

Annual variation of community biomass is lower in more diverse stream fish communities

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Anthropogenic influences have disproportionately affected freshwater ecosystems, and a loss of biodiversity is forecasted to greatly reduce ecosystem function and services. Loss of species may destabilize communities by limiting the stabilizing forces of compensatory dynamics and/or statistical averaging, both of which are effects that can buffer variation in aggregate community properties. Currently, support for positive diversity–stability relationships stems from experiments with simple communities at small spatial and temporal scales, and application to natural communities is limited. Using a long-term dataset of 35 stream fish communities matched with hydrologic data, we show that community stability (annual variation of standing biomass of fishes) was less variable in more species-rich communities and was not associated with stream hydrology. Only the statistical averaging model of community stability was consistent with observed patterns of lower biomass variation in more species-rich communities. Our findings suggest anthropogenically induced extirpation of vertebrate consumers may lower community biomass stability in complex ecosystems.

Rapid loss of global biodiversity has prompted concern for the effects of reduced species richness on ecosystem stability and functioning (Naeem et al. 1994, Naeem and Li 1997, Loreau et al. 2001). The diversity–stability hypothesis predicts that higher species richness can reduce variation in community aggregate properties – such as biomass – through compensatory dynamics or statistical averaging; i.e. total community biomass remains relatively stable, whereas population biomass fluctuates over time (McNaughton 1977, Pimm 1984, Tilman and Downing 1994, Doak et al. 1998, Lehman and Tilman 2000). Experimental evidence from grassland and microbial communities suggests that increased species richness can indeed stabilize community aggregate properties and subsequently affect ecosystem-level processes (Cottingham et al. 2001, Balvanera et al. 2006, Cardinale et al. 2006, Hector et al. 2010). However, the effect of species richness on the stability of consumer communities (e.g. primary and secondary consumers) has received less attention, despite the fact that consumer biomass at least partially regulates energy availability to both higher trophic levels and decompositional components of food webs.

Although a positive relationship between species richness and community stability is supported by evidence from simple communities in field and laboratory experiments conducted at small spatial and temporal scales (Cardinale et al. 2002, Seabloom 2007, Jiang and Pu 2009), the influence of natural environmental gradients on both species richness and stability has been largely ignored (Hooper et al. 2005, Hughes et al. 2007, Ives and Carpenter 2007). Because of

potential nonlinear relationships between species richness and ecosystem function, extrapolation from small-scale empirical studies of simple communities to more complex community dynamics at larger spatial scales may be difficult (Emmerson et al. 2001, Hooper et al. 2005, Srivastava and Vellend 2005), and logistics often preclude manipulation of natural communities. Thus, observational studies have assessed relationships between species richness and community-level dynamics using natural ecological gradients or environmental variation (Frank and McNaughton 1991, Troumbis and Memtsas 2000, Valdivia and Molis 2009). Whereas directly testing mechanistic linkages between diversity and stability in observational studies may be limited, such studies can be used to evaluate relationships predicted from small-scale experiments at scales relevant to conservation (Hooper et al. 2005). Such studies are particularly needed in freshwater ecosystems (Dudgeon et al. 2006) and for species in higher trophic level communities (Petchey et al. 2004) that are disproportionately threatened by anthropogenic influences.

To assess the relationships between species richness and community stability in consumers, we investigated patterns between temporal fish community biomass stability (hereafter, community stability) and fish species richness using long-term community surveys at 35 sites in the central plains of North America (Supplementary material Appendix A). Because our fish communities were distributed over a large spatial scale (i.e. hundreds of kilometers), they naturally varied in species richness and composition, and were exposed to gradients of stream size and flow conditions. Streams in this

region are subjected to extreme flow conditions that can alter numerical abundances of fishes (Ross et al. 1985) and generally make these streams harsh environments (Dodds et al. 2004). Therefore, we tested for associations between species richness, hydrologic fluctuations and temporal community stability.

