



Fish species diversity among spatial scales of altered temperate rivers

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ABSTRACT

Aim The alteration of flowing systems over the past century has led to significant changes to the processes that drive these complex environments as well as to the scales at which these processes act. Recently, efforts have begun in earnest to restore some semblance of ecosystem diversity, but there is little understanding of exactly on what spatial scale or scales biotic diversity is responding. We investigated the manner in which fish diversity is partitioned at multiple spatial scales in two rivers in the central United States.

Location The Missouri and Illinois rivers of the central United States.

Methods We analysed how fish diversity was partitioned within the Illinois River and Missouri River systems by sampling each river under hierarchical frameworks that allowed analysis at section (large), reach (intermediate), and site (small) scales. We tested the hypothesis that there are scale-dependent responses of fish diversity using an additive partitioning approach.

Results Site alpha diversity was significantly higher than expected in both the Illinois and Missouri rivers. The relative contribution of alpha diversity to total diversity at a given spatial scale increased for the Illinois River, but not for the Missouri River, in that the highest alpha diversity contribution peaked at the reach scale. Diversity patterns from both rivers suggest that diversity at the site scale plays a significant role in determining the overall diversity in these systems. However, there is a substantial contribution at larger scales that warrants consideration when attempts are being made to protect or restore diversity and other ecosystem parameters.

Main conclusions Understanding the variation of diversity in riverine systems is crucial for providing insight not only into how biotic communities respond to scale-dependent factors, but also into the underlying abiotic and biotic factors that generate patterns of diversity across scales. These insights, in turn, are important for ensuring that restoration and management activities are targeting the appropriate scales for remediation. A lack of understanding of this issue could have negative outcomes for the recovery of a community in a restoration scenario, as well as resulting in a low economic return on restoration investments, which could hinder future efforts.

Keywords

Additive partitioning, biodiversity, Illinois River, Missouri River, nested hierarchy analysis, spatial structure.

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INTRODUCTION

Fish species diversity is influenced by biotic and abiotic processes that function across various scales of space and time

in riverine systems (Bain *et al.*, 1988; Angermeier & Schlosser, 1989; Rahel & Hubert, 1991). Some of these processes operate over very coarse spatial and temporal scales. For instance, abiotic processes such as plate tectonics (geomorphology) and

climate (latitude; Ricklefs & Schuller, 1993), interacting with biotic temporal processes involving rates of evolutionary speciation and dispersal (Livingston *et al.*, 1982; Hughes *et al.*, 1987; Hugueny, 1989), have strongly influenced patterns of fish species diversity within and among riverine systems. However, at finer spatial and temporal scales, the flow of water across a fluvial landscape is thought to be one of the key driving variables used to describe fish species diversity, as it can have a strong effect on many other abiotic factors (Johnson *et al.*, 1995; Poff & Allan, 1995; Sparks, 1995; Pegg & Pierce, 2002). Abiotic factors such as river-channel morphology, the distribution of reach and pool habitats, localized hydrology, microhabitat refugia, substrate stability, and sediment deposition are all largely determined by the interaction between the flow regime of a river and local geology (Frissell *et al.*, 1986; Junk *et al.*, 1989; Sparks, 1995; Poff *et al.*, 1997; Bunn & Arthington, 2002), and flow plays a crucial role in determining the types of suitable habitat available for riverine fishes throughout the various stages of their life history. Furthermore, many riverine fishes have evolved life-history strategies to capitalize on this complex interaction between biotic and abiotic factors (Southwood, 1977; Frissell *et al.*, 1986; Bunn & Arthington, 2002; Lytle & Poff, 2004).

Unfortunately, human usage has substantially altered many of the world's large river systems (Sparks, 1995; Nillson *et al.*, 2005). These alterations have generally been the result of public demand directed towards reducing annual flow variability for flood control, and towards maintaining a reliable source of water for navigation, hydropower, and irrigation. Such alterations include the isolation of rivers from their floodplains, the destruction of wetland habitat through draining and filling for agricultural purposes, the construction of levees to contain floods, and the construction of dams, thereby creating impoundments to regulate flow (Galat & Lipkin, 2000). These alterations are believed to have disrupted fish species composition and diversity in many river systems. For example, alterations to both the Illinois River and Missouri River in the United States, coupled with the historical effects of pollution, are thought to have led to significant changes in both the spatial and temporal patterns of fish community structure (Funk & Robinson, 1974; Pegg & Pierce, 2002; Pegg & McClelland, 2004). Therefore, it is not surprising that many large river ecosystem restoration programmes have focused either implicitly or explicitly on maximizing aquatic biodiversity as a means to establishing processes that are more natural (Poff *et al.*, 1997; Bunn & Arthington, 2002). Consequently, it is crucial to understand variation in aquatic biological diversity in order to gain insight into the underlying abiotic and biotic factors that generate patterns of diversity across multiple scales in these modified systems.

