Processes governing riverine fish species richness are scale-independent

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Abstract: The ability of macroecological approaches to identify the mechanisms that underlie spatial patterns in species richness has been heavily debated in part because of continued attention to the role of scale-dependence in the mechanisms regulating biodiversity. Here we show that species abundance is a scale-independent predictor of species richness for riverine fish. We modelled local species richness of riverine fish in 976 rivers in the continental United States and used this parameterized local model to predict regional species richness at increasingly coarser scales that were defined according to U.S. Environmental Protection Agency (EPA) Ecoregion classes (Ecoregion III: fine scale, Ecoregion II: medium scale, and Ecoregion I: coarse scale). We found that the locally parameterized model predicted species richness most accurately at the coarsest scale, explaining 80% of the variability in total species richness. An inverse set of models, which used the coarsest scale data to parameterize models tested at finer scales, showed that 38% of the variability in local species richness was explained by the coarse scale model. Total abundance was the single most important predictor of species richness across all scales with a slope ranging from 0.4-0.56 on a log-log plot. Although the specific mechanisms linking total species richness and energetic constraints may be scale-dependent, total abundance may be a scale-independent predictor of the total number of species that can be supported in a given area.

Introduction

Whether the mechanisms regulating biodiversity might be scale-independent (Blondel 1987, Gaston 2000, Whittaker et al. 2001, Marquet 2002, Evans et al. 2005) is a central issue in debates on what determines the number of species in a given area (Brown 1995, Rosenzweig 1995, Allen et al. 2002, Whittaker et al. 2003, Ricklefs 2004). It has been argued that some processes, such as the relationship between available energy and the number of species that can be supported in an area, are so fundamental that they must operate across all scales even if they are not easily detectable at all scales (Brown 1999, Venevsky and Veneskaia 2003, Evans et al. 2005). However, a large body of empirical data has shown that processes that determine patterns at larger scales may have little impact in determining patterns at local scales (Lawton 1999, Chown et al. 2004). Here we take advantage of an unusually comprehensive data set on the species richness of riverine fish in 976 rivers in the continental United States to examine the degree to which the mechanisms regulating riverine fish species richness might be scale-independent.

Hutchinson (1959) was one of the first ecologists to propose that available energy sets a limit on the maximum number of species that can co-exist in an area. Today, species-energy theory, which states that the species richness of a given region is a function of the total or average amount of available energy (Brown 1981, Wright 1983, Wright et al. 1993, Srivastava and Lawton 1998), has emerged as the primary hypothesis attempting to explain large-scale variation in species richness (Hawkins et al. 2003, Willig et al. 2003, Hunt et al. 2005). The idea underlying species-energy theory, which has been dubbed the "More Individuals Hypothesis" (Srivastava and Lawton 1998), is that greater amounts of available energy can support more individuals, thus allowing a greater number of large populations to be supported in areas where available energy is higher (Wright 1983). Since large populations are less prone to extinction than small popula-

tions, areas with higher available energy should have more species (Wright 1983, Rosenzweig and Abramsky 1993, Srivastava and Lawton 1998).

Although there is variability in the relationship between species diversity and energy availability at different scales (Rosenzweig and Abramsky 1993, Wright et al. 1993), a positive relationship has been confirmed by a number of large-scale studies (Allen et al. 2002, Hawkins et al. 2003, Currie et al. 2004, Hurlbert 2004) despite differences in the various proxies used to measure available energy (e.g., temperature (Allen et al. 2002); evapotranspiration (Hawkins et al. 2003); climate (Currie et al. 2004); the "normalised vegetation difference index" (a measure of primary productivity, Hurlbert 2004)).