We observed patterns to evaluate three potential, non-mutually exclusive mechanisms that could contribute to more species-rich communities being more stable: statistical averaging, overyielding and covariance effects (Doak et al. 1998, Lehman and Tilman 2000, Cottingham et al. 2001). Statistical averaging (*sensu* portfolio effect; Tilman 1999) draws analogy with financial investments as relative fluctuations in a diversified portfolio are lower compared to a single or few investments. Statistical averaging effects would be supported if: 1) the temporal variance of species (s^2) scales with their mean biomass (m) with a constant (c) ($s^2 = cm^z$), such that $1 < z < 2$, and increases in strength as z approaches 2 (Doak et al. 1998, Tilman et al. 1998) and, 2) sum variances decrease in more species-rich communities. In addition, increased biomass evenness among species would strengthen this effect by reducing the relative 'investment' in each species and increased synchrony of assets (i.e. species abundances) over time will weaken the strength of statistical averaging (Schindler et al. 2010). Accordingly, the lowered relative fluctuation in biomass of species-rich communities has been referred to as the 'insurance value' of species richness (Naeem and Li 1997). Overyielding occurs when total community biomass is increased while variation in total community biomass remains relatively constant. This may happen if higher species richness increases overall niche occupancy, allowing more resources to be converted to biomass. For example, consider two communities over time: community A has five species with a mean annual biomass of 100 g per unit area and community B has 10 species with 200 g per unit area. If both communities demonstrate the same annual variation in biomass (e.g. standard deviation = 10 g), community B is relatively more stable than community A. The overyielding effect would be supported if mean community biomass increases as communities become more species rich while variability of biomass stays constant. Finally, the covariance effect stabilizes community biomass by reducing the covariance in biomass over time among species. Over time, the abundances of species can covary positively (species increase and decrease synchronously), neutrally (species increase and decrease randomly relative to each other), or negatively (species increase and decrease asynchronously, i.e. as species A increases, species B decreases proportionally). Higher species richness can increase niche overlap among community members, hence increasing competition and asynchronous species abundances over time. To support the covariance effect, total covariance (summed covariance between all species pairs) should be negatively associated with species richness. If increased species richness results in more asynchronous species fluctuations overtime, community stability may increase, however average species stability (population stability) may actually decrease in more species-rich communities.

In the present study, we tested for associations between species richness, environmental variability, and community and population stability. Overall, we show that the annual standing community biomass of more species-rich communities was more stable over time and demonstrate that statistical averaging could explain this positive association.

Material and methods

Stream hydrology

To assess possible effects of variation in environmental conditions on community and population stability, we quantified stream hydrology using discharge data obtained from United States Geological Survey (USGS) gauging stations located at each sampling location (<http://waterdata.usgs.gov/ok/nwis/rt>), Supplementary material Appendix B). Specifically, we enumerated the magnitude, duration and timing of extreme flow conditions to characterize stream hydrology using Indicators of Hydrologic Alteration (IHA) software, ver. 7, 2007 (Richter et al. 1996, Supplementary material Appendix C). Each site had sufficient data to quantify flow parameters for a minimum of 20 years as suggested by Richter et al. (1996, Supplementary material Appendix B). Parameters incorporated flow characteristics that potentially affect fishes over a wide range of temporal scales (i.e. days to years) and were chosen based on their potential influence on annual habitat availability (mean annual flow, number of zero flow days), variation and predictability of flow (annual coefficient of variation (CV) in flow, flow predictability, constancy/predictability), predictability of floods (percent of floods in 60 day period), flow constancy (base flow index), annual difference in extreme flows (date of minimum and maximum flow), and the rate of flow change during high flow events (rise rate, fall rate, number of reversals; Supplementary material Appendix C). The parameters chosen could affect fishes directly, e.g. through physical loss of habitat or disruption of reproductive efforts, and indirectly by affecting resource availability (i.e. algae growth or abundance of aquatic invertebrates). Each parameter was appropriately transformed to approximate normality (Supplementary material Appendix C) and a principal components analysis (PCA) based on a correlation matrix was used to summarize variation in flow conditions among sites. Only axes with eigenvalues above 1 were retained for analyses.

Fish communities

Fish communities were monitored at 35 sites located along 19 streams in Oklahoma, USA, between 1978 and 2008 (Supplementary material Appendix B). On average, each site was sampled 2.2 times a year for 21 years (range = 12–23 years; Supplementary material Appendix B). Fishes were collected from wadable habitats with seines along ~200 m of shoreline for 1 hr during each sampling event. All specimens were preserved on site in 10% formalin and each species' mean annual biomass was quantified for each site to the nearest 10 mg. Because high or very low flow conditions during a given sampling event may have created potential sampling biases, annual fish community biomass was estimated by averaging species biomass from multiple collections each year (Supplementary material Appendix B). Only small-bodied species (<200 mm maximum length; Miller and Robison 2004; Supplementary material Appendix D) were included in analyses because seines are inefficient at capturing adult large-bodied fishes.

We assumed sampling efficiency was constant across all years and sites, species did not vary in susceptibility of capture at each site, all species present at a site were captured,

and species were not falsely reported as being present at a site. Sampling efficiency could potentially have been lower in larger streams, possibly violating efficiency assumptions and artificially inflating community biomass variation at these sites. We quantitatively tested this possibility by including the effects of stream hydrology (which largely varied as a function of stream size) as a possible driver of community stability. Furthermore, lower sampling efficiency in larger, more species-rich streams would decrease community biomass stability in our dataset, a pattern opposite to theoretical expectations. Consequently, biomass stability in larger, more species-rich streams is likely under- not overestimated. Because of the geographic distances among collection locations, we also assumed fish populations varied independently among sites.