The existence of multiscale species diversity patterns within ecological systems complicates formal analyses as a result of the inherent interdependence of the data at varying hierarchical scales (Schneider, 2001). However, one revitalized approach that is gaining attention is additive partitioning (MacArthur, 1965; Levins, 1968; Lande, 1996;

Veech *et al.*, 2002; Noda, 2004). Additive partitioning is an operational method that allows researchers to analyse patterns of species diversity across multiple spatial scales. In this method the total diversity (gamma) found in a pooled set of communities sampled from a habitat at any spatial scale can be partitioned into the average diversity that occurs within a sample (alpha) and the average diversity among samples (beta; Lande, 1996; Gering & Crist, 2002; Veech *et al.*, 2002; Crist *et al.*, 2003; Fleishman *et al.*, 2003). Traditional analyses of alpha diversity often involve comparisons of some measure of mean diversity (e.g. species richness) found in two or more sets of samples using analysis of variance. Analyses of beta diversity often involve metrics (e.g. Bray-Curtis) based on pairwise similarity or dissimilarity (Magurran, 1988) in order to contrast changes in species composition. Unlike the case for Whittaker's (1960) multiplicative concepts of alpha-, beta-, and gamma diversity, the total species diversity in a set of samples can be partitioned into additive components ($\gamma = \alpha + \beta$) within and among spatial scales (Lande, 1996; Veech *et al.*, 2002; Crist *et al.*, 2003). The resulting components of diversity are all measured in the same units, allowing gamma diversity to be broken into alpha and beta components for comparison across multiple spatial and/or temporal scales.

Many large river systems can be organized as a spatially nested hierarchy based on ecologically relevant differences in river geomorphological and hydrological characteristics (Frissell *et al.*, 1986; Amoros *et al.*, 1987; Townsend, 1996). Additive partitioning can then be used to evaluate multiscale patterns of species diversity in these rivers by simultaneously exploring the contribution of each nested level to the total diversity of a given landscape. The partitioning of spatially explicit diversity can also assist in identifying which spatial scale provides the greatest contribution to species diversity (Wagner *et al.*, 2000; DeVries & Walla, 2001; Fournier & Loreau, 2001; Gering & Crist, 2002; Crist *et al.*, 2003; Fleishman *et al.*, 2003). The objective of our study was to assess patterns of fish diversity within the Illinois River and Missouri River, two highly modified temperate rivers in the central United States, using the additive partitioning approach. Specifically, we tested the core null hypothesis that the within-sample (alpha) diversity and between-sample (beta) diversity observed in this study exhibit no scale dependence.

STUDY AREA

The Illinois (440 km) and Missouri (3768 km) rivers are large tributaries of the Mississippi River located in the Upper Mississippi River Basin of the central United States (Fig. 1). Physical modifications to these rivers have followed a parallel temporal sequence, ranging from a series of dams constructed during the first half of the 20th century to channel deepening and levee construction/repairs, which continue to the present day. Therefore, both rivers have an established history of anthropogenic modifications that have changed the fish communities (Starrett, 1971; Funk & Robinson, 1974; Hesse & Mestl, 1993) and influenced the scale of pressures driving diversity in these systems.