Factors other than energy availability are also important determinants of species richness (Wright et al. 1993). Habitat heterogeneity, for example, is a key determinant of species richness (Guégan et al. 1998, Ritchie and Olff 1999). Similarly, biogeographic history (Brown and Lomolino 1998, Weins and Donoghue 2004), area (Rosenzweig 1995), and geometric constraints on species distributions (Colwell and Lees 2000) have all been shown to be determinants of global patterns of species richness. However, as Hutchinson (1959) suggested, energy must place an ultimate limit on the number of individuals that can be supported in a given area, and it seems reasonable that this limitation may have important implications for species diversity which cut across observational scales.

In this paper, we test the hypothesis that there is scale-dependence in the mechanisms driving species richness using a bottom-up (fine to coarse scale) and a top-down (coarse to fine scale) approach to model fitting (Allen and Starr 1982). Specifically, we test whether a model parameterized at a small scale can be scaled-up to predict patterns at increasingly aggregated larger scales and vice versa. This methodology directly assesses the proportion of variance in species richness that can be explained by models developed at different scales. We can then ask whether the mechanisms that drive species richness change according to scale. We used this top-down and bottom-up model fitting approach to predict geographical patterns in riverine fish species richness in the continental United States. To accomplish this we used US EPA Ecoregion classes I, II, and III, which define areas of general similarity in ecosystems (Fig. 1), to delineate three scales of aggregation: fine (Ecoregion class III), medium (Ecoregion class II), and coarse (Ecoregion class I; Fig. 1a-c). We hypothesized that if models developed for local species richness could predict regional patterns in species richness and vice versa, this would suggest that the processes that determine species richness are similar for local and regional patterns despite the different spatial scales at which these mechanisms operate. We used six variables in our models. Four of the variables, distance to river source measured at each location where a fish community sample was taken, flow velocity, elevation, and total fish abundance have previously been shown to affect river fish species richness

(Guégan et al. 1998) and were chosen to facilitate comparison with previous studies. We also used latitude and longitude to assess the impact of potential broad-scale ecological and evolutionary constraints on species richness (Willig et al. 2003, Chown et al. 2004, Currie et al. 2004).

Methods

We assembled data on fish communities for 976 rivers in 51 major river basins across the United States into a GIS. These data included 1780 fish community samples, collected from 1993 through 2002 by the National Water-Quality Assessment (NAWQA) Program. Distance to river source was measured at each location where a fish community sample was taken, along with flow velocity, elevation, latitude, longitude, and total fish abundance.
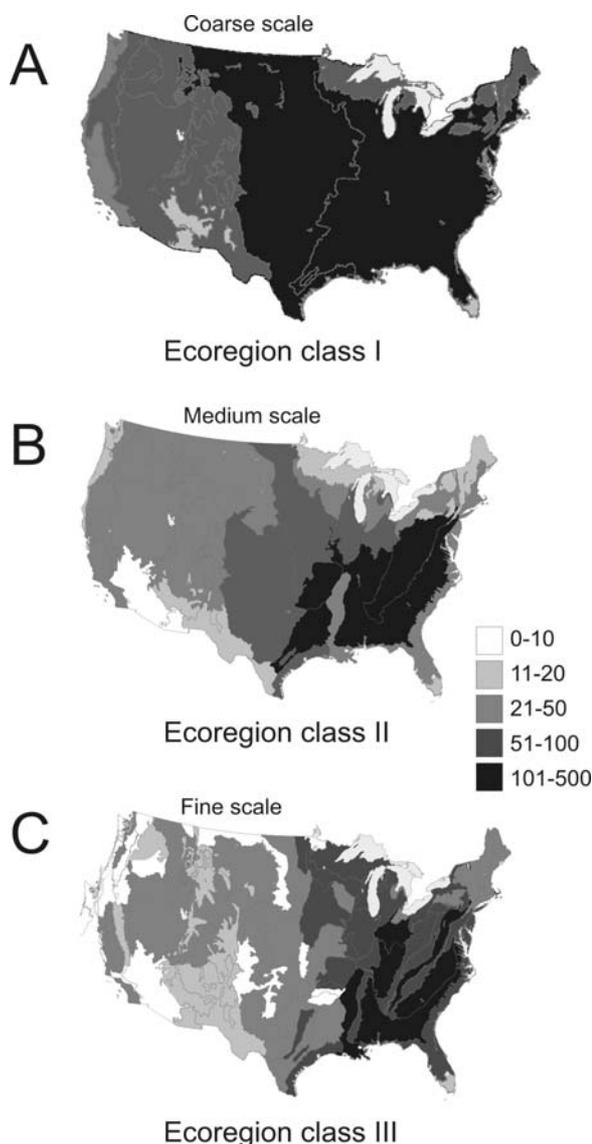
Figure 1. Distribution of species richness of riverine fish in the continental United States for **a:** coarse scale (Ecoregion I), **b:** medium scale (Ecoregion II), and **c:** fine scale (Ecoregion III).

