillingua*), rosyface shiner (*Notropis rubellus*), longnose dace, fallfish, white sucker, margined madtom (*Noturus insignis*, rock bass (*Ambloplites rupestris*), smallmouth bass, tessellated darter (*Etheostoma olmstedi*), and banded darter. Two of these (17%) were nonindigenous species of the Susquehanna River drainage. Overall Fisher's exact test showed no relation between the presence of non-indigenous species (as a generic class) in a stream segment and stream order (2-tailed, $P = 0.99$). Species richness per 100 m of stream reach was strongly related to stream order, overall and by native and non-native categories (Table 5). However, both the number of individual fish per 100 m$^2$ of stream area and the total lengths of fish per m$^2$ were unrelated to stream order in all cases. Stream order significantly affected diversity of both species ($H_s$) and tolerance ($H_t$; i.e. 1st order streams supported species that were

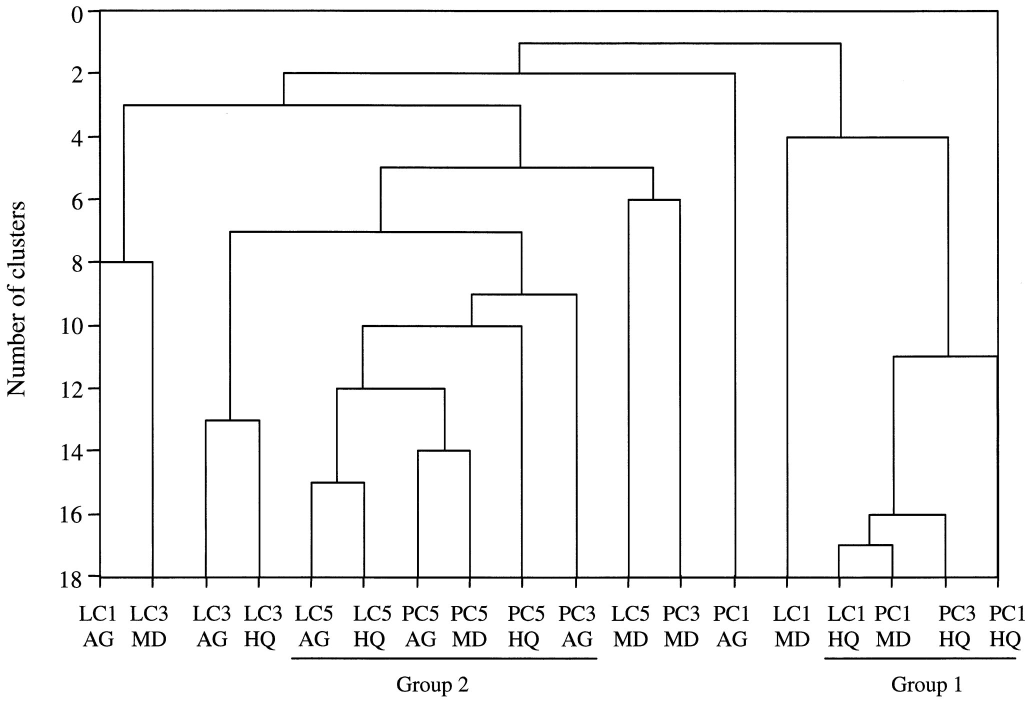


*Figure 3.* Cluster analysis of the 18 stream fish assemblages in Pine and Loyalsock Creeks. Highlighted are the two groups of assemblages that cluster earliest (group 1 = non-agriculturally influenced headwaters; group 2 = most 5th order streams). Stream codes as in Figure 1 with PC = Pine Creek and LC = Loyalsock Creek.

*Table 3.* Analyses of variance to show the effect of stream order and land use on water-quality variables in Pine Creek and Loyalsock Creek drainages (all model and error degrees of freedom are 2 and 14 except calcium (2, 9)).

| Water-quality variable | Stream order | | Land use | |
|---|---|---|---|---|
| | *F* | *P* | *F* | *P* |
| pH | 1.37 | 0.29 | 1.50 | 0.26 |
| Alkalinity | 0.29 | 0.75 | 4.71 | 0.03* |
| Manganese | 0.62 | 0.55 | 7.35 | 0.01* |
| Sulfate | 1.07 | 0.37 | 1.96 | 0.18 |
| Iron | 0.87 | 0.44 | 1.09 | 0.36 |
| Calcium | 0.79 | 0.48 | 4.21 | 0.05* |
| Magnesium | 0.81 | 0.46 | 1.77 | 0.21 |
| Chloride | 0.90 | 0.43 | 4.01 | 0.04* |
| Nitrate | 0.41 | 0.67 | 4.41 | 0.03* |
| DO[a] | 0.08 | 0.93 | 1.77 | 0.21 |
| TDS[a] | 0.12 | 0.89 | 3.91 | 0.04* |

*Significant at $P \leq 0.05$.
[a]DO = dissolved oxygen, TDS = total dissolved solids.

