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I am submitting herewith a dissertation written by Jeffrey Robert Duncan entitled "From Second Creek to New Pangea: A Multi-Scale Analysis of Patterns and Trends in Aquatic Biodiversity." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

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FROM SECOND CREEK TO NEW PANGEA:

A Multi-Scale Analysis Of Patterns And Trends In Aquatic Biodiversity

A Dissertation
Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Jeffrey Robert Duncan
December 2001

DEDICATION

For those who have and will stand in harm's way for the sake of freedom and pluralism,

And

To future conservationists who will reap the fruits of my generation's successes and struggle through the challenges of our failures.

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My personal journey from Second Creek to New Pangea would not have been possible without the technical assistance and inspiration of many. Since the road has been long, it would be impossible to mention them all, but whether called out by name or not, you know who you are, and you have my sincere thanks. A once prominent role model and old friend who had a profound early influence on my development as a scientist is Dr. Robert Brustad. Thanks Brew, where ever you are.

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ABSTRACT

The Earth's freshwater ecosystems are undergoing a period of dramatic change. The simultaneous expansion and contraction of aquatic species' ranges is leaving an indelible mark on the evolutionary histories of the world's freshwater species. This dissertation represents a compilation of research efforts that quantify, explain, and propose policy recommendations concerning current trends in aquatic biodiversity. Part II provides an appraisal of the status of the world's freshwater fishes that asks two primary questions—are all taxonomic groups equally susceptible to extinction, and can we identify a unifying suite of extinction risk factors? Although I concluded, that extinction risk is not randomly distributed among freshwater fish families, the identification of a unifying set of extinction predictors remains elusive. In Part III, focusing on the U.S., a species list was compiled for each of the lower 48 states to represent their historic and future freshwater fish faunas. Species richness was calculated for each state, and the degree of change in faunal similarity was estimated between neighboring states. Comparisons indicated that states are likely to become more distinct from their neighbors in the future. In Part IV, I evaluate aquatic diversity trends along a natural gradient within the state of Tennessee. Changes in species richness and faunal similarity occurring between historic and future faunas were calculated between ecoregions. Species richness was found to decrease statewide. Similarity increased for virtually all ecoregion-taxonomic combinations indicating that Tennessee is losing its historic biological distinctiveness. Part V represents a study of biophysical homogenization at a fine spatial scale. I compared the frequency of debris dams in a forested reference stream to a stream in a heavily urbanized watershed. I found that debris dams occurred in greater frequency within the forested reference stream compared to the urban stream. A follow-up analysis determined that although there was a significantly greater amount of riparian canopy litter within the urban stream corridor, the quality and timing of litter inputs prevented debris dam genesis and retention. It is believed that the scouring flows that typically accompany highly impervious urban watersheds contributed to decreased frequency of debris dams in the urban stream.

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PART I

PROLOGUE

Map of Pangea drawn by Jessica, Pattie Elementary School, Dumfries, Virginia

Nearly 300 million years ago, the Earth's landmasses drifted together to form the super-continent known as Pangea. Comprising of virtually all of the world's land area, Pangea was an epicenter of an evolutionary convolution among species that induced species radiations among some taxa and mass extinctions among others (Futumya, 1986). An age of unprecedented connectivity was established between previously isolated terrestrial ecosystems. The freshwater habitats of Pangea inherited a diverse ensemble of aquatic organisms, including the ancestors of our modern bony fishes, many of which had arisen in unique and isolated habitats within a 100 million year period prior to the uniting of Pangea (Long, 1996).

The influence of geographic isolation on evolutionary and ecological processes was temporarily replaced by the ecological pressures and opportunities created through biotic mixing. Some species invaded novel territories while others, evolutionarily ill-prepared for the invasion of new competitors, were pushed to, and in some cases beyond, the brink of extinction. Then, about 50 million years later, the landmass began to fragment, once again creating continents with isolating boundaries and setting the stage for a new period of rapid radiation among the terrestrial and freshwater assemblages that had synergistically evolved on Pangea. Although Pangea was relatively short-lived (at least in geologic terms), its effect in altering the course of evolution was no doubt significant.

Today, as a result of unprecedented evolutionary advancement within the brain of a single species—*Homo sapiens*—a new Pangea is forming. Although not driven by the force of plate tectonics, geographic boundaries that once restrained terrestrial and freshwater species from intermingling between continents are collapsing. Within the last 500 years, global exploration, the advent of modern modes of travel, and the globalization of commerce have begun providing a bridge for species that were once geographically constrained. As the title implies, aquatic biodiversity is undergoing a period of dramatic change. The simultaneous expansion and contraction of aquatic species ranges is likely to leave an indelible mark on the evolutionary and ecological histories of

the world's freshwater biota. The extent of this phenomenon encompasses multiple spatial scales. Even within continents, ecological boundaries are collapsing.

The efficiency of humans in manipulating aquatic communities and ecosystems for economic gains and recreational pleasure further exemplifies an analogy to Pangea. The draining and filling of wetlands and the impoundment and manipulation of stream flows has exacerbated changes in the biosphere. For example, more than half of the wetland habitats in the U.S. have been lost or degraded within the last 200 years (Maltby, 1988). Management policies concerning freshwater fisheries of the U.S. have historically been geared toward enhancement of a few commercially and recreationally desirable species, despite the fact that approximately 90 percent of freshwater fishes are considered nongame species (Shute et al., 1997). Although the present biodiversity crisis remains in its early stages, the rate at which significant biotic changes are taking place is unprecedented in evolutionary history (Erwin, 1998, McKinney and Lockwood, 2001).

This dissertation represents a cohesive and original compilation of distinct research efforts that quantify, explain, and propose policy recommendations concerning the current biodiversity trends among freshwater communities when observed at a variety of scales. These trends can be viewed both as a spatial phenomenon, the effects of which are measurable at a variety of levels ranging from a comparison of two small Southern Appalachian streams to the six major bioregions of the world, and as a temporal phenomenon by comparing ecological patterns of the past, present, and future. Although the unifying title of this volume is indicative of the temporal transition from the present day state of aquatic biodiversity to a hypothetical future state, I have elected to first establish a global context to this work by presenting its corresponding parts in a sequence of increasing spatial resolution—beginning at a global level and ending at a local level. Despite this sequence of presentation, the reader should remain aware of the big picture—that the present biodiversity

crisis represents a journey through biological time to the not so distant streams, rivers, lakes, and wetlands of New Pangea.

I begin the analysis with Part II, "Extinction in a Field of Bullets." Because human actions alter the physical nature of aquatic ecosystems similarly worldwide, the extinction risk among many freshwater fishes that share particular life-history traits may also be similar. Determining whether taxonomic selectivity (i.e., the non-random loss or persistence of certain species groups) exists among the world's freshwater fish families is a key step in predicting future species declines and triaging future conservation efforts. We use binomial statistics to look for taxonomic patterns among the world's freshwater fish families currently at risk of extinction. We find that families inhabiting well-studied regions of the world contain more threatened species. However, we find no indication of a unifying set of extinction-promoting biological or ecological traits that contribute to extinction risk among freshwater families. A possible explanation for this discrepancy is that aquatic alterations worldwide are so severe that extinction is being driven by extrinsic rather than intrinsic factors.

In Part III, "How's the Fishing in New Pangea," the level of resolution is refined to focus on the fishes of the U.S. Historic and future species lists are developed for each of the lower 48 states based on conservation rankings and whether or not a species is believed to be native to the state. Although species ranges are obviously not constrained by political boundaries, the use of states as a foundation for assessing patterns in biodiversity on a national level is an appropriate approach given that policy and management constructs operate according to political jurisdictions rather than environmental gradients. After calculating changes in species richness, we estimate the degree of faunal similarity between states in the past and compare it to estimated similarity in the future. Contrary to our initial prediction that states will become more similar to one another in the future, we find that the level of similarity changes very little between western states and that it actually decreases in the historically species rich eastern U.S. We hypothesize that this decrease in similarity may be a transient state in our drift toward Pangea and be caused by the differentiation

between extinction and invasion rates—extinctions taking much longer to occur than invasions.

Part IV, "Spatial Homogenization of the Aquatic Fauna of Tennessee," further refines the resolution to the regional level by evaluating the effects of extinction and invasion on aquatic species within a single state. We obtained distribution information for fishes, mussels, and amphibians inhabiting the state of Tennessee. To evaluate the role of environmental gradients in mediating extinction and invasion, we superimpose the species distributions over the ecoregions of the state. As in Part III, we evaluate the changes in faunal similarities occurring through time as one moves from the past into the future. We find that habitat degradation, particularly the impoundment and fragmentation of medium-sized rivers, likely plays a significant role in removing the geographic distinctness within the aquatic faunas of Tennessee.

Finally, in Part V, "Assessing the Structure of Debris Dams in Urban Streams: A Case Study of Biophysical Homogenization," I narrow the focus to one of the underlying biophysical influences on the aquatic biodiversity crisis—physical homogenization of riparian ecosystems. Specifically, I compare the frequency and composition of debris dams within an urban stream to those of a forested reference stream, both located within the Ridge and Valley ecoregion of Tennessee. Although I find that the frequency of debris dams was significantly higher in the reference stream, the dry weight of leaf litter collected within the urban stream corridor was significantly greater. I conclude that riparian zone management (specifically the type and quality of vegetation) and the degree to which watershed imperviousness alters urban stream flow are important factors in regulating the generation and retention of biophysical structure in small streams.

While the intent of this dissertation and its component parts is to shed light on the extent of the current biodiversity crisis, it is important to place this discussion within the context of the contemporary environmental movement. Within the last 30 years, a variety of efforts by national, regional, and local

governments as well as non-profits has developed an assortment of conservation policies and tools and has posted a handful of conservation successes (McKinney and Lockwood, 2001) in an effort to stabilize the ongoing drift toward New Pangea. The promise of long-term success at altering our course will depend on the ability of humankind to modify habitual behaviors and develop a new understanding of its relationship within the biosphere. The magnitude of change needed within the human psyche will require worldwide environmental education and will ultimately rely on a high level of environmental consciousness. This new environmental awareness must permeate all levels of society and induce change ranging from individual lifestyles to the operations of multinational corporations (Hawken, 1999). This dissertation is intended to represent a minor contribution toward increasing awareness of the ecological consequences of our individual actions, governmental policies, and cultural paradigms.

LITERATURE CITED

Erwin, D.H. 1998. The end and the beginning: recoveries from mass extinctions. *Trends in Ecology and Evolution* 13:344-349.

Futumya, D.J. 1986. Evolutionary Biology. Second edition. Sinauer Associateds, Inc. Publishers, Sunderland, Massachusetts.

Hawken, P., Lovins, A.B. and L.H. Lovins. 1999. Natural Capitalism. Little Brown & Company.

Long, J.A. 1996. The Rise of Fishes. Johns Hopkins University Press. Baltimore, MD.

Maltby, E. 1988. Wetland resources and future prospects: an international perspective. In Zelazny, J. and J.S. Feierabend (eds.), Wetlands: Increasing Our Wetland Resources. National Wildlife Federation, Washington, D.C.

McKinney, M.L. and J.L. Lockwood. 2001. Biotic homogenization: a sequential and selective process. In Lockwood, J.L. and M.L. McKinney (eds.), Biotic Homogenization. Klewer Academic/Plenum Publishers, New York.

Shute, P.W., Biggins, R.G. and R.S. Butler. 1997. Historical perspectives of management and conservation of aquatic resources. In Benz, G.W. and D.E. Collins (eds.), Aquatic Fauna in Peril: the Southeast Perspective. Southeast Aquatic Research Institute, Decatur, Georgia.

PART II

EXTINCTION IN A FIELD OF BULLETS:

A Search For Causes In The Decline Of The World's Freshwater Fishes

Part II is presented as a slightly altered version of a paper that appears in the journal Biological Conservation:

Duncan, J.R. and J.L. Lockwood. 2001. Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. Biological Conservation 102:97-105.

My use of "we" in this chapter refers to the collaboration of my co-author and myself. My contribution to this paper includes (1) selection of the topic and development of the problem into a work relevant to the central core of this dissertation, (2) acquisition compilation of the data, (3) data analysis and interpretation, and (4) the majority of the writing. I wish to express my gratitude to my co-author, Dr. Julie L. Lockwood, for her assistance and guidance throughout the development of this work.

INTRODUCTION

Predicting which species are likely to go extinct is perhaps one of the most fundamental yet challenging endeavors of conservation biology (McKinney, 1997; McKinney & Lockwood, 1999; Russell et al., 1999). Efforts at prediction in conservation biology reflect a basic dilemma between the need to act and the need to know more. Ideally, conservationists need the capacity to identify some set of biological or ecological traits that predispose species to extinction. This ability enables priority ranking of potentially vulnerable species, before the species actually become threatened. Practically speaking, these traits must be amenable to accurate and efficient measurement such that large groups can be assessed rapidly. Although this may be a reasonable approach for well known, easily studied, and conspicuous groups such as mammals and birds, it may not be realistic when confronted with difficult to observe and species-rich groups such as fishes.

Freshwater fishes are not only the most diverse of all vertebrate groups, with nearly 10,000 described species, but they are also the most highly

threatened. Perhaps more than 20% of described fish species are at risk of extinction in the near future (Leidy and Moyle 1998). Various studies have sought to assess risk by identifying extinction-promoting characteristics among certain groups of fishes or within specific geographic regions (e.g., Angermeier, 1995; Etnier, 1997; Leidy and Moyle, 1998). However, none has succeeded in identifying a comprehensive and unifying set of extinction-promoting traits on a global scale. Nevertheless, our ability to effectively combat the current extinction crisis requires that we adopt a broad taxonomic and global perspective. Although research efforts at finer taxonomic and geographic scales are valuable in supporting local and regional management efforts, their conclusions may be inadequate for influencing conservation policy at the national and international levels.

One approach to broad-scale prediction assumes that extinction-biasing traits are evolutionarily conserved within lineages, thus producing a patterned distribution of extinction vulnerability within higher taxa (McKinney, 1997; Owens and Bennett, 2000, Purvis et al., 2000a; Purvis et al., 2000b; Russel et al. 1999). This allows us to target higher fish taxa for conservation action without needing a detailed understanding of every species' life history. Further, if we are able to tease apart the critical biological and ecological characteristics that produce taxonomic patterns (i.e., group-defining characters), we may be more effective in designing management and conservation schemes.

To assess the global status of freshwater fishes and, if possible, to identify a suite of unifying extinction-promoting traits, we asked three fundamental questions. First, does extinction occur randomly among freshwater fish families? We use binomial statistics to ascertain which, if any, fish families are extinction-prone beyond the background level that we would expect if extinction occurred randomly among families. Unlike other vertebrate groups, the diversity among fishes has precluded them from being thoroughly studied in vast areas of the world, producing geographic gaps in our understanding of their conservation status (Bruton, 1995). Thus, our second question is whether the extinction-prone families are more likely to inhabit more thoroughly studied

regions of the world. If so, we should be cautious when exploring for characteristics to explain global taxonomic patterns. Third, we asked if there were identifiable group-defining physical or biological characteristics (i.e., intrinsic factors) that could serve as useful predictors of extinction risk at the family level. The ability to pinpoint these traits, if they exist, would facilitate proactive placement of extinction-prone families at the top of our conservation triage lists (Vane-Wright *et al*., 1991). The absence of such traits could suggest that extinction risk is driven by extrinsic factors such as the preferential loss of broad habitat types (e.g., springs or medium-sized rivers).

DATA SOURCES

Among vertebrates, fish taxonomy is perhaps the most dynamic (Nelson, 1976; 1984; 1994). As more evolutionary history is uncovered through the discovery of previously undescribed species and use of molecular genetic techniques, the total number of known fish species worldwide is increasing. To present the most current accounts of global fish diversity, we obtained the number of species per family using Nelson (1994). Although there is undoubtedly a degree of uncertainty in our estimates of family size, we believe our data are as valid as permitted by the current state of fish systematics. Using information in Nelson (1994), we limited our focus to families inhabiting primarily freshwater environments. To assess which freshwater fish families are particularly susceptible to extinction, the number of threatened species per family was taken from the International Union for the Conservation of Nature (IUCN) Red List of Threatened Animals (Groombridge & Baillie, 1996). Caution was exercised in attempting to reconcile discrepancies in nomenclature and taxonomy between Nelson (1994) and Groombridge and Baillie (1996) by using Eschmeyer (1990) to confirm genus-family relationships. However, due to the dynamic nature of fish taxonomy, we recognize that some errors in our data inevitably persist. Although, it is widely suspected that IUCN accounts of species vulnerability are biased toward the better-studied taxonomic groups of the western world, particularly freshwater species of North America (Leidy and Moyle, 1998), we

know of no other data source that offers a more detailed, accurate, and up-to-date account of the world's imperiled fishes.

The IUCN categorizes species based on their relative risk of global extinction. We include only those species listed as extinct (E), extinct in the wild (EW), critically endangered (CR), endangered (EN), and vulnerable (VU). Although the latter three categories include fish species that are not yet extinct, they are considered at high risk of becoming extinct in the near future (Groombridge & Baillie, 1996). For more detailed information on how these definitions were derived see Groombridge and Baillie (1996).

STATISTICAL ANALYSES

Our first goal was to pinpoint which freshwater fish families, if any, hold more threatened species than expected by chance. If the probability of extinction is distributed randomly among higher taxa, the number of threatened species per family should be proportional to the overall percentage of species that are threatened (Zar, 1984). However, a family may hold many more (or many less) threatened species than the overall average, thus indicating a taxonomic bias—taxonomic selectivity (McKinney, 1997; Bennett and Owens, 1997; Lockwood, 1999; Russell et al., 1999).

We can estimate the chance of obtaining a value equal to, or greater than, the observed number of threatened fish species using the binomial equation, $R = (n!/X!(n\text{-}X)!)p^{x}q^{n\text{-}x}$, where n is family size, X is the observed number of threatened species, p is the overall percentage of threatened species, and q is $1\text{-}p$ (Bennett & Owens, 1997; Lockwood, 1999). Since we made more than 30 independent comparisons, the R-value of each family was compared to a sequentially derived Bonferroni critical value to judge significance (Rice, 1989). This process was carried out using "CRITBINOM" function in Microsoft Excel. Using a Bonferroni correction forced us to state the critical value (α=0.05) *a priori*, thus we could not calculate the degree to which the observed value deviated from the expected. However, we calculated the number of standard deviations the

observed value fell from the expected and used this as a measure of relative selectivity.

Next, we used a series of chi-square analyses to test the final two questions: Is there a sampling bias toward better-known families from more accessible regions of the world, and are there identifiable biological or geographic characteristics that may serve as useful predictors of extinction risk? Chi-square was selected because the data for each of the attributes were generally non-normally distributed and because the sample size for extinction-prone families was relatively small (18 in most cases) (Zar, 1984). For each of these separate analyses, we obtained the total frequency of a given trait by dividing the number of families in which the trait was present by the number of freshwater families for which data were available (111 in most cases). From this, we calculated the expected frequency among extinction-prone families by multiplying the observed frequency for all freshwater families by the number of threatened families for which data were available. This procedure allowed us to statistically compare the frequency of various traits within extinction-prone families to the trait frequency observed for all freshwater families worldwide. A critical value of 0.05 was again used to judge significance (Zar, 1984).

To determine whether geographic location was a factor in extinction risk, we tested for differences in the distribution of families among major bioregions of the world using information in Berra's (1981) atlas of freshwater fish families. Bioregions listed by Berra were Nearctic, Palearctic, Neotropical, Ethiopian, Oriental, and Australian. Assessing the number of threatened families within each bioregion, we were able to approximate the degree of geographic sampling bias within the IUCN database. That is, were threatened families more generally found in the better-studied portions of the world, namely the Nearctic?

Next, we tested for differences in geographic patterns among families. Geographic patterns included dispersion (i.e., number of bioregions inhabited by a family), endemism (i.e., widespread or localized distribution), habitat (i.e., inland, coastal, or islandic), and latitude (i.e., arctic, northern temperate, tropical,

southern temperate). To test the effect of geographic dispersion on taxonomic selectivity, we tallied the number of bioregions occupied by each family. We then assessed the effect of endemism at the family level by classifying families as widespread if they occupied relatively large contiguous areas (e.g., >1,000 km in diameter) or several dispersed smaller areas, and as endemic when a family's entire worldwide range was <1,000 km in diameter. To test the influence of habitat preference, we classified inland families as those with ranges that were predominantly landlocked, coastal families as those found along coastal regions of major continents, and island families as those inhabiting oceanic islands.

