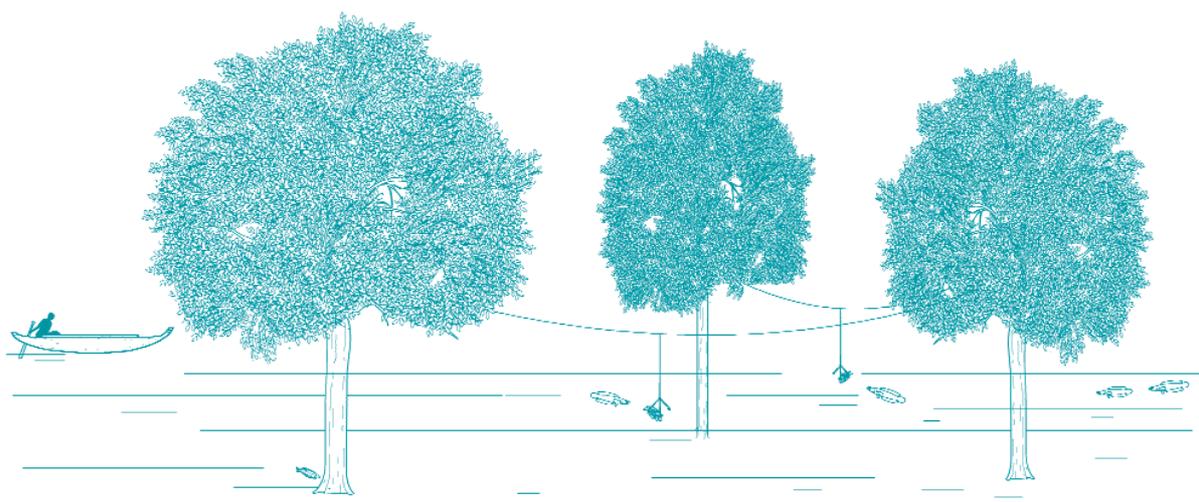


ORGANIZATION AND MAINTENANCE OF FISH DIVERSITY IN SHALLOW WATERS OF TROPICAL FLOODPLAIN RIVERS

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ABSTRACT

Historical and zoogeographic factors appear to explain the origin of Neotropical freshwater fish diversity, but proximate factors maintaining such remarkable levels of regional diversity, particularly in large floodplain rivers, remains unknown. Floodplain rivers are characterized by high levels of landscape and temporal heterogeneity. The littoral zone is composed of a mosaic of habitat templates upon which local communities are assembled and represents a highly dynamic component of the landscape due to seasonal water level fluctuations associated with the annual flood pulse. Results presented indicate littoral species are forced to continually disperse across the landscape in association with a moving land-water interface

Key Words: beta diversity, colonization, community assembly, fishes, flood pulse, gamma diversity, spatiotemporal heterogeneity, Venezuela

and lend support to an implicit theoretical trade off between colonization and competition ability among fishes of tropical floodplain rivers. The continual disassembly and reassembly (due to dispersal) of local communities across a spatially heterogeneous landscape should result in low extinction rates (i.e. at the regional level) and could theoretically maintain a nearly infinite regional species pool. Consequently, we suggest that the flood pulse paradigm should be expanded to include a potential mechanistic understanding of maintenance of high levels of beta and gamma diversity in floodplain rivers. Interactions among seasonal hydrology, variability in habitat structural complexity and landscape heterogeneity appear to maintain high aquatic species richness in these lowland rivers. It follows that alteration of seasonal water level fluctuation (e.g. damming) and habitat heterogeneity (e.g. channelization) should have substantial and negative consequences on the maintenance of regional biodiversity pools in floodplain rivers.

INTRODUCTION

Tropical floodplain rivers are home to the largest fraction of freshwater fish biodiversity (Dudgeon 2000; Lundberg 2001) and as such should be a focal point of global conservation efforts. Recently, conservationists have focused their efforts on species conservation through identification and conservation of hotspots (i.e. areas with high levels of endemism) (Meyers *et al.* 2000). Unfortunately, tropical rivers and associated fish faunas are absent from this conservation initiative (Meyers *et al.* 2000; Brooks *et al.* 2002). Not only have rivers been undervalued in conservation efforts, but also ecological understanding of community and assemblage dynamics in lowland rivers lags behind other fields of study (e.g. limnology in temperate lakes). We suggest that better conceptual understanding of these systems will lead to more effective conservation and restoration practices.

Recent studies have made great headway in understanding large-scale patterns of freshwater fish diversity. In an insightful review of the source of South American freshwater fish fauna richness, Lundberg (2001) identified area and latitudinal gradient as suit-

able explanations for large-scale maintenance of neotropical riverine freshwater fish diversity, but suggested that a historic-zoogeographic perspective is needed to understand the genesis of this diversity. Lundberg presented evidence that river basins were repeatedly transformed during periodic geological upheavals and changes in basin boundaries and inter-basin connections resulted in sympatric speciation opportunities. Lundberg reasoned that low baseline extinction rates resulted in the present-day richness of neotropical freshwater fish species.