*Table 4.* Analyses of variance to show the effect of stream order and land use on instream habitat-quality variables in Pine Creek and Loyalsock Creek drainages (model and error degrees of freedom are 2 and 15 except for gradient (2, 14)).

| Habitat-quality variable | Stream order | | Land use | |
|---|---|---|---|---|
| | *F* | *P* | *F* | *P* |
| Gradient | 10.8 | 0.001** | 1.24 | 0.32 |
| Width | 40.4 | 0.0001*** | 0.17 | 0.85 |
| Depth | 20.3 | 0.0001*** | 0.32 | 0.73 |
| Current velocity | 15.7 | 0.0003*** | 1.78 | 0.20 |
| Diel water temperature | 33.9 | 0.0001*** | 0.52 | 0.60 |
| Substrate particle size | 2.1 | 0.16 | 1.47 | 0.26 |
| Surface turbulence | 0.4 | 0.66 | 2.46 | 0.19 |
| Bank overhang | 7.1 | 0.007** | 0.79 | 0.47 |
| Canopy cover | 7.8 | 0.005** | 0.70 | 0.51 |
| Instream veg. zone | 1.8 | 0.19 | 0.61 | 0.56 |
| Woody debris density | 13.7 | 0.0004*** | 0.05 | 0.95 |

*,**,***Significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

more uniformly intolerant) in the 18 streams but did not affect functional ($H_f$) diversity (Table 5).

*Land use.* Six of eleven water-quality variables, alkalinity, manganese, calcium, chloride, nitrate, and total dissolved solids, were significantly affected by land-use category (Table 3). Mine-influenced streams had the highest manganese levels, while streams of agricultural land use had the highest levels of the

*Table 5.* Analyses of variance to show the effects of stream order and land use on species density; total fish density; and species, functional (trophic), and tolerance diversity ($H_s$, $H_f$, and $H_t$) for the 18 sampled streams.

| Dependent variable | Independent variable | | | | | |
|---|---|---|---|---|---|---|
| | Stream order | | | Land use | | |
| | df | $F$ | $P$ | df | $F$ | $P$ |
| No. of species/100 m | | | | | | |
| Native | 2, 15 | 17.8 | 0.0001*** | 2, 15 | 0.52 | 0.61 |
| Non-native | 2, 15 | 4.8 | 0.02* | 2, 15 | 0.96 | 0.40 |
| All | 2, 15 | 19.1 | 0.0001*** | 2, 15 | 0.63 | 0.55 |
| No. of individuals/m$^2$ | | | | | | |
| Native | 2, 15 | 1.06 | 0.37 | 2, 15 | 1.78 | 0.20 |
| Non-native | 2, 12 | 0.45 | 0.65 | 2, 12 | 0.15 | 0.86 |
| All | 2, 14 | 0.61 | 0.56 | 2, 14 | 0.79 | 0.47 |
| Total fish length/m$^2$ | | | | | | |
| Native | 2, 14 | 1.21 | 0.33 | 2, 15 | 2.84 | 0.09 |
| Non-native | 2, 15 | 1.01 | 0.39 | 2, 15 | 1.76 | 0.21 |
| All | 2, 14 | 0.90 | 0.43 | 2, 14 | 2.60 | 0.11 |
| Diversity | | | | | | |
| $H_s$ | 2, 15 | 10.0 | 0.002** | 2, 15 | 1.62 | 0.23 |
| $H_f$ | 2, 15 | 0.85 | 0.45 | 2, 15 | 0.55 | 0.59 |
| $H_t$ | 2, 15 | 3.65 | 0.05* | 2, 15 | 3.81 | 0.07 |