Collection of NAWQA fish community data

Sampling reaches were established at a site using a combination of geomorphic characteristics, such as stream width and stream depth (wadeable or non-wadeable), and geomorphology (type and distribution of geomorphic channel units). In general, reach length ranged from 150 to 300 m for wadeable streams and from 500 to 1000 m for non-wadeable streams. A representative sample of the fish community was collected from the entire reach using a combination of electrofishing and seining. Electrofishing was conducted in two separate passes of the reach and fish collected from the first pass were processed before the second pass was conducted. Seining was performed after electrofishing to ensure that smaller fish were adequately sampled. Three seine collections were taken and combined before processing fish.

We used the entire NAWQA fish dataset to develop the models, which included data collected from 1993 to 2002. Each sample was used in the models across all dates, thus for Ecoregion I, there were 56 data points corresponding to 6 ecoregions from 1993-2002. For complete information on sampling protocols and data collection see (http://water.usgs. gov/nawqa/protocols/OFR02-150/index. html).

Ecoregions

Ecoregions were established according to US EPA Ecoregion criteria. According to the Ecoregion I classification, there are 15 broad ecological regions which highlight major ecological areas at an intercontinental scale. The Ecoregion II class has 52 regions to provide a more detailed description of the large ecological areas nested within the level I regions. The Ecoregion III class has 120 ecoregions. Not all ecoregions contain rivers, nor were all of them sampled. Within the Level I classification scheme, 10 of 15 regions included data on fish species richness. Fish species richness data were available for 20 of the 52 regions in Ecoregion class II and for 66 of the 120 regions in Ecoregion class III. Detailed descriptions of ecoregion classification can be found at (http://www.epa.gov/wed/pages/ecoregions/ecoregions.htm) and (ftp://ftp.epa.gov/wed/ecoregions/na/ CEC_NAeco.pdf.).

Modelling

Total species richness is defined as the total number of species in a reach or in an ecoregion. Mean species richness is defined as the average number of species across reaches for the ecoregions. Total abundance is defined as the number of individual fish of all species present in a reach or in an ecoregion. Our modelling procedure was done in three steps. First, we evaluated distance to source, flow velocity, abundance, elevation, latitude, and longitude as predictors of total and mean species richness at four different spatial scales: local (all reaches), fine (Ecoregion III), medium (Ecoregion II), and coarse (Ecoregion I) scales. Second, we used the model parameterized using the local spatial scale to explain variation in species richness at increasingly aggregated scales of