Species richness at each site was calculated as the mean number of fish species observed each year over the entire sampling period. To address potential sampling biases, we also scrutinized our species richness estimate at each site using individual-based rarefaction in EcoSim ver. 7 (Gotelli and Entsminger 2004). Estimates of rarefied species richness were based on 1000 individuals and 1000 iterations for each yearly collection and site. Two sites did not have any yearly collections of >1000 individuals and were dropped from the analysis. \log_{10} mean species richness and \log_{10} mean rarefied species richness were highly correlated (Pearson correlation, $n = 33$; $r = 0.945$; $p < 0.001$), and the use of mean rarefied species richness opposed to mean number of actually observed species in subsequent analyses did not yield qualitatively different results (not shown). Based on a standardized sampling effort among sites, use of average biomass, and exclusion of large bodied fishes, our protocol represented an estimate of annual standing biomass and temporal variation in biomass of small-bodied fishes from shallow, wadable habitats at each site.

Species richness of community/population stability

We defined community stability (S) at each site as the mean annual biomass relative to its standard deviation (μ/σ) over time (inverse of CV; Tilman 1999, Lehman and Tilman 2000, Tilman et al. 2006). Mean population stability for each community was calculated as the mean annual species biomass stability over the sampling period, averaged across all species in the community.

Separate stepwise multiple regressions were used to predict community stability and mean population stability using four independent variables: stream hydrology (PC axes I, II and III) and species richness. Observed relationships between species richness and community stability may be confounded by correlations between species richness and environmental factors. Species richness often increases with stream size (i.e. flow variability, see stream hydrology results below; Angermeier and Schlosser 1989). Species richness positively and significantly correlated with stream hydrology (only the first PC axis, Pearson correlation, $n = 35$, $r = 0.37$, $p = 0.028$). We therefore interpreted partial correlation coefficients from variables that were not selected in the final models to assess their contribution to predicting each dependant variable.

Community stabilizing mechanisms

To test whether statistical averaging was driving a positive species richness–community stability relationship, a power

function was fitted between each species' mean annual biomass (m) and their temporal variance of biomass (s^2). Because statistical averaging effects will reduce the sum variance in more species-rich communities, we also tested this relationship using linear regression. Furthermore, because increased biomass evenness among species strengthens the effects of statistical averaging, we assessed the relationship between species richness and community evenness using linear regression. Mean community evenness was calculated from evenness of biomass among species during each year and site using Pielou's evenness index (J ; Pielou 1966):

$$J = (H/H')$$

where H is the Shannon diversity index and H' is the maximum possible H .

To assess potential overyielding effects on community stability, each community's species richness was regressed against mean total annual community biomass, whereby more diverse communities would be expected to have a higher total community biomass. Finally, to evaluate the covariance effect, sum covariance among species were made positive by adding a constant (60 000) to all data points, then square root transformed to approximate normality, and regressed against species richness. If competitive interactions were important in maintaining community stability, sum of covariance would be expected to become more negative as species richness increases.

Community structures

Because of high environmental variability and the mobile nature of fishes, species turnover within sites may be high. We tested whether species turnover in communities could be predicted with stream hydrology or species richness using stepwise linear regression. We assessed mean annual species turnover at each site by quantifying presence/absence of species in each year and site (Diamond and May 1977, Meffe and Berra 1988). Species turnover was calculated as:

$$T = (C + E)/(S_1 + S_2)$$

where T is species turnover, C is the number of species colonized, E is the number of species extirpated, and S_1 and S_2 are the number of species in each sample. T ranges from 0 (no turnover) to 1 (complete turnover).

To approximate normality, all variables were \log_{10} transformed prior to analyses described above unless otherwise stated. Mean community turnover and evenness were arcsine-square-root transformed prior to analyses. All statistical analyses were performed in SPSS 16.0 (SPSS, Inc., Chicago, IL, USA). Sum covariances and sum variances were quantified using MATLAB 6.5 (The MathWorks, Natick, MA, USA).

Results

Stream hydrology

The first three PC axes explained 75.2 % of the variation in stream hydrology among sites (Supplementary material Appendix C). Along PC axis I (explaining 50.6 % of the variation), positive scores were associated with mean annual flow, date of minimum flow, and rise and fall rates; negative

scores were associated with coefficient of variation in flow and number of zero flow days per year. The first PC axis predominantly reflected a gradient of stream discharge across our study area. In general, stream localities increased in size due to increased precipitation and greater drainage areas from west to east as they drain this region (Supplementary material Appendix E). There were no other obvious spatial correlations with the other two PC axes.

Species richness and community/population stability

In a regression model with stream hydrology (PC axes I, II and III) and species richness as independent variables, species richness was the only variable retained in predicting

community stability ($n = 35$, $F_{1,34} = 7.38$, $R^2 = 0.18$, $p = 0.01$; Fig. 1a). On average, total community biomass variation with 19 species was predicted to be 1.7 times less than the variation of biomass in communities with five species. None of the stream hydrology PC axes were significant enough to be included in the final model, but stream size (PC I) showed the strongest (and negative) association with community stability (Table 1). Conversely, PC I was the only variable retained when predicting population biomass stability ($n = 35$, $F_{1,34} = 23.59$, $R^2 = 0.42$, $p < 0.001$; Fig. 1b); population stability significantly declined in larger streams with less flow variability. Contrary to our prediction, the relationship between species richness and population stability was not significant (Table 1).