*,**,***Significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

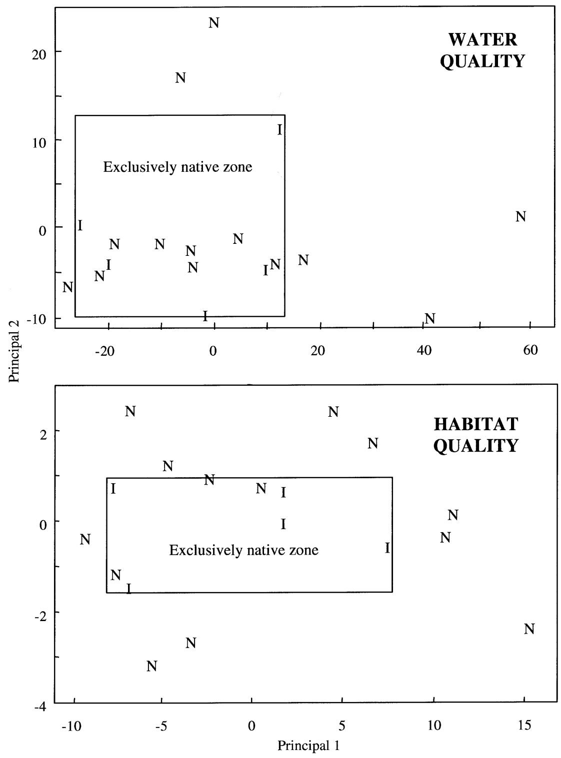


*Figure 4.* Principal components analysis relating water-quality and habitat-quality variables to stream fish assemblages. Assemblages with nonindigenous species are designated 'N' while those with exclusively native species are 'I'. Rectangles represent the limit of water-quality or habitat-quality variability beyond which exclusively native assemblages do not exist. Axes (principals 1 and 2) represent principal components that explain the greatest amount of variation among environmental variables.

remaining five variables. On the other hand, none of the habitat-quality variables were significantly affected by land-use category (Table 4).

Direct effects of land use on the presence of fish species in the 18 streams were observed for only the two native sculpin species (Fisher's exact test, $P \leq 0.05$). With one exception, cottids were not found in stream segments influenced by mining. Overall, Fisher's exact test showed no relationship between the presence of nonindigenous species (as a generic class) in a stream segment and land-use type (2-tail, $P = 0.53$), though only half the mine-influenced streams had nonindigenous species versus five of six streams for both of the other land uses. Nor did land-use category significantly affect the number of species per 100 m of stream reach, the number of individuals per 100 m$^2$ stream area, or the total fish length per m$^2$ of stream area (Table 5), except for the latter variable, 1st order streams, where agriculturally influenced streams had significantly greater fish length per m$^2$ than streams with other land uses ($F_{2,3} = 77$, $P = 0.04$). Species, functional (trophic), and tolerance diversities were likewise found to be independent of land use, although there was a trend toward increased tolerance diversity in agricultural land use ($P = 0.07$, Table 5).

### *Differential response of native and nonindigenous species to integrated abiotic and biotic stream attributes*

The proportion of nonindigenous individuals in a stream segment was not significantly related to the number of trophic levels represented ($F_{2,12} = 2.73$, $P = 0.11$), though the mean nonindigenous proportion for four-level streams was numerically greater than that for streams with two or three trophic levels. Removing nonindigenous fishes from all samples did not affect functional diversity in samples ($F_{1,34} = 0.02$, $P = 0.88$), nor did it change trophic structure in streams with few trophic levels ($<4$) differently than those with many ($>3$) trophic levels ($Z = -0.39$, $P = 0.35$). However, principal components analysis relating water-quality variables to stream fish assemblages revealed narrower distributions of exclusively native assemblages along the major principal axes, showing a more restricted response of exclusively native assemblages to water-quality variation than for mixed assemblages (Figure 4). Similarly, the same type of analysis relating habitat-quality variables to the 18 fish assemblages showed the same narrower distributions and restricted response of exclusively native assemblages to habitat-quality variation than for mixed assemblages (Figure 4).

## Discussion

### *General watershed characteristics*

The Susquehanna River drains 71,200 km$^2$ in northern Appalachia and provides the largest (50%) single source of freshwater to the Chesapeake Bay, itself the largest estuary in the United States (Carlson 1968; Reshetiloff 1995). Pine and Loyalsock Creeks are West Branch tributaries in the Appalachian Plateau, which is underlain by largely undisturbed sedimentary rock strata. Surface features, however, of both drainages reflect historical as well as current patterns of land use that include conservation, agriculture, and coal mining. These land uses typify the northcentral Appalachian region.