observation: fine (Ecoregion III), medium (Ecoregion II) and coarse (Ecoregion I). Specifically, the relationship between the six independent variables and both total and mean local species richness was determined for all local sites (n=1780). This resulting model was then used to generate predictions for total and mean regional species richness for fine, medium, and coarse scales based on the values of independent variables averaged for each scale. The independent variables were averaged for each ecoregion scale separately using mean values for each independent variable across all reaches in the ecoregion. Third, we used the coarsest scale (Ecoregion I) to parameterize a regional model which was then used to attempt to explain variation in total and mean species richness at the local, fine (Ecoregion III), and medium (Ecoregion II) scales. It is important to note that in step two and three separate models were not developed for each scale as in the first step. Instead, a model parameterized on local data was used to predict total and mean regional species richness at the more highly aggregated scales and a model parameterized on the coarsest scale was used to predict total and mean species richness at less aggregated scales. Species richness and abundance were non-normally distributed and thus were log_{10} transformed. All of the variables were included in the models. We did not use any stepwise procedure for model fitting as stepwise methods are not robust when there is collinearity in the independent variables (Derksen and Keselman 1992) and many of the variables in the model were correlated (see Table 2). We report adjusted R^2 for all analyses. All statistical analyses were conducted in JMP 5.1 (1989 - 2004 SAS Institute Inc. http://www.sas.com).

Results

Models of total and mean species richness for each scale

The six variables explained 61.5% of the variability in total local species richness (P>0.0001; Table 1). Abundance was the most important predictor, contributing 60% to the explained variance followed by elevation (21%), longitude (8.9%), latitude (5.5%), distance to source (4.4%), and flow velocity (0.26%; Table 1). For fine, medium, and coarse scales, the six independent variables explained 70.2%, 69.3%, and 89.4% of the variability in total species richness (e.g., cumulative number of species) and 62.3%, 54.2%, and 67.6% of mean species richness (e.g., average number of species per site), respectively. For total species richness, abundance explained the highest proportion of the total variance regardless of scale (Table 1). In contrast, mean species richness was more dependent on elevation, abundance, and longitude (Table 1).

There were a number of collinear variables in the models for each scale, ranging from 7 of 15 possible correlations at the coarsest scale to 11 of 15 possible correlations at the local scale (Table 2). On average, however, the correlation coefficients were relatively weak, ranging from an average $\bar{r} = 0.22$ at the local scale to an average of $\bar{r} = 0.27$ at the coarse scale.

Table 1. Results of multiple regression models for A) total and B) mean species richness of riverine fish for the local scale and for the three Ecoregion aggregations.

A) Total species richness

	Local		Ecoregion III		Ecoregion II		Ecoregion I	
	Adj. R^2	P	Adj. R^2	P	Adj. R^2	P	Adj. R^2	P
	0.615	<0.0001	0.702	<0.0001	0.693	<0.0001	0.894	<0.0001
	F	P	F	P	F	P	F	P
Abundance	860.611	<0.0001	278.706	<0.0001	121.375	<0.0001	174.871	<0.0001
Elevation	300.917	<0.0001	33.587	<0.0001	5.618	0.019	0.769	0.384
Distance to source	62.971	<0.0001	10.037	0.002	5.954	0.016	2.029	0.160
Flow velocity	3.688	0.055	2.005	0.158	3.105	0.081	8.422	0.005
Latitude	78.231	<0.0001	13.343	0.000	1.384	0.242	0.344	0.560
Longitude	127.771	<0.0001	43.006	<0.0001	29.940	<0.0001	13.446	0.001

B) Mean species richness

	Ecoregion III		Ecoregion II		Ecoregion I	
	Adj. R^2	P	Adj. R^2	P	Adj. R^2	P
	0.623	<0.0001	0.542	<0.0001	0.676	<0.0001
	F	P	F	P	F	P
Abundance	68.782	<0.0001	29.914	<0.0001	1.667	0.202
Elevation	71.460	<0.0001	9.581	0.002	38.223	<0.0001
Distance to source	14.600	0.000	7.504	0.007	3.016	0.088
Flow velocity	1.359	0.245	2.849	0.094	2.464	0.122
Latitude	7.477	0.007	1.304	0.256	0.499	0.483
Longitude	48.024	<0.0001	25.419	<0.0001	14.037	0.000

Table 2. Pearson correlation co-efficient for the six independent variables and total species richness at each scale (local scale, fine (Ecoregion I), medium (Ecoregion II), and coarse (Ecoregion III) scales). Significant correlations are shown in bold type.