Although historical and zoogeographic factors may explain the origin of neotropical freshwater fish diversity, there is little understanding of proximate factors (*sensu* Resetarits and Bernardo 2001) maintaining this remarkable diversity across the landscape at regional and local scales, particularly in large floodplain rivers. Fish assemblages in European and North American temperate forested lakes are structured by a series of nested filters operating first at regional and subsequently at local scales (Tonn 1990; Tonn *et al.* 1990). Stream fish assemblages in the same two regions (Europe and North America) also exhibited hierarchical structure with regional zoogeography and local habitat templates structuring local fish assemblages (Matthews 1998; Lamouroux, Poff and Angermeier 2002). Characterization of the relationship between regional and local fauna richness has been identified as a useful metric to evaluate the degree that species interactions regulate local community dynamics (Cornell and Lawton 1992; Hugueny and Cornell 2000). Cornell and Lawton (1992) stated that unsaturated assemblages are ubiquitous in nature and as a consequence regional richness is free of local constraints, although this logic has been seriously challenged (Shurin *et al.* 2000). Cornell and Lawton (1992) speculated that the regional species pool regulates local richness, which should be a function of landscape heterogeneity and evolutionary diversification. Empirical data have revealed that contemporary energy availability and habitat heterogeneity successfully predict the current global distribution of riverine fish diversity (Guégan, Lek and Oberdorff 1998). Furthermore, fish assemblages in Africa, North

America and Western Europe may be either unsaturated i.e. non-interactive (Tonn *et al.* 1990; Hugueny and Paugy 1995; Griffiths 1997; Oberdorff *et al.* 1998) or saturated i.e. interactive (Tonn *et al.* 1990; Angermeier and Winston 1998). In their comparative study, Tonn *et al.* (1990) demonstrated that North American assemblages exhibited an asymptotic relationship between local and regional richness (i.e. interactive local assemblages), whereas European assemblages did not (i.e. non-interactive local assemblages). Similar to temperate lakes, North American stream fish assemblages (i.e. Virginia) also showed local community saturation (Angermeier and Winston 1998). The likelihood that neotropical fish assemblages are saturated seems high, because regional diversity in these settings is remarkably high (Jepsen 1997; Arrington and Winemiller 2003) yet alpha diversity is not substantially greater than similar North American samples (Matthews 1998), that have much lower regional diversity levels. Though a consensus on this subject has not been reached (Cornell and Lawton 1992; Shurin *et al.* 2000), the possibility exists that local community interactions may regulate regional species richness for fishes in neotropical rivers.

Much attention has focused on spatiotemporal dynamics in lotic environments as a mechanism for maintaining biodiversity (e.g. Schlosser 1987; Townsend 1989; Ward 1989, 1998; Poff and Allan 1995; Matthews 1998; Schlosser and Kallemeyn 2000; Oberdorf, Hugueny and Vigneron 2001). Recent work conducted on European floodplain rivers has characterized landscape attributes of floodplain rivers as shifting mosaics of habitat features with varying levels of among-habitat connectivity (Ward, Tockner, Arscot *et al.* 2002; Amoros and Bornette 2002). The combination of landscape heterogeneity and temporally variable among-patch connectivity are common features of floodplain rivers that result in observed patterns and levels of biodiversity (Ward 1998; Ward *et al.* 1999; Ward *et al.* 2001; Tockner *et al.* 1999; Amoros and Bornette 2002; Robinson *et al.* 2002). The general synopsis is that a dynamic landscape composed of a mosaic of habitat patches in various successional states maintains the high regional diversity levels observed

in floodplain rivers. This should be the case whether or not local communities are saturated, because effects of landscape and temporal heterogeneity should overcome competitive exclusion (Levin and Paine 1974; Chesson and Huntley 1997; Hurtt and Pacala 1995).

In this limited review, we hope to address the following questions based on experience with fish assemblages in neotropical floodplain rivers. How are neotropical fishes organized across the river-floodplain landscape? What factors influence assemblage structure in these local communities? How are such large regional species pools maintained?

ORGANIZATION OF FISH DIVERSITY IN TROPICAL FLOODPLAIN RIVERS

Characterization of patterns of species occurrences and relative abundance is a major goal in community ecology (Hubbell 2001). A central debate among community ecologists has been the role of deterministic versus stochastic processes often inferred through examination of random or non-random patterns in assemblage data. Studies of fish assemblages in temperate streams have demonstrated both random (Grossman, Moyle and Whitaker 1982; Grossman *et al.* 1998) and non-random patterns (Meffe and Sheldon 1990; Jackson, Somers and Harvey 1992; Taylor 1996), with results often strongly dependent on the spatial, temporal and numerical scale of the study (Rahel 1990, Angermeier and Winston 1998). Tropical floodplain rivers have been studied less frequently and have yielded mixed results. Goulding, Carvalho and Ferreira (1988) concluded that fish assemblages of the Río Negro (Brazil) were random associations of species. More recent studies also support the random association hypothesis (Jepsen 1997; Saint-Paul *et al.* 2000).