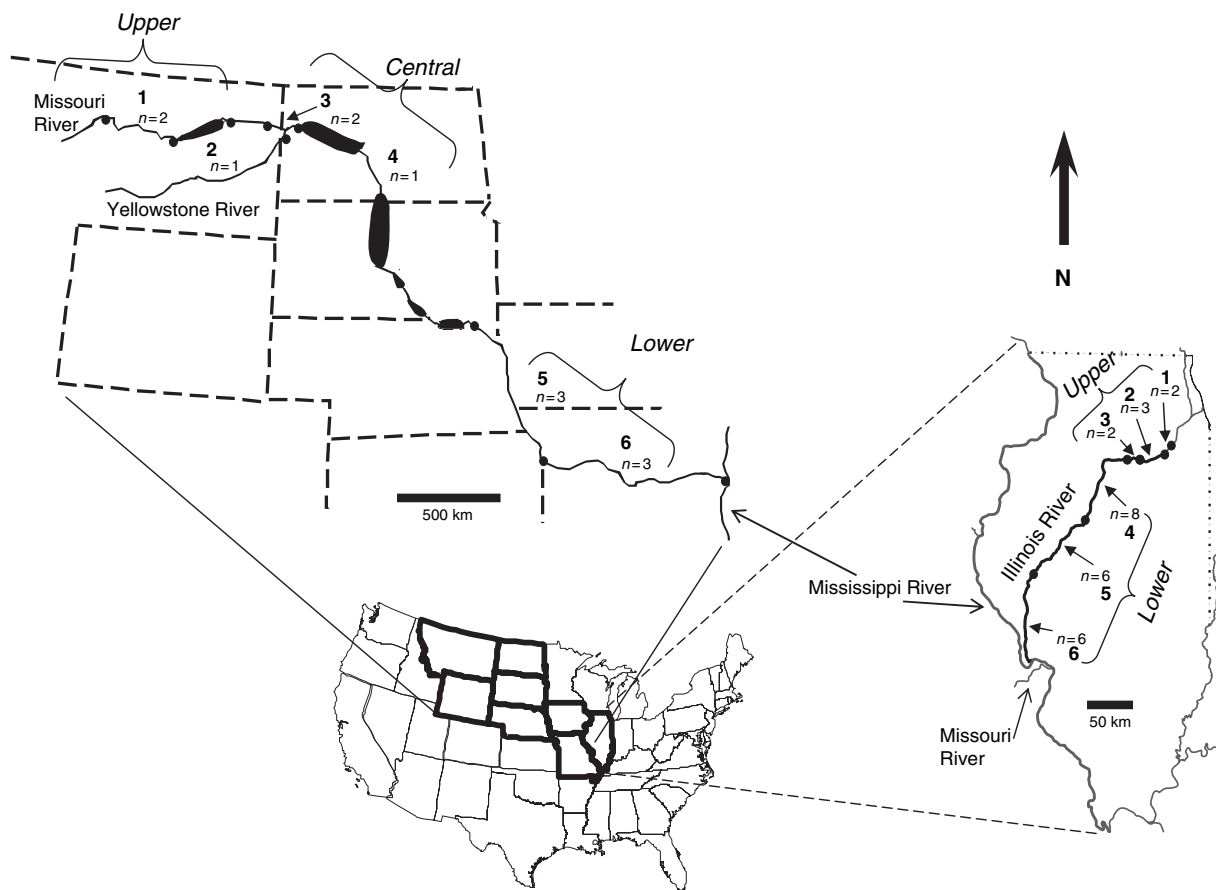


Figure 1 Geographic location of the Illinois River and Missouri River in the United States. Spatial scales are broken into section (italics) identified by brackets, reach (bold) identified by ●, and sites identified by sample sizes within a reach for each river system.

METHODS

Illinois river fish data collection

Twenty-seven fixed sites were sampled annually along the Illinois River between 1996 and 1998 as part of the Illinois Natural History Survey's Long-term Illinois River Fish Population Assessment Project (Koel & Sparks, 2002; Fig. 1). Although the sites were initially selected based on accessibility, they were all located in backwater, side-channel and main-channel habitats that remained permanently connected to the main channel, regardless of river stage. The number of sampling sites was generally stratified to reflect the size of each reach (Fig. 1). Fish sampling methodology and technology were standardized throughout the life of the project to ensure comparability within and among years. Annual sampling was conducted during a 6-week period from late August to early October, when both water level and water temperature tend to be relatively stable and fish movements associated with seasonal migrations are likely minimal. Each site was typically sampled for 1 h using a 3000-W, three-phase AC boat-mounted electrofisher. All captured fish were identified to species and immediately released near each sample site.

Hierarchical framework

We partitioned the Illinois River into three nested spatial levels based upon natural and anthropogenic differences in geomorphology and hydrology (Fig. 1). First, we separated the Illinois River into two sections (upper and lower) based upon natural differences in river geomorphology (river 'section' nested within 'river'). We then further separated each river section into three reaches as a result of a series of locks and dams (river 'reach' nested within river 'section'). Finally, we separated each river reach into a number of river sampling sites (river 'site' nested within river 'reach'), with the number of sites varying depending on the reach. Explicit justification for these spatial scales is outlined in Koel & Sparks (2002) and Pegg & McClelland (2004).