Local scale	ELE	DS	FV	LAT	LON	AB
Elevation (ELE)						
Distance to source (DS)	0.013					
Flow velocity (FV)	**-0.122**	**0.609**				
Latitude (LAT)	0.147	0.061	0.007			
Longitude (LON)	**-0.460**	-0.135	0.022	**-0.254**		
Abundance (AB)	**-0.248**	**0.030**	0.049	-0.056	**0.400**	
Species richness (S)	**-0.519**	0.103	0.118	**-0.248**	**0.546**	**0.643**
Fine scale (Ecoregion III)						
Elevation (ELE)						
Distance to source (DS)	0.047					
Flow velocity (FV)	**-0.149**	**0.597**				
Latitude (LAT)	0.198	-0.035	0.033			
Longitude (LON)	**-0.550**	-0.158	0.039	-0.119		
Abundance (AB)	**-0.262**	-0.035	0.024	0.082	**0.377**	
Species richness (S)	**-0.536**	0.093	**0.184**	-0.148	**0.588**	**0.706**
Medium scale (Ecoregion II)						
Elevation (ELE)						
Distance to source (DS)	**0.316**					
Flow velocity (FV)	-0.033	**0.498**				
Latitude (LAT)	0.107	-0.102	-0.014			
Longitude (LON)	**-0.571**	**-0.317**	-0.058	0.039		
Abundance (AB)	**-0.234**	**-0.176**	-0.102	0.033	**0.394**	
Species richness (S)	**-0.447**	-0.052	0.104	-0.059	**0.609**	**0.720**
Coarse scale (Ecoregion I)						
Elevation (ELE)						
Distance to source (DS)	0.021					
Flow velocity (FV)	-0.211	**0.516**				
Latitude (LAT)	0.094	-0.003	0.146			
Longitude (LON)	**-0.334**	-0.214	-0.018	0.019		
Abundance (AB)	**-0.441**	0.169	**0.277**	-0.058	**0.567**	
Species richness (S)	**-0.462**	0.231	**0.399**	0.002	**0.615**	**0.926**

