

Non-native species, size distributions, and nutrient recycling
in southwestern stream communities

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Abstract

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Non-native species introductions are a ubiquitous form of environmental change. However, the role of introductions in ecosystem functioning is still poorly understood, especially in highly invaded systems with multiple non-native species. This thesis employs a functional trait framework— in which the net ecosystem effect of changing community structure is evaluated by quantifying change in the community-level distribution of biological traits— to assess the potential effects of multi-species introductions on ecosystem functioning in the Verde River, Arizona, USA. Specifically, I assess changes in body size distributions associated with non-native fish and crayfish introductions to estimate change in consumer-mediated nutrient recycling— an important size-scaling function in which aquatic consumers can control the rates and ratios of inorganic nutrient availability. In chapter 1, I compare the central moments of

individual size distributions of basin-wide native and non-native fish species pools. Native and non-native species pools were characterized by significantly different mean, coefficient of variation, and skewness moments of individual size distributions. These differences were more pronounced within trophic guilds than across the whole community, and notably differences in higher order moments (CV, skewness) were relatively greater than differences in the mean of size distributions. In Chapter 2 I evaluated whether such changes in the variance of size distributions affected nutrient recycling independent of the mean. I coupled nutrient recycling incubations and field sampling of habitat-specific size distributions of a non-native crayfish (*Orconectes virilis*) to scale up nutrient recycling from individuals to aggregate ecosystem functioning using mean-only or variance-incorporating approaches. A mean-only approach overestimated true rates of aggregate nutrient recycling by as much as 20% in habitats with low mean body size, but the bias induced by ignoring variance declined with the mean of the distribution. Given that the relationship between individual body size and nutrient recycling is a general representation of many size-functioning relationships, these qualitative results likely hold for other consumer-mediated functions. In Chapter 3 I determined whether body size provided a common functional currency to predict individual nutrient recycling across multiple fish species, and in turn whether native to non-native fish turnover was expected to generate large differences in aggregate nutrient recycling in the Verde River. Body size-recycling models with species-specific parameters were more parsimonious than global models with parameters shared across species. Using species-specific models I found that non-native dominated communities excreted ammonium at similar rates as native-dominated communities, but phosphate at significantly lower rates. The resultant difference in the N:P ratio was surprisingly large, generally independent of body size, and potentially important for aquatic microbial communities in this

system. By contrast, the global model incorporating body size but not taxonomy did not capture this significant N:P difference. Together these chapters suggest that quantifying change in body size distributions yields important ecological insights, but taxonomic identity or additional traits are still necessary for a full evaluation of the ecosystem-level effects of multi-species introductions.

Contents

| | |
|---|----|
| Non-native introductions influence fish body size distributions within a dryland river | 8 |
| ABSTRACT..... | 9 |
| INTRODUCTION | 11 |
| METHODS | 14 |
| RESULTS | 20 |
| DISCUSSION | 23 |
| ACKNOWLEDGEMENTS | 27 |
| REFERENCES | 27 |
| TABLES | 35 |
| FIGURE CAPTIONS..... | 38 |
| FIGURES..... | 40 |
| Disentangling the influences of mean body size and size structure on ecosystem functioning | 43 |
| ABSTRACT..... | 44 |
| INTRODUCTION | 46 |
| METHODS | 49 |
| RESULTS | 54 |
| DISCUSSION | 56 |
| DATA ACCESSIBILITY | 60 |
| ACKNOWLEDGEMENTS | 60 |
| REFERENCES | 61 |
| TABLES | 68 |
| FIGURE CAPTIONS | 69 |
| FIGURES..... | 70 |
| SUPPORTING INFORMATION | 74 |
| Estimating the effects of species turnover on nutrient recycling requires species-specific allometric models | 77 |
| ABSTRACT..... | 78 |
| INTRODUCTION | 80 |
| METHODS | 84 |
| RESULTS | 88 |
| DISCUSSION | 91 |
| ACKNOWLEDGEMENTS | 95 |

| | |
|------------------------------|-----|
| DATA AVAILABILITY | 95 |
| REFERENCES | 96 |
| SUPPORTING INFORMATION | 103 |
| TABLES | 104 |
| FIGURE CAPTIONS..... | 107 |
| FIGURES..... | 109 |
| SUPPORTING INFORMATION | 114 |

Running Head: Non-natives and size distributions

Non-native introductions influence fish body size distributions within a dryland river

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ABSTRACT

1. Species introductions are a ubiquitous form of environmental change, but assessing the ecological effects of multiple introductions remains a challenge. Quantifying the influence of non-native species on functional trait distributions may provide greater predictive insight into the effects of multiple introductions and changing assemblage structure on ecosystem functioning.
2. Body size is a particularly important trait with which many per capita rates of ecosystem functioning scale. Freshwater fish introductions have altered species-level body size distributions globally. However, it is difficult to interpret the functional consequences of these macroecological patterns because animals contribute to ecosystem functioning at smaller spatial scales and at the individual, not species, level.
3. In this study we