Missouri river fish data collection

Fish were collected from 12 river sites located throughout the riverine portions of the Missouri and Lower Yellowstone rivers during late summer and early autumn of the years 1996–98 following standardized protocols as part of the Missouri River Benthic Fishes Project (Sappington *et al.*, 1998; Fig. 1). Within each site, six macrohabitat types were sampled, including

inside and outside bend, main channel at the cross-over point between bends, tributary mouth, connected side channel, and unconnected side channel. Sampling gears used included a boat electrofisher, beam trawl, bag seine, stationary gill net, and drifted trammel net. Effort was typically consistent among sites, and at least two gears were used in each macrohabitat to account for the size-selective bias inherent within each gear. All captured fish were identified to species and immediately released near each sample site.

Hierarchical framework

We partitioned the Missouri River study landscape into three hierarchical spatial levels following an approach similar to that used for the Illinois River. First, we separated the Missouri River into three mainstem sections based upon observable differences in channel morphology resulting from human alteration ('section' nested within River). We further separated each section into reaches based upon differences in hydrology within each section ('reach' nested within 'section'). Finally, each reach was further separated into a number of sites ('site' nested within 'reach'; Fig. 1), with the number of sites varying depending on the reach size. Explicit justification for these spatial scales is described in Sappington *et al.* (1998), Berry & Young (2001) and Pegg & Pierce (2002).

Additive partitioning

Using the additive partitioning approach, total fish gamma-diversity is the sum of alpha diversity (α_1) within sites, beta-diversity (β_1) among sites, beta diversity (β_2) among reaches, and beta diversity (β_3) among river sections:

$$\gamma_{(\text{totaldiversity})} = \alpha_1(\text{withinsite}) + \beta_1(\text{amongsites}) + \beta_2(\text{amongreaches}) + \beta_3(\text{amongsections})$$

These diversity estimates can then be used to evaluate spatial differences and/or influences that may not be immediately apparent from looking solely at diversity at one or a select subset of sites. We used PARTITION (Crist *et al.*, 2003) to test for the presence of any scale-dependent spatial patterns of fish species richness across all hierarchical levels for the Illinois River and Missouri River fish data sets. Specifically, we tested the null hypothesis that the observed alpha species richness and beta species richness data at each hierarchical level were

not significantly different within each river from those obtained by a random distribution of fish species among samples at all hierarchical levels (i.e. no scale dependence; Crist *et al.*, 2003). We used the complete randomization procedure option in PARTITION to generate 10,000 random distributions of fish species among samples at all hierarchical levels to form a null distribution of each alpha and beta estimate for each level within the hierarchy. We then tested the observed diversity components (alpha and beta) at each hierarchical level to the expected mean diversity component values generated by assessing the proportion of null values that were greater than (or less than) the actual estimate. Our highest hierarchical scale of analysis was at the river scale rather than total diversity for the entire data set that included both rivers, because site sizes, effort, and gears differed substantially between river systems, which could readily bias system-scale comparisons.

Finally, we compared the relationship between scale-specific alpha diversity and gamma diversity at each hierarchical scale using linear regression (Gering & Crist, 2002). Assessing the nature of this relationship can provide valuable information on the overall diversity contribution both within and among spatial scales (Noda, 2004).

RESULTS

River-specific Gamma diversity

Forty-eight fish species were collected in the Illinois River between 1996 and 1998 (Appendix S1 in Supplementary Material). Seventy-four fish species were collected from the Missouri River between 1996 and 1998 (Appendix S2).

Additive partitioning

The observed mean alpha diversity was considerably greater than the beta diversity at each spatial scale along the Illinois River (Table 1). The total species richness within and among site components (α_1 and β_1) accounted for 64% of the total species richness. Mean species richness (α_1) within sites contributed the most to overall species richness, followed by beta diversity (β_1) among sites, beta diversity (β_2) among reaches, and beta diversity (β_3) among sections (Fig. 2a).