Only two variables were correlated with abundance across all four scales: elevation, which was negatively correlated with abundance, and longitude, which was positively correlated with abundance. No other consistent correlations between abundance and the other predictor variables were observed across all four scales. The only other variables that were strongly consistently correlated across all four scales were distance to source and flow velocity, which were positively correlated (Table 2).
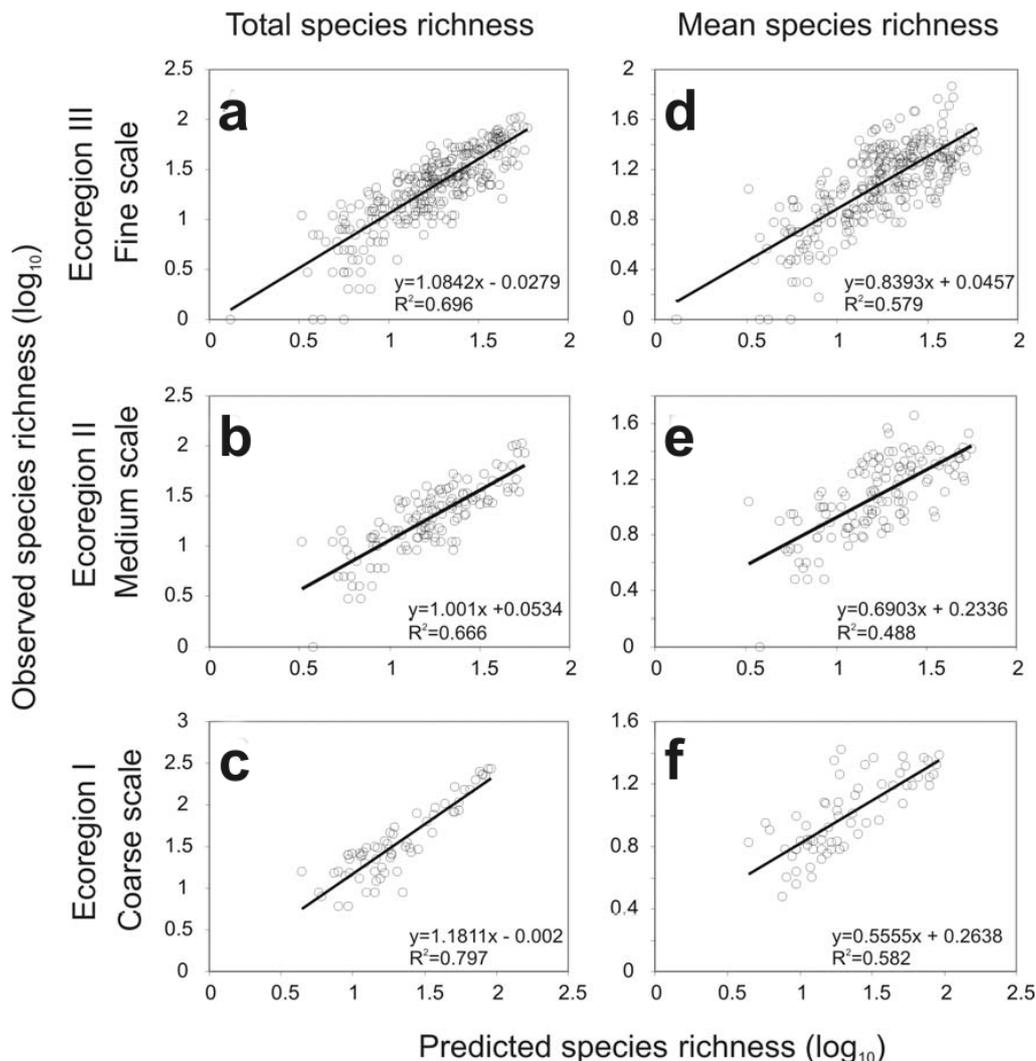
Parameterized models for predicting species richness at different scales

The locally parameterized model predicted 69.6%, 66.6%, 79.7% of the variation in total regional species richness for fine, medium, and coarse scales, respectively (Fig. 2a-c). For mean species richness, the locally parameterized model predicted 57.9%, 48.8%, and 58.2% of the variance in mean regional species richness for fine, medium, and coarse scales, respectively (Fig. 2d-f).

We also examined the ability of the model parameterized for the coarsest scale (Ecoregion I; Table 1) to predict variation at the less aggregated scales. The regionally parameterized model predicted 58.3%, 54.1%, and 36.6% of the variation in total species richness at the medium, fine, and local scales and 41.6% and 40% of the variation in mean species richness at the medium and fine scales.

Species richness and abundance

Total species richness increased with total abundance across all scales (Fig 3a-d). The ability of total abundance to explain variation in species richness was highest at the coarse scale (85.7%) and lowest at the local scale (41.3%). The slopes of the relationships between total abundance and total species richness were very similar across the local, fine, and medium scales ranging from 0.39 to 0.43. At the coarsest scale the slope was 0.57. In contrast to the results for total species richness, mean species richness only contributed sig-

Figure 2. Prediction of fish species richness in the three aggregated Ecoregions using the model for species richness parameterized at the reach (local) scale. Scatterplots compare predicted and observed species richness values for (**a-c**) total species richness and (**d-f**) mean species richness for (**a,d**) coarse (Ecoregion I), (**b,e**) medium (Ecoregion II), and (**c,f**) fine (Ecoregion III) scales.

nificantly to the models for total abundance at the fine and medium scales and not at the coarse (p=0.202; Table 1b).