For assigning latitude, arctic families were those that extended above the Arctic Circle. Northern temperate families were those with ranges between the Tropic of Cancer and the Arctic Circle. Tropical families were those found within the tropics of Cancer and Capricorn, and southern temperate families were those inhabiting areas south of the Tropic of Capricorn. None of the habitat or latitudinal categories was considered mutually exclusive (i.e., some families were found to occupy more that one category). In these cases the families were assigned to all appropriate categories for analysis. However, in some cases we used professional judgment to assign families to one predominant latitudinal area, although their range extended slightly into an adjacent region.

Unfortunately, few data were available that describe biological traits (e.g., trophic status, body size, etc.) at the family level; however, Nelson (1994) provides a listing of maximum lengths for families. Although using maximum length as a surrogate description of body size within families undoubtedly introduces a degree of uncertainty to our results (maximum may in some cases be an extreme value), we know of no other globally comprehensive listing for body size. Nelson lists maximum lengths for 86 of the 111 freshwater families we analyzed. Families were classified as *small* or *large* using the statistical mode of all families' maximum lengths (0.48 m). For simplicity, we rounded this value to 0.5 m.

TAXONOMIC SELECTIVTY

Nelson (1994) estimates that globally there are 482 families containing 24,618 fish species, of which 9,966 inhabit freshwater. Reconciling data presented by Berra (1981) and Nelson (1994), we considered 111 families to inhabit predominantly freshwater (see appendix). Groombridge and Baillie (1996) list 441 (4.4%) freshwater species as threatened with extinction. Thirty-five freshwater families contain at least one threatened species with 18 families containing a greater number of threatened species than expected by chance (Table 1). The degree of taxonomic selectivity, measured as standard deviations in excess of the expected mean, ranged from 1.27 for bonytongues (Osteoglossidae) to 21.78 for sturgeons (Acipenseridae). The remainder of freshwater families that hold more threatened species than expected were Belontiidae (gouramies), Salmonidae (salmonids), Adrianichthyidae (ricefishes), Goodeidae (goodeids), Percidae (perches), Galaxiidae (galaxiids), Ictaluridae (North American catfishes), Amblyopsidae (cavefishes), Cichlidae (cichlids), Polyodontidae (paddlefishes), Catostomidae (suckers), Heteropneustidae (airsac catfishes), Diplomystidae (diplomystid catfishes), Umbridae (mudminnows), Elassomatidae (pygmy sunfishes), and Clariidae (airbreathing catfishes).

ANALYSIS OF FAMILY TRAITS

In comparing the bioregional distributions of all families to those that were statistically extinction-prone, we rejected our null hypothesis that threatened families were evenly distributed across all six bioregions ($X^2 = 15.38$, $0.005 < P < 0.01$). This finding, for lack of any other readily testable explanation, appears to statistically validate the common perception that the IUCN data are biased by a disproportionate number of well-known taxa that primarily inhabit the Nearctic region (Bruton, 1995; Leidy and Moyle, 1998). Simply stated, poorly studied taxa are less likely to be listed as threatened. Because of this apparent bias, we performed the remaining analyses in two ways, one comparing all 18 taxonomically selected threatened families to the group of nontaxonomically selected families worldwide, and alternatively by comparing a subset of the

taxonomically selected families, those with representative species in the Neartic, to nontaxonomically selected families with Nearctic representation. If a true discrepancy existed between extinction-prone and extinction-resistant families, then the pattern should remain among the subset of well-known Nearctic families.

Assessing whether the number of bioregions inhabited (i.e., geographic dispersion) by a family had any bearing on extinction risk, we again rejected our null hypothesis ($X^2 = 6.37$, $0.025 < P < 0.05$). Although the majority of families inhabited a single bioregion (62.2%), the extinction-prone families were likely to come from two (38.9%) or more than two bioregions (27.8%). Our follow-up analysis, focusing solely on Nearctic families, allowed us to accept our null hypothesis that the number of bioregions a family inhabits likely has no bearing on its risk of extinction ($X^2 = 0.31$, $0.75 < P < 0.90$). Thus, we were able to conclude that there is likely no difference in extinction risk associated with the number of bioregions inhabited.

Separate comparisons of endemism (i.e., widespread or endemic) and habitat type (i.e., inland, coastal, islandic) among threatened families versus all families revealed no significant difference between threatened families and all families. Chi-squared values were 3.17 ($0.05 < P < 0.10$) for endemism and 1.51 ($0.25 < P < 0.50$) for habitat type. Our Nearctic follow-up analyses validated these conclusions with chi-squared values of 3.77 ($0.10 < P < 0.05$) and 3.29 ($0.10 < P < 0.25$) for endemism and habitat type, respectively.

Our test for latitudinal effects indicated that arctic and northern temperate families were significantly more extinction-prone than families inhabiting lower latitudes ($X^2 = 9.54$, $0.005 < P < 0.01$). In our follow-up analysis of Nearctic families, we pooled the arctic with the northern temperate category and the tropical with the southern temperate category to maintain an adequate sample size. Similar to the bioregional test, we found that there was no latitudinal pattern in extinction risk ($X^2 = 0.25$, $0.50 < P < 0.75$). Thus, we were able to conclude that there is likely no difference in extinction risk attributed to

latitude. Our final analysis concerned maximum length. Again, we were unable to detect any difference in the frequency of small versus large body size between the globally extinction-prone families and freshwater families in general (X^2 = 0.60 ($0.25 < P < 0.50$). Our follow-up analysis ($X^2 = 0.09$, $0.75 < P < 0.90$) validated our initial finding that there is likely no difference in maximum body for families at risk of extinction versus families in general for families that occur in the Nearctic.

DISCUSSION

Fishes are by far the most diverse group of living vertebrates. Species that inhabit freshwater habitats show a high degree of endemism, thus providing the geographic regions they inhabit a unique evolutionary heritage (Bruton, 1995). However, ongoing widespread human manipulation of aquatic habitats threatens much of this heritage. Globally, evidence suggests that we will likely lose at least 4% of all known fish species within the near future (Bruton, 1995; Groombridge & Baillie, 1996). Considering the scarcity of information on the conservation status of lesser-known taxa, the rate at which we are losing species is likely greater even than that suggested by red lists such as IUCN's. In fact, Leidy and Moyle (1998) speculate that extinction in excess of 20% of freshwater fish species may be a more realistic estimate. Further, our results indicate that the world's most jeopardized taxa are not located randomly on the evolutionary tree. Rather, the majority (71%) of species at risk of extinction come from a disproportional subset of 18 freshwater families including the sturgeons, gouramies, and salmonids (Table 1).

Angermier (1995) suggests that specific life history traits–such as small range size (or endemism), habitat specificity (e.g., gravel shoals), and habitation of nearshore environments–may play a significant role in extinction risk, at least among the taxa of Virginia. Beyond such region-specific conclusions, our ability to generalize globally appears futile. Sweeping generalizations at the broad scale of global freshwater families are replete with exceptions. Although taxonomic selectivity appears to exist among imperiled freshwater families, predicting

which factors cause this selectivity remains elusive. The only clear pattern is that better-studied families are more likely to contain threatened species. However, even among the better-studied families, we are currently unable to identify traits that may predispose these taxa to extinction.

Our inability to identify a unifying set of predictive extinction-promoting traits among fishes may stem from a variety of underlying causes. The first could simply be because we are not looking at the right traits. Body size, degree of endemism, habitat type, and latitude have all been implicated as promoting extinction in many groups (McKinney, 1997) and are readily available from data sources such as Nelson (1994) and Berra (1981). Given that we are unable to detect extinction-promoting patterns among families for which these traits are known, perhaps more information is needed. This may be particularly true for lesser-known families in poorly studied regions of the world. Similarly, it is possible that we have not looked at the right taxonomic level. Increasing our taxonomic resolution to the genus or species level requires information that is currently unavailable. Given the urgency of the current crisis, increasing our information base in order to determine what species may ultimately be at risk of extinction seems an inefficient, costly, and unrealistic alternative.

Table 1. Freshwater families containing at least one jeopardized species (Groombridge and Baillie, 1996). Families with significantly higher risk of extinction are in bold.

Family	Common Name	Number of threatened species	Number of Species in family	Standard Dev. from Expected Mean
Acipenseridae	**Sturgeons**	**23**	**24**	**21.78**
Belontiidae	**Gouramies**	**12**	**18**	**12.84**
Salmonidae	**Salmonids**	**23**	**66**	**12.02**
Percidae	**Perches**	**35**	**162**	**10.63**
Cichlidae	**Cichlids**	**136**	**1300**	**10.58**
Adrianichthyidae	**Ricefishes**	**10**	**18**	**10.55**
Goodeidae	**Goodeids**	**14**	**36**	**10.06**
Galaxiidae	**Galaxiids**	**13**	**40**	**8.63**
Ictaluridae	**NA Catfishes**	**13**	**45**	**7.98**
Amblyopsidae	**Cavefishes**	**4**	**6**	**7.41**
Catostomidae	**Suckers**	**15**	**68**	**7.07**
Polyodontidae	**Paddlefishes**	**2**	**2**	**6.57**
Heteropneustidae	**Airsac catfishes**	**1**	**2**	**3.13**
Diplomystidae	**Diplomystid catfishes**	**1**	**4**	**2.00**
Clariidae	**Airbreathing catfishes**	**8**	**100**	**1.74**
Umbridae	**Mudminnows**	**1**	**5**	**1.69**
Elassomatidae	**Pygmy sunfish**	**1**	**6**	**1.46**
Osteoglossidae	**Bonytongues**	**1**	**7**	**1.27**
Amblycipitidae	Torrent catfishes	1	10	0.86
Poeciliidae	Livebearers	16	293	0.86
Salangidae	Icefishes	1	11	0.75
Balitoridae	Hillstream loaches	17	350	0.39
Phallostethidae	Phallostethids	1	19	0.18
Pangasiidae	Pangasiids	1	21	0.08
Centrarchidae	Sunfishes	1	29	-0.26
Anabantidae	Climbing gouramies	1	30	-0.29
Cobitidae	Loaches	4	110	-0.40
Sisoridae	Sisorid catfishes	1	85	-1.46
Siluridae	Sheatfishes	1	100	-1.67
Cyprinidae	Minnows	73	2010	-1.73
Bagridae	Bagrid catfishes	4	210	-1.78
Trichomycteridae	Parasitic catfishes	2	155	-1.90
Mochokidae	Upside-down catsfishes	1	167	-2.40
Pimelodidae	Long-whiskered catfishes	2	300	-3.17
Characidae	Characins	1	885	-6.24
Total threatened families		441	6694	
Total Freshwater spp			9966	

Each of these explanations for the apparent lack of detectable extinction-promoting traits assumes that extinction risk is produced by an underlying intrinsic force. That is, certain extinction-prone taxa exhibit particular genotypic or phenotypic traits that inhibit their ability to cope with stressors. It is equally plausible that extinction may be driven by extrinsic factors. In other words, freshwater fishes may be going extinct simply because they inhabit the wrong place at the wrong time, or as Raup (1991) puts it, because they have "bad luck." For example, 23 of the 24 species within the Acipenseridae (sturgeons) are listed as threatened, making them by far the most taxonomically threatened of the freshwater fishes. Although some sturgeons inhabit strictly freshwater, many are anadromous (i.e., spending significant portions of their life cycles in both fresh and saltwater environments), and nearly all are migratory to some degree. With the damming of many medium to large rivers (their primary habitat throughout the Northern Hemisphere) migration corridors have been reduced if not eliminated, thus becoming a key factor in their demise. Although the behavior of migrating can be considered a biological trait, it is not explanatory for the majority of taxonomically selected families, and is thus not a useful indicator of extinction risk. In essence, the decline of sturgeons is more a product of the fact that they inhabit dammed rivers as it is any specific biological trait.

Further, paleontologists have identified five major episodes of mass extinction during which >50% of the world's biodiversity was lost (Erwin, 1997). Depending on the relative rate and magnitude of environmental change associated with these events, the relative effect on extant biodiversity at the time likely varied. When environmental change was extreme and occurred rapidly, taxon-specific traits appear to have played less of a role in determining who survived and who went extinct (Raup, 1991).

From this point of view, the importance of bad luck in the extinction of fishes may reflect the extreme nature of alterations within the aquatic environment. In response to human demands on water resources, aquatic ecosystems have suffered the effects of pollution, dewatering, impoundment, and channelization (Mason, 1991; Moyle & Randall, 1998; Holmquist *et al*., 1998).

Since the 1950s, the construction of approximately 40,000 large dams has transformed portions of many major drainages throughout the world into punctuated staircases of slackwater reservoirs (McCully, 1996). To fishes, the effect of damming a river occurs rapidly and causes extreme environmental consequences resulting in conditions of altered flow, depth, dissolved oxygen, light availability, temperature, habitat heterogeneity, and energy sources (Mason, 1991). Further, dams simplify the physical structure of natural waterways with enormous losses of shoals, shallow banks, and complex habitats such as pools and riffles (Auster, 1998; Allan & Flecker, 1993). But, dams are not the only source of extreme and rapid environmental change in the aquatic world. Other forms of human activity threaten regionally unique small aquatic systems such as springs, headwater streams, and wetlands which are routinely paved over, drained, filled, polluted, and otherwise degraded (Richter *et al*., 1997).

The combined effect of these human alterations to aquatic environments may be so extreme and rapid that intrinsic extinction-promoting factors among fishes are swamped. Raup (1991) discusses how extremely intense and widespread catastrophic disturbances (e.g., large meteorite impacts) may produce what he terms "field of bullets" selectivity whereby extinction essentially becomes unpredictable in relation to life history traits. Given that freshwater fishes are arguably among the most highly human-impacted faunal group, our tentative findings of such "field of bullets" selectivity is perhaps unsurprising. Assuming we are witnessing the early stages of a rapidly occurring sixth mass extinction (Pimm *et al.*, 1995), fishery conservation efforts may be better-suited toward identifying, prioritizing, and limiting extrinsic extinction-promoting factors rather than looking for intrinsic biological causes.

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LITERATURE CITED

Allan, J.D. and A.S. Flecker. 1993. Biodiversity conservation in running waters: identifying the major factors that affect destruction of riverine species and ecosystems. *Bioscience* 43:32-43.

Angermeier, P.L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. *Conservation Biology* 9:143-158.

Auster, P.J. 1998. A conceptual model of the impacts of fishing gear on the integrity of fish habitats. *Conservation Biology* 12:1198-1203.

Bennett, P.M. and I.P.F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? *Proc. R. Soc. London B* 264:401-408.

Berra, T.M. 1981. *An Atlas of Distribution of the Freshwater Fish Families of the World.* University of Nebraska Press. Lincoln and London.

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

Erwin, D.H. 1998. The end and the beginning: recoveries from mass extinctions. *Trends in Ecology and Evolution* 13:344-349.

Eschmeyer, W. N. 1990. *Catalog of the Genera of Recent Fishes*. California Academy of Sciences, San Francisco, CA.

Etnier, D.A. 1997. Jeopardized southeastern freshwater fishes: a search for causes. In Benz, G.W. and D.E. Collins (eds.). *Aquatic Fauna in Peril.* Southeast Aquatic Research Institute, Decatur, GA.

Groombridge, B. and J. Baillie. 1997. *1996 IUCN Red List of Threatened Animals.* IUCN Gland, Switzerland and Cambridge, UK.

Harcourt, A. 1998. Ecological indicators of risk for primates, as judged by species' susceptibility to logging. In Caro, T. (ed.) *Behavioral ecology and conservation biology.* Oxford University Press, Oxford, UK.

Holmquist, J.G., Schmidt-Gegenbach, J.M., and Y.B. Buchanan. 1998. High dams and marine-freshwater linkages: effects on native and introduced fauna in the Carribean. *Conservation Biology* 12:621-630.

Leidy, R.A. and P.B. Moyle. 1998. Conservation status of the world's freshwater fish fauna: an overview. In Fieldler, P.L. and P.M. Karieva (eds.). Conservation Biology for the Coming Decade 2nd edition. Chapman and Hall, New York.

Lockwood, J.L. 1999. Using taxonomy to predict success among introduced aviafauna: the relative importance of transport and establishment. *Conservation Biology* 13:560-568.

Mason, C.F. 1991. *Biology of Freshwater Pollution*. Longman Scientific and Technical, New York, NY.

McCully, P. 1996. Silenced Rivers: the ecology and politics of large dams. Zed Books. Atlantic Highlands, NJ.

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

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

Moyle, P.B. and P.J. Randall. 1998. Evaluating the biological integrity of watersheds in the Sierra Nevada, California. *Conservation Biology* 12:1318-1326.

Nelson, J.S. (1976). *Fishes of the World*. John Wiley & Sons, New York, NY.

Nelson, J.S. (1984). *Fishes of the World* 2nd Edition. John Wiley & Sons, New York, NY.

Nelson, J.S. (1994). *Fishes of the World* 3rd Edition. John Wiley & Sons, New York, NY.

Owens, I.P.F. and P.M. Bennett. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. *Proceedings of the National Academy of Science.* 97:12144-12148.

Purvis, A., Gittleman, J.L., Cowlishaw, G., and G. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society* 267:1947-52.

Purvis, A., Agapow, P.M., Gittleman, J.L. and G.M. Mace. 2000. Nonrandom extinction and the loss of evolutionary history. *Science* 288:328-330.

Pimm, S.L., Russell, G.J., Gittleman, J.L. and T.M.Brooks. 1995. The future of biodiversity. *Science* 269:347-350.

Raup, D.M. 1991. *Extinction: Bad Genes or Bad Luck?* Norton Publishers, New York.

Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223-225.

Richter, B.D., Braun, D.P., Mendelson, M.A., and L.L. Master. 1997. Threats to imperiled freshwater fauna. *Conservation Biology* 11:1081-1093.

Russell, G.J, Brooks, T.M., McKinney, M.L. and C.G.,Anderson. 1999. Present and future taxonomic selectivity in bird and mammal extinctions. *Conservation Biology* 12:1365-1376.

Vane-Wright, R.I., Humprhies, C.J. and P.H. William. 1991. What to protect? – systematics and the agony of choice. *Biological Conservation* 55:235-254.

Zar, J.H. (1984). *Biostastical Analysis*. Prentice-Hall, Engle Cliffs, NJ.