Site alpha diversity (α_1) was significantly higher than expected ($P < 0.01$) in the Illinois River; that is, none of the

Spatial scale	Diversity component	Observed mean diversity	Expected mean diversity	Contribution to gamma diversity (%)	<i>P</i>
River	γ	48.0			
Section	α_3	40.0	42.6	83	0.99
	β_3	8.0	5.4	17	< 0.01
Reach	α_2	30.7	32.3	77	0.99
	β_2	9.3	10.3	23	0.85
Site	α_1	19.7	14.6	64	< 0.01
	β_1	11.0	17.8	36	1.00

Table 1 Additive partitioning results for fish communities along the Illinois River (1996–98). Spatial scales are shown in Fig. 1. Values of *P* indicate the probabilities resulting from the null hypothesis test that a given diversity parameter is from a random distribution

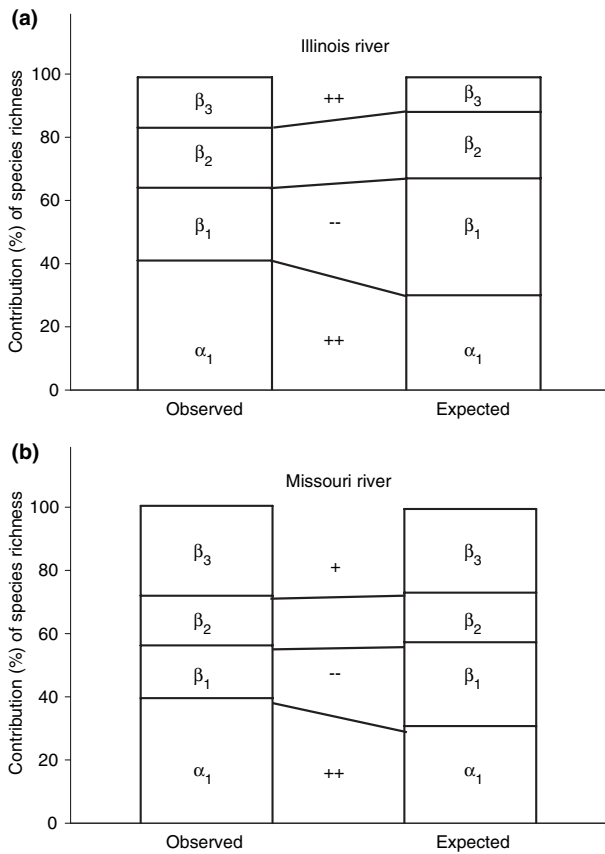


Figure 2 Diversity partition results for (a) the Illinois River and (b) the Missouri River at all spatial scales analysed. Each variable in the bar represents the percentage contribution to total diversity. The symbol ‘++’ indicates that the observed diversity was much greater than expected ($P < 0.01$), ‘--’ indicates that the observed diversity was much lower than expected ($P < 0.01$), and ‘+’ indicates that the observed diversity was higher than expected ($P = 0.07$).

10,000 randomizations produced data sets in which alpha-diversity was higher than observed. In contrast, level-one observed beta-diversity (β_1) was significantly lower than expected ($P < 0.01$) because all randomizations produced data sets in which β_1 was greater than the value observed. The fact that the α_1 and β_1 site diversity estimates are significant in opposite directions is not entirely unexpected, given the complementary nature of the additive approach. Diversity at higher spatial scales had mixed results. Beta diversity (β_2) at the reach level was not significantly higher or lower than expected ($P > 0.05$). However, beta diversity (β_3) at the section scale was significantly higher ($P < 0.05$) than expected (Table 1; Fig. 2a).

The relative contribution of alpha diversity to gamma-diversity at a given spatial scale increases with hierarchical scale (Table 1). Similarly, deviations from the assumption that alpha and beta diversity will make an equal contribution to scale-specific diversity can be evaluated using regression information defining the relationship between alpha diversity and gamma diversity at the site and reach levels. Here, our