Discussion

Both local and regional models for total species richness were most sensitive to variation in abundance. The high sensitivity of the models for total species richness to abundance supports recent analyses of patterns in riverine fish species richness at global scales (Oberdorff et al. 1997, Guégan et al. 1998). Guégan et al. (1998) analyzed fish species richness for 183 basins around the world. They suggest that global riverine fish species richness is determined by a combination of available energy (calculated as terrestrial NPP using data on temperature and rainfall) and habitat heterogeneity (measured as flow velocity) when viewed at the scale of entire river basins. At the river basin scale, they were able to predict 93% of the variation in fish species richness (Guégan et al. 1998). Our results, using a much more highly resolved dataset for

Figure 3. Relationship between total abundance and total species richness for (**a**) all reach (local) data and (**b-d**) data aggregated at (**b**) coarse (Ecoregion I), (**c**) medium (Ecoregion II), and (**d**) fine (Ecoregion III) scales.

1780 reaches in 976 rivers, suggest that local and regional variation in fish species richness is also highly sensitive to abundance and the processes that drive abundance. Total fish abundance explained 85.7% of the variability in total species richness at the coarsest scale (Ecoregion I) and the full model, which incorporated all six variables, explained 89.4% of the variability (Adj. R^2) in total species richness.

The abundance of species in any ecological system is determined by a complex set of variables which include factors such as available space (Marquet et al. 1990, Blackburn et al. 1993), hydrologic variability (Hugueny and Paugy 1995), seasonality (Currie et al. 2004) , habitat complexity (Guégan et al. 1998), resource supply rates (Enquist et al. 1998, Enquist et al. 2003, Brown et al. 2004), environmental temperature (Allen et al. 2002, Brown et al. 2004), and the body sizes of the organisms in the ecosystem (Enquist et al. 1998, Allen et al. 2002, Enquist et al. 2003, Brown et al. 2004). While non-energetic factors such as hydrologic variability can have significant effects on abundance, rates of resource supply and the sum of the total rates of resource use ultimately place an upper cap on potential abundance (Enquist et al. 1998, Marquet 2002, Long and Morin 2005, Makarieva et al. 2005, Marquet et al. 2005). From this upper limit of potential abundance, negative deviations will occur (Marquet et al. 1995) due to both non-energetic factors, such as available space, and energetic factors, such as body size and environmental temperature.

To some extent all of the variables used in our models may reflect aspects of energy availability. For example, NPP, which is often used as an approximation of energy availability (Allen et al. 2002, Hurlbert 2004), generally decreases with increasing elevation and increases with increasing distance to source (Degens et al. 1991). In our models, we observed a negative correlation between abundance and elevation and a positive correlation between abundance and longitude at all four scales (Table 2). Latitude, longitude, distance to source, flow velocity, and elevation may additionally reflect geographical or local determinants of species richness that can modulate the role of energy availability or have direct or other indirect effects on species richness. For example, while increasing elevation should lead to lower abundances and lower species richness directly due to lower temperature (Allen et al. 2002), increased elevation also limits dispersal opportunities in headwaters which in turn constrain species richness which would indirectly effect species richness (Robinson and Rand 2005) independently of energetic constraints.