A few studies in tropical river systems have concluded fish assemblages are structured in a non-random manner. Working in the same system as Jepsen (1997), Arrington (2002) documented non-random structure of fish and macroinvertebrate assemblages among major habitat types (e.g. sandbank, leaf litter, submerged wood) located in the moving littoral. Fish

assemblages in these local habitats were maximally structured during the low-water period and less structured in rising- and falling-water periods. Consequently, juxtaposition of multiple habitat types and the resulting landscape heterogeneity resulted in high levels of observed beta diversity, which substantially influenced the estimate of the regional species pool. Similarly, fish assemblages on the floodplain of the Brazilian Amazon were found to be non-randomly structured among major habitat types (Petry, Bayley and Markle 2003), though habitats in this study were characterized by dominant macrophytes. Others have shown fish assemblage structure in tropical rivers is influenced by water type (Ibarra and Stewart 1989; Cox Fernandes 1999), sample depth (Lundberg *et al.* 1987; Stewart, Ibarra and Barriga-Salazar 2002; Hoeinghaus *et al.* 2003), seasonally falling water levels (Cox Fernandes 1999) and diel period sampled (Arrington and Winemiller 2003). Rodriguez and Lewis (1997) found structured assemblage patterns in Orinoco floodplain lakes that were correlated with water clarity. They inferred predation by alternative predators in clear or turbid lakes was driving assemblage structure. As Winemiller (1996) hypothesized, tropical floodplain river fish assemblages appear to be structured by both stochastic and deterministic processes and the magnitude of these processes varies seasonally (Arrington 2002).

MAINTENANCE OF FISH DIVERSITY IN TROPICAL FLOODPLAIN RIVERS

We suggest that the flood pulse paradigm be expanded to include a potential mechanistic understanding of maintenance of high levels of beta and gamma diversity in floodplain rivers. We hypothesize that the flood pulse (Junk, Bayley and Sparks 1989), i.e. the annual hydrologic pattern of predictable flooding of lateral floodplain habitats in large tropical rivers, regulates community assembly patterns and regional diversity levels. As conceived by Junk *et al.* (1989), the flood pulse concept linked riverine productivity to predictable annual patterns of flooding and characterized the main channel as a passageway for fish migrations. Although some fish species undoubtedly use the main channel for migration (Junk *et al.*

1989; Fernandes 1997; Wei *et al.* 1997; Duque, Taphorn and Winemiller 1998), many species either seasonally (low water) or consistently occupy main channel habitats (e.g. deep channel, shifting sandbanks, snag complexes). We shift our focus from the main channel / highway analogy (Junk *et al.* 1989) to the moving littoral as a dynamic habitat template. We define the moving littoral as the dynamic land-water ecotone occurring along main channel margins and extending onto the floodplain during high water. The moving littoral, thus, represents a highly dynamic component (i.e. shallow water) of the landscape composed of a mosaic of habitat templates upon which local communities are assembled (Southwood 1988; Townsend 1989; Bayley 1995; Arrington 2002; Petry *et al.* 2003). Furthermore, local habitat templates in the moving littoral may be thought of as being disturbed at some intermediate level (Connell 1978; Townsend, Scarsbrook and Dolédec 1997; Ward *et al.* 1999; Sheil and Burslem 2003) due to the seasonally predictable patterns of drying and wetting in lowland rivers (Junk *et al.* 1989; Arrington and Winemiller 2003).

As discussed above, there is considerable debate regarding the roles of deterministic and stochastic processes regulating local fish assemblages. A new hypothesis receiving considerable attention is Hubbell's (2001) "neutral theory", which assumes per capita equivalence of within-trophic-level community members. Community change is assumed to occur through stochastic ecological processes and random speciation. Application of the neutral theory has resulted in the generation of multiple testable predictions, which can serve as working null hypotheses in community studies. For example, local communities are expected to be sub-sets of the larger metacommunity, with species relative abundance equal between the two when migration rates into the local community are non-trivial (Hubbell 2001).

Previous studies have shown the importance of immigration rates on the structure (including richness) of local communities (MacArthur and Wilson 1967). Dispersal rates determine the importance of local community regulators in zooplankton assemblages