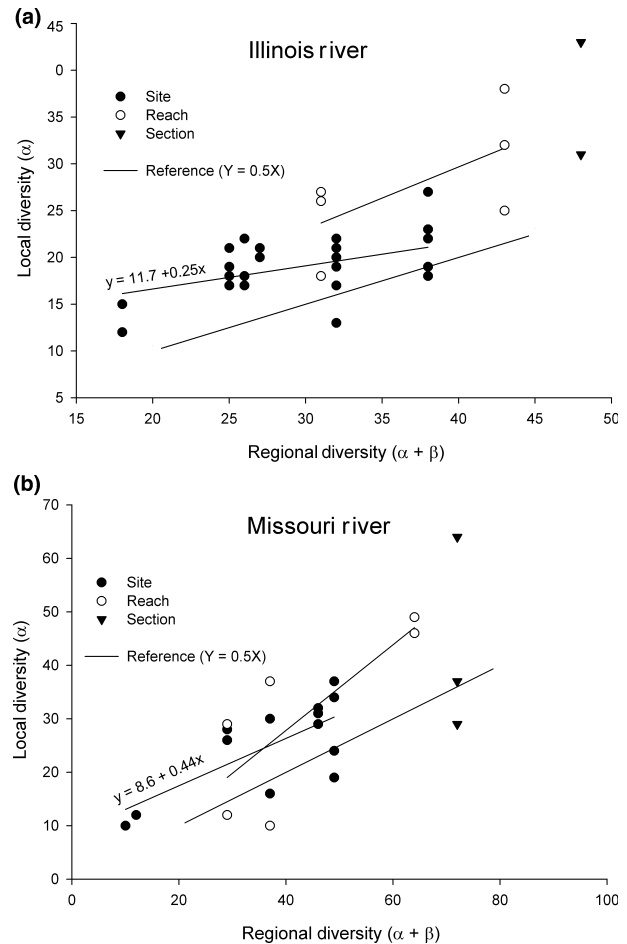


Figure 3 Relationship of alpha diversity to gamma diversity at several scales for (a) the Illinois River and (b) the Missouri River. Regressions for site-scale data are significant ($P < 0.05$) and above the reference line, indicating that alpha diversity is playing a large role in contributing to the diversity of each system.

results indicate, based on the slopes of the lines, that the relative contribution of alpha diversity increases both with scale and overall species richness. However, at the site level there is more parity between alpha and beta diversity than at the reach level (Fig. 3a).

For the Missouri River, the mean alpha diversity was also considerably greater than the beta diversity at each spatial scale (Table 2). The total species richness (α_1 and β_1) within and among sites contributed 55% of the total diversity in the Missouri River. Mean alpha-diversity (α_1) within river sites contributed the most to overall species richness (38%), followed by beta diversity (β_1) among sites (17%), beta diversity (β_2) among reaches (16%) and beta diversity (β_3) among sections (29%; Fig. 2b).

Site alpha diversity was also significantly higher than expected ($P < 0.01$) in the Missouri River. Similar to the case for the Illinois River, none of the 10,000 randomizations produced data sets for the Missouri River that had higher alpha diversity estimates than those we observed. At the same time, observed beta diversity (β_1) was significantly lower than

Spatial scale	Diversity component	Observed mean diversity	Expected mean diversity	Contribution to gamma diversity (%)	<i>P</i>
River	γ	74.0			
Section	α_3	52.3	54.2	71	0.92
	β_3	21.7	19.8	29	0.07
Reach	α_2	40.6	42.2	78	0.92
	β_2	11.7	12.1	22	0.60
Site	α_1	27.9	21.8	69	< 0.01
	β_1	12.7	20.3	31	1.00

Table 2 Additive partitioning results for fish communities along the Missouri River (1996–98). Spatial scales are shown in Fig. 1. Values of *P* indicate the probabilities resulting from the null hypothesis test that a given diversity parameter is from a random distribution.

expected, because all 10,000 randomizations produced data sets in which β_1 was greater than that observed ($P < 0.01$). Beta diversity (β_2) at the reach scale was not significantly higher or lower than expected ($P > 0.05$). Beta diversity (β_3) at the section scale was higher than expected ($P < 0.07$).

The macrohabitat samples (nested within site) along the Missouri River provided an additional hierarchical scale of evaluation that could shed light on a finer spatial scale. Therefore, we conducted a second analysis of Missouri River diversity using macrohabitat data as the lowest hierarchical scale for comparative purposes against analyses using the hierarchical levels presented for both rivers. The resulting partition of species diversity was largely similar to that of the Missouri River analysis without using macrohabitat. However, beta diversity values at the macrohabitat and site levels were significantly lower than expected ($P < 0.01$), suggesting that within-site diversity is contributing a substantial portion of the diversity at the site and higher spatial scales.

Our results indicate that the relative contribution of alpha-diversity increases both with scale and with overall species richness (Fig. 3b). However, the relative contribution of alpha-diversity to gamma diversity at a given spatial scale is not linear in the Missouri River, in that the highest alpha diversity contribution peaked at the reach hierarchical spatial scale (Table 2). Our analyses including macrohabitats indicated a similar trend for the site (71%), reach (80%), and section (67%) relationships, but the alpha diversity contribution was highest at macrohabitat level (82%).