Community stabilizing mechanisms

When fitting a power function between population biomass (m) and variance in biomass (s^2), mean-variance scaled such that $z = 1.69$ ($n = 980$, $F_{1,977} = 39207.05$, $r^2 = 0.98$, $p < 0.001$; Fig. 2a). The power function fitted to the most abundant populations at each site (i.e. species that comprised at least 20% of the total biomass during any year and contributed the most biomass to communities) scaled by $z = 1.60$ ($n = 218$, $F_{1,216} = 1764.98$, $r^2 = 0.89$, $p < 0.001$; Fig. 2b). Our data also indicated a significant inverse relationship between summed variances of species over time and species richness ($n = 35$, $F_{1,34} = 6.53$, $r^2 = 0.17$, $p = 0.015$; Fig. 2c). In more species-rich communities, biomass was further spread out more evenly among species ($n = 35$, $F_{1,34} = 636$, $r^2 = 0.16$, $p = 0.017$; Fig. 3).

Mean annual community biomass did not increase in more species-rich communities ($n = 35$, $F_{1,34} = 2.09$, $p = 0.16$). In contrast, covariance among species significantly decreased in more species-rich communities ($n = 35$, $F_{1,34} = 12.23$, $r^2 = 0.27$, $p < 0.001$; Fig. 4). However, only three of the 35 communities had negative sum covariance, and these communities were only moderately species rich (Fig. 4).

Community structures

Stream hydrology presumably influenced the identity and persistence of species in each community during the sampling period. Community structure varied over time, and PC I was the only variable retained when predicting species turnover (i.e. higher species turnover in larger streams with less flow variability; $n = 35$, $F_{1,34} = 20.69$, $r^2 = 0.39$, $p < 0.001$; Fig. 5). Variables not selected in the final model only showed non-significant relationships with community turnover (Table 1.)

Discussion

Similar to other studies at smaller spatial and temporal scales, we found a positive relationship between species richness and community stability. In addition, community stability was not significantly related to stream hydrology. Conversely, population stability did not decrease in more species-rich communities, but varied as a function of stream size (PC I). Of the three possible

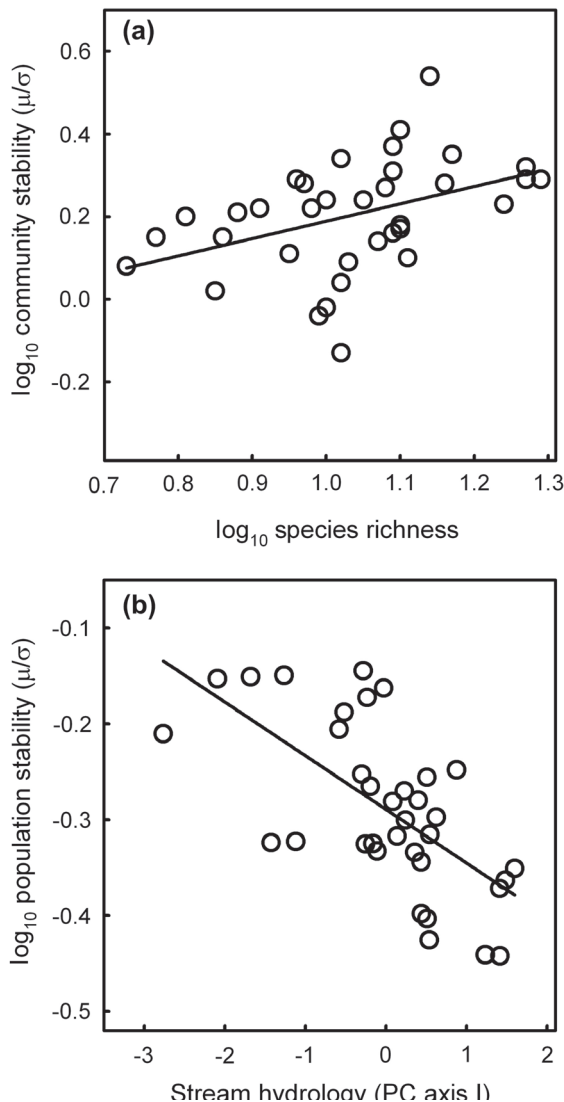


Figure 1. (a) Relationship between \log_{10} species richness and \log_{10} community stability ($n = 35$, $F_{1,34} = 7.38$, $R^2 = 0.18$, $p = 0.01$). (b) Relationship between stream hydrology (PC I) and \log_{10} mean population stability ($n = 35$, $F_{1,34} = 23.59$, $R^2 = 0.42$, $p < 0.001$). Positive PC I scores associated with mean annual flow, date of minimum flow, and flow rise and fall rates; negative PC I scores associated with coefficient of variation of mean annual flow, and median number of days with no flow.