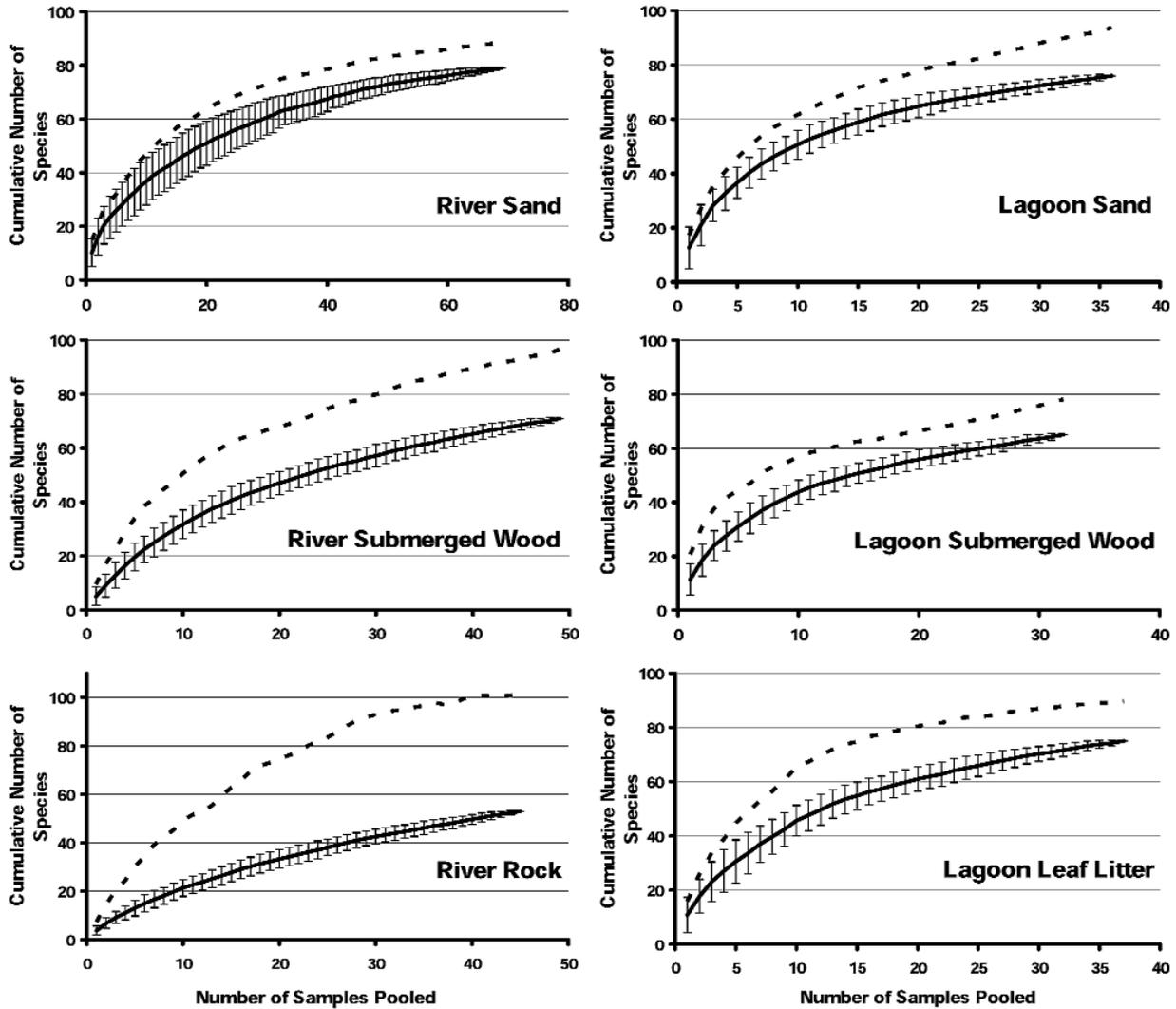
(Jenkins and Buikema 1998) and predominantly limit diversity in newly formed assemblages (Shurin *et al.* 2000). Temporal variation of fish assemblage structure in a Brazilian estuary has been linked to fish immigration and emigration dynamics (Garcia, Vieira and Winemiller 2001). For temperate streams, Schlosser (1987) offered a conceptual model indicating the generalized importance of immigration and extinction processes for the development of fish assemblage attributes. Using Schlosser's model as a starting point, Taylor and Warren (2001) showed stream fish immigration rates were positively related to stream size and negatively related to flow variability. They then documented patterns of nestedness in fish assemblage structure that were positively related to extinction rates and negatively related to immigration rates. They also observed that colonization and extinction dynamics of species appeared "more or less random" in habitats with high immigration rates, a result predicted by Townsend's (1989) patch dynamics concept.

Recent work by Arrington, Winemiller and Layman (in review) examined the influence of colonization rate and habitat complexity on the dynamics of local fish assemblages in the Cinaruco River, a floodplain river located in the Venezuelan *llanos*. Habitat patches of varying complexity and colonization rates were created within broad main-channel sandbanks and were colonized by fishes and macroinvertebrates for a period of 21 days. In accordance with island biogeography theory, Arrington *et al.* found a significant positive influence of colonization rate on the number of species in local habitat patches. Furthermore, they observed more complex habitats contained significantly more species. Results varied when treatment effects were evaluated separately for two distinct subsets of the fish assemblage. Richness of fish taxa with low vagility was positively related to colonization rate and habitat patch complexity, whereas richness of highly vagile fishes was positively related to patch complexity but not colonization rate. Presumably, increased colonization ability by vagile species swamped the influence of habitat patch isola-

tion. These results suggest local community dynamics in this neotropical floodplain river are dominated by near continuous dispersal and colonization of habitat patches in the moving littoral (*sensu* "patch dynamics concept" Townsend 1989) by adult fishes (Arrington *et al.* in review). Furthermore, low concordance was observed between ranks of species from the meta-community and local habitat patches; thus falsifying one of Hubbell's (2001) hypotheses (see above). In a parallel experiment, Arrington *et al.* (in review) documented largely stochastic structure of local assemblages in newly formed habitat patches, but increasing levels of non-random organization were observed in patches as time progressed (> 24 days). Taken together, these data suggest dispersal is most important in structuring assemblages in newly formed patches, whereas the influence of local processes on assemblage structure increases as time progresses.

A considerable body of ecological theory has been developed that indicates tradeoffs in colonization and competitive abilities should preclude competitively dominant species from occupying all suitable habitats in a spatially heterogeneous landscape (i.e. the moving littoral of floodplain rivers) and as a consequence competitive subordinates should persist in the regional species pool (Levin and Paine 1974; Hurtt and Pacala 1995). The experiments by Arrington *et al.* lend support to an implicit theoretical trade off between colonization and competition ability in fishes of tropical floodplain rivers, where littoral species are forced to continually disperse across the landscape in association with a moving land-water interface. This continual disassembly and reassembly (due to dispersal) of local communities across a spatially heterogeneous landscape should result in low extinction rates (i.e. at the regional level) and could theoretically maintain a nearly infinite regional species pool (Hurtt and Pacala 1995).