As mean species richness is not predicted to vary with abundance due to energetic factors, and thus should show scale-dependence, one way to tease apart energetic versus other determinants of species richness is to compare the results for mean species richness to the results for total species richness. We found that while mean species richness per site increased with abundance for the fine and medium scales, there was no relationship between abundance and mean species richness at the coarse scale (Table 1). For the fine scale,
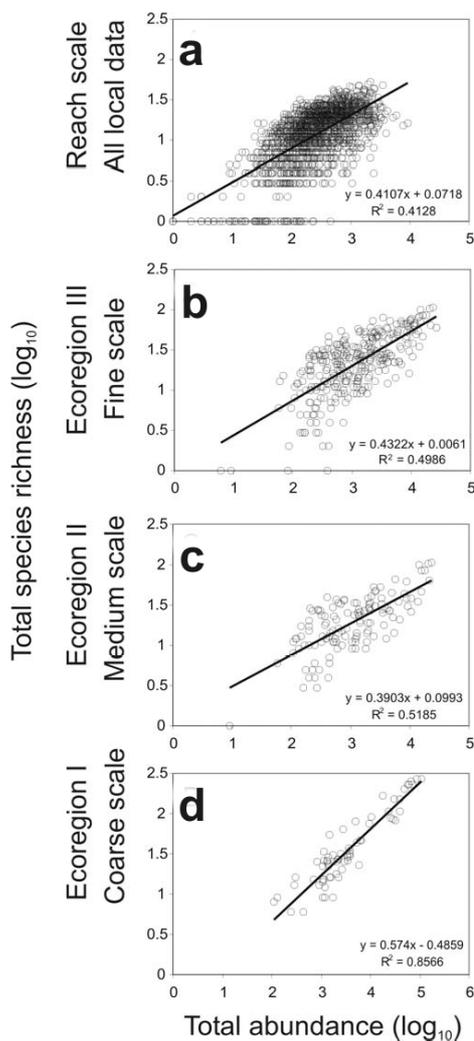
mean species richness was as sensitive to elevation and longitude as it was to total abundance, whereas for the coarse scale elevation and longitude were the most important predictor variables (Table 1). These results suggest the relationship between abundance and mean species richness per site, unlike the relationship between abundance and total species richness, appears to be a function of local scale-dependent constraints (Marquet et al. 1995).

The high proportion of variance explained at subsequent scales using the bottom-up and top-down scaling approach used here suggests scale-independence in the processes determining total species richness across scales. Evidence for a scale-independent constraint of abundance on total species richness is provided by both the slope of the relationship between abundance and total species richness, which varies by only 0.17 across scales, as well as by the top-down modelling scenario where the coarsest ecoregion model, which was almost entirely driven by abundance, explained 36.6% of the variability in the local data. This coarse scale model was parameterized on 56 data points yet still accounted for more than a third of the variability in a data set of 1780 data points. In addition, the local model, which explained 61% of the variability in total species richness, explained 80% of the variability at the coarsest scale (Ecoregion I). These patterns are congruent with the idea that at smaller scales there is greater variability in the mechanisms determining species richness, which is illustrated by the decrease in the number of significant correlations between independent variables at increasingly larger scales (Table 2) and the less equitable distributions of the strengths of the predictor variables at larger scales (Table 1). The slopes of the relationships between observed and expected total species richness based on the parameterized models were also strongly constrained with a slope of 1.08, 1.01, and 1.18 at the fine, medium, and coarse scales respectively (Fig. 2a-c).

Conclusion

Our results suggest that species abundance may be a scale-independent predictor of species richness for riverine fish. Not only are the processes that drive patterns in total species richness partially scale-independent but it is also possible that available energy, which sets an upper limit on species richness, is the primary scale-independent constraint. This is not to say that specific mechanisms are scale-invariant: the relevant sources of energetic limitation will likely take different forms at different scales of observation. For example, at large scales, energy availability may act to set limits to regional diversity through rainfall and climatic patterns, whereas at local scales, energy availability may set limits of species richness through local variability in productivity. However, energy availability provides an ultimate limit to the amount of biomass that can be supported in a given area and is, consequently, a fundamental determinant of the number of species that can be supported in an area regardless of the scale of observation (Wright 1983, Hurlbert 2004). Thus, although the path of causality linking species and en-

ergy is not simple (Lawton 1999, Wright et al. 1993, Srivastava and Lawton 1998, Gaston 2000, Hurlbert 2004) and the specific mechanisms linking species and energy may change with scale, we suggest that energy, through its effect on abundance, may be a scale-independent driver of species richness for riverine fish.

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