Table 1. Regression results of independent variables not included in the final model from stepwise regression predicting community stability, population stability, and community turnover using species richness and flow variability (PC I, II and III) as independent variables. Each estimate is the standardized regression coefficient that would result if the variable were entered into the equation at the next step.

Dependant	Independent	Estimate	t	p	Partial r	Partial r ²
Community stability	PC 1	-0.312	-1.912	0.065	-0.320	0.102
	PC 2	-0.073	-0.433	0.668	-0.076	0.006
	PC 3	0.026	0.163	0.872	0.029	0.001
Population stability	Richness	0.239	1.717	0.096	0.290	0.084
	PC 3	-0.229	-1.776	0.085	-0.300	0.090
	PC 2	0.002	0.016	0.987	0.003	0.000
Community turnover	PC 2	-0.161	-1.179	0.247	-0.204	0.042
	PC 3	0.132	0.955	0.346	0.167	0.028
	Richness	-0.111	-0.743	0.463	-0.130	0.017

mechanisms we investigated explaining the stabilizing effects of species richness on community stability, our data only supported the statistical averaging model.

Community stabilizing mechanisms

Several pieces of evidence suggest statistical averaging likely stabilized species-rich communities. First, the mean-variance scaling of population biomasses was greater than 1 both for all species and the most abundant species present at each site. Second, as predicted, sum variance of species decreased in more species-rich communities. Finally, as communities became more species-rich, biomass was distributed more evenly among species.

Because mean annual community biomass did not increase in more species-rich communities, the overyielding effect was not a major contributor in stabilizing community biomass. The overyielding effect is thought to occur when adding species increases the over-all niche space occupied and allows for conversion of more resources to biomass. However, the increase in richness across the species richness gradient was largely attributable to increases of species in the families Cyprinidae and Percidae (Fig. 6a). This phenomenon is common in freshwater fish communities, where species richness increases with additions of species in the same families rather than by adding species from new families (Fig. 6b; Matthews 1998). Because we assessed small-bodied fish communities and species of Cyprinidae and Percidae can be ecologically similar, the addition of species from the same family likely did not increase total niche occupancy as much as if species richness increased by additions of species from different families.

If the increased frequency of ecologically similar species (i.e. species in the same family, Fig. 6b) in more species-rich communities increased competitive interactions, the decline in the sum covariance among species along the richness gradient could have reduced the variation in annual community biomass in some communities. However, this was not a consistent trend across the species richness gradient, suggesting the covariance effect was not stabilizing communities. Only three of the 35 communities had a negative sum covariance, and the decline in sum covariance along the richness gradient was not due to more negative covariances but rather covariances nearing zero. Summed covariance nearing zero suggests populations in more species-rich communities did not increasingly covary as predicted if competitive interactions

were strong, but to a certain extent fluctuated randomly relative to each other.

Competitive interactions for food resources, overall, may be relatively weak in this system because of where these fishes feed in the food web. The species investigated feed on invertebrates, algae and detritus. Invertebrate production can be limiting for stream fishes, but food resources like detritus and algae are rarely, if ever, limiting (Moyle and Light 1996). Although we used a long-term data set, environmental conditions during this period could have been favorable for most species, and competitive interactions may have only been observed if communities had experienced "ecological crunches" (Weins 1977). If competitive or trophic interactions are relatively weak in this system (as suggested by weak interactions among the fishes investigated here), entire food webs may be stabilized similarly by low interaction strengths (McCann et al. 1998).

Although community stability was significantly associated with species richness, other environmental factors could have contributed to stabilizing species-rich communities. Species richness generally increases from west to east in Oklahoma with the highest species richness occurring in the Ozark uplands in northeastern and the Ouachita mountain region and Red River in southeastern Oklahoma. Most urban centers in Oklahoma are found in central and north central regions of the state, with much lower population densities in east and southeast Oklahoma, which coincide with the highest fish species richness. Consequently, fish communities in these regions have likely experienced lesser habitat modifications compared to communities in central parts of the state. Therefore, community structures in these species-rich regions may have been kept more intact and experienced fewer human induced disturbances compared to more urbanized areas.