Additional studies on the Cinaruco River appear to support such a mechanism in maintaining a very large regional species pool in a tropical floodplain river (Arrington 2002). Through most of 1999, six



■ **Figure 1.** Species accumulation curves for standardized seine samples collected from six habitats located in the moving littoral zone of the Cinaruco River, Venezuela reveal the diversity of tropical floodplain fish assemblages. Samples were collected through most of 1999, excluding the peak-wet season (see Arrington 2002). Number of samples collected per habitat was: river rock 45, river sand 69, river snag 47, lagoon leaf 36, lagoon sand 36 and lagoon snag 31. Each point along the solid line represents an estimate of the total community richness (including taxa not sampled) for specific littoral zone habitats based on the relative abundances of the most rare species in our samples (see Colwell 1997).

habitats were sampled from the moving littoral zone in the Cinaruco River. These habitats function as habitat templates, upon which local communities are assembled (Arrington 2002) and their spatial distribution in the main channel and floodplain is a dominant component of spatial habitat heterogeneity. Each month seven replicate diurnal samples were collected using the same seine (see Arrington 2002 for a description of methods). We plotted fish species accumulation curves for each habitat independently (Figure 1). In each habitat, we observed a continual and positive slope of the

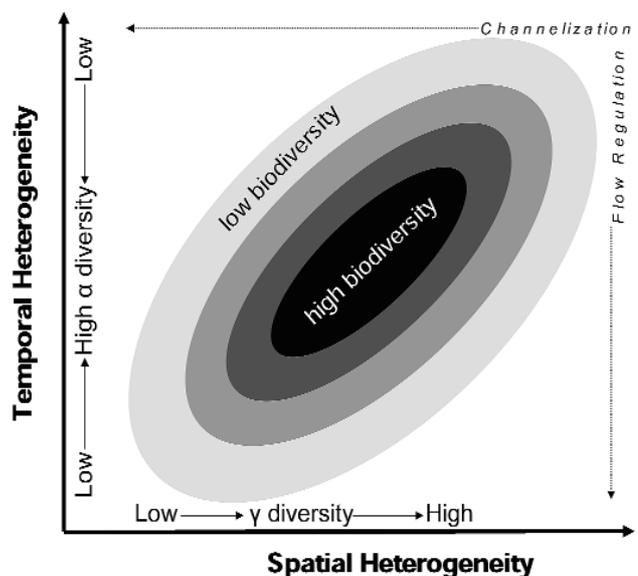
accumulation curve, with observed total assemblage richness (γ diversity) reaching 50 to 80 fish species per habitat type. In addition to observed species richness values, we estimated γ diversity for specific littoral zone habitats using a non-parametric estimator based on observed relative abundance data. The technique, known as abundance-based coverage estimator, assumes information about un-sampled species is held in the rarest classes of species collected (Chao and Lee 1992; Colwell and Coddington 1994; Chazdon *et al.* 1998) and can be computed using freely-available soft-

ware (Estimate S , Colwell 1997). In some habitats, such as river rock (Figure 1), the estimated size of the species pool far exceeds observed values. These local communities were consistently composed of relatively rare species. Thus, it appears that community assembly within isolated habitat patches, such as our river rock habitats, are more dependent upon stochastic colonization processes (i.e. colonization limitation). Furthermore, these patches often contained species characteristic of adjacent open sandbank habitats, which suggests leaky boundaries may lead to “mass effects” (Townsend 1989) in local patches that are not biologically saturated. Others have hypothesized that low dispersal or connectivity among patches should result in lowered α diversity, but promote β and γ diversity (Hubbell 1997), particularly in floodplain rivers that are characterized by high levels of spatiotemporal heterogeneity (Ward *et al.* 1999; Tockner *et al.* 1999; Amoros and Bornette 2002). In more contiguous (higher connectivity) patches, lower estimates of total richness may reflect reduced persistence of rare (Hubbell 2001) or competitively inferior (Hurt and Pacala 1995) species with higher colonization rates (higher α diversity but lower β diversity; Amoros and Bornette 2002). At present we are unable to identify the mechanism(s) driving the difference between observed and expected diversity (Figure 1). But, our experimental results indicate that a combination of colonization limitation (dispersal) and biotic interactions result in low α diversity but high β diversity (Arrington *et al.* in review). We submit that the annual flood pulse interacts with basin geomorphology and adds temporal heterogeneity to an already spatially heterogeneous landscape, both of which are critical in maintaining high levels of γ diversity observed in lowland tropical rivers (Figure 2).