Though single water-quality measurements from the streams cannot capture the full range of variation or stresses exhibited by the streams over the long run or even in a single year, the chemical profiles we observed indicate variation consistent with the major land uses within the watersheds. Cluster analysis supported this characterization with distinct clusters of variables identifying mine-drainage and agricultural gradients. Geomorphic and physical habitat variation appeared to co-vary with stream size in some cases or was consistently small in others (Figure 2).

Fish communities of the two drainages were moderately rich for northern Appalachia. Our 29 and 30 species found in Pine and Loyalsock Creeks at 9 sites each in a single season compare to 38 and 31 species at 98 and 20 stations sampled over 1 and 4 years, respectively (Cooper and Wagner 1971; Hughey 1991, 1992). Historically, collections with vouchered specimens total 43 and 41 species for Pine and Loyalsock Creeks (Argent et al. 1997). Richness in major Pennsylvania drainages decreases in an easterly direction (Ohio to Susquehanna to Delaware) due to a number of factors related to biogeography and recent geology (Cooper 1983; Argent et al. 1997). For the entire Susquehanna River drainage, 10–14 species have been identified as nonindigenous among an estimated 84 total species (Argent 2000).

Of the seven nonindigenous fish species collected in this study (21% of total), only two (brown trout and common carp) are continental exotics. All others are major-drainage exotics that have entered the Susquehanna basin via stocking (bluegill and smallmouth bass; see Richardson 1995), accidental release aided by natural causes (banded darter; see Raesly et al. 1990; LoVullo and Stauffer 1993), or other unknown events, including those related to the retail baitfish industry (mimic shiner and fantail darter; see LoVullo and Stauffer 1993). The most ubiquitous species found were not exotic, but rather include coldwater and coolwater fishes that require moderate-to-high water quality (Halliwell et al. 1999). The most diverse stream samples were from large, nominally 'high-quality,' watersheds, while the most depauperate were from small high-quality or mine-influenced drainages, consistent with the inverse species richness-water quality principle for coldwater systems (Lyons et al. 1996). Cluster analysis (Figure 3) confirmed this pattern of assemblage groups, separated primarily on the basis of richness or diversity and secondarily by land use.

### *Cascading landscape influences on ichthyofauna*

We found that both the scale and quality of landscape attributes influenced stream hydrogeomorphology and fish communities. Perhaps not unexpectedly, stream order, the principal surrogate of watershed size, strongly affected stream geomorphology as well as habitat variation related to fish cover, but not water quality. On the other hand, land use in watersheds significantly affected some measured water-quality variables but not stream geomorphology or habitat quality. Failure to detect land-use effects on instream habitat conditions was contrary to some known effects, such as agricultural/urban-related sedimentation (Richter et al. 1997) and riparian-integrity impacts (Jones et al. 1999; Stauffer et al. 2000). We measured sedimentation rates only indirectly (transect substrate particle-size estimation; sedimentation loads not measured) and our indicator of riparian health, canopy cover, did not adequately capture the extent of the riparian buffer zone. Fish communities were also influenced by stream order in terms of both the presence/absence of particular species found in the various watersheds and species density. However, the effect was transparent to the native-origin status of particular species. Angermeier and Winston (1998) also found scale to be an important determinant of native fish diversity in mid-Atlantic-slope streams, but introduced species, though pervasive, were less abundant and unpredictable in occurrence.

Landscape scale effects were also observed in patterns of species and tolerance diversity. The more uniformly intolerant headwater assemblages suggest physical barriers for species tolerant to water-quality degradation, such as common carp, bluntnose minnow (*Pimephales notatus*), common shiner (*Luxilus cornutus*), fallfish, and bluegill. No such barrier occurred in the case of green sunfish (*Lepomis cyanellus*) invading first-order North Carolina Piedmont streams (Lemly 1985). However, diel temperature range and gradient are two of several physical factors that differ greatly, unlike their counterparts of the mid-Atlantic Piedmont, between headwater and third order or large streams of the Appalachian Plateau.