Effects of environmental variability and community structure

In spite of the fact that highly variable stream flows can increase the variation in the number of fish individuals present at a given site over time (Ross et al. 1985, Oberdorff et al. 2001), we found no evidence of stream flow variability influencing the variation in total biomass of fishes. This is perhaps because the streams we investigated were larger and less variable in annual flow compared to previously studied systems. Oberdorff et al. (2001) showed increased variation (CV) in

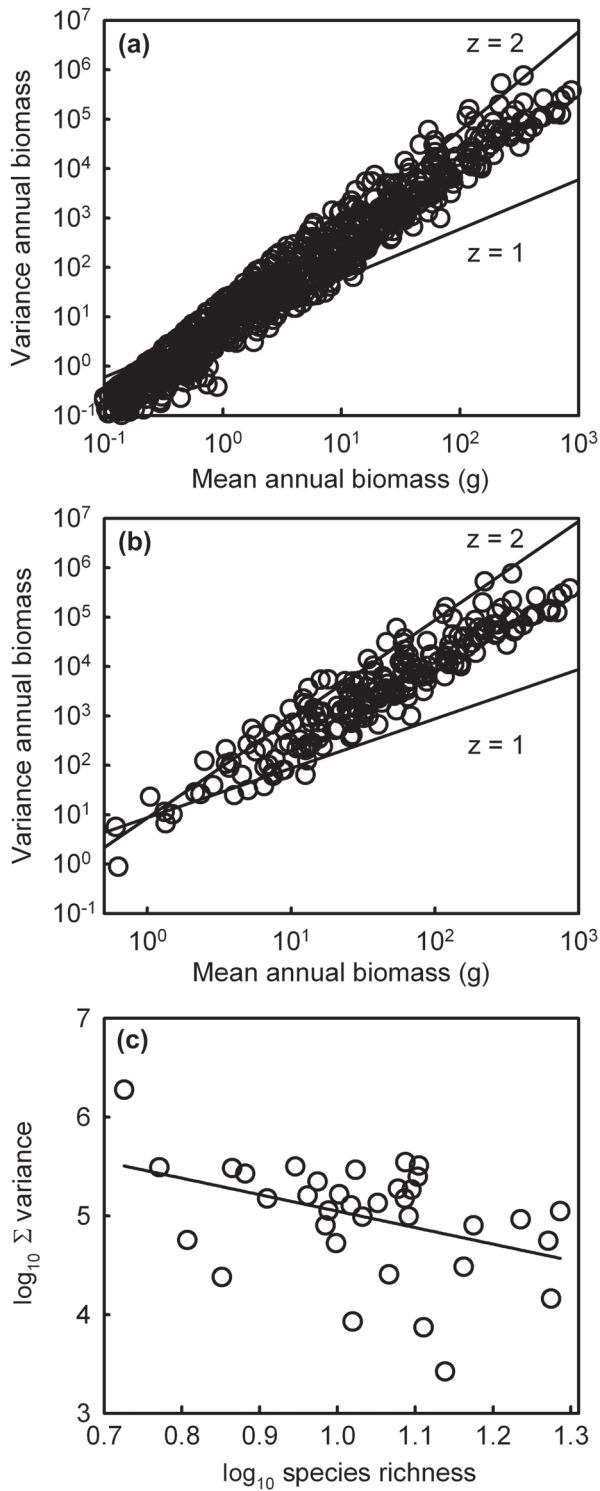


Figure 2. (a) Relationship between all species' mean annual biomass and their temporal variance ($s^2 = 5.95m^{1.69}$; $n = 979$, $F_{1,977} = 39207.05$, $r^2 = 0.98$, $p < 0.001$). The fitted lines are the power functions where $z = 1$ and $z = 2$ using the constant 5.95. Axes are \log_{10} scaled to allow maximum separation of points. (b) Relationship between the most abundant species' mean annual biomass (i.e. species that comprised at least 20% of yearly biomass collections at each site) and their temporal variance ($s^2 = 8.70m^{1.60}$; $n = 218$, $F_{1,216} = 1764.98$, $r^2 = 0.87$, $p < 0.001$). Fitted lines are power functions where $z = 1$ and $z = 2$ using the constant 8.70. Axes are \log_{10} scaled to allow maximum separation of points. (c), Relationship between species richness and sum variance of population biomass ($n = 35$, $F_{1,34} = 6.53$, $r^2 = 0.17$, $p = 0.015$).

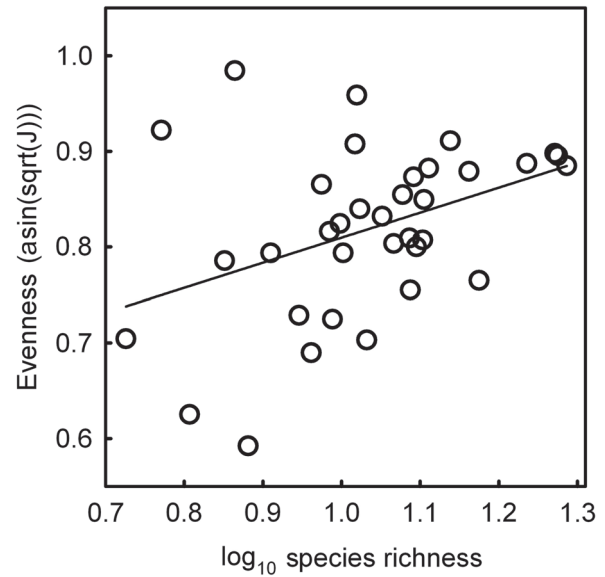


Figure 3. Relationship between \log_{10} species richness and mean community evenness (J) ($n = 35$, $F_{1,34} = 6.36$, $r^2 = 0.16$, $p = 0.017$).