Appendix

Summary of all freshwater families and their associated traits

Family	Common Name	Bioregion[1]	Salinity Tolerance[2]	Number Bioregions	Maximum Length (m)	Distribution[3]	Location[4]	Latitude[5]
Acipenseridae	Sturgeons	1,3,5	3	3	4.2	W	IN, C	AR, NT
Belontiidae	Gouramies	3,5	1	2	NA	W	IN, C, IS	NT, T
Salmonidae	Salmonids	1,3	3	2	1.5	W	IN, C	AR, NT
Adrianichthyidae	Ricefishes	3,5	2	2	0.2	W	IN, C, IS	NT,T
Goodeidae	Goodeids	1	2	1	0.2	I	IN	T
Percidae	Perches	1,3	1	2	0.9	W	IN, C	AR, NT
Galaxiidae	Galaxiids	2,4,6	3	3	0.58	W	IN, C	ST
Ictaluridae	NA catfishes	1	1	1	1.6	W	IN, C	NT, T
Amblyopsidae	Cavefishes	1	1	1	0.09	I	IN, C	NT
Cichlidae	Cichlids	1,2,4,5	2	4	0.8	W	IN, C	T
Polyodontidae	Paddlefishes	1,3	1	2	3	I	IN, C	NT
Catostomidae	Suckers	1,3	1	2	1	W	IN, C	AR, NT, T
Heteropneustidae	Airsac catfishes	5	1	1	NA	I	IN, C	T
Diplomystidae	Diplomystid catfishes	2	1	1	0.28	I	IN, C	ST
Umbridae	Mudminnows	1,3	1	2	0.2	I	IN, C	NT
Elassomatidae	Pygmy sunfish	1	NA	1	0.045	I	IN, C	NT
Osteoglossidae	Bonytongues	2,4,5,6	1	4	2.5	W	IN, C, IS	T
Clariidae	Airbreathing catfishes	3,4,5	1	3	NA	W	IN, C, IS	NT, T, ST
Amblycipitidae	Torrent catfishes	5	1	1	NA	I	IN, C, IS	T
Salangidae	Icefishes	3,5	3	2	0.15	I	C, IS	NT, T

Family	Common Name	Bioregion[1]	Salinity Tolerance[2]	Number Bioregions	Maximum Length (m)	Distribution[3]	Location[4]	Latitude[5]
Phallostethidae	Phallostethids	5	3	1	0.037	W	IN, C, IS	NT, T
Pangasiidae	Pangasiids	5	1	1	3	I	IN, C, IS	T
Centrarchidae	Sunfishes	1	1	1	0.83	I	IN, C	NT
Anabantidae	Climbing gouramies	4,5	1	2	0.3	W	IN, C, IS	NT, T, ST
Poeciliidae	Livebearers	1,2	2	2	0.18	W	C	NT, T, ST
Cobitidae	Loaches	3,4,5	1	3	0.4	W	IN, C, IS	NT, T
Balitoridae	Hillstream loaches	5	1	1	NA	W	IN, C, IS	NT, T
Sisoridae	Sisorid catfishes	3,5	1	2	2	W	IN, C, IS	NT, T
Siluridae	Sheatfishes	3,5	1	2	5	W	IN, C, IS	NT, T
Trichomycteridae	Parasitic catfishes	2	1	1	NA	W	IN, C	T, ST
Bagridae	Bagrid catfishes	3,4,5	1	3	2	W	IN, C, IS	NT, T, ST
Mochokidae	Upside-down catfishes	4	1	1	0.72	W	IN, C	NT, T, ST
Pimelodidae	Long-whiskered catfishes	2	1	1	3	W	IN, C	T, ST
Cyprinidae	Minnows	1,3,4,5	1	4	3	W	IN, C	NT, T, ST
Characidae	Characins	1,2,4	1	3	1.4	W	IN, C	NT, T, ST
Petromyzontidae	Lampreys	1,2,3,6	3	4	0.9	W	IN, C, IS	AR, NT, ST
Dasyatidae	Stingrays	2	3	1	NA	W	IN	T, ST
Ceratodontidae	Australian lungfishes	6	1	1	NA	I	IN	ST
Lepidosirenidae	South American lungfishes	2	1	1	NA	W	IN	T, ST
Protopteridae	African lungfishes	4	1	1	1.8	W	IN ,C	T
Polypteridae	Bichirs	4	1	1	0.9	W	IN, C	T
Lepisosteidae	Gars	1	2	1	3	W	IN, C, IS	NT, T
Amiidae	Bowfin	1	1	1	0.9	W	IN, C	NT
Denticipitidae	Denticle herrings	4	1	1	0.06	I	C	T
Pantodontidae	Butterflyfishes	4	1	1	0.1	I	IN, C	T

Family	Common Name	Bioregion[1]	Salinity Tolerance[2]	Number Bioregions	Maximum Length (m)	Distribution[3]	Location[4]	Latitude[5]
Hiodontidae	Mooneyes	1	1	1	0.51	W	IN	NT
Notopteridae	Old World knifefishes	4,5	1	2	1.5	W	IN, C, IS	T
Mormyridae	Elephantfishes	4	1	1	1.5	W	IN, C	T
Gymnarchidae	Gymnarchids	4	1	1	1.5	W	IN	T
Osmeridae	Smelts	1,3	3	2	0.4	W	C, IS	AR, NT, T
Retropinnidae	New Zealand smelts	6	3	1	0.35	W	IN, C, IS	T, ST
Lepidogalaxiidae	Salmanderfishes	6	NA	1	0.06	I	IN	ST
Esocidae	Pikes	1,3	1	2	1.4	W	IN, C	AR, NT
Kneriidae	Kneriids	4	1	1	0.15	W	IN, C	T
Phractolaemidae	Snake mudheads	4	1	1	0.16	I	IN, C	T
Erythrinidae	Trahiras	2	1	1	1	W	IN, C	T, ST
Ctenoluciidae	Pike characins	2	1	1	1	W	IN, C	T
Hepsetidae	Hepsetids	4	1	1	0.65	W	IN, C	T
Lebiasinidae	Lebiasinids	2	1	1	NA	W	IN, C	T
Gasteropelecidae	Freshwater hatchetfishes	2	1	1	NA	W	IN, C	T, ST
Curimatidae	Curimatids	2	1	1	0.45	W	IN, C	T, ST
Anostomidae	Anostomids	2	1	1	0.4	W	IN, C	T, ST
Hemiodontidae	Hemidontids	2	1	1	0.3	W	IN, C	T, ST
Distichodontidae	Distichodontids	4	1	1	0.84	W	IN, C	T
Gymnotidae	Naked-back knifefishes	2	1	1	0.6	W	IN, C	T, ST
Electorphoridae	Electric knifefishes	2	1	1	2.3	W	IN, C	T, ST
Apteronotidae	Ghost knifefishes	2	1	1	NA	W	IN, C	T, ST
Rhamphichthyidae	Sand knifefishes	2	1	1	NA	W	IN, C	T, ST
Gyrinocheilidae	Algae eaters	5	1	1	0.3	I	IN, C	T
Cranoglanididae	Armorhead catfishes	5	1	1	NA	I	C, IS	T

Family	Common Name	Bioregion[1]	Salinity Tolerance[2]	Number Bioregions	Maximum Length (m)	Distribution[3]	Location[4]	Latitude[5]
Schilbeidae	Schilbeid catfishes	4,5	1	2	NA	W	IN, C, IS	T
Amphiliidae	Loach catfishes	4	1	1	0.17	W	IN, C	T
Akysidae	Stream catfishes	5	1	1	NA	W	IN, C, IS	T
Chacidae	Frogmouth catfishes	5	1	1	0.24	W	IN, C, IS	NT, T
Olyridae	Olyrids	5	1	1	NA	I	IN, C	NT, T
Malapteruridae	Electric catfishes	4	1	1	1.2	W	IN, C	T
Doradidae	Thorny catfishes	2	1	1	0.8	W	IN, C	T, ST
Auchenipteridae	Driftwood catfishes	2	1	1	NA	W	IN, C	T, ST
Aspredinidae	Banjo catfishes	2	1	1	0.42	W	IN, C	T, ST
Ageneiosidae	Barbelless catfishes	2	1	1	1	W	IN, C	T, ST
Hypophthalmidae	Lookdown catfishes	2	1	1	0.6	W	IN, C	T
Helogeneidae	Helogeneids	2	1	1	0.1	W	IN, C	T
Cetopsidae	Whalelike catfishes	2	1	1	NA	W	IN, C	T, ST
Callichthyidae	Callichthyid armored catfishes	2	1	1	NA	W	IN, C	T, ST
Loricariidae	Suckermouth armored catfishes	2	1	1	NA	W	IN, C	T, ST
Astroblepidae	Climbing catfishes	2	1	1	0.3	I	IN	T
Aphredoderidae	Pirate perches	1	1	1	0.13	W	IN, C	NT
Percopsidae	Trout–perches	1	1	1	0.2	W	IN	AR, NT
Cyprinodontidae	Pupfishes	1,2,3,4,5	2	5	0.22	W	IN, C, IS	NT, T, ST
Anablepidae	Anablepids	2	2	1	0.32	W	IN, C	T, ST
Melanotaeniidae	Rainbowfishes	6	2	1	0.12	W	IN, C, IS	T, ST
Gasterosteidae	Sticklebacks	1,3	3	2	0.18	W	IN, C, IS	AR, NT
Indostomidae	Indostomids	5	3	1	0.27	I	IN	NT
Channidae	Snakeheads	4,5	1	2	1.2	W	IN, C, IS	NT, T
Synbranchidae	Swampeels	2,3,4,5,6	3	5	1	W	IN, C, IS	NT, T, ST

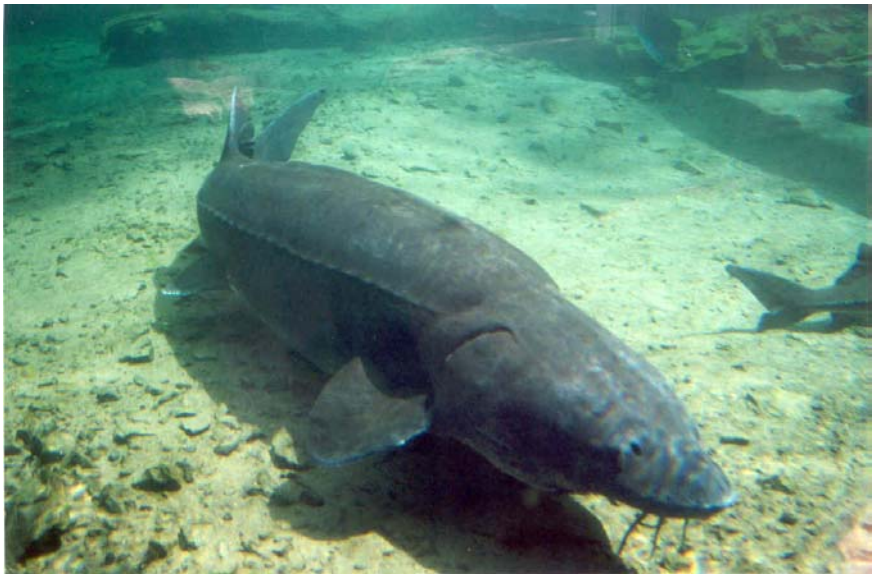
Family	Common Name	Bioregion[1]	Salinity Tolerance[2]	Number Bioregions	Maximum Length (m)	Distribution[3]	Location[4]	Latitude[5]
Cottidae	Sculpins	1,3	3	2	0.78	W	IN, C, IS	AR, NT
Comphoridae	Baikal oilfishes	3	3	1	0.2	I	IN	NT
Percicthyidae	Temperate perches	1,2,3,6	3	4	NA	W	IN, C, IS	NT, T, ST
Toxotidae	Archerfishes	5,6	3	2	0.4	W	C, IS	T
Scatophagidae	Scats	4,5,6	3	3	0.35	W	C, IS	T, ST
Enoplosidae	Enoplosids	6	3	1	NA	I	C	ST
Nandidae	Leaffishes	2,4,5	1	3	0.21	W	IN, C, IS	T
Embiotocidae	Surfperches	1,3	3	2	0.45	W	C, IS	NT
Bovichthyidae	Bovichthyids	2,6	3	2	NA	W	C, IS	ST
Rhyacichthyidae	Loach gobies	5,6	3	2	0.32	W	IS	T
Kurtidae	Nurseryfishes	5,6	3	2	0.6	W	C, IS	T
Helostomatidae	Kissing gouramies	5	1	1	NA	W	C, IS	T
Osphronemidae	Giant gouramies	5	1	1	0.8	W	C, IS	T
Luciocephalidae	Pikeheads	5	1	1	0.18	W	C, IS	T
Mastacembelidae	Spiny eels	3,4,5	1	3	0.009	W	IN, C, IS	NT, T
Chaudhuriidae	Chaudhurids	5	1	1	0.08	I	IN	T

a	b	c	d	e
1 = Nearctic	1 = Intolerant	W = Widespread	IN = Inland	AR = Arctic
2 = Neotropical	2 = Somewhat tolerant	I = Isolated	C = Coastal	NT = Northern temperate
3 = Palearctic	3 = Tolerant		IS = Islandic	T = Tropical
4 = Ethiopian				ST = Southern temperate
5 = Oriental				
6 = Austalian				

PART III

HOW'S THE FISHING IN NEW PANGEA?

An Assessment of Changing Patterns in the Diversity of America's Freshwater Fishes



White sturgeon (Acipenser transmontanus), Bonneville Fish Hatchery, Columbia River (photo by J. Duncan)

Part III has not yet been published, although submission of this work to a scholarly journal is planned for the near future. Authorship of the submitted version will likely be the following:

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My use of "we" within this work refers to the collaboration of my co-authors and myself. My contribution to this paper includes (1) selection of the topic and development of the problem into a work relevant to the central core of this dissertation, (2) acquisition and compilation of the data, (3) data analysis and interpretation, and (4) the majority of the writing. I wish to express my gratitude to my co-authors, especially Dr. Julie L. Lockwood for her statistical assistance and general guidance throughout the development of this work.

INTRODUCTION

Until recently, few studies have attempted to address the processes of species extinction and invasion simultaneously. However, a recent flurry of studies (e.g., Hobbs and Mooney, 1998; Lockwood et al., 2000; Lockwood and McKinney, 2001; McKinney, 1998; McKinney and Lockwood, 1999; Rhymer and Simberloff, 1996) focusing on biotic homogenization—the process of simultaneous invasions and extinctions—has begun to shed light on this global phenomenon. Perhaps nowhere else have the effects of biotic homogenization been so profound than within the freshwater fishes (Duncan and Lockwood, 2001[a and b]; Marchetti et al., 2001; Rahel, 2000). In this chapter, we assess the effect of homogenization on regional biodiversity patterns by using the freshwater fishes of the continental United States as case study.

The term homogenization implies a process of mixing objects or materials, in our case fish species. Although humans have clearly succeeded in inducing homogenization among freshwater fishes in the purest sense of the term, our findings suggest that the end result may not be as simple as it appears from

the surface. Rosenzweig (2001), quoting other sources, stated that we are embarking on a journey into a new ecological period, the "Homogocene," where ecosystems are dominated by communities of abundant and widespread cosmopolitan species. The resulting effects on biodiversity patterns, however, are clouded.

Conservation biologists have asserted that faunas of the Homogocene will in some ways mimic those of Pangea (Vitousek et al. 1993, McKinney 1997, Brown 1995). On this ancient super-continent, which was composed of all the Earth's landmasses above sea level, geographic isolating boundaries were much less restrictive than today and provided a different set of evolutionary constraints. Although this analogy is at a minimum intriguing and provides a vivid mental picture of the future of the biosphere, we show that predicting the biogeographic structure of "New Pangea," particularly for freshwater fishes, may be considerably more complex than previously believed.

Our assessment of homogenization within the fish fauna of the U.S. is not entirely novel. Rahel (2000) conducted a descriptive study of biotic homogenization of U.S. freshwater fishes by comparing historic to present-day faunas. He found that when comparing all 1,128 possible pairings of state-to-state combinations (limited to the contiguous lower 48 states), the number of shared species increased on average by 15.4 species relative to pre-European settlement assemblages. Although we generally concur with his conclusions—that the freshwater fishes of the United States have undergone a process of homogenization—we believe that the geographic and temporal scope of Rahel's study may have strongly influenced the patterns he observes, and thus the conclusions he draws. By predicting faunal assemblages for the states of "New America," we find that states will share an average of 24.4% *fewer* fish species than they do today.

To account for this discrepancy, we hypothesize that the process of homogenization, as well as the ultimate results of it, may vary according to the spatial and temporal scales upon which they are assessed. Rahel's study draws

conclusions by comparing historic faunas to those of the present. Although this approach tells us, in effect, where we have been and where we are today, it neglects to say anything about the future given current trends. For example, species that are currently considered at risk of becoming extinct are implicitly assumed to persist according to Rahel's model; an unlikely scenario. Further, we suspect the technique of comparing all pairwise combinations of states may have unnecessarily biased the average degree of similarity that he suggests exists between states. This method includes the comparison of faunas from states that have little in common with regard to ecological, evolutionary, and disturbance histories (e.g., Nevada compared to Rhode Island). In addition, physical characteristics of distant states, such as size and climate, exacerbate ambiguity resulting in a comparison of ecological apples and oranges. Thus, the underlying temporal and spatial assumptions of Rahel's approach restricts our ability to accurately evaluate and, if necessary, adapt environmental policies and management schemes such that they proactively address future ecological threats and conditions.

To account for these shortcomings, our study differs from Rahel (2000) in two primary regards. First, our estimates of homogenization are based on comparing historic faunas to predicted future faunas. We believe that characterizing and reacting to the process of homogenization can best be accomplished by not only examining the past but also by comparing it to a predicted future state. To this end, we compare historic faunas within each state to those predicted to exist in the future by assuming that those species currently at risk of extinction will likely become extinct in the future and that the current number of established exotic species will likely increase in the future. Second, to estimate the future extent of homogenization across the U.S., we limited our state-to-state comparisons to states that border one another. We believe that by restricting the geographic scale of our assessment to neighboring states, we can limit uncertainty and obtain a more realistic picture of the future spatial homogenization between states.

METHODS

Our approach consisted of three discrete steps: (1) assembling historic and future species lists for each state, (2) estimating the change in species richness within each state and the change in faunal similarity through time between neighboring states, and (3) a search for underlying causes for this change in future biodiversity.

Assembling Species Lists

We began by assembling a master species list for each of the lower 48 states using state- and species-specific data acquired from the Association for Biodiversity Information (Natureserve, 2000). Although Natureserve provided data that included sub-species, we restricted our focus to the species level. The Natureserve data ranked each species according to its global (G) and state (S) conservation status. Global and state status was indicated by either an "X" or an "H", or by a whole number ranging from 1 to 5. An "X" indicated that a species is believed to be extinct throughout its range, that it has not been located despite intensive searches of historical sites and other appropriate habitat, and that there is virtually no likelihood that it will be rediscovered. An "H" indicates that the species is possibly extinct. It is known from only historical occurrences, but may nevertheless still be extant, although further searching is needed. Numeric rankings are defined as follows: (1) Critically imperiled—because of extreme rarity or because of some factor(s) making it especially vulnerable to extinction. Typically five or fewer occurrences or very few individuals (<1,000) remain; (2) Imperiled—because of rarity or because of some factor(s) making it very vulnerable to extinction or elimination with typically 6 to 20 occurrences or few remaining individuals (1,000 to 3,000); (3) Vulnerable—either because it is very rare throughout its range, found only in a restricted range (even if abundant at some locations), or because of other factors making it vulnerable to extinction or elimination with typically 21 to 100 occurrences or between 3,000 and 10,000 individuals; (4) Apparently secure—uncommon but not rare, and usually widespread; apparently not vulnerable in most of its range, but possibly cause for

long-term concern; typically more than 100 occurrences and more than 10,000 individuals; (5) Secure—common, widespread, and abundant (although it may be rare in parts of its range, particularly on the periphery); not vulnerable in most of its range typically with considerably more than 100 occurrences and more than 10,000 individuals.

Next, we combined the Natureserve data with exotic species data obtained from Fuller et al. (1999). Fuller's data contained state-specific information that conveyed whether the species was believed established, collected but not necessarily established, intentionally stocked, or likely extirpated from the state. (Updated data through 1999 were obtained directly from P. Fuller).

Once the master species lists were complete, we screened each list according to conservation rank and introduction status to derive our estimated historic and future assemblages for each state. In the historic screening we assumed that all native species recorded for a state were present in the past. This included species now believed extinct or extirpated but excluded species noted as being non-native. Conversely, the screening process that derived the future state lists retained non-native species believed established as well as those that were intentionally stocked and those collected but not confirmed to exist within the state at present. The practice of retaining species listed as collected, but not established, may result in an inflation of our results. However, this inflation is likely offset by future invasions and by the fact that Fuller et al. (1999) suggest that many species listed as collected may in fact already be established. Non-native species that Fuller listed as extirpated were not retained.

The Natureserve data also included undescribed species and hybrids. These data elements were considered full species under the future scenario, assuming that undescribed species will ultimately be described and that hydrids will ultimately function as organic species. In the rare case where Naureserve and Fuller conflicted (e.g., Natureserve data occasionally contained S-ranks that indicated a species was non-native to the state), Natureserve was generally

accepted with regard to conservation status (e.g., extinct vs. non extinct) and Fuller generally ruled for whether or not a species was deemed native or non-native to a state.

Estimating Changes in State Faunal Similarities

Biotic homogenization occurs on a spatial scale when two or more distinct geographic regions (e.g., states) grow increasingly similar through time in the proportion of shared species relative to the overall species pool (Duncan and Lockwood, 2001). In this study, we estimate temporal homogenization using a Russel's (1999) equation for species turnover,

(Eq. 1) $$t_{xy} = E_{xy} + I_{xy} / S_x + S_y$$

where t_{xy} is the observed turnover per species, E_{xy} is the number of species found in state *x* but not state *y*, I_{xy} is the number of species found in state *y* but not state *x*, and *S* is the number of species present in states *x* and *y*, respectively. Simply, Russel's equation provides a measure of similarity (or beta diversity) between adjacent states. We calculated turnover for the historic and future faunas separately for each of the contiguous state pairs. For example, we calculated turnover between the historic faunas of Oregon and Washington. Subsequently, we calculated turnover for the same states' predicted future faunas. The degree of temporal homogenization is the resulting difference between the historic and future turnover scores.

(Eq. 2) $$\Delta t_s = t_h - t_f$$

where Δt_s is the change in turnover for state *s* between the historic (*h*) and future (*f*) scenarios.