THREATS TO FISH DIVERSITY IN TROPICAL FLOODPLAIN RIVERS

Rivers face a number of anthropogenic threats (Allan and Flecker 1993; Crisman *et al.* 2003) and dam building appears particularly damaging to tropical riverine biodiversity (Grossman, Dowd and Crawford 1990; Goulding, Smith and Mahar 1996; Pringle *et al.* 2000). Large floodplain rivers are characterized by a

remarkable degree of spatiotemporal heterogeneity in their natural state (Ward *et al.* 1999, 2001, 2002) and this heterogeneity is maintained by fluvial dynamics acting on landscape features. In the Tagliamento River (Italy) corridor, for example, landscape features experienced up to 80 percent turnover in a 3-year period, but features maintained similar relative proportions across the landscape (Ward *et al.* 2001). Construction of dams for flood control or hydroelectric power generation constrains these fluvial dynamics and can result in dramatic loss of spatial heterogeneity (Toth *et al.* 1995; Schmidt *et al.* 1998). If the interaction between the natural rise and fall of flood waters and floodplain spatial heterogeneity (habitat templates for organisms) maintains regional diversity levels in tropical floodplain rivers (Figure 2), then loss of the flood pulse not only will impact biological production (Junk



■ **Figure 2.** A conceptual model illustrating the importance of spatiotemporal heterogeneity in maintaining biological diversity in floodplain rivers. This model is derived from the intermediate disturbance hypothesis (Connell 1978; Shiel and Burslem 2003) and the “patch dynamics concept” (Townsend 1989) and is supported by fish data collected from the Cinaruco River, Venezuela, an unregulated, tropical lowland river. Anthropogenic alterations such as channelization and flow regulation are expected to result in compromised heterogeneity; direction of impact is indicated by dotted lines.

et al. 1989; Bayley 1995), but impoverish regional species pools (Grossman *et al.* 1990; Ward *et al.* 1999). Furthermore, reduction of landscape heterogeneity may impair the resilience typically observed in these systems (Townsend 1989; Meffe and Sheldon 1990; Townsend *et al.* 1997). Consequently, restoration strategies for floodplain rivers must emphasize the return of hydrologic variability characteristic of the pre-impacted system (e.g. Toth, Arrington and Begue 1997) as well as re-establishing among-habitat connectivity (Toth *et al.* 1998).

Interactions among seasonal hydrology, variability in habitat structural complexity and landscape heterogeneity appear to maintain high aquatic species richness in these lowland rivers. It follows that alteration of seasonal water level fluctuation (e.g. damming) and habitat heterogeneity (e.g. channelization) should have substantial and negative consequences on the maintenance of regional biodiversity pools in floodplain rivers. Better ecological understanding is needed to properly manage and preserve biological diversity in tropical floodplain rivers.

ACKNOWLEDGEMENTS

Our research was funded by the National Science Foundation (NSF DEB-0107456), The National Geographic Society, L.T. Jordan Institute and the International Sportfish Fund. This work would not have been possible without the help and assistance of J. Arrington, C. Garcia, J. Garcia, C. Layman, C. Lofgren, C. Marzuola, J. Marzuola, E. Pelaez, A. Stergios, B. Stergios, D. Taphorn and G. Webb. C. Layman and an anonymous reviewer provided helpful comments on this manuscript.

LITERATURE CITED

- Allan J.D. & Flecker A.S. 1993. Biodiversity conservation in running waters. *Bioscience*, 43: 32-42.
- Amoros C. & Bornette G. 2002. Connectivity and bio-complexity in waterbodies of riverine floodplains. *Freshwater Biology*, 47: 761-776.
- Angermeier P.L. & Winston M.R. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. *Ecology*, 79: 911-927.
- Arrington D.A. 2002. Evaluation of the relationship between habitat structure, community structure, and community assembly in a neotropical blackwater river. Texas A&M University, Texas, College Station. (Doctoral dissertation)
- Arrington D.A. & Winemiller K.O. 2003. Diel changeover in sandbank fish assemblages in a neotropical floodplain river. *Journal of Fish Biology*, 63: 1-18.
- Arrington D.A., Winemiller K.O. & Layman C.A. *In* Review community assembly at the patch scale in a speciose tropical river. *Oecologia*.
- Bayley P.B. 1995. Understanding large river-floodplain ecosystems. *Bioscience*, 45: 153-158
- Brooks T.M., Mittermeier R.A., Mittermeier C.G., da Fonseca G.A., Rylands B., Konstant A.B., Flick W. R., Pilgrim R., Oldfield J., Magin G. & Hilton-Taylor C. 2002. Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, 16: 909-923.
- Chao A. & Lee S.M. 1992. Estimating the number of classes via sample coverage. *Journal of the American Statistical Association*, 87: 210-217.