several metrics of fish densities and population sizes in relation to increased CV of annual discharge of streams. However, the CV of annual discharge of our stream sites ranged from 1.3 to 12.09, far below the range of CV (roughly 30–75) in annual discharge Oberdorff et al. (2001) observed. Indeed, fishes subject to higher relative flow variability in smaller and especially intermittent streams experience more environmental stressors (e.g. low/high temperature, low oxygen, drying) compared to larger streams with more stable flows (Schlosser 1990). In our system, stream hydrology likely had little influence on the variation in community biomass because of the relative contribution of stream flow versus other abiotic (e.g. habitat availability/suitability) or biotic (e.g. species richness) drivers of community biomass variation.

Although population stability did not decrease in more species-rich communities, relationships between population stability and stream hydrology and species turnover confounded

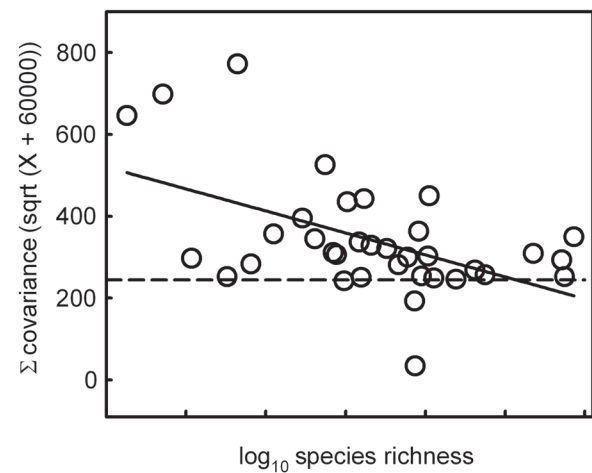


Figure 4. Relationship between \log_{10} species richness and sum covariance (square root($X + 60000$)); ($n = 35$, $F_{1,34} = 12.23$, $r^2 = 0.27$, $p < 0.001$). The dashed line indicates zero covariance on untransformed data.

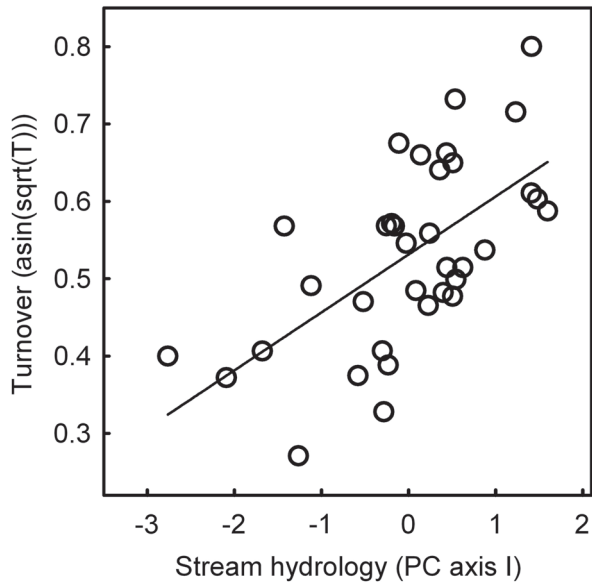


Figure 5. Relationship between stream hydrology (PC I) and mean species turnover in each community ($n = 35$, $F_{1,34} = 20.69$, $r^2 = 0.39$, $p < 0.001$). Positive PC I scores associated with mean annual flow, date of minimum flow, and flow rise and fall rates; negative PC I scores associated with coefficient of variation of mean annual flow, and median number of days with no flow.

this observation. Population biomass stability significantly decreased in larger and less variable streams. The negative association between stream size and flow variability is attributable to the averaging of tributary inflows in larger streams. We suggest the variation in population biomass over time could have been inflated in larger streams for several reasons. First, population stability could be reduced if species – albeit present – were more inconsistently collected in larger streams on a year-by-year basis. Because only wadable habitats were sampled, collection efficiency was likely higher in smaller streams with less deep-water habitats compared to larger streams. Larger streams also usually provide more heterogeneous habitats that may not have been represented in the 200 m of stream shore sampled at each site. Second, higher species turnover in larger and less variable streams could be attributable to vagrant species emigrating and immigrating in sample reaches. Lastly, because sampling occurred over a relatively long time period (i.e. up to 30 years), the lower population stability in larger streams may reflect long-term alteration of community structure by habitat modification. Because of the hierarchical nature of stream networks, downstream reaches likely suffer accumulative effects of impoundments and water withdrawal in upper reaches. Although we cannot be certain, sampling efficiency could have been more variable in larger streams, thus lowering population stability in these habitats. Indeed, population and community stability were positively correlated (Pearson correlation, $r = 0.55$, $p = 0.001$), and thus more variable sampling efficiency in larger streams possibly introduced artificial variation in community biomass in these habitats (evidenced by the non-significant negative trend between PC I and community stability; Table 1). If sampling efficiency reduced community stability in larger, more species-rich streams (species richness and PC I were slightly correlated), our estimate of community stability may actually represent a conservative estimate. Therefore, even if