Thus, comparing turnover rates between adjacent states provides a means of detecting broad-based geographic patterns in faunal similarities between historic and future periods. Further, changes in similarities between adjacent

states through time can be said to be the result of variation among three ecological attributes—rate of extinction, rate of invasion, number of state endemics, and historic species richness (i.e., historic alpha diversity). Future species richness (i.e., future alpha diversity) becomes altered when the numbers of extinctions and invasions are in disequilibrium, and it provides a useful measure of future biotic characteristics.

Next, because all of the lower 48 states, except Maine, share borders with two or more other states, we calculated the average change in historic and future turnover between a given state and all of its adjacent neighboring states (i.e., states with adjoining borders) to provide a measure of change in geographically distinct faunas. The resultant value is termed "average neighborhood turnover change" or simply, ΔT_A and is calculated as

(Eq. 3) $$\Delta T_A = \Sigma(\Delta t_n)/n$$

where ΔT_A is the net increase or decrease in turnover for a given state pairwise comparison averaged over *n* number of neighboring states. Values of ΔT_A are provided for each state in Table 1 (see appendix). Calculating ΔT_A for each state allows us to quantitatively characterize the degree of biotic homogenization likely to occur in each state in the future. A positive ΔT_A value indicates that a state will on average share a greater proportion of species with its neighbors in the future. Conversely, a negative value indicates that the state will share fewer species in the future, and thus be more biologically distinct.

The Search for Pattern

Characterizing changes in ichthyodiversity on a state-by-state basis allows us to detect regional trends. If regional trends exist, we can then look for underlying cause, which we hypothesize, may differ according to geography. Once we calculated and sorted ΔT_A for all states, we noticed an apparent trend that differentiated ΔT_A scores according to a given state's longitude (Table 1).

Although we found that ΔT_A increased in all states (except NM, OR, and VT) the greatest increases were in eastern states. For example, nine of the ten states that displayed the greatest increases in ΔT_A occur within the eastern half of the U.S. To confirm this apparent zonal trend, we conducted a *t*-test that compared ΔT_A scores for eastern versus western states. We used the 100th meridian as the point of separation dividing eastern from western states. From a hydrologic perspective, the 100th meridian has been used to symbolize the boundary between the humid east and the arid west (Wilkinson, 1992). For simplicity, we categorized those states that straddle 100th meridian as western states because their ΔT_A scores were comparable to other western states. The *t*-test confirmed our hypothesis that eastern and western states (including middle states) differ significantly with regard to ΔT_A ($t = 2.1$, $df = 46$, $P=0.044$).

To compare and explain the east versus west differences in ΔT_A, we calculated state values for each of the parameters needed to estimate turnover. These were historic species richness, number of extinctions, number of endemics, and number of exotics (Table 1). These values were standardized according to state area to eliminate the effect of species-area relationships. Further, when performing statistical analysis we log-transformed the variables to improve normality (Zar, 1984).

To determine the relative influence of each of these parameters on geographic zone we first judged colinearity between the variables using standard correlation coefficients. For any pair of variables that had correlation coefficient >0.80, we considered one a proxy for the other (SAS 1998). Only historic richness and extinction/area were significantly intercorrelated ($R = 0.88$). We retained only historic richness for the remainder of our analyses. We then performed a logistic regression where the dependent variable was geographic zone and the independent variables the constituents of the ΔT_A. Following the recommendations of Hosmer and Lemeshow (2000), we first fitted a regression equation using all independent variables. We then deleted variables that did not show an independent relationship to zone beginning with the variable with the

lowest absolute value of the logistic likelihood X^2. After each variable was deleted, a new regression equation was fitted and the process was repeated until all included variables were significant at the $\alpha = 0.05$ level.

Although assessing the effect of each of the components of turnover allowed us to determine which of these forces were most important in driving turnover between eastern and western states, it said little of the underlying causes that initiate the process of turnover change, let alone differences in the causes between regions. To address this, we cataloged a variety of state-specific physical, biological, and cultural variables that we believed could influence ΔT_A and that were readily available from the literature. These variables were state population (U.S. Census, 2000), rate of urbanization (USDA, 2001), rate of cropland change (USDA, 2001), number of dams (USACE, 2001), and median recorded precipitation (Table 2, see appendix). As with the turnover-related variables, these values were standardized according to state area and log-transformed to improve normality. We then calculated correlation coefficients, and removed variables, as above. The only variables to show intercorrelation were population change/area and urban change/area ($R = 0.95$). We only included urban change/area for the remainder of our analyses. To understand the role of each of these variables on $\Delta T_{A,}$ we performed a stepwise multiple regression following the methods of Zar (1999). First, a regression equation was fitted for the full model (i.e. one containing all independent variables). The relationship of each independent variable to ΔT_A was assessed using *t*-tests. The independent variable showing the lowest absolute value of *t* was removed, and a new regression equation fitted. This procedure continued until only significant independent variables remained.

RESULTS

Our efforts to compile state historic and future species lists allowed for the calculation of a variety of state-specific diversity-related values (Table 1). Historic species richness (i.e., alpha diversity) ranged from 1 species per hectare

(Arizona) to 205 spp/ha (species per hectare) in Rhode Island with a mean of 21 and a standard deviation of 36 spp/ha. Future species richness ranged from 3 spp/ha in New Mexico to 216 spp/ha in Delaware with a mean of 24 and a standard deviation of 41 spp/ha. On average, species richness declined by 2 spp/ha; however, change in richness ranged from a decrease of 51 spp/ha in Delaware to a net gain of 19 spp/ha in Rhode Island. Nineteen of the lower 48 contiguous states had a net decrease in richness with Rhode Island, Tennessee, and Virginia topping the list for the greatest decline in richness. Sixteen states showed increases in alpha diversity with Delaware, Connecticut, and Massachusetts demonstrating the largest increases. Invasions balanced extinctions in 12 states (i.e., where there was no change in richness), all of which lie in the western U.S. with the exception of Kentucky.

Factors contributing to richness change, invasions and extinctions, varied similarly, although invasions exceeded extinctions with means of 8 spp/ha and 5 spp/ha invasions and extinctions, respectively. Texas had the lowest rate of invasion with 1 spp/ha and Delaware had the highest invasion rate with 58 spp/ha. Extinction rate was greatest in Rhode Island with 69 spp/ha and lowest in Montana with 0.4 spp/ha. Values for ΔT_A (i.e., average change in turnover relative between neighboring states) ranged from –0.057 (New Mexico) to 0.609 (Rhode Island) with a mean of 0.244. New Mexico, Oregon, and Vermont were the only states with negative values for ΔT_A indicating increased faunal similarity with their neighbors in the future.

When we compare these measures of diversity grouped according to geographic zone (i.e., east and west of the 100^{th} meridian), the data become more revealing. Average historic species richness in the east exceeded historic richness in the west by an order of magnitude with 32 spp/ha and 4 spp/ha, respectively. The case was similar for future species richness with an average of 35 spp/ha in the east and 4 spp/ha in the west. On average, species richness increased by 3 spp/ha species in the east but essentially stayed the same among western states (i.e., mean of – 0.05 spp/ha). Both extinctions and invasions occurred more frequently in the east compared to the west with means of 8

spp/ha in the east and 1 spp/ha in the west for extinctions, and 11 spp/ha in the east and 2 spp/ha for invasions. Since the primary factors that contribute to turnover were greater in the east compared to the west, it is perhaps unsurprising that ΔT_A increases more in the east than in the west. Mean ΔT_A in the east was 0.278 with a standard deviation of 0.164 compared with a mean of 0.181 and a standard deviation of 0.135 in the west. Figure 1 clearly illustrates the distinction between eastern and western states. Although, all states (excluding NM, OR, and VT) become somewhat more distinct in the future, the primary distinction between east and west (as confirmed by our previously mentioned *t*-test) is that eastern states diverge most significantly from their neighbors, while western states diverge only slightly.

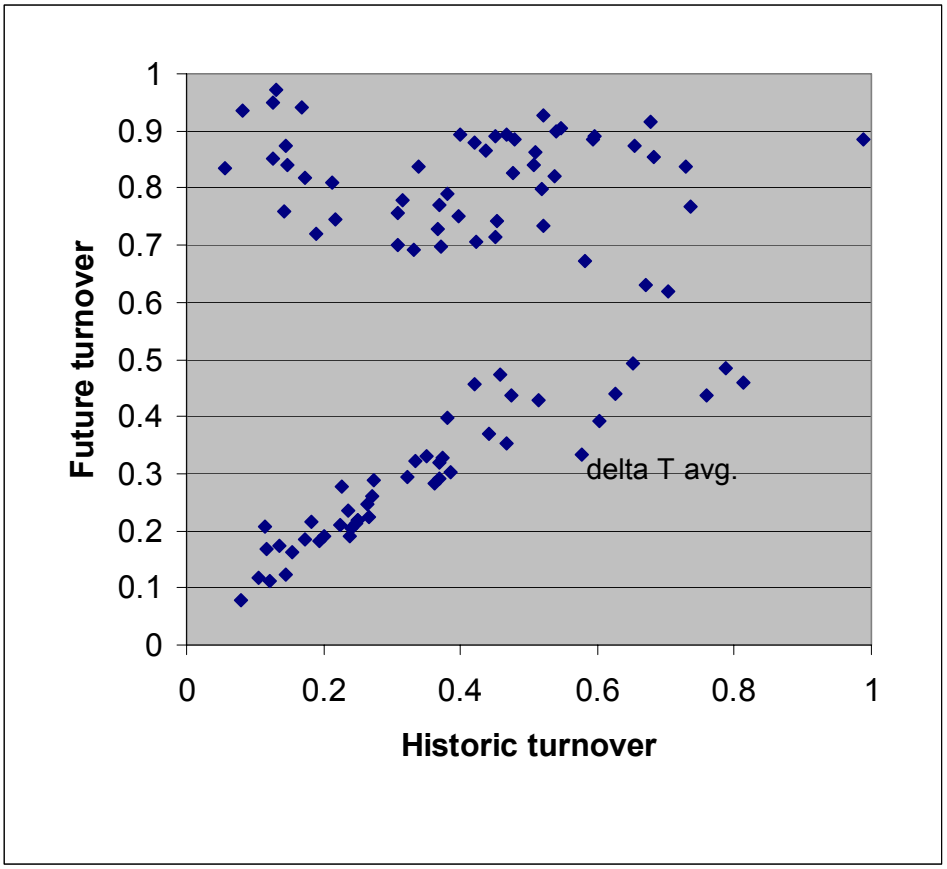


Figure 1. Scatter diagram of turnover values for state-state comparisons for all neighboring states.

Statistical Analysis

Once we confirmed the existence of a zonal trend in ΔT_A, our next challenge was to determine which of the primary components of turnover (i.e., extinctions, invasions, endemics, historic species richness) were driving differences in ΔT_A scores between zones. The logistic regression model indicated that only historic richness/state area correlated significantly with zone ($R^2 = 0.854$, Whole Model Logistic Likelihood X2 = 53.3, P <0.0001). That is, eastern states historically held many more species per hectare of land than did western states. Thus, the historically more species rich eastern states will likely diverge in faunal similarity in the future to a greater extent than the historically species sparse west.

Given that historic richness apparently buffers the turnover change in the future, our final challenge was to assess the degree to which physical, biological, and cultural factors influence ΔT_A . Specifically, we assessed the influence of mean annual precipitation, number of dams, degree of urbanization, and rate of cropland conversion for each state. We used stepwise multiple regression to determine which, if any, of these factors are predictive of ΔT_A. Only degree of urban change/area correlates significantly with ΔT_A (R2 = 0.10, ANOVA F = 6.5, df = 1, P = 0.014). Simply, as urbanization increases, ΔT_A increases.

DISCUSSION

Our findings that species richness and state-state turnover rates increased in the future was counter-intuitive to contemporary thought among conservation biologists (Lodge 1993, Mooney and Hobbs 1998, McKinney and Lockwood 1998) and at odds with Rahel's (2000) present state conclusions. After all, logic would tell us that augmenting highly diverse, co-evolved assemblages with a handful of cosmopolitan invaders, while coincidentally losing native species to extinction, would lead to a state of increased similarity among adjacent areas. In many state-state comparisons, we find just the opposite. Why does future species richness increase in all but three states? Why do nearly all state faunas within the

US appear to diverge from neighboring states in the future? And, why is this trend more drastic in the humid east than in the arid west?

Let's begin with the first and second questions since they are closely tied. Rosenzweig (2001) suggests that the current biodiversity crisis represents a transition from one steady-state to another. More simply, the world's flora and fauna are experiencing a period of rapid, human-enhanced, change in ecological and evolutionary history—the punctuation within the concept of punctuated equilibrium—that will ultimately come to a close when human pressures lessen or cease to exist and a new state of biodiversity is reached. During this period, he predicts that local areas will undergo boosts in biodiversity simply because invasions occur at a much faster rate than extinctions. Even in extreme cases where an alien species directly induces the extinction of a native species, the extinction process takes time to unravel, and for at least a period, the two species co-exist. On the other hand, species invasions can occur literally in an instant, for example, when invader-infested ballast water is released in a novel port or when a jetliner lands delivering ecological stowaways capable of colonizing new habitats. Indeed, our results indicate that the current proportion of exotic species within the freshwater fishes of the U.S. outweighs the proportion of current and predicted future extinctions, with exotics accounting for 18.2% of historic species richness and extinctions making up 14.1% of historic richness.

Whether or not this is the correct explanation of the increasing future richness and turnover rates we predict, there is a high level of uncertainty within the number of invasions we predict. Although we can assess extinction risk with a relatively high degree of certainty (e.g., Groombridge and Baillie, 1996), predicting which species will invade where and when remains largely a matter of ecological roulette. As previously mentioned, by retaining established as well as collected (but not established) non-native species, we may be over-estimating the extent of exotic species within future state faunas. Conversely, given the uncertainty in predicting species colonization, it is equally plausible that the future state faunas will hold an even greater proportion of non-native species. Therefore, assuming the probabilities of these uncertainties cancel one another,

we believe our estimates of future faunal composition are as close to reality as our currently level of knowledge with allow.

Assuming our results are indicative of Rosenszweig's boost in diversity, how do we explain the differences we see among eastern and western states? To answer this, we must tease apart the components of this transition from a historic biotic state of similarity to some future corresponding state. The primary factors that contribute to our estimates of future turnover include the rates of invasion and extinction, the degree of historic endemism, and the historic species richness within each distinct geographic region. As we have shown, endemism, invasions and extinctions, relative to state size, appear to be higher in the east compared to the west. Perhaps not surprising is the fact that historic turnover was on average 16% higher in the arid west than the humid east (i.e., averaging 0.48 and 0.32, respectively). Perhaps the most drastic difference in eastern and western states is historic richness, which was greater in the east by an order of magnitude.

Although some may find the species-area relationships for exotics particularly surprising, especially given the notoriety of inter-specific effects of invaders on native fishes of the west (e.g., see Marchetti et al. 2001, Rahel 2000, Moyle and Light, 1996), the underlying causes of this distinction may be obvious and, in fact, in line with the trend of historic richness. Turnover is historically higher in the west because there are relatively few species spread out over vast areas. Hydrologic connectivity between states may also be less in the west since states are generally larger and tributaries to larger rivers are often ephemeral, dependent on snowmelt or highly episodic rain events. In the east, climate moderates runoff resulting in more stable flows, a condition favoring species nad habitat diversification. Generally, there is more water within smaller states that are better connected by streams and rivers with major tributaries that typically flow year round. For example, the Tennessee River drainage encompasses 105,000 km^2 and drains portions of seven states. This compared to major drainages and biodiversity sinks in the west, such as the Rio Grande and the Columbia, which are more restricted in terms of the number of states they drain and by extreme seasonal runoff events. Further, freshwater assemblages of the

east are generally older allowing more time for speciation to occur. Changing sea level and Pleistocene glaciation have interrupted diversification of aquatic species in the west while sparing vast portions of the east (Abell et al. 2000). These processes have also contributed to the diversification of major habitat types in eastern states allowing for sustained development of eastern faunas.

Similarly, species-area relationships for exotics are likely influenced by the abundance and diversity of aquatic habitats in the east compared to the west. Further, McKinney (2001) concludes that species-area relationships for fishes correspond to human factors such as population—where there are more people there will be more exotics—and to the time elapsed since European colonization. It is logical to conclude that the same may be said for extinctions—the more human pressures, the more extinctions. Thus, we can conclude that in the future there will be greater differentiation in the east compared to the west, and that this is the result of is historic species richness, historic turnover, and effects associated with human population densities and conversion of non-paved natural areas to hardened urban landscapes (Weaver and Garman, 1994).

However, as Rosenzweig (2001) notes this increase in regional diversity (and therefore turnover) may well be a transient property, an artifact of a transition into the Homogocene. Although the characteristics and consequences that will ultimately shape this revised system may take centuries to develop, and we cannot predict what they will be, we can say with certainty that New Pangea, or in our case New America, will lack many of its unique and intriguing cast of characters and will contain a host of cosmopolitan species. Further, Rosenzweig suggests that New Pangea will be smaller in area due to loss of habitat, a factor that will ultimately influence species-area relationships and hence global diversity. Although we agree that global and regional diversity will ultimately decrease in the future, the view that this is due to a "loss of area" is an oversimplification.

To the contrary, global area is obviously conserved (i.e., assuming the volcanistic processes of subduction and adduction are in equilibrium), however

habitat is being converted from a diversity of types that support and are evolutionarily linked to a multitude of species, into a uniform monotony that benefits a relative few. In the case of America's freshwater fishes, physical homogenization of the environment through watershed urbanization, channelization of small streams, damming and/or diversions of stream flows, and alteration riparian corridors, sets the stage for the process of biotic homogenization.

Any effort to effectively halt or slow our journey toward a New Pangea will require a broad-based approach entailing paradigm shifts in social and political constructs. Our present-day toolbox for combating and managing the crisis has thus far proven inadequate. The doctrine established by various environmental laws, such as the Endangered Species Act (ESA) and the Clean Water Act (CWA), is limited in its ability regulate the comprehensive and long-term nature of biotic homogenization as it relates to America's freshwater fishes. Further, the process of biotic mixing is currently beyond the scope of regional differences in state water quality and water allocation laws. A handful of laws and policies exist to control exotic species (e.g., the Aquatic Nuisance Species Act), but because they fail to recognize biodiversity as a long-term and geographically diffuse process, they too fail to address the current crisis in any meaningful way. Clearly, society and the laws it has created tend to be reactionary and responds only to real or perceived threats that have already occurred. For example, the ESA is protective of species that are already imperiled. Until such time as a species becomes eminently at risk of extinction, it is afforded no protection under the ESA. Although the literature is full of references to the current biodiversity "crisis," the crisis is yet to gain the societal and political attention it deserves. While threats to species existence have long been the subject of public and political debate, the process of biotic homogenization and its potential consequences lies just beyond the current consciousness horizon of natural resource managers, the public, and politicians. Perhaps the most important key toward managing New Pangea lies with building better understanding and awareness of its prospect and underlying causes.

LITERATURE CITED

Abell, R. A. et al. 2000. Freshwater Ecoregions of North America: A Conservation Assessment. Island Press, Washington, D.C.

Duncan, J.R. and J.L. Lockwood. 2001 (a). Spatial homogenization of the aquatic fauna of Tennessee: extinction and invasion following land use change and habitat alteration. In: Lockwood, J.L. and M.L. McKinney (eds.). Biotic Homogenization. Klewer Academic/Plenum Publishers. New York.

Duncan, J.R. and J.L. Lockwood. 2001(b). Extinction in a field of bullets: a search for causes in the decline of the world's freshwater fishes. *Biological Conservation* 102:97-105.

Fuller, P.L., Nico, L.G. and J.D. Williams. 1999. Nonindigenous Fishes Introduced into Inland Waters of the U.S. American fisheries Society, Bethesda, MD.

Groombridge, B., and J. Baillie. 1997. 1996 IUCN Red List of Threatened Animals. IUCN Gland, Switzerland and Cambridge, UK.

Hobbs, R.J. and H. Mooney. 1998. Broadening the extinction debate: population deletions and additions in California and Western Australia. *Conservation Biology* 12:271-283.

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

Lockwood, J.L. and M.L. McKinney (eds.). 2001. Biotic Homogenization. Kluwer Academic/Plenum Publishers, New York.

Lodge, D.M. 1993. Biological Invasions: Lessons for Ecology. *Trends in Ecology and Evolution* 8:133-136.