DISCUSSION

The diversity patterns we observed in the Illinois and Missouri rivers provide an interesting insight into some of the driving forces in these systems. For example, the contributions of alpha diversity at the section scale on the Illinois River and reach scale on the Missouri River indicate strong contributions within recognizable hydro-geomorphic features in each river. The major break between sections on the Illinois River is a result of substantial changes in morphology: the upper section is characterized as a relatively narrow floodplain with a higher gradient, whereas the lower section of the river has a much wider floodplain and a lower gradient (Starrett, 1971). These differences, and the fact that the lower section is in close proximity to the Mississippi River as a source for fish diversity,

probably provide at least an historical basis for differences between sections. However, anthropogenic influences are also at play in these same hierarchical units and may be the overriding driver of the system at present. Industrial and domestic pollution decimated the native fish community in the upper half of the river in the early 1900s (Starrett, 1971). Exposure of fish to high levels of pollution was fairly brief (*c.* 50 years), but it substantially and abruptly altered the overall fish community (Pegg & McClelland, 2004). There have also been changes to the lower river through floodplain isolation, increased sediment deposition, and flow modifications, which influence diversity, but their direct impacts have been less abrupt. Therefore, it seems reasonable that the highest contribution to diversity would come at these clearly delineated spatial scales, at which recent driving forces are exerting the most pressure on fish communities in the Illinois River.

A similar scenario exists on the Missouri River, in that the reaches represent significant changes in basin morphology or changes in river management practices. The Missouri River traverses nearly 4000 km across a broad climatic and latitudinal gradient. This gradient has operated on a lengthy temporal scale that has probably had an evolutionary influence on diversity patterns and biogeographical constraints in establishing the diversity of fishes. This phenomenon is not uncommon in many systems, but may be less evident with recent shifts in diversity following anthropogenic changes. Hawkins & Porter (2003) found evidence of some historical influence on biodiversity, but that present factors or forces (e.g. fragmentation, land-use patterns) have the most profound effect on North American bird and mammal diversity. River fish diversity is seemingly operating in a parallel context. For example, the prevailing concepts on the ecology of large, modified river systems provide support for the idea that diversity is regulated by processes at larger, anthropogenic-induced scales. The Serial Discontinuity Concept (Ward & Stanford, 1983) allows that placing dams along a river can 'reset' areas downstream of the dam to environmental conditions reflecting headwater areas, with dramatic impacts on the biota. Furthermore, impoundments are impediments to fish dispersal and are prevalent in both rivers. These impediments are probably influencing diversity at the reach and section levels because the species compositions change markedly between the larger spatial scales. Reaches located within the upper two sections on the Missouri River are interspersed

above and below a series of reservoirs that have isolated riverine fish communities to some extent (Pegg & Pierce, 2002). Reach 5 on the lower Missouri River has been subjected to a combination of channelization and flow modifications from upstream impoundments, among other modifications, where a substantial amount of wetted area has been removed (Funk & Robinson, 1974). Collectively, the reduction in habitat has caused substantial changes in riverine species compositions within the Missouri River (Pegg & Pierce, 2002) and has ultimately led to recovery plans for at-risk species, for example the federally endangered pallid sturgeon *Scaphirhynchus albus* Forbes & Richardson (Quist *et al.*, 2004) and several other native species.

The determination of scale-influenced diversity has important consequences for an appropriate understanding of river biota as well as for management and ecosystem restoration strategies (Veech *et al.*, 2002). If the scale at which river management and naturalization strategies are implemented is dissimilar to the scale(s) at which they should be applied, efforts to mitigate the impacts of human activity on fluvial ecosystems may fail (Wiens, 1989, 2002). With this in mind, it appears that targeting large-scale (section or reach) management practices that influence the prevalent forces on biodiversity in today's landscape will have the most profound effect on conserving biodiversity in these modified riverine systems. However, diversity issues should not be ignored at smaller spatial scales, because patterns from both of the rivers that we studied showed that α_1 -diversity also plays a meaningful role in determining overall diversity in these systems. This result implies that smaller-scale processes such as habitat availability, competition for resources, and other niche interactions are having a considerable influence on fish communities at the site scale that have resounding influence at broader spatial scales. Ultimately, the management of altered riverine systems will probably require a delicate balance of optimizing microhabitat or other small-scale issues to establish a suitable environment for individual species, while also attempting to control larger landscape issues such as land-use practices, flow management, and floodplain connectivity. Many other large rivers around the world face similar threats, so it is reasonable to expect a comparable response to multiscale influences on diversity in these systems as well. Fortunately, many of the resource-management and restoration plans currently in place (e.g. Vivash *et al.*, 1998; Poudevigne *et al.*, 2002; USCOE, 2006) identify and attempt to mediate processes that operate both at the coarse scale (i.e. land use, impoundment, flow modification) and at finer scales (i.e. localized habitat restoration and connection to floodplain), because they are the scales at which physical modifications can be performed. In this context, it seems eminently important to protect diversity at the site level, but also to provide integrity at coarser spatial scales.