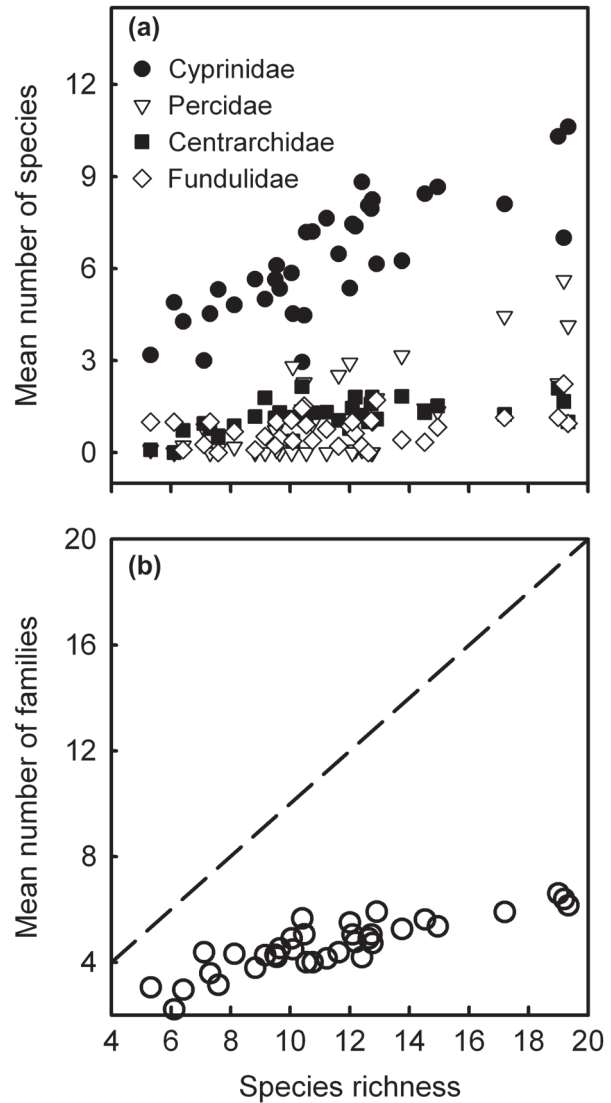


Figure 6. (a) Mean number of species in each family and mean number of species at each site over the sampling period. (b) Relationship between mean species richness and mean numbers of families present at each site over the sampling period. Dashed line represents a 1:1 relationship.

potential sampling efficiency biases affected stabilizing effects of species richness on annual variation in community biomass, we have likely underestimated the effects of species richness on community biomass stability in this system.

Community stability and conservation

Although consumer community stability across sites was relatively low compared to communities of primary producers (Tilman et al. 2006), the predicted insurance value of species in these communities suggests species richness can increase the constancy of annual biomass in higher trophic levels. Species richness effects on community biomass stability in higher trophic levels would be especially important for ecosystems with inverted biomass pyramids (e.g. lakes, marine systems; Odum 1971). Indeed, biomass available to detritivores and top predators can at least partially depend on the biomass of consumers, such as the fishes investigated

here. The trophic ecology of most freshwater fishes and their role in ecosystem processes are largely unknown. However, top-down effects of fishes can physically structure habitats for aquatic invertebrates and influence primary production (Gelwick and Matthews 1992, Power 1992, Flecker and Taylor 2004). Fishes also can act as energy conduits to higher trophic levels (Steinmetz et al. 2003) and have profound effects on nutrient cycling in aquatic ecosystems (McIntyre et al. 2007, 2008, Schindler 2007).

The long-term effects of anthropogenically induced extirpations and altered community structures are unknown, but will likely have unforeseen consequences to ecosystem processes (Tilman et al. 1994). Based on the data presented here, species richness may influence the constancy of annual vertebrate community biomass, but species richness in this region and other aquatic systems will likely continue to be threatened by water withdrawal and development (Poff et al. 2007). Because statistical averaging effects were likely responsible for stabilizing communities in this system, these stabilizing effects could be reduced by not only by extirpation of species, but also by altered community structures (e.g. lower evenness). Although the ecosystem level effects of these fishes are relatively unknown, our data suggest species richness has community stabilizing effects at scales that are relevant to conservation.

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Supplementary material (available online as Appendix O18810 at <www.oikosoffice.lu.se/appendix>). Appendix A–E.