Marchetti, M.P., Light, T., Feliciano, J., Armstrong, T., Hogan, Z., Viers, J. and P.B. Moyle. 2001. Homogenization of California's fish fauna through abiotic change. In: Lockwood, J.L. and M.L. McKinney (eds.). Biotic Homogenization. Klewer Academic/Plenum Publishers. New York.

McKinney, M.L. 1998. On predicting biotic homogenization: species-area patterns in marine biota. *Global Ecology and Biogeography Letters* 7:297-301.

McKinney, M.L. 2001. Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biological Conservation* 100:243-252.

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

Natureserve. 2000. Data for species and sub-species listing state distribution and conservation status obtained via Excel spreadsheets in June, 2000. Natureserve serves as a clearinghouse organization for biodiversity information and was previously associated with The Nature Conservancy.

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

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

Rosenzweig, M.L. 2001. The four questions: What does the introduction of exotic species do to diversity? *Evolutionary Ecology Research* 3:361-367.

Russel, G.J. 1999. Turnover dynamics across ecological and geological scales. In: McKinney, M.L. and J.A.Drake (eds). Biodiversity Dynamics. University of Columbia Press, New York.

United States Army Corps of Engineers. 2001. National Inventory of Dams.

United States Department of Agriculture. 2001. Economic Research Service. Online database of major land uses of the U.S. http://www.ers.usda.gov/data/majorlanduses/

Weaver, L.A., and G.C. Garman. 1994. Urbanization of a watershed and historical changes in a stream fish assemblage. *Transactions of the American Fisheries Society* 115:162-172.

Wilkinson, C.F. 1992. Crossing the Next Meridian: Water, Power, and the Future of the American West. Island Press. Washington, D.C.

Zar, J.H. 1984. Biostatistical Analysis. Prentice-Hall, Engle Cliffs, NJ.

APPENDIX

Table 1.

State	Zone	Average Change in Neighborhood Turnover	Area (1000ha)	Historic Richness/Area	Future Richness/Area	Extinctions/ Area	Invasions/ Area
NM	West	-5.73E-02	3.13E+04	-1.83E-06	2.62E-03	1.34E-03	1.66E-03
OR	West	-4.50E-02	2.49E+04	-1.81E-06	4.22E-03	5.23E-04	2.09E-03
VT	East	-2.80E-02	2.33E+03	-1.20E-05	4.29E-02	4.72E-03	9.87E-03
MT	West	4.88E-03	3.78E+04	1.29E-07	2.62E-03	3.97E-04	1.40E-03
NY	East	1.24E-02	1.22E+04	1.02E-06	1.26E-02	7.48E-03	5.01E-03
CA	West	3.29E-02	4.04E+04	8.13E-07	3.91E-03	7.18E-04	2.55E-03
TN	East	3.39E-02	1.06E+04	3.19E-06	2.08E-02	1.22E-02	3.77E-03
MS	East	6.69E-02	1.22E+04	5.49E-06	1.97E-02	3.04E-03	2.30E-03
AL	East	7.61E-02	1.32E+04	5.76E-06	2.21E-02	4.16E-03	1.74E-03
MO	East	9.98E-02	1.79E+04	5.58E-06	1.24E-02	2.13E-03	2.74E-03
ND	West	1.20E-01	1.79E+04	6.72E-06	4.92E-03	1.29E-03	1.62E-03
WY	West	1.47E-01	2.51E+04	5.85E-06	3.34E-03	1.19E-03	2.19E-03
KS	West	1.51E-01	2.12E+04	7.11E-06	6.97E-03	1.37E-03	2.35E-03
GA	East	1.72E-01	1.50E+04	1.15E-05	1.87E-02	5.19E-03	4.26E-03
UT	West	1.80E-01	2.12E+04	8.49E-06	3.81E-03	6.12E-04	2.97E-03
NJ	East	1.85E-01	1.94E+03	9.50E-05	4.94E-02	2.06E-02	1.85E-02
ID	West	1.90E-01	2.15E+04	8.83E-06	3.95E-03	7.91E-04	2.88E-03
IL	East	1.90E-01	1.44E+04	1.32E-05	1.49E-02	2.85E-03	3.76E-03
SD	West	2.00E-01	1.97E+04	1.02E-05	4.22E-03	2.13E-03	1.73E-03
KY	East	2.02E-01	1.04E+04	1.95E-05	2.36E-02	5.31E-03	5.31E-03
VA	East	2.05E-01	1.04E+04	1.98E-05	1.85E-02	1.06E-02	6.76E-03
IN	East	2.16E-01	9.32E+03	2.32E-05	2.17E-02	3.65E-03	4.50E-03
AZ	West	2.39E-01	2.95E+04	8.09E-06	3.15E-03	7.11E-04	2.74E-03
LA	East	2.50E-01	1.14E+04	2.19E-05	1.75E-02	2.11E-03	2.63E-03
PA	East	2.51E-01	1.17E+04	2.16E-05	1.32E-02	7.21E-03	4.55E-03
NC	East	2.65E-01	1.27E+04	2.09E-05	1.83E-02	6.70E-03	6.46E-03
CO	West	2.69E-01	2.69E+04	9.99E-06	4.60E-03	4.08E-04	3.16E-03
DE	East	2.79E-01	5.18E+02	5.38E-04	2.16E-01	5.79E-03	5.79E-02
NE	West	2.97E-01	1.99E+04	1.49E-05	4.11E-03	2.71E-03	2.41E-03
AR	East	2.97E-01	1.35E+04	2.20E-05	1.51E-02	1.86E-03	2.08E-03
WA	West	3.00E-01	1.74E+04	1.73E-05	4.78E-03	5.19E-04	2.13E-03
WV	East	3.16E-01	6.22E+03	5.08E-05	2.36E-02	1.05E-02	9.17E-03
MI	East	3.26E-01	1.48E+04	2.21E-05	1.08E-02	1.42E-03	2.84E-03
CT	East	3.27E-01	1.30E+03	2.52E-04	8.03E-02	1.54E-03	3.86E-02
MA	East	3.29E-01	2.07E+03	1.59E-04	5.21E-02	6.27E-03	2.65E-02
TX	West	3.32E-01	6.79E+04	4.90E-06	3.01E-03	1.41E-03	1.36E-03
IA	East	3.49E-01	1.45E+04	2.40E-05	1.07E-02	1.52E-03	2.48E-03

State	Zone	Average Change in Neighborhood Turnover	Area (1000ha)	Historic Richness/Area	Future Richness/Area	Extinctions/ Area	Invasions/ Area
NV	West	3.59E-01	2.85E+04	1.26E-05	3.51E-03	9.13E-04	2.70E-03
OK	West	3.60E-01	1.79E+04	2.01E-05	8.06E-03	3.92E-03	2.46E-03
MD	East	3.68E-01	2.59E+03	1.42E-04	5.44E-02	7.72E-03	1.93E-02
NH	East	3.69E-01	2.33E+03	1.58E-04	2.53E-02	1.20E-02	9.87E-03
MN	East	3.70E-01	2.07E+04	1.78E-05	7.82E-03	1.45E-03	2.36E-03
FL	East	3.80E-01	1.45E+04	2.62E-05	1.90E-02	1.93E-03	9.86E-03
OH	East	4.05E-01	1.06E+04	3.81E-05	1.26E-02	6.22E-03	4.14E-03
SC	East	5.35E-01	7.77E+03	6.89E-05	1.76E-02	5.66E-03	4.38E-03
WI	East	5.45E-01	1.40E+04	3.90E-05	9.94E-03	4.58E-03	3.50E-03
ME	East	6.07E-01	8.03E+03	7.56E-05	9.84E-03	9.96E-04	3.61E-03
RI	East	6.09E-01	2.59E+02	2.35E-03	1.85E-01	6.95E-02	5.02E-02
Min		**-5.73E-02**	**259.0016**	**-1.20E-05**	**2.62E-03**	**3.97E-04**	**1.36E-03**
Max		**6.09E-01**	**67858.42**	**2.35E-03**	**2.16E-01**	**6.95E-02**	**5.79E-02**
Avg		**2.44E-01**	**16004.14**	**9.12E-05**	**2.39E-02**	**5.37E-03**	**7.66E-03**
Stdev		**1.60E-01**	**12129.88**	**3.45E-04**	**4.06E-02**	**1.03E-02**	**1.20E-02**
EastMin		**-2.80E-02**	**5.18E+02**	**-1.20E-05**	**7.82E-03**	**9.96E-04**	**1.74E-03**
EastMax		**6.09E-01**	**4.04E+04**	**5.38E-04**	**2.16E-01**	**6.95E-02**	**5.79E-02**
EastAvg		**2.78E-01**	**1.72E+04**	**2.94E-05**	**3.47E-02**	**7.64E-03**	**1.06E-02**
EastStdev		**1.64E-01**	**9497.649**	**9.61E-05**	**4.73E-02**	**1.22E-02**	**1.41E-02**
WestMin		**-5.73E-02**	**2.59E+02**	**4.90E-06**	**2.62E-03**	**3.97E-04**	**1.36E-03**
WestMax		**3.60E-01**	**6.79E+04**	**2.35E-03**	**8.06E-03**	**3.92E-03**	**3.16E-03**
WestAvg		**1.81E-01**	**1.38E+04**	**2.04E-04**	**4.22E-03**	**1.23E-03**	**2.26E-03**
WestStdev		**1.35E-01**	**15961.44**	**5.58E-04**	**1.43E-03**	**9.31E-04**	**5.55E-04**

Table 2.

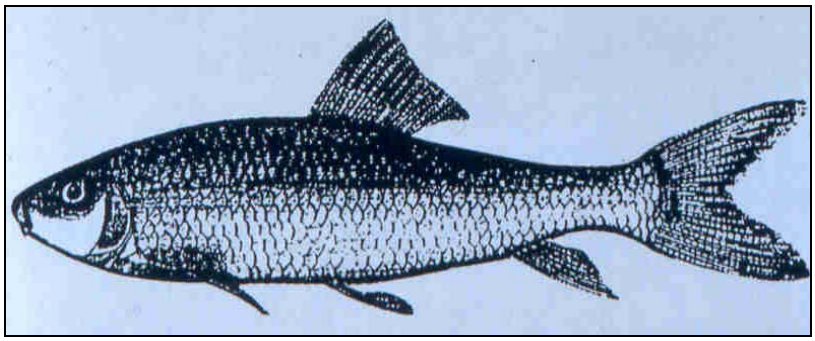
State	Zone	Population/ Area	Endemics/ Area	Urban change/ Area	Cropland Change/ Area	Dams/ Area	Median Precip (inches)
AL	East	3.18E-04	1.14E-03	5.48E-02	-1.20E-01	1.59E-01	60.11
AR	East	1.86E-04	3.71E-04	2.34E-02	8.35E-03	8.76E-02	58.83
CT	East	2.55E-03	0.00E+00	2.03E-01	-9.53E-02	5.58E-01	51.07
DE	East	1.37E-03	0.00E+00	1.02E-01	7.81E-04	1.18E-01	47.07
FL	East	9.65E-04	3.45E-04	9.46E-02	1.74E-02	5.36E-02	66.80
GA	East	4.73E-04	3.33E-04	4.77E-02	-7.31E-02	2.80E-01	64.65
IA	East	1.93E-04	0.00E+00	1.08E-02	2.04E-02	1.91E-01	43.31
IL	East	8.21E-04	0.00E+00	4.18E-02	4.15E-02	8.79E-02	45.59
IN	East	6.22E-04	0.00E+00	4.28E-02	9.13E-02	1.18E-01	58.03
KY	East	3.67E-04	3.86E-04	2.44E-02	-1.91E-02	1.11E-01	47.10
LA	East	3.77E-04	0.00E+00	3.35E-02	1.67E-02	3.20E-02	70.09
MA	East	2.90E-03	0.00E+00	2.07E-01	-1.97E-01	7.56E-01	46.98
MD	East	1.93E-03	3.86E-04	1.68E-01	-6.47E-02	1.05E-01	45.18
ME	East	1.62E-04	1.25E-04	2.44E-02	-2.16E-02	8.08E-02	49.35
MI	East	6.43E-04	1.35E-04	3.41E-02	-4.21E-02	5.96E-02	39.83
MN	East	1.30E-04	0.00E+00	1.88E-02	3.75E-03	4.39E-02	29.67
MO	East	2.57E-04	2.24E-04	2.36E-02	-4.49E-02	2.31E-01	54.46
MS	East	4.35E-04	2.46E-04	2.31E-02	-1.14E-02	2.72E-01	65.17
NC	East	5.59E-04	4.73E-04	4.52E-02	-1.70E-02	2.32E-01	76.15
NH	East	6.43E-04	4.29E-04	5.47E-02	-7.03E-02	2.76E-01	76.23
NJ	East	5.66E-04	0.00E+00	1.98E-01	-1.70E-01	3.87E-01	52.87
NY	East	1.49E-03	0.00E+00	4.48E-02	1.03E-01	1.62E-01	49.85
OH	East	1.05E-03	9.42E-05	6.63E-02	-1.31E-02	1.60E-01	43.89
PA	East	1.04E-03	0.00E+00	4.28E-02	-8.60E-02	1.21E-01	48.68
RI	East	3.86E-03	0.00E+00	1.83E-01	-6.41E-02	7.14E-01	47.15
SC	East	4.63E-04	3.86E-04	4.74E-02	-1.31E-01	3.04E-01	61.19
TN	East	4.90E-04	1.60E-03	5.58E-02	-6.16E-02	9.42E-02	70.06
VA	East	6.27E-04	2.90E-04	5.64E-02	-3.24E-02	1.53E-01	47.15
VT	East	2.49E-04	4.29E-04	1.28E-02	-2.44E-01	1.52E-01	57.93
WI	East	3.65E-04	0.00E+00	2.05E-02	-2.43E-02	4.77E-02	37.04
WV	East	2.90E-04	0.00E+00	9.38E-03	-1.83E-01	9.25E-02	51.76
AZ	West	1.42E-04	2.37E-04	2.33E-02	2.06E-02	1.08E-02	29.50
CA	West	7.77E-04	8.17E-04	4.47E-02	1.03E-02	3.69E-02	76.77
CO	West	1.37E-04	0.00E+00	1.45E-02	3.53E-02	6.13E-02	47.27
ID	West	4.65E-05	1.40E-04	3.24E-03	4.84E-02	1.88E-02	41.57
KS	West	1.18E-04	0.00E+00	9.66E-03	5.32E-02	2.76E-01	35.90
MT	West	2.30E-05	0.00E+00	1.57E-03	7.25E-02	7.57E-02	29.24
ND	West	3.58E-05	0.00E+00	1.92E-03	1.27E-03	3.34E-02	21.00
NE	West	8.02E-05	0.00E+00	3.13E-03	-7.28E-03	1.04E-01	35.41
NM	West	2.52E-04	1.60E-04	6.70E-03	-5.06E-02	1.29E-02	31.73
NV	West	5.62E-05	4.91E-04	1.10E-02	-2.39E-02	1.75E-02	29.52

State	Zone	Population/ Area	Endemics/ Area	Urban change/ Area	Cropland Change/ Area	Dams/ Area	Median Precip (inches)
OK	West	1.85E-04	0.00E+00	2.91E-02	-1.03E-01	2.59E-01	45.75
OR	West	1.25E-04	3.22E-04	7.55E-03	8.95E-03	3.28E-02	86.11
SD	West	3.66E-05	0.00E+00	1.75E-03	1.54E-03	1.20E-01	25.66
TX	West	2.74E-04	5.31E-04	2.96E-02	-3.37E-02	1.03E-01	55.51
UT	West	8.95E-05	1.41E-04	6.75E-03	-1.91E-04	2.97E-02	54.94
WA	West	3.11E-04	2.31E-04	2.62E-02	5.92E-02	3.90E-02	93.59
WY	West	1.91E-05	3.98E-05	2.75E-03	2.50E-03	5.38E-02	28.37
Min		**1.91E-05**	**0.00E+00**	**1.57E-03**	**-2.44E-01**	**1.08E-02**	**21.00**
Max		**3.86E-03**	**1.60E-03**	**2.07E-01**	**1.03E-01**	**7.56E-01**	**93.59**
Avg		**6.06E-04**	**2.19E-04**	**4.66E-02**	**-2.89E-02**	**1.57E-01**	**50.64**
Stdev		**7.81E-04**	**3.15E-04**	**5.50E-02**	**7.30E-02**	**1.64E-01**	**16.11**
EastMin		**1.30E-04**	**0.00E+00**	**9.38E-03**	**-2.44E-01**	**3.20E-02**	**29.67**
EastMax		**3.86E-03**	**1.60E-03**	**2.07E-01**	**1.03E-01**	**7.56E-01**	**76.23**
EastAvg		**8.51E-04**	**2.38E-04**	**6.50E-02**	**-4.78E-02**	**2.01E-01**	**53.65**
EastStdev		**8.73E-04**	**3.53E-04**	**6.06E-02**	**7.93E-02**	**1.82E-01**	**11.27**
WestMin		**1.91E-05**	**0.00E+00**	**1.57E-03**	**-1.03E-01**	**1.08E-02**	**21.00**
WestMax		**7.77E-04**	**8.17E-04**	**4.47E-02**	**7.25E-02**	**2.76E-01**	**93.59**
WestAvg		**1.59E-04**	**1.83E-04**	**1.31E-02**	**5.58E-03**	**7.55E-02**	**45.16**
WestStdev		**1.83E-04**	**2.37E-04**	**1.28E-02**	**4.35E-02**	**7.95E-02**	**21.78**

PART IV

SPATIAL HOMOGENIZATION OF THE AQUATIC FAUNA OF TENNESSEE:

Extinction and Invasion Following Land Use Change and Habitat Alteration



The extinct harelip sucker, *Lagochila lacera* (Modified from Etnier and Starnes,1993).

Part III is presented as a slightly revised version that appears as chapter12 under the same title in the book, "Biotic Homogenization" published in 2001 and edited by J.L. Lockwood and M.L. McKinney:

Duncan, J.R. and J.L. Lockwood. 2001. Spatial homogenization of the Aquatic Fauna of Tennessee: Extinction and Invasion Following Land Use Change and Habitat Alteration. In: Lockwood, J.L. and M.L. McKinney (eds.). Biotic Homogenization. Klewer Academic/Plenum Publishers, New York. ISBN 0-306-46542-6.

My use of "we" in this chapter refers to the collaboration of my co-author and myself. This paper originated in part as a presentation and discussion topic of a graduate seminar on biotic homogenization in fall, 1998. My contribution to the chapter includes (1) selection of the topic and development of the problem into a work relevant to the central core of this dissertation, (2) acquisition and compilation of most of the data, (3) data analysis and interpretation, and (4) the majority of the writing. I wish to express my gratitude to my co-author, Dr. Julie L. Lockwood, for her assistance and guidance throughout the development of this work.

INTRODUCTION

One of the most profound legacies of modern society is the global transformation of the world's flora and fauna due to biotic homogenization (McKinney and Lockwood 1999, Lockwood et al. In press). The systematic loss of vulnerable taxa to extinction is a common theme in our discussions of aquatic ecosystems (Allan and Flecker 1993). Similarly, increasing rates of invasion of fresh- and saltwater communities by non-native species continue to invoke social, economic, and ecological consequences (Carlton 1996, 1992). Together, the sum of simultaneous human-facilitated extinction and invasion has resulted in the non-random homogenization of aquatic faunas worldwide. Certain higher taxa (e.g., families) may be more likely to become extinct or to invade novel

territories than would be predicted by chance (Angermeier 1995, McKinney 1998, Lockwood 1999). This non-random pruning and geographic rearranging of the aquatic and marine evolutionary tree has resulted in the loss of diversity among higher taxa as well as a loss of global species richness (McKinney and Lockwood 1999).

An equally important component to biotic homogenization is the decline of diversity among historically distinct faunas (Harrison 1993). Historically, restriction of species ranges has resulted from a host of factors including physical isolation (e.g., mountain ranges), evolutionary isolation (e.g., speciation, co-evolution), and ecological isolation (e.g., inter-specific competition, habitat requirements) (Huston 1994). These isolating pressures inevitably produce regionally distinct communities. In the face of habitat alterations, land use changes, and taxonomic homogenization, the effects of isolating pressures have lessened such that formerly distinct regional communities tend to resemble one another more so than if the isolating boundaries were still functional (Lodge 1993). If one combines the loss of isolation with the loss of endemic species, ecological similarity between formerly unique regions increases. Here, we explore the fate of the freshwater fish, mussels, and amphibians of Tennessee in order to understand how human activities have spatially homogenized this biologically unique region.