Our results ultimately indicate that the Illinois and Missouri rivers are influenced by unbalanced scale dependence where the fish communities are responding to many scale-related gradients (e.g. competition, habitat availability, hydrology, climate, etc.) where a large amount of diversity is

dependent upon the coarsest and finest scales. This differs somewhat from Stendera & Johnson's (2005) findings that aquatic macroinvertebrate communities were dominated by diversity at the smallest scale in boreal forests, but that this was less the case in arctic alpine areas. These findings were attributed to latitudinal gradients in species richness, in that the alpine systems had lower diversity than boreal systems, so the contribution of abundant and common species at the finest scale played a major role in gamma diversity. Beau-grand *et al.* (2001) noted a similar gradient in diversity for marine plankton. For terrestrial systems, Fournier & Loreau (2001) found that the smaller scale also appeared to have a large input to diversity for carabid beetle diversity, but others have reported that fine-scale influences have less of an effect (e.g. forest canopy beetles, *sensu* Crist *et al.*, 2003). These studies, and our own, highlight the fact that there is not a comprehensive paradigm that can be applied to all systems when considering spatial diversity patterns among an array of terrestrial and aquatic ecosystems. However, it is logical that similar ecosystems, subjected to similar temporal and spatial forces, will have complementary diversity patterns, as has been demonstrated for the Missouri and Illinois rivers here.

The additive partition approach is not without structural and computational limitations. Noda (2004) emphasized the need to ensure that sample design is sensitive to the spatial scales sampled, and to ease this concern argued that it should be uniformly scaled (e.g. 1, 10, 100, 1000 m² as uniform scale increments of area) with uniform sample sizes. Compliance with spatial uniformity can be accomplished relatively easily in some systems, but becomes logistically difficult in linear ecosystems such as rivers. The hierarchical scales that we used in this study are generally structured in a uniform fashion, but there are some inconsistencies in sample size within the scales that mean that caution needs to be applied in the interpretation of our results. Similarly, there is always concern that the data may have some inherent hierarchical characteristics that do not accurately represent the biological meaning of the analyses (Ricotta, 2005). Nevertheless, the similar trends that are obtained from data independently collected across two rivers that span considerably different longitudinal and latitudinal gradients provide an indirect means of validating our hypotheses.

The study of diversity across several spatial scales in complex systems can be difficult given that these systems are typically driven by a myriad of factors, both biotic and abiotic. However, Crist *et al.* (2003) suggest that using the diversity partitioning approach may increase our understanding of diversity across several spatial scales in continual ecosystems. The diversity partitioning approach does provide a formal analytical framework from which to begin fleshing out how diversity changes across a landscape. This information may then lead to testable hypotheses and to a better understanding of the processes that drive community structure at all scales. Here, we have used additive partitioning to describe diversity-scale patterns for two river systems. This approach is valuable because it uses information from the entire community at each

spatial scale in the hierarchy and therefore provides a better cumulative perspective for understanding community responses to river processes. However, diversity is not the only issue influenced by scale: for example, ecosystem structure and function are much more dynamic than species richness and warrant considerable attention in the future. Gaining a firm grasp of these aspects may prove challenging, yet is desperately needed in order to provide further understanding into mechanisms that influence scale-dependent biotic responses.

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SUPPLEMENTARY MATERIAL

The following material is available for this article:

Appendix S1 Illinois River fishes caught 1996–98.

Appendix S2 Missouri River fishes caught 1996–98.

This material is available as part of the online article from: <http://www.blackwell-synergy.com/http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2006.01624.x> (This link will take you to the article abstract).

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BIOSKETCHES

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