Land-use effects on fish community composition and function, though more modest, were also identified. Both cottid species were largely absent from mine-influenced streams, and fish were significantly larger in agriculturally influenced streams of 1st order (but see Walser and Bart 1999). In addition, a trend in tolerance diversity was found, with agricultural drainages showing greatest tolerance diversity in fish communities, followed by mine-influenced drainages. The hierarchical nature of these landscape influences is illustrated in Figure 5.

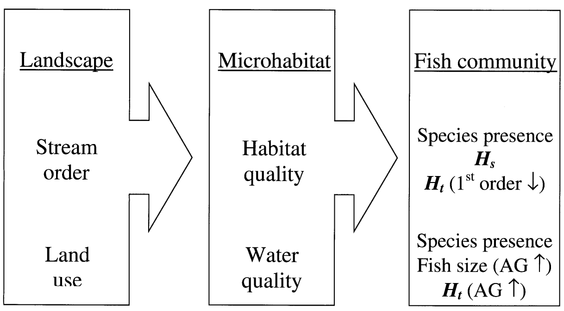


*Figure 5.* Model of cascading landscape influences on ichthyofauna in northern Appalachian lotic systems.

Landscape effects of quality on fish communities, as in the case of scale, were transparent to the native-origin status of fish species, i.e., did not affect the two classes differently. Therefore, hypothesis $H_1$ (type of land use in watershed affects fish communities and their ability to resist invasion by nonindigenous species) was only weakly supported by the data and needs further testing. In the Willamette basin of Oregon, mixed land use was associated with relatively high abundance of introduced species (Waite and Carpenter 2000). Argent (2000) found that over half the species showing significant declines across Pennsylvania landscapes over the past half century were general insectivores, followed in importance by benthic insectivores (which include the two cottids for which we identified impacts). Species that declined in response to increasing agriculture across Pennsylvania landscapes included central stoneroller, spotfin shiner (*Cyprinella spiloptera*), satinfin shiner (*Cyprinella analostana*), and tessellated darter.

In sum, fish community structure and function were clearly affected by stream order and land use. Since direct correlations to specific physical or chemical variables were also identified, we believe these overall effects were mediated largely through geomorphic or physical habitat variables, in the case of stream order effects, and through chemical variables related to water quality, in the case of land-use effects. These factors affected nonindigenous species no differently than native species. Therefore hypothesis $H_2$ (biotic factors are more important than abiotic in the invasion potential of nonindigenous fishes) is not supported. Our findings are consistent with those of California streams, where hydrologic regime compatibility apparently is the principal determinant of successful invasion by exotic fishes, rather than biotic factors (Moyle and Light 1996; Brown and Moyle 1997). Biotic factors such as predation play a role in some systems, however (Garman and Nielsen 1982; Scoppettone 1993).

*Mechanism for nonindigenous fish invasion*

No relationships were identified between the occurrence of nonindigenous species in watersheds and trophic structure. Nor did removal of nonindigenous species from samples significantly affect either the number of trophic levels in a sample or functional diversity within samples. Therefore we find no support for the hypothesis ($H_3$) that reduced ecosystem diversity increases vulnerability to exotic or nonindigenous species by increasing available limiting resources (Stachowicz et al. 1999; Tilman 1999). This conclusion must be considered tentative, however, because a rigorous test of the hypothesis would require comparisons among healthy and degraded speciose and depauperate lotic systems.

We did, however, identify some measurable characteristics of streams with nonindigenous species present that are different from those with natives only. The variation associated with both water-quality and habitat-quality variables was greater in mixed assemblages than in exclusively native assemblages. In a study of the effects of a changing landscape on Pennsylvania's fish fauna, Argent (2000) found some influence of nonindigenous fishes on native community structure but no resulting one-to-one species loss.

Our findings suggest that the mechanism for successful invasion of lotic systems in northern Appalachia by nonindigenous or exotic species is through change in water quality or habitat quality associated with human or natural disturbances, including agriculture and mining activities in watersheds. Even 'depauperate' streams apparently resist incursion by non-native fishes, so long as the relatively narrow instream physical and chemical conditions are maintained. Relative to physical-habitat and water-quality factors, biotic factors appear to play no or a lesser role in the invasibility of northern Appalachian streams by exotic or nonindigenous fishes. Abiotic conditions may establish a sufficiently strong barrier to many potential invasives, essentially constituting limiting factors to those species, where biotic resistance might otherwise prevail.

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## Note

[1] Mention of tradenames does not imply endorsement.

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