- Chazdon R.L., Colwell R.K., Denslow J.S. & Guariguata M.R. 1998. Statistical methods for estimating species richness of woody regeneration in primary and secondary rain forests of NE Costa Rica. In F. Dallmeier & J.A. Comiskey eds. *Forest biodiversity research, monitoring and modeling: Conceptual background and old world case studies*. Paris, Parthenon Publishing. pp. 285-309.
- Chesson P. & Huntly N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist*, 150: 519-553.
- Colwell R.H. 1997. Estimate S: Statistical estimation of species richness and shared species from samples. Version 5. User's Guide and application published. (Available at: <http://viceroy.eeb.uconn.edu/estimates/>.)
- Colwell R.H. & Coddington J.A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London Series B*, 345:101-118.
- Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199: 1302-1310.
- Cornell H.V. & Lawton J.H. 1992. Species interactions, local and regional processes and limits to the richness of ecological communities: A theoretical perspective. *Journal of Animal Ecology*, 61: 1-12.
- Cox Fernandes C. 1999. Detrended canonical correspondence analysis (DCCA) of electric fish assemblages in the Amazon. In A.L. Val & V.M.F. Almeida-Val eds. *Biology of Tropical Fishes*. Manaus, INPA. pp. 21-39.
- Crisman T.L., Chapman L.J., Chapman C.A. & Kaufman L.S. eds. 2003. Conservation, ecology, and management of African fresh waters. Gainesville, FL, University Press of Florida.
- Dudgeon D. 2000. Large-scale hydrological changes in tropical Asia: Prospects for riverine biodiversity. *Bioscience*, 50: 793-806.
- Duque A.B., Taphorn D.C. & Winemiller K.O. 1998. Ecology of the coporo, *Prochilodus mariae* Characiformes, Prochilodontidae, and status of annual migrations in western Venezuela. *Environmental Biology of Fishes*, 53: 33-46.
- Fernandes C.C. 1997. Lateral migration of fishes in Amazon floodplains. *Ecology of Freshwater Fish*, 6: 36-44.
- Garcia A.M., Vieira J.P. & Winemiller K.O. 2001. Dynamics of the shallow-water fish assemblage of the Patos Lagoon estuary Brazil during cold and warm ENSO episodes. *Journal of Fish Biology*, 59: 1218-1238.
- Goulding M., Carvalho M.L. & Ferreira E.G. 1988. *Río Negro: Rich life in poor water*. The Hague: SPB Academic Publishing.
- Goulding M., Smith N.J.H. & Mahar D.J. 1996. *Floods of fortune: Ecology and economy along the Amazon*. New York, Columbia University Press.
- Griffiths D. 1997. Local and regional species richness in North American lacustrine fish. *Journal of Animal Ecology*, 66: 49-56
- Grossman G. D., Dowd J.F. & Crawford M. 1990. Assemblage stability in stream fishes: A review. *Environmental Management*, 14: 661-671.
- Grossman G.D., Moyle P.B. & Whitaker J.O. 1982. Stochasticity in structural and functional characteristics of an Indiana stream fish assemblage: A test of community theory. *American Naturalist*, 120: 423-454.

- Grossman G.D., Ratajczak R.E. Jr., Crawford M. & Freeman M.C. 1998. Assemblage organization in stream fishes: Effects of environmental variation and interspecific interactions. *Ecological Monographs*, 68: 395-420.
- Guégan J., Lek S. & Oberdorff T. 1998. Energy availability and habitat heterogeneity predict global riverine fish diversity. *Nature*, 391: 382-384.
- Hoeinghaus D.J., Layman C.A., Arrington D.A. & Winemiller K.O. 2003. Spatiotemporal variation in fish assemblage structure in tropical floodplain creeks. *Environmental Biology of Fishes* 49: 421-433.
- Hubbell S.P. 1997. A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* 16: Suppl., S9-S21.
- Hubbell S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ., Princeton University Press.
- Hugueny, B. & Cornell H.V. 2000. Predicting the relationship between local and regional species richness from a patch occupancy dynamics model. *Journal of Animal Ecology*, 69:194-200.
- Hugueny, B. & Paugy D. 1995. Unsaturated fish communities in African rivers. *American Naturalist*, 146: 162-169.
- Hurtt G.C. & Pacala S.W. 1995. The consequences of recruitment limitations: Reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, 176: 1-12.
- Ibarra M. & Stewart D.J. 1989. Longitudinal zonation of sandy beach fishes in the Napo River Basin, Eastern Ecuador. *Copeia*, 1989: 364-381.
- Jackson D.A., Sommers K.M. & Harvey H.H. 1992. Null models and fish communities: Evidence of nonrandom patterns. *American Naturalist*, 139: 930-951.
- Jenkins D.G. & Buikema Jr. A.L. 1998. Do similar communities develop in similar sites? A test with zooplankton structure and function. *Ecological Monographs*, 68: 421-433.
- Jepsen D.B. 1997. Fish species diversity in sand bank habitats of a Neotropical river. *Environmental Biology of Fishes*, 49: 449-460.
- Junk W.J., Bayley P.B. & Sparks R.E. 1989. The flood pulse concept in river-floodplain systems. In D.P. Dodge ed. *Proceedings of the international large rivers symposium*. *Can. J. Fish. Aquat. Sci. Spec. Publ.*, 106: 110-127.
- Lamouroux N., Poff N.L. & Angermeier P.L. 2002. Intercontinental convergence of stream fish community traits along geomorphic and hydraulic gradients. *Ecology*, 83: 1792-1807.
- Levin S.A. & Paine R.T. 1974. Disturbance, patch formation, and community structure. *Proceedings of the National Academy of Sciences USA* 71, 2744-2747.
- Lundberg J. 2001. Freshwater riches of the Amazon. *Natural History*, 110: 36-43.
- Lundberg J.G., Lewis Jr. W.M., Saunders J.F. III & Mago-Leccia F. 1987. A major food web component in the Orinoco River Channel: Evidence from planktivorous electric fishes. *Science*, 237: 81-83.
- MacArthur R.H. & Wilson E.O. 1967. *The Theory of island biogeography*. Princeton, NJ., Princeton University Press.
- Matthews W.J. 1998. *Patterns in Freshwater Fish Ecology*. New York, Chapman and Hall.