THE ECOREGIONS OF TENNESSEE AND THEIR INFLUENCE ON FRESHWATER FAUNA

Tennessee boasts what is perhaps the most diverse assemblage of freshwater aquatic organisms in North America (Etnier and Starnes 1993). Contributing to its diversity is the juxtaposition of major ecoregions that transect the state (Griffith et al. 1997). Ecoregions are classified hierarchically according to spatial patterns and composition among biotic and abiotic factors including geology, physiography, hydrology, land use, soils, vegetation, and wildlife. Ecoregions are identified at four levels of resolution corresponding to Roman numerals I-V. Beginning at the coarsest level (i.e., Level I), North America

contains 15 major ecoregions, and at a slightly higher resolution (Level II), North America is divided into 51 ecoregions. Griffith et al. (1997) subdivides Tennessee into seven Level III and 25 Level IV ecoregions. In this study, we used Level III resolution since it was broad enough to allow mapping of species ranges from existing atlases, yet specific enough to depict a gradient of landscape types across Tennessee. From west to east, the seven Level III ecoregions of the state include the Coastal Plains (CP), the Western Highland Rim (WHR), the Nashville Basin (NB), the Eastern Highland Rim (EHR), the Cumberland Plateau (CuP), the Ridge and Valley (RV), and the Blue Ridge Mountains (BR) (Figure 1).

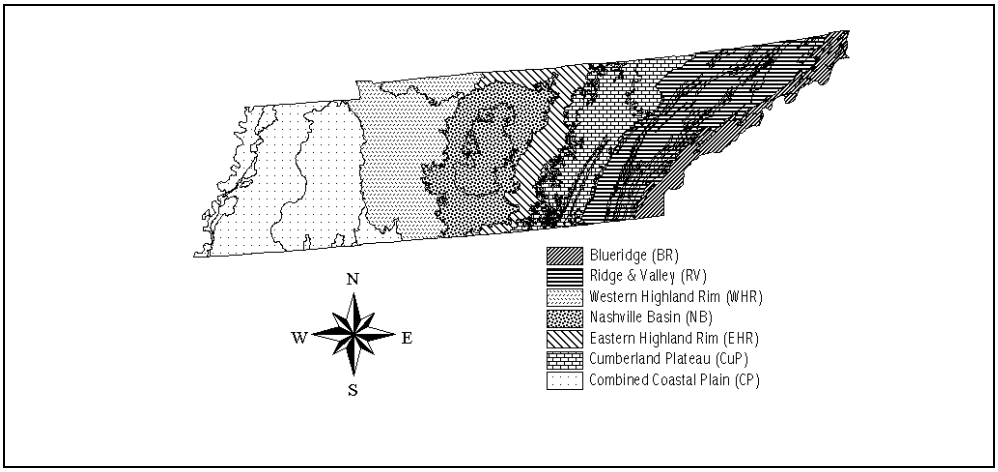


Figure 1. Ecoregions of Tennessee as presented by Griffith et al. 1997.

It should be noted that some authors (e.g., Etnier and Starnes 1993) have characterized Tennessee's landscape using physiography. Physiographic provinces contained within Tennessee are very similar to the ecoregions of Griffith et al. (1997); however, the Eastern and Western Highland Rim regions are combined to make one physiographic region called the Highland Rim (HR) encircling the Nashville Basin. In this analysis, we retained Etnier and Starnes use of physiography in determining distribution of fishes; however, we used ecoregions based on Griffith et al. (1997) in assessing the ranges of mussels and amphibians. Regardless of the classification scheme, Tennessee's geographic situation, that of extending across multiple and distinct environmental regions,

has not only produced a diverse aquatic fauna but also provides an intriguing setting for analyzing the spatial dynamics of biodiversity.

Examining major taxa such as fish, mussels, and amphibians illustrates the richly diverse aquatic ecosystems of Tennessee. Of fish alone, Tennessee's waters harbor 29 families within 18 orders, accounting for 293 species, most within the Percidae (darters and perches, 93 spp.) and Cyprinidae (minnows, 83 spp.)(Etnier and Starnes, 1993). Parmalee and Bogan (1998) report approximately 150 species of freshwater mussels, 17 of which are believed to be extinct. Among amphibians, Tennessee contains 66 species in seven families within two orders. Over the past 65 years, the actions of such federal agencies as the Tennessee Valley Authority and United States Army Corps of Engineers have resulted in impounding virtually all of the medium to high order rivers in state (Etnier and Starnes 1993). The effects of these impoundments, exacerbated by silt from development, nutrient rich run-off from farming, acid mine drainage, and stresses of impervious surfaces due to urban sprawl have led to the federal or state listing of 51 fish, 39 mussels, and 12 amphibians as endangered, threatened, or in need of management (TDEC 1999).

In this analysis, we quantify the number of aquatic species within each ecoregion based on information published in Etnier and Starnes (1993) for fish, Parmalee and Bogan (1998) for mussels, and Redmond and Scott (1996) for amphibians. With the exception of fish, information on conservation status for each taxon was obtained from the Tennessee Department of Environment and Conservation (TDEC 1999). Conservation status for fish was extracted from Etnier and Starnes (1993). For a more detailed account of ecoregion descriptions, refer to Griffith et al. (1997).

QUANTIFYING SPATIAL DIVERSITY

Quantifying spatial homogenization of aquatic species across the ecoregions of Tennessee requires calculating within–ecoregion and between–ecoregion diversity. Within–ecoregion diversity is measured by simply tallying the number

of species whose ranges are contained within a particular ecoregion. Between–ecoregion diversity is much more complex to calculate. Several authors have used slightly different formulas to answer various questions (e.g., Whittaker 1960, Cody 1986, MacArthur 1965) resulting in a hodge-podge of formulas (all typically called 'beta' diversity) each saddled with their own assumptions (Shmida and Wilson 1985, Huston 1994).

We followed the method of Russell (1999) by defining between–ecoregion changes in diversity simply as spatial turnover. Spatial turnover can be calculated in exactly the same way as temporal turnover and is useful for comparing any kind of community difference in species composition (Russell 1999). Spatial turnover is measured by tallying the number of species "lost" or "gained" as one moves from one location to another along a spatial continuum. The resultant value is then standardized to the size of the community. We have slightly modified Russell (1999) to obtain the following formula for spatial turnover, $T_S = (G_S + L_S)/\alpha$, where S is a given ecoregional comparison (i.e., the spatial extent under consideration), G_S is the number of species found in the first ecoregion but not the second, L_S is the number of species found in the second ecoregion but not the first, and α is the total number of species found within both. Thus, T_S reflects the degree of faunal similarity between two adjacent ecoregions. (Note: Russell (1999) calculates α for each community separately and then adds the two together to arrive at the denominator. Our slight modification to Russell's method is that we sum the total number of species in both communities collectively. Thus, we do not over-inflate the denominator by counting species that are present in both communities more than once.)

Spatial turnover will be high if the two ecoregions have evolved largely separate faunas due to ecological or physiographic isolation (e.g., drastically different habitat types, watershed divides). These pressures increase as the distance between ecoregions increases, resulting in greater and greater turnover values. We limit our ecoregion comparisons to only those adjacent to one another, thus minimizing this effect. Spatial turnover will be low if the ecoregions have many species in common. This latter scenario can be due to

several natural reasons including historic stream capture, waterway connections, regular catastrophic flooding, climatic fluctuations, or merely by accident. It can also result from intentional or accidental widespread release of exotic species, or anthropogenic waterway connections (e.g., the Tenn-Tom Waterway, the Saint Lawrence Seaway, etc.).

Following Harrison (1993) we calculated within– and between–ecoregion diversity at two different temporal states in order to understand how extinction and invasion are shaping regional faunas. The first temporal state is a historical scenario where all species that are believed to be extinct or locally extirpated are still extant and introduced species do not exist. This is intended to represent what the faunal assemblage may have been prior to significant human disturbance. The second temporal state is an estimated future scenario where extinct or locally extirpated species as well as those listed by federal or state agencies as threatened, endangered, or vulnerable are omitted from the data set. We make the assumption that future conservation measures, if taken for a given species, will be ineffective in saving the species from future decline. That is not to say that we believe all species currently deemed imperiled to some degree will ultimately become extinct. Likely, some will continue to survive; however, their survival as rare species will contribute negligibly to ecological and evolutionary processes in the future.

Although numerous species-level and some ecosystem-level conservation efforts are underway (and some have been successful), the pressures of an ever-increasing human population combined with detrimental land use practices, make the long term prognosis for Tennessee's aquatic fauna appear bleak. Further, because exotic species can sometimes be controlled but rarely if ever eliminated from their novel environs, we include all currently established exotic species within the future scenario. We consider this a conservative approach to predicting the future of biological invasions. The number of non-native aquatic species is likely to increase in the future (Etnier and Starnes 1993) within Tennessee waters; however, it is difficult to predict which species will invade and which ecoregions will be invaded.

RESULTS

We begin by comparing historic and future statewide and within–ecoregion diversity values. A summary for the changes in within–ecoregion diversity for each taxon is provided in Table 1 (see appendix). Statewide diversity decreased for all taxonomic groups (12% for fish, 43% for mussels, and 18% for amphibians) when comparing historic and future scenarios. Currently, more than a quarter (25.7%) of the state's mussel species are vulnerable to extinction, as are nearly one-fifth of fish and amphibian species (17.4% and 18.2%, respectively). Twenty-two of the state's present-day 294 species of fish are considered exotic (7.5%) as are three of 136 mussels (2.2%). There are no known exotic amphibians established within the borders of Tennessee. There are believed to be at least two fish species that formerly inhabited the Tennessee River basin that are now extinct. The white-line topminnow (*Fundulus albolineatus*) is known only from about 20-25 specimens collected at Big Spring near Huntsville, Alabama (Etnier, pers. comm.) on the lower bend of the Tennessee River. It is not included in the historic fauna of the state of Tennessee and was excluded from our analysis. Conversely, the harelip sucker (*Lagochila lacera*) is believed to have been widespread throughout several major drainages in eastern North America including the Tennessee and Cumberland until the late nineteenth century. No modern records of it are known and it is almost surely extinct. Etnier and Starnes (1993) provides thorough summary of its former distribution in Tennessee. While many species of amphibians are considered vulnerable to extinction, we know of none that have already vanished from the state's fauna.

Unlike fishes and amphibians, freshwater mussels leave behind fossil evidence in the form of shells when they perish. As a result, it is known that at least 16 species (10.4%) no longer inhabit the waters of Tennessee. Future within–ecoregion diversity decreased for nearly all taxa and ecoregions when compared to historic values. Exceptions included fish in Cumberland Plateau and Blue Ridge where within–ecoregion diversity increased by 1.9% and 7.3%, respectively, and mussels in the Coastal Plain where it increased by 5.7%. The Ridge and Valley ecoregion displayed the largest decline in within–ecoregion

diversity among fish and mussels, dropping in total species richness from 160 to 148 for fish (representing an 8% loss), and from 106 to 45 (a 58% loss) in mussel species. This ecoregion has the highest number of vulnerable fishes (24) and mussels (31), but ranks among the lowest in the percentage of exotic species among these two groups (8% and 2%, respectively). Among amphibians, the largest decrease was in the Blue Ridge where species richness dropped from 50 to 42 species, a 16.0% decline.

Between–ecoregion diversity, or spatial turnover, decreased for all taxa/ecoregion combinations excluding amphibians between the Coastal Plain and Western Highland Rim where it increased by 38.8% (Table 2, see appendix). Statewide, average spatial turnover decreased for all groups, ranging from a 16% drop in fishes to a 20% drop in amphibians. Maximum declines in spatial turnover among amphibians and fish occurred between the Cumberland Plateau and the Ridge and Valley where amphibian turnover dropped 62.4%, and fish turnover decreased by 23.3%. The maximum decrease in spatial turnover among mussels occurred between the Cumberland Plateau and the Eastern Highland Rim with a 35.4% decrease. Historically, spatial turnover is relatively low for mussels and amphibians indicating a high level of faunal similarity between ecoregions; however, a clear trend of increasing spatial turnover exists among historical fish faunas moving from west to east across the state. This large break in fish faunal similarity is particularly apparent as one moves from the Highland Rim ecoregion into the Cumberland Plateau. This rapid turnover in fish species continues as one moves eastward. Overall, if we assume that vulnerable taxa will ultimately become extinct and exotic species will continue to thrive, then it appears that the ecoregions of western Tennessee will continue to support aquatic fauna that maintain a high degree of similarity. That said, it is equally true that the historically diverse faunas of central and eastern Tennessee will lose their distinctiveness.

DISCUSSION

Tennessee maintains a rich aquatic natural heritage, the face of which has been drastically altered largely as the result of human activities throughout the twentieth century. Mussels appear to be taking the brunt of the punishment. The loss of mussels from Tennessee and neighboring states stands among the most alarming extinction events in modern history (Williams et al. 1992). This loss of mussels, and other aquatic organisms, is primarily the result of the construction of numerous dams, primarily from 1935 on, that rapidly converted dynamic and complex flowing systems to a series of sluggish reservoirs lacking in habitat diversity. Today, most of the state's medium-sized rivers are entombed by reservoirs (Etnier 1997), leaving their habitats and faunas extremely vulnerable to extinction. In addition, poor (and largely unregulated) agricultural and silviculture practices, in tandem with the effect of urban sprawl, continue to destroy isolated spring habitats and headwater creeks (Etnier 1997).

Unlike traditional assessments of biodiversity, biotic homogenization is an attempt to better understand the entire effect on a given fauna by including both species decline and invasions. By including exotic species in our analysis of species declines, fish diversity remains comparatively high with respect to amphibians and (especially) mussels. As Marchetti et al. (2001) point out, the inclusion of exotics in standard biodiversity calculations complicates our view of how to interpret such measures. For example, Marchetti et al. conclude that the introduction of novel species appears to be a driving force behind biotic homogenization among California's fish fauna. This provides and intriguing contrast to our results in that there are comparatively few exotics among Tennessee's aquatic fauna, an undoubted artifact of being an inland state. The aquatic fauna of Tennessee still decreases in biodiversity when we include exotic species in our counts; however, it tends to mask the loss of regional distinctiveness (see below).

On a non-political spatial scale (i.e., ecoregions), future losses in species diversity are non-random in that they are not spread evenly through space.

Within the Cumberland Plateau and Blue Ridge ecoregions, future fish diversity actually increased. In this ecoregion, lost fishes are 'replaced' by exotic fishes. However, this is not a niche-for-niche ecological replacement. That is, most fish that are lost inhabit medium-sized rivers or small springs whereas most exotics live in lentic systems (Etnier 1997), making the long-term effect of homogenization a spatially non-random event. In short, we are witnessing a transition from flowing water habitats to standing water habitats (i.e., lotic systems are replaced by quasi-lentic impoundments). This change in habitat is, to a degree, mirrored by a change from lotic-adapted to lentic-adapted species and a wholesale replacement of functional groups, community structure, and ecological dynamics.

Similarly, mussel diversity increased in the future within the Coastal Plain. This can be attributed in part to the fact that mussel diversity is generally low in this ecoregion relative to the remainder of the state and that no species are listed as vulnerable to extinction. Hence, the primary long-term impact on this fauna will likely be due to exotic species. Of course, because the fauna is historically few in number, inter-specific interactions such as interference competition with zebra mussels, may induce extinction particularly for those species which may be inherently rare.

Most future losses in diversity occur within the Ridge and Valley ecoregion for mussels and fish and within the Blue Ridge for amphibians. We discuss the possible causes of sharp declines in diversity within the Ridge and Valley below. Among amphibians, future drops in within–ecoregion diversity generally increased in magnitude from west to east. The reason for this trend is unclear but may be related to habitat complexity. Western ecoregions are characterized by large, sluggishly flowing systems (similar to reservoirs). In the east, habitats are more variable and include numerous seeps, springs, and small creeks. As this habitat variety is diminished, species that are co-evolved for a narrow range of habitat types are lost first.

Finally, in almost all ecoregional comparisons and across all taxa, future spatial turnover decreases. Maximum decreases in amphibian and fish spatial turnover occurred between the Cumberland Plateau and Ridge and Valley ecoregions. Most of this decrease may be attributed to the large projected future declines in amphibian and fish diversity within the Ridge and Valley ecoregion. A very small portion of this ecoregion contains the unique Consasauga watershed. The headwater forests of this watershed remain largely untouched (Etnier and Starnes 1993); thus, this region contains the last stronghold of several threatened fish and amphibians (and mussels). If we assume these unique species do not survive into the future, spatial turnover inevitably drops. This suggests that if we were to know the pre-impoundment fauna of the Mississippi and Tennessee watersheds (i.e. the primary river systems that make up the remaining ecoregions) the future decrease in spatial turnover within other ecoregion comparisons would have likely been greater.

For mussels, maximum decreases in spatial turnover occur between the Eastern Highland Rim and the Cumberland Plateau. The Cumberland Plateau region suffers from a recent and continued history of extreme land use change, most notably the presence of coal mining. A particularly devastating result has been the strip-mining of many of the region's watersheds over the last 30 years. In some cases, strip-mining has resulted in the virtual elimination of a watershed's aquatic fauna (Etnier and Starnes 1993). Today, acid mine drainage is a limiting factor in addition to continued strip-mining. The loss of several unique species within this ecoregion, combined with similarly high losses in the Eastern Highland Rim, essentially leaves a depauperate mussel fauna of broadly adapted, wide ranging species that can successfully survive in highly altered waterways (Parmalee and Bogan 1998).

The presence of several spatially common exotic fish and mussels further drives future turnover values down. With an increase in commercial river traffic, intentional sport fish stocking, and the dumping of bait buckets, several exotic fish and mussels have colonized almost all of Tennessee's ecoregions. This is very apparent among the fishes. Sport fishes such as rainbow trout

(*Oncorhynchus mykiss*) are intentionally stocked throughout Tennessee waters. An entire suite of minnows (family Cyprinidae) has been transported as bait fish, and the ever-ubiquitous goldfish (*Carassius auratus*) has become well established probably as an intentionally released aquarium fish. These exotic fishes decrease the spatial diversity of Tennessee's waterways simply by existing throughout the state. However, they may further decrease spatial diversity by directly causing the decline of many of their native congeners either by predation or competition (Etnier and Starnes 1993).

The main impact of aquatic habitat alteration and land use change on Tennessee waters has been the loss of regional faunal distinction and an overall decrease in species richness. To appreciate such an effect may significantly aid our efforts to offset the current extinction crisis; however, to do so takes a broader view than that of traditional population-based conservation biology. By adopting a landscape– or watershed–based perspective toward land management, planning, and species conservation, we may be able to stabilize and avert future damage. Measuring diversity between–ecoregions (i.e., calculating spatial turnover) can not only determine whether regional faunas are increasing or decreasing in similarity, it can also identify conservation "hotspots" whereby efforts can be targeted toward specific local regions.

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LITERATURE CITED

Allen, J.D. and A.S. Flecker. 1993. Biodiversity conservation in running waters: identifying the major factors that affect destruction of riverine species and ecosystems. *Bioscience* 43:32-43.

Angermeier, P.L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. *Conservation Biology* 9:143-158.

Carlton, J.T. 1992. Dispersal of living organisms into aquatic ecosystems as mediated by aquaculture and fisheries activities. In Rosenfield, A. and R. Mann (eds.) Dispersal of Living Organisms into Aquatic Habitats. Maryland Sea Grant Publication, College Park, Maryland.

Carlton, J.T. 1996. Biological invasions and cryptogenic species. *Ecology* 77:1653-1655.

Cody, M.L. 1986. Diversity, rarity, and conservation in Mediterranean-climate regions. In Soule, M.E. (ed.). Conservation Biology: the science of scarcity and diversity. Sinauer Associates Inc. Sunderland, MA.

Etnier, D.A. 1997. Jeopardized southeastern freshwater fishes: A search for causes. In Benz, G.W. and D.E Collins (eds.). Aquatic Fauna in Peril. Southeast Aquatic Research Institute, Decatur, GA.

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

Griffith, G.E., Omernik, J.M., and S.H. Azevedo. 1997. Ecoregions of Tennessee. EPA/600/R-97/022. Western Ecology Division, National Health and Environmental effects Research Laboratory, U.S. Environmental Protection Agency, Corvalis, Oregon.

Harrison, S. 1993. Species diversity, spatial scale, and global change. In Karieva, P., Kingslover, J.G., and R.B. Huey (eds.). Biotic interactions and global change. Sinauer Associates Inc. Sunderland, MA.

Huston, M.A. 1994. Biological diversity : the coexistence of species on changing landscapes. Cambridge University Press. New York.

Lockwood, J.L. 1999. Using taxonomy to predict success among introduced avifauna: relative importance of transport and establishment. *Conservation Biology* 13: 560-567.

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

MacArthur, R.H. 1965. Patterns of species diversity. *Biological Review* 40: 510-533.

Marchetti, M.P.; Light, T.; Feliciano, J.; Armstrong, T.; Hogan, Z.; Viers, J.; and P.B. Moyle. 2001. Homogenization of California's fish fauna through abiotic change. In: Lockwood, J.L. and M.L. McKinney (eds.). Biotic Homogenization. Klewer Academic/Plenum Publishers. New York.

McKinney, M.L. 1998. On predicting biotic homogenization: species-area patterns in marine biota. *Global Ecology and Biogeography Letters* 7:297-301.

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

Parmalee, P.W. and A.E. Bogan. 1998. The Freshwater Mussels of Tennessee. University of Tennessee Press. Knoxville, Tennessee.

Redmond, W.H. and A.F. Scott. 1996. Atlas of Amphibians in Tennessee. Miscellaneous Publication Number 12, The Center for Field Biology, Austin Peay State Univesity. Clarksville, Tennessee.

Russell, G.J. 1999. Turnover dynamics across ecological and geological scales. In: McKinney, M.L. and J.A. Drake (eds.) Biodiversity dynamics: turnover of populations, taxa, and communities. Columbia University Press, New York.

Shmida, A. and M.V. Wilson. 1985. Biological determinants of species diversity. *Journal of Biogeography* 12:1-20.

Tennessee Department of Environment and Conservation: Division of Natural Heritage website http://www.state.tn.us/environment/nh/

Whittaker, R.H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs* 30:279-338.

Williams, J.D. and D.A. Etnier. 1982. Description of a new species, *Fundulus julisia*, with a redescription of *Fundulus albolineatus* and a diagnosis of the subgenus *Xenisma* (Teleostei: Cyprinodontidae). Occasional Papers of the Museum of Natural History, The University of Kansas, Lawrence, Kansas.

Williams, J.D., M.L. Warren Jr., K.S. Cummings, J.L. Harris, and R.J. Neves. 1992. Conservation status of the freshwater mussels of the United States and Canada. Fisheries 18: 6-22.

APPENDIX

Table 1. Historic to future projected changes in statewide and ecoregion diversity. See text for abbreviation definitions.

Amphibians

	CP	WHR	NB	EHR	CuP	RV	BR	Statewide
Past Species	34	38	33	38	41	38	50	66
Future Species	32	34	31	33	36	34	42	54
Percent change	-5.88	-7.89	-6.06	-10.53	-12.20	-10.53	-16.00	-18.18
Vulnerable Species	2	4	2	5	5	4	8	12
% vulnerable	5.88	7.89	6.06	10.53	12.20	10.53	16.00	18.18
Extinct	0	0	0	0	0	0	0	0
% extinct	0	0	0	0	0	0	0	0
Exotic	0	0	0	0	0	0	0	0
% exotic	0	0	0	0	0	0	0	0

Fish

	CP	HR	NB	CuP	RV	BR	Statewide
Past Species	128	163	91	52	159	64	272
Future Species	126	156	90	52	144	67	242
Percent Change	-0.79	-2.50	-1.10	1.89	-8.11	7.25	-11.93
Vulnerable species	14	19	5	6	27	8	51
% vulnerable	9.29	9.09	5.21	8.62	13.95	8.00	17.35
Extinct	0	0	0	0	0	0	0
% Extinct	0	0	0	0	0	0	0
Exotic Species	13	12	5	7	13	11	22
% Exotic	8.57	6.82	4.17	10.34	6.98	14.67	7.48

Mussels

	CP	WHR	NB	EHR	CuP	RV	BR	Statewide
Past Species	35	90	91	41	54	106	20	149
Future Species	37	56	47	34	30	45	13	85
Percent change	5.71	-35.56	-47.25	-17.07	-44.44	-57.55	35.00	-42.95
Vulnerable species	0	19	22	6	13	31	2	35
% vulnerable	0.00	22.35	25.93	14.63	26.53	33.70	11.11	25.74
Extinct	0	9	12	1	6	16	3	16
% Extinct	0.00	8.89	13.19	2.44	11.11	15.09	15.00	10.74
Exotic	2	3	2	1	1	2	1	3
% exotic	5.41	3.53	2.47	2.44	2.04	2.17	5.56	2.21

Table 2. Historic to future projected changes in spatial turnover within Tennessee's ecoregions. See text for abbreviation definitions.

Amphibians

	Historic	Future	Deviation from Historic	Percent Deviation from Historic
CP-WHR	0.20	0.28	0.08	38.89
WHR-NB	0.31	0.24	-0.07	-21.41
NB-EHR	0.27	0.22	-0.05	-17.17
EHR-CuP	0.20	0.14	-0.07	-33.93
CuP-RV	0.41	0.15	-0.26	-62.39
RV-BR	0.37	0.31	-0.06	-16.00
Mean	0.31	0.21	-0.10	-30.18

Fish

	Historic	Future	Deviation from Historic	Percent Deviation from Historic
CP-HR	0.67	0.65	-0.03	-3.75
HR-NB	0.97	0.84	-0.13	-13.25
HR-CuP	2.89	2.24	-0.64	-22.22
CuP-RV	2.69	2.06	-0.63	-23.34
RV-BR	2.19	1.72	-0.47	-21.45
Mean	1.88	1.50	-0.38	-16.80

Mussels

	Historic	Future	Deviation for Historic	Percent Deviation from Historic
CP-WHR	0.71	0.56	-0.15	-21.57
WHR-NB	0.15	0.13	-0.02	-12.65
NB-EHR	0.57	0.42	-0.16	-27.00
EHR-CuP	0.52	0.33	-0.18	-35.35
CuP-RV	0.53	0.43	-0.10	-19.46
RV-BR	0.83	0.73	-0.10	-11.74
Mean	0.55	0.43	-0.12	-21.29

PART V

ASSESSING THE STRUCTURE OF DEBRIS DAMS IN URBAN STREAMS:

A Case Study of Biophysical Homogenization

Field assistant, Mango, and litter trap along Whites Creek, Union County, Tennessee, December,1999.

Part V is a slightly revised version of a paper by a similar title published in the Proceedings of the American Water Resources Association:

Duncan, J.R. 2001. Assessing the structure of debris dams in urban stream restoration and management. In: Proceedings of the American Water Resources Association: International conference on Riparian Ecology and Management in Multi-Land Use Watershed, August 28-31, 2000, Portland, Oregon.

This peer-reviewed paper was initiated as a course project for Dr. Carol Harden's graduate seminar on watershed dynamics in fall, 1998. The final version was the result of fieldwork, laboratory analysis, literature searches, statistical analysis, and writing that I exclusively conducted that extended well beyond the temporal scope of the initial class project.

INTRODUCTION

As anthropogenic activities continue to exact heavy tolls on our streams and rivers, the growing science of watershed restoration remains in its infancy. Numerous efforts to restore degraded stream channels have been undertaken (e.g., Duncan et al., 1998; Riley, 1998; Schauman and Salisbury, 1998) with varying degrees of success depending upon what endpoints are measured (e.g., economics, aesthetics, hydrology, ecosystem function, biodiversity). In many cases, the intangible nature of ecosystem function and the complexity of restoring the structure of ecological communities has resulted in ecological attributes being largely ignored. Despite this, their importance as indicators of restoration success is paramount if our goal is to restore self-sustaining aquatic ecosystems capable of supporting and preserving a significant level of biodiversity.

The process of watershed restoration must account for a variety of stressors including flashy runoff due to impervious surfaces, accelerated flow velocities and discharge within streams due to channel alteration, and the multiple adverse effects of riparian corridor devegetation. A key component that is often overlooked in the restoration equation (and apparently from the literature) is the importance of debris

dams in regulating nutrient cycling, in-stream habitat diversity, and biophysical barrier within small streams. Traditional mitigation of watershed stressors may not be enough. For example, Hauer (1989) found that organic materials and debris dams were absent 15 years following restoration activities of a stream.

In naturally functioning stream ecosystems of eastern North America, debris dams made up of allochthonous organic matter are critical for nutrient retention, cycling, and transport as well as providing aquatic habitat (Bilby and Likens, 1980; Jones and Smock, 1991; Agradi, 1997; Casas, 1997). As leaves and other organic debris find their way into streams, debris dams serve as traps where coarse particulate organic material (CPOM) is retained and ultimately processed by stream organisms (e.g., shredders). The importance of debris dams in the retention of CPOM and as refugia for aquatic fauna is unmistakable. For example, Smock et al. (1989) found that debris dams accounted for the retention of up to 85% of CPOM in small streams and that density of aquatic invertebrates was 10 times higher in and around debris dams than in adjacent areas. In addition, Palmer et al. (1996) tested the effect of flooding on assemblages of aquatic invertebrates in streams both with and without debris dams. They found that in channels where debris dams were intentionally removed, abundance of aquatic invertebrates may decrease as much as 75-90% following extreme storm events, whereas in streams with debris dams, there was no significant decrease in faunal abundance. The implication is that debris dams provide food and refugia for aquatic organisms, buffering the effect of disturbance.

In light of the overwhelming evidence that debris dams serve as important biophysical elements in natural streams, thus providing nutrient retention and habitat heterogeneity, it seems fitting they should be a chief consideration in the restoration and management of degraded streams. Stream restoration can be a broad-ranging endeavor with efforts that often focus on a handful of stream characteristics such as channel morphology, bank stabilization, or the presence of a particular species, rather than on ecosystem sustainability and function. As a result, the noncharismatic presence and importance of debris dams and their associated allochthonous sources may be overlooked. This results in a critical piece of the puzzle being omitted,

preventing the establishment of a self-sustaining stream community. In this study, I compare the frequency of debris dams in a degraded urban stream to that of a relatively unimpacted forested watershed to determine if debris dams may be a limiting factor in the ecological restoration of urban streams. To assess the differences among allochthonous inputs, I also measure and compare the amount of canopy litter falling within the riparian corridors of each of the two streams.

METHODS

To test the hypotheses that (1) urban streams are deficient in debris dams and (2) that this difference is primarily the result of insufficient riparian canopy litter, I conducted a paired watershed survey of debris dams and their allochthonous sources. The study compared the frequency, size, and prominent materials (only frequency is presented here) of debris dams on two second to third order streams in eastern Tennessee (Figure 1). Both watersheds were of similar size and occur within the same ecoregion (i.e., southern limestone/dolomite valleys and low rolling hills of the Ridge and Valley) (Griffith et al., 1997), but each had a markedly different ecological history and present-day land use.

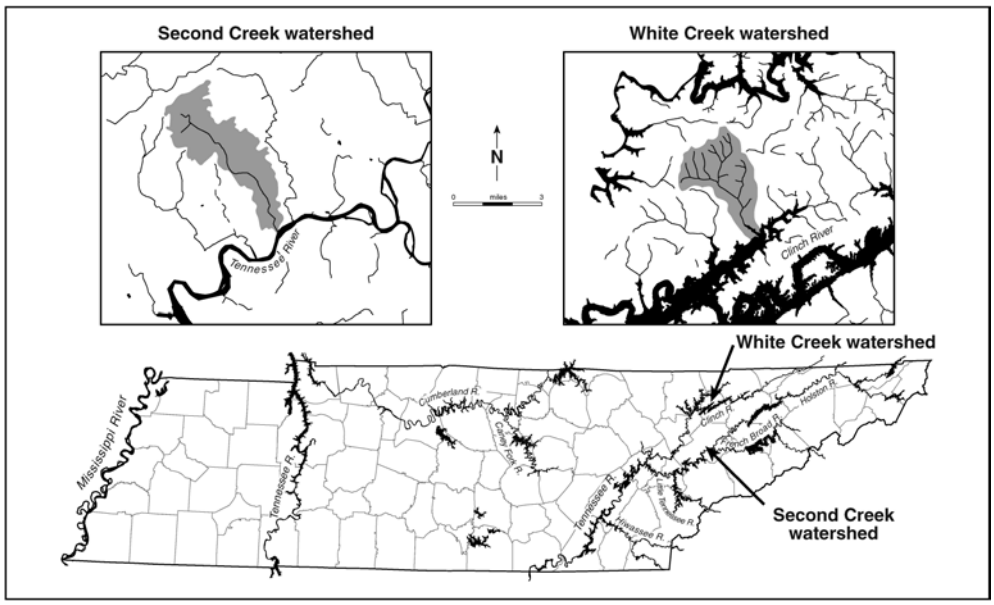

Figure 1. Relative location of watersheds

Site Description and Selection

Second Creek lies within a heavily urbanized watershed encompassing approximately 15 km^2 within the city of Knoxville, Tennessee and discharges into the Fort Loudoun impoundment of the upper Tennessee River. Historically, Second Creek has been the site of severe anthropogenic degradation dating to the 1790s. Today, Second Creek is impacted by nonpoint source pollution, altered hydrology due to urbanization throughout the watershed, in-stream channelization, and extensive clearing of its riparian corridor. Its current land uses vary from residential to heavy industry. Forested, agricultural, and vacant lands occupy less than 10 percent of the watershed. I selected Second Creek in part because it has been the focus of numerous studies and restoration efforts over the past several years (e.g., Duncan et al., 1998).

White Creek lies within an entirely forested watershed located within the Chuck Swan Wildlife Management Area in Union County, Tennessee, and discharges into the Norris Lake impoundment of the Clinch River. The White Creek watershed is of similar size to that of Second Creek, encompassing approximately 10 km^2. Dominant vegetation within the watershed is second growth mixed deciduous hardwoods. While timber harvest has historically occurred within the watershed, in its current state most canopy trees, including those associated with or in close proximity to the riparian corridor, are at or near maturity and include such species as red maple (*Acer rubrum*), oaks (*Quercus sp.*), poplar (*Liriodendron tulipifera*), and sycamore *(Platanus occidentalis*). I selected White Creek as a reference watershed for three reasons, (1) because it likely approximates the predisturbance condition of Second Creek, (2) because it falls within the same sub-ecoregion, and (3) because it has been adopted as the ecoregion reference stream by the Tennessee Department of Environment and Conservation due to its relatively intact fish and aquatic invertebrate faunas.

Data Collection and Analysis

To compare debris dams between the watersheds, I first established three 100-meter longitudinal transects along each of the streams, one near the headwaters, one midway through the watershed, and one near the mouth of each stream. Placing the transects along a similar gradient in both watersheds allowed me to minimize variation that could be associated with differential discharge between the two systems. Reaches were determined ad hoc based on position in the watershed, accessibility, and minimization of direct anthropogenic activities (e.g., I avoided residential areas where children playing in the stream might construct dams using various debris).

Within Second Creek, all three reaches had some degree of riparian vegetation; however, the riparian corridors of all three reaches lacked the characteristics of a natural riparian forest and were generally dense with invasive plants such as privet (*Ligustrum* sp.) and early successional species such as willows (*Salix* sp.). The uppermost reach was located adjacent to a community baseball field on one bank and a relatively intact wetland on the opposite bank. Overhanging vegetation was abundant but consisted primarily of shrub-type understory species. The middle reach was located within an industrial area. Again, there was abundant overhanging vegetation dominated by shrubby invasive and early successional species (e.g., willow and privet). The downstream reach was situated along a forested greenway extending through the University of Tennessee campus. While this site maintained a relatively closed canopy with minimal understory, species richness and abundance were minimal, consisting almost exclusively of widely spaced mature sycamores (*Platanus occidentalis*). Along White Creek, all three reached exhibited similar riparian communities characterized by mature second-growth deciduous species as previously mentioned. Exotic and early successional species were not abundant.

Fieldwork to quantify the number of debris dams was conducted along each stream in early October 1998 and was preceded by a prolonged dry period resulting in low flow conditions. Estimated discharge within the study areas was less than 10

cubic feet per second for both streams. Along each transect, I recorded the frequency of debris dams within the channel, canopy closure, and approximate width of the riparian corridor. The riparian corridor was generally defined as those trees in close enough proximity to contribute litter to the stream. Riparian corridor width varied according to topography and surrounding land use. For the purposes of this study, I defined debris dams as any obstruction in the channel greater than 0.5 meters in width and composed of predominantly allochthonous materials (e.g., leaves, woody debris, trash, etc.). Natural inorganic streambed materials (e.g., rocks) were not specifically evaluated in the survey, although streambed substrates often trapped organic debris initiating dam formation. For each debris dam, I recorded the width of the dam (estimated to the nearest 0.5 m), the prominent materials composing the dam, and the approximate percentage of the channel constricted in cross section. Dam materials were categorized to include leaf packs, small woody debris (sticks, branches, and logs < 10 cm in diameter), large woody debris (woody materials > 10 cm in diameter), and emergent and overhanging vegetation including root wads. (Due to the length constraints of this paper, I have elected to present only frequency and canopy litter data here. However, it should be noted that leaf packs comprised the dominant material in a statistically significant majority of dams in the forested stream. This observation led me to assess the canopy inputs for each stream.)

To measure canopy litter inputs in each stream, I evenly distributed fifteen litter traps (i.e., standard plastic laundry baskets with drain holes in the bottoms, each approximately 0.5 m in diameter), five in each of the three reaches discussed above, for a period lasting from mid-October to mid-January. The litter traps were positioned as close as possible to the stream channel to estimate litter inputs while avoiding the possibility of them being washed away (generally less than 2 meters from the channel). All litter traps were placed in both watersheds on the same day in mid-October and similarly retrieved on the same day in mid-January. After being collected, litter samples were independently dried and weighed.

The frequency of debris dams was calculated for each reach within both streams. Since each reach was selected at random, and because dam data were

nominal in nature, a chi-square test was determined to be an appropriate test to determine if a difference existed in debris dam frequencies between the two watersheds. Similarly, differences among canopy litter samples were compared between both streams using a nonparametric Mann-Whitney test (Zar, 1984).

RESULTS

Since input and retention of organic debris is directly related to in-stream faunal biomass and diversity, the frequency of debris dams is an appropriate indicator of organic retention within small streams (Smock et al. 1989). Combining all three reaches, 22 dams were recorded in the urban stream and 78 in the reference stream. The frequency of dams in the reference stream was significantly higher than that of the test stream ($\alpha < 0.01$). Frequency of debris dams per 100 m reach within the test stream ranged from 3-10 with a mean of 7.3. Dam frequency per reach in the reference stream was significantly higher, ranging from 21-30 with a mean of 24.3 (Table 1).

Table 1. Chi-Square Analysis of Debris Dam Frequency

Reach	Urban (observed)	Forested (expected)	Chi-square	alpha < 0.01
Upstream	10	23	7.4	
Midstream	9	30	14.7	
Downstrea m	3	21	15.4	
Total	22	74	37.5	4.6
Mean/100m	7.3	24.7		
St. Dev.	3.8	10.2		

Because dam frequency was significantly greater in the forested stream compared to the urban stream, I reasoned that I would find greater amounts of canopy litter in the forested stream as well. This was not the case. In each watershed, I was able to recover 10 of 15 litter traps, the fates of the remaining five being unknown (an interesting sociological note given the remoteness of the reference stream and accessibility of the urban stream). Litter composition in all samples was primarily leaf matter with lesser and varying degrees of small woody material and other detritus. Dry weight of the reference stream samples ranged from 7.17g to 52.58g with a mean of 23.54g and a standard deviation of 14.68g. This was significantly less than the amounts collected in the urban creek which ranged from 37.90g to 117.11g with a mean of 60.06g and a standard deviation of 23.02g.

DISCUSSION

Urban watersheds are often characterized by increased amounts of impervious surfaces, point- and nonpoint-source pollution, and various stream corridor alterations ranging from devegetation to severe channelization. Together, these factors preclude urban streams from functioning as their nonimpacted counterparts.

Recently, a growing understanding of the role of imperviousness and land use in limiting in-stream biodiversity has emerged (e.g., Shuler et al., 1998). While we remain in the early stages of watershed-level retrofitting to reduce imperviousness, extensive stream corridor restoration projects have been widely initiated. These efforts have used a variety of bioengineering techniques targeted primarily at erosion reduction and bank stabilization.