- Meffe G.K. & Sheldon A.L. 1990. Post-defaunation recovery of fish assemblages in southeastern blackwater streams. *Ecology*, 71: 657-667.
- Meyers N., Mittermeier R.A., Mittermeier C. G., da Fonseca G.A.B. & Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature*, 403: 853-858.
- Oberdorff T., Hugueny B., Compin A. & Belkessam D. 1998. Non-interactive fish communities in the coastal streams of North-western France. *Journal of Animal Ecology*, 67: 472-484.
- Oberdorff T., Hugueny B. & Vigneron T. 2001. Is assemblage variability related to environmental variability? An answer for riverine fish. *Oikos*, 93: 419-428.
- Petry P., Bayley P.B. & Markle D.F. 2003. Relationships between fish assemblages, macrophytes and environmental gradients in the Amazon River floodplain. *Journal of Fish Biology*, 63.
- Poff N.L. & Allan J.D. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, 76: 606-627.
- Pringle C.M., Freeman M.C. & Freeman B.J. 2000. Regional effects of hydrologic alterations on riverine macrobiota in the New World: Tropical-temperate comparisons. *Bioscience*, 50: 807-823.
- Rahel F.J. 1990. The hierarchical nature of community persistence: A problem of scale. *American Naturalist*, 136: 328-344.
- Reseraris W.J., & Bernardo J. eds. 2001. *Experimental Ecology: Issues and perspectives*. New York, Oxford University Press.
- Robinson C., Tockner K. & Ward J.V. 2002. The fauna of dynamic riverine landscapes. *Freshwater Biology*, 47: 661-677.
- Rodríguez M.A. & Lewis W.M. 1997. Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecological Monographs*, 67: 109-128.
- Saint-Paul U., Zuanon J., Villacorta Correa M.A., García M., Noemi Fabré N., Berger U. & Junk W.J. 2000. Fish communities in central Amazonian white- and blackwater floodplains. *Environmental Biology of Fishes*, 57: 235-250.
- Schlosser I.J. 1987. A conceptual framework for fish communities in small warmwater streams. In W.J. Matthews and D.C. Heins eds. *Community and evolutionary ecology of North American stream fishes*. Norman, OK, USA, University of Oklahoma Press. pp. 17-24.
- Schlosser I.J. & Kallemeyn L.W. 2000. Spatial variation in fish assemblages across a beaver-influenced successional landscape. *Ecology*, 81: 1371-1382.
- Schmidt J.C., Webb R.H., Valdez R.A., Marzolf R. & Stevens L.E. 1998. Science and values in river restoration in the Grand Canyon. *Bioscience*, 48: 735-747.
- Sheil D. & Burslem D.F.R.P. 2003. Disturbing hypotheses in tropical forests. *Trends in Ecology and Evolution*, 18: 18-26.
- Shurin J.B., Havel J.E., Leibold M.A. & Pinel-Alloul B. 2000. Local and regional zooplankton species richness: A scale-independent test for saturation. *Ecology*, 81: 3062-3073
- Southwood T.R.E. 1988. Tactics, strategies and templets. *Oikos*, 52: 3-18.
- Stewart D.J., Ibarra M. & Barriga-Salazar R. 2002. Comparison of deep-river and adjacent sandy-beach fish assemblages in the Napo River Basin, Eastern Ecuador. *Copeia*, 2002: 333-343.

- Taylor C.M. 1996. Abundance and distribution within a guild of benthic stream fishes: Local processes and regional patterns. *Freshwater Biology*, 36: 385-396.
- Taylor C.M. & Warren M.L. 2001. Dynamics in species composition of stream fish assemblages: Environmental variability and nested subsets. *Ecology*, 82: 2320-2330.
- Tockner K., Schiemer F., Baumgartner C., Kum G., Weigand E., Zweimüller I. & Ward J.V. 1999. The Danube restoration project: Species diversity patterns across connectivity gradients in the floodplain system. *Regulated Rivers: Research & Management*, 15: 245-258.
- Tonn W.M. 1990. Climate change and fish communities: a conceptual approach. *Transactions of the American Fisheries Society*, 119: 337-352.
- Tonn W.M., Magnuson J.J., Rask M. & Toivonen J. 1990. Intercontinental comparison of small-lake fish assemblages: The balance between local and regional processes. *American Naturalist*, 136: 345-375.
- Toth L.A., Arrington D.A. & Begue G. 1997. Headwaters restoration and reestablishment of natural flow regimes: Kissimmee River of Florida. In J.E. Williams, C.A. Wood & M.P. Dombeck eds. *Watershed restoration: Principles and practices*. Bethesda, MY., American Fisheries Society. pp. 425-444.
- Toth L.A., Arrington D.A., Brady M.A. & Muszick D.A. 1995. Conceptual evaluation of factors potentially affecting restoration of habitat structure within the channelized Kissimmee River ecosystem. *Restoration Ecology*, 3: 160-180.
- Toth L.A., Melvin S., Arrington D.A. & Chamberlain J. 1998. Hydrologic manipulations of the channelized Kissimmee River. *Bioscience*, 48: 757-764.
- Townsend C.R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society*, 8: 36-50.
- Townsend C.R., Scarsbrook M.R. & Dolédec S. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. *Limnology and Oceanography*, 42: 938-949.
- Ward J.V. 1989. The four-dimensional nature of lotic ecosystems. *Journal of the North American Benthological Society*, 8: 2-8.
- Ward J.V. 1998. Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation*, 83: 269-278., 47: 517-539.