While many of these actions have proven successful in promoting local bank stabilization, few if any have focused on the linkage between watershed characteristics (e.g., land use and imperviousness), riparian corridor structure, and the formation and presence of debris dams in urban streams. In fact, because many stream restoration efforts are based on aesthetics, debris dams are often looked upon as eyesores. Urban planners and stormwater engineers often view stream debris as a hazard to infrastructure and as a contributor to localized flooding. As a result, community and government stream initiatives often make "debris removal" a top priority (e.g., Sadler, 1999). While a proportion of riparian debris consists of human-generated refuse, debris removal practices generally do not attempt to segregate naturally-occurring debris from trash. The total removal of all stream debris likely further inhibits stream ecosystem functioning by reducing habitat and organic matter retention. While short- term social and economic benefits may be gained from debris removal as a management or restoration strategy in urban streams, the significance of stream debris must not be overlooked if in-stream biodiversity and ecosystem sustainability are to be included as long-term goals.

Within this study, I have found that debris dams are fewer and of a different quality in an urban stream relative to a forested reference stream, despite litter inputs that appear to be greater in the urban stream. Although urban streams are often viewed as having an abundance of dissolved nutrients (due to nonpoint-source pollution), retention of canopy litter in the form of CPOM is minimized making nutrient flows inaccessible to trophic groups other than autotrophs. For example, stream invertebrate communities display complex food webs structured according to various functional feeding groups. These groups include shredders, scrapers, collectors, and predators, all maintaining a critical role in processing organic debris

(Merritt and Cummins, 1996). In the absence of CPOM, the structure of this food web will be severely altered, the shredders having nothing to shred, collectors having nothing to collect, and predators left with a diminished prey base. Assuming that this deficiency of debris dams can be extrapolated to other degraded urban streams, these systems in general may be nutrient and/or habitat limited. Thus, despite efforts to improve streambank conditions, this limitation may persist in the absence of watershed-wide remedies, precluding the re-establishment of a self-sustaining in-stream community.

Despite the preliminary of nature of this study, clearly there are differences in the frequency and quality of debris dams in urban versus forested streams. The altered quality of streamside vegetation in the urban setting is likely to account for this difference. Because tree species vary in the timing and duration of their leaf drop throughout the fall, and because different species have varying rates of in-stream decay and nutrient availability, managing streamside communities to account for these factors seems worthy (Paul and Meyer, 1996). Extant and recovering riparian corridors should be maintained in a manner that allows for significant leaf and woody debris inputs (Welsch, 1999). However, as the data in this study suggest, the sheer amount of canopy litter is not enough. While this study provides an initial attempt to understand the formation and importance of debris dams in small urban streams, further research will require more robust data that cover a greater variety of ecosystem types and take into account seasonal fluctuations in dam formation and abundance. In addition, more study is needed to determine the effect on dam genesis and stability given altered hydrology and allochthonous input quality.

Litter quality (i.e., the types of overhanging species present) and stream hydrology (as influenced by watershed imperviousness) likely interact synergistically to impede dam formation and stability in the urban stream. Amundsen (1995) suggests that disturbed riparian canopies such as those along urban streams produce greater amounts of litter because of increased competition among r-selected species. Generally, these canopies are more open and edge-like. These traits simultaneously allow greater light penetration and increased amount of

edge-associated species. As a result, riparian species divert greater amounts of energy to foliage production as opposed to roots and shoots. Despite greater amounts of leaf matter, the size, timing, and species composition of litter likely interacts with flashy discharge during storm events that scours potential debris, transporting it downstream and inhibiting dam formation.

Watershed management, especially in urbanizing watersheds where human activities are on the increase, should incorporate and manage for the presence of debris dams. The frequency of debris dams is directly dependent on the quality and spatial extent of the riparian forest as well as general land use within the watershed. Additional study is needed to determine riparian management practices that specifically promote the formation of debris dams so that urban watershed planners can be afforded the tools necessary for sustainable watershed management. However, until stream managers account for scouring flows caused by impervious watershed surfaces, the effect of even the most well-founded riparian zone management may have little effect on improving in-stream conditions.

CONCLUSIONS

This study compared the frequency of debris dams in two small streams in eastern Tennessee. There were significantly fewer debris dams in the urban stream relative to the forested reference stream, likely due to a synergism between flashy hydrology and riparian corridor deforestation. The capacity of streams to retain CPOM is directly related to species richness among aquatic biota. The results of this study suggest that (1) retention of CPOM in urban streams is greatly reduced, (2) that urban stream management activities should take measures to promote a riparian plant community capable of contributing the quantity and type of material necessary for debris dam formation and sustainability, and (3) that riparian corridor management needs to be augmented by watershed-wide management practices to reduce the impact of stream scour caused by imperviousness.

LITERATURE CITED

Agradi, T.R., 1997. Hydrologic Context and Macroinvertebrate Community Response to Floods in an Appalachian Headwater Stream. *American Midland Naturalist* 138:371-386.

Amundsen, C.C. 1995. Reservoir riparian zone characteristics in the upper Tennessee River Valley. In Trettin, C.C., et al. (eds.), Wetlands of the Interior Southeastern U.S. Klewer Publishing. New York.

Bilby, R.E., and G.E. Likens, 1980. Importance of Organic Debris Dams in the Structure and Function of Stream Ecosystems. *Ecology* 61:1107-1113.

Casas, J.J., 1997. Invertebrate Assemblages Associated with Plant Debris in a Backwater of a Mountain Stream: Natural Leaf Packs vs. Debris Dams. *Journal of Freshwater Ecology* 12:39-49.

Duncan, J.R., R.A. Hanahan, M.E. Pleasant, T.R. Gangaware, and D.L. Feldman, 1998. Techniques for Urban Stream Restoration. In: Proceedings of the American Society of Civil Engineers, Conference on Water Resources. Memphis, TN, August, 6-9, 1998.

Griffith, G.E., J.M. Omernik, and S.H. Azevedo, 1997. Ecoregions of Tennessee: Corvallis, OR, U.S. E.P.A., National Health and Environmental Effects Research Laboratory, EPA/600/R-97/022, p.51.

Hauer, F.R., 1989. Organic Matter Transport and Retention in a Blackwater Stream Recovering from Flow Augmentation and Thermal Discharge. *Regulated Rivers Research & Management* 4: 371-380.

Jones, J.B. Jr., and L.A. Smock, 1991. Transport and Retention of Particulate Organic Matter in Two Low-Gradient Headwater Streams. *Journal of the North American Benthological Society* 10:115-126.

Merritt, R.W. and K.W. Cummins, 1996. An Introduction to the Aquatic Insects of North America. Kendall/Hunt. 862pp.

Palmer, M.A., P. Arensburger, A.P. Martin, and D.W. Denman, 1996. Disturbance and Patch-Specific Responses: The Interactive Effects of Woody Debris and Floods on Lotic Invertebrates. *Oecologia* 105:247-257.

Paul, M.J, and J.L. Meyer, 1996. Fungal Biomass of 3 Litter Species During Decay in an Appalachian Stream. *Journal of the North American Benthological Society* 15:412-432.

Riley, A.L. 1998. Restoring Streams in Cities: A Guide for Planners, Policy Makers, and Citizens. Island Press, Boca Raton, FL.

Sadler, J.F., 1999. Talking trash II: A Return to Debris Removal (extended abstract). In Proceedings from the Ninth Annual Tennessee Water Resources Symposium, Tennessee Section of the American Water Resources Association.

Schauman, S., and S. Salisbury, 1998. Restoring Nature in the City: Pugent Sound Experiences. *Landscape and Urban Planning* 42: 287-295.

Shuler, T. 1998. Rapid Watershed Planning Handbook: A Comprehensive Guide for Managing Urbanizing Watersheds. Center for Watershed Protection. Ellicott City, Maryland.

Smock, L.A., G.M. Metzler, and J.E. Gladden, 1989. Role of Debris Dams in the Structure and Functioning of Low-Gradient Headwater Streams. *Ecology* 70:764-775.

Welsch, D.J., 1999. Riparian Forest Buffers: Function and Design for Protection and Enhancement of Water Resources. United States Department of Agriculture, Forest Service, Northeastern Area, State and Private Forestry, Forest Resources Management, Randnor, PA NA-PR-07-91.

Zar, J.H., 1984. Biostatistical Analysis, 2nd Ed. Prentice-Hall, Inc. Englewood Cliff, New Jersey. 718 pp.

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PART VI

EPILOGUE

Fisherman wading upper Clinch River, Tennessee circa 1925
(Photo courtesy Tennessee Valley Authority archives)

As renowned ecologist, Charles Elton, profoundly stated, "We must make no mistake, we are witnessing one the great convolutions of the world's flora and fauna" (Elton, 1958). The distinct chapters presented within this dissertation comprise an up-to-date empirical assessment of Elton's supposition with a specific focus on the freshwater environment. Although each chapter relies on differing data sources and analytical methods, together, they shed light on the processes responsible for Elton's "great convolution"—namely the human-induced collapse of isolating ecological boundaries and subsequent synergistic effects of extinction, invasion, and land use change. For the past 500 years, global exploration, increasing rates of human consumption, and modernization of transportation technology has resulted in simultaneous species range expansions and contractions among aquatic biota resulting in profound and irreversible consequences to the evolutionary and ecological histories of the world's freshwater ecosystems.

Combined, this assessment takes into account four distinct spatial scales, ranging from the six major bioregions of the world to a small Southern Appalachian stream. In addition, historical species assemblages are used as a baseline for evaluating predicted faunas likely to persist under future conditions. In the case of Part V, a historical surrogate is used for the basis of comparison. Specifically, a relatively pristine reference stream ecosystem is compared to the present day conditions within a highly altered urban stream ecosystem.

In concert, the chapters presented within this dissertation offer unanimous and confounding evidence that Elton was indeed correct. Continuing increases in human population, consumption, and mobility are resulting in the wholesale reorganization of the Earth's freshwater ecosystems. Regardless of the scale from which we view freshwater systems, the results are clear—we are significantly affecting the structure and function of aquatic ecosystems and irreversibly altering the course of their evolution.

Despite this conclusion, the present state of our knowledge is such that accurate predictions concerning the specific structure and function of future

aquatic environments are entangled with uncertainties and point to the need for additional research. Although change is a natural phenomenon of biological systems, the rate at which the current change is taking place is unprecedented in geologic and evolutionary history (Erwin, 1998). These uncertainties, coupled with the urgency of the biodiversity crisis, exemplify a common dilemma within the discipline of conservation biology—the need to have more specific information versus the need to act.

For those who require a more thorough analysis of the problem and its implications, this concluding section is an attempt to point out some of the major underlying uncertainties inherent within each of the preceding chapters and to identify some reasonable next steps toward refining the uncertainties. For those who may find themselves with an overriding compulsion to act in lieu of more precise evidence, this section also proposes a cursory set of potential solutions and actions to slow or divert our journey toward New Pangea.

It is reasonable to assert that Elton's great convolution exists within a temporal continuum beginning within the last 500 years, and coinciding with major advances in human civilization, and that it will not conclude until the world's biota are thoroughly spatially homogenized marking the beginning of a new period of evolutionary equilibrium and symbolizing the formation of New Pangea (Rosenzweig, 2001). Although the concept of New Pangea denotes a philosophical endpoint to the analysis presented within this volume, establishing a foundational global context required that I tell the story beginning at the global scale and moving sequentially toward the local level.

Following this rationale, I begin here with Part II. "Extinction in a Field of Bullets" provides an up-to-date appraisal of the status of the world's freshwater fishes. With at least 4 percent, and estimates ranging as high as 20 percent, of freshwater fishes facing an elevated risk of extinction (Leidy and Moyle, 1998), two questions arise. Are all taxonomic groups equally susceptible to extinction? And, if not, can we identify a unifying suite of risk factors capable of predicting extinction among predisposed higher taxonomic groups of fishes

(i.e., families)? Although it can be concluded, using binomial statistics, that extinction risk is not randomly distributed among freshwater fish families, the identification of a unifying set of extinction predictors remains elusive.

Evidence from previous mass extinctions known from the fossil record suggests that the rate of environmental change can influence whether or not certain taxonomic groups are more susceptible than others (Erwin, 1998). Based on this, it can be inferred that the rate of change within the current crisis is such that taxonomically conserved traits have little if any bearing on extinction risk. Simply stated, the rate of change within the aquatic environment may be such that extinction is more a factor of bad luck than bad genes (Raup, 1991).

On the other hand, our difficulty in identifying a smoking gun of extinction risk may lie in that we have not examined the right set of biological traits or that we have not looked at the correct taxonomic scale. Clearly, certain species-level traits such as migration are indicative of extinction risk, although such traits are not useful as statistically significant indicators across all taxa and all global bioregions. A possible remedy to this situation would be to look at finer geographic and taxonomic scales. Angermier (1995) successfully identified a suite of extinction risk factors for the freshwater fishes of Virginia; however, the ability to extrapolate these factors to the diversity of fishes and aquatic ecosystems worldwide is for now futile. Perhaps a more reliable and productive alternative would be to seek to identify and minimize the extrinsic causes of extinction. For example, research relating to the global effects and mitigation of dammed rivers, diverted flows, and fragmented aquatic habitats may be a more tangible and meaningful goal.

In “How’s the Fishing in New Pangea?” (Part III), the focus shifts to the United States. A species list was compiled for each of the lower 48 states to represent their historic freshwater fish faunas. By adding non-native species recorded from each state and deleting those species deemed at risk of extinction, a predicted future fauna was derived for each state. Species richness was calculated for each state, and the degree of faunal similarity, or turnover, was

estimated between neighboring states in the past and compared to the projected similarity between future state faunas. Intriguingly, these comparisons indicated that states are likely to become more distinct from their neighbors in the future.

Moreover, similarity changes very little between western states but decreases substantially in the historically species rich eastern U.S. Based on the conclusions of Rosenzweig (2001), it is likely that this decrease in similarity represents a transition in states' ichthyodiversity that is driven by the differentiation between rapid rates of invasion and the comparatively slow process of extinction. The difference in turnover rates between eastern and western states is likely due to differences in historic species richness between the regions. Further, additional patterns may exist by comparing the faunas along north-south gradients. Since successive periods of glaciation have left northern regions with comparatively low levels of aquatic diversity, the anthropogenic addition of exotics may result in biotic changes that are worthy of further consideration and research.

In addition, the approach used within Part III introduced uncertainty in two primary ways. First, by including species that were collected, but not known to have established populations within a given state, it is possible that future species richness and turnover rates were overestimated. The degree to which this is the case remains unclear. Further, assessing the extent of non-native species known to be established would likely provide an underestimation of the species that will ultimately make up the state faunas of the U.S. Although some non-native species that have been collected within particular states are most certainly accidentals, with virtually no probability of developing self-sustaining populations, others most likely represent yet-to-be confirmed permanent additions to state faunas. In either case, the number of non-native species extant in nearly all states is likely to increase in the future, a notion that could to a degree offset the level of uncertainty of the approach used. A more refined approach to this analysis that examines the probability of collected species becoming established is required to further reduce this uncertainty.

Second, species hybrid (primarily gamefish) were included in future faunas based on the assumption that hybrids will ultimately function as new species within the state faunas of the future. The degree to which this is true remains in question. As with collected, but non-established, non-native species, further study is needed to determine the probability of hybrids performing a significant role in future faunas of the U.S.

Part IV narrows the focus further and shifts from evaluating biodiversity trends according to political boundaries to an approach that relies on natural gradients. First, distribution information for fishes, mussels, and amphibians was obtained for the state of Tennessee. To evaluate the process of biodiversity change across an environmental gradient, ecoregions were superimposed over the species distributions. As in the previous chapter, changes in species richness and faunal similarity occurring between historic and future faunas were calculated moving from one ecoregion to the next. Unlike Part III, species richness was found to decrease statewide with a 12 percent, 43 percent, and 18 percent decreases among fishes, mussels, and amphibians, respectively. Accordingly, similarity increased for virtually all ecoregion-taxonomic combinations indicating that Tennessee is likely losing its historic intrastate biological distinctiveness. Specifically, this loss in regional distinctiveness is most certainly due to habitat degradation, most notably the impoundment and fragmentation of medium-sized rivers.

Although the results of Part IV are fairly conclusive, further research capable of aiding natural resource managers and policy makers is needed. Specifically, studies that focus on other non-political gradients, such as watersheds, will be useful tools in responding to biological trends that may otherwise go unnoticed. Identification and analysis of biological "hot spots," geographic areas or habitats that harbor a disproportional number of species, may also be of use to regional managers. Part IV also points to the need for additional investigation focusing on the importance of transition zones within environmental gradients in harboring rare species. Although Part IV focused on

the state of Tennessee, a recent flurry of state and regional atlases of aquatic and terrestrial species distributions lend themselves to the approach discussed here.

Finally, Part V, "Assessing the Structure of Debris Dams" represents a study of biophysical homogenization at a fine spatial scale. The process of simplifying diverse aquatic habitats is at least in part responsible for the convolution of the world's aquatic faunas. Urbanization of watersheds and their associated impervious surfaces has been implicated in the decline of species diversity and abundance in small streams. Further, maintaining riparian buffers along urban stream corridors is seen as a means of counteracting the effects of urbanization.

Within this paired watershed study, I compared the frequency of debris dams in a forested reference stream to a stream in a heavily urbanized watershed. I found that debris dams occurred in greater frequency within the forested reference stream compared to the urban stream. A follow-up analysis determined that although there was a significantly greater amount of riparian canopy litter within the urban stream corridor, the quality and timing of litter inputs prevented debris dam genesis and retention. It is believed that the scouring flows that typically accompany highly impervious urban watersheds also contributed to decreased frequency of debris dams in the urban stream.

The influence of debris dams on stream biota has been an area of considerable study, particularly for forest managers, although little if any attention has been devoted to understanding the influence of debris dams in providing habitat and nutrient availability within urban streams. While the field of stream restoration has gained momentum in recent years, a thorough understanding of the role of biophysical structures in recovering stream ecosystems is an essential next step toward maximizing the success of these efforts. Although the conclusions stated in Part V are intriguing, they represent a mere snapshot of the existence, function, and importance of debris dams in small streams. Further, the conclusions of Part V are based upon limited data collected during a single season from a single urban stream. To support stream restoration

and riparian zone management in human-dominated landscapes, a better understanding of the genesis, retention, and importance of debris dams will require a greater amount of data from a greater variety of disturbed stream corridors.

Together, the individual components of this dissertation demonstrate that the aquatic environment is undergoing a period of unprecedented reorganization at the hands of modern civilization. The conclusions garnered from each section confirm that the world's aquatic biota is undergoing an irreversible convolution in evolutionary history. The interaction of simultaneous species declines, extinctions, and invasions, areas traditionally considered individually, warrant further study toward the goals of improved knowledge of the consequences, greater sociopolitical awareness, and comprehensive mitigation.

Further research will be necessary to dispel many of the uncertainties within this work and to provide specific solutions for averting the present trends. Specifically, Parts II-IV provide evidence that extinction risk is not evenly distributed spatially or taxonomically. Certain geographic locales will likely see disproportionate numbers of extinctions and invasions, and similarly particular species groups will become extinct or invade novel territories at higher rates than expected. Although the implicit assumption of each of these sections is that presently imperiled species will ultimately become extinct, the impacts of decreasing abundance within taxa and the effect this may have on community dynamics and ecosystem functions is an area worthy of deeper consideration. Moreover, parts II and V suggest that the understanding of certain extinction- or invasion-promoting extrinsic factors, those that are explicitly unrelated to species biology, offer perhaps the most promising and realistic opportunity for further study and the minimization of human activity on aquatic evolution.

Deriving solutions such as international accords targeted toward preserving and restoring aquatic diversity and habitats by eliminating extrinsic causes of extinction and invasion may become increasingly useful as international commerce accelerates. Prioritization of imperiled aquatic habitat

and designation of aquatic reserves, much like the protection afforded national parks, may also provide near-term means of offsetting current global trends. Only with additional research, multi-scale governmental cooperation, and increased social awareness can our drift toward New Pangea be averted.

LITERATURE CITED

Angermeier, P.L. 1995. Ecological attributes of extinction-prone species: loss of freshwater fishes of Virginia. *Conservation Biology* 9:143-158.

Elton, C.S. 1959. The Ecology of Invasions by Animals and Plants. John Wiley. New York.

Erwin, D.H. 1998. The end and the beginning: recoveries from mass extinctions. *Trends in Ecology and Evolution* 13:344-349.

Leidy, R.A. and P.B. Moyle. 1998. Conservation status of the world's freshwater fish fauna: an overview. In Fieldler, P.L. and P.M. Karieva (eds.). Conservation Biology for the Coming Decade 2nd edition. Chapman and Hall, New York.

Raup, D.M. 1991. *Extinction: Bad Genes or Bad Luck?* Norton Publishers, New York.

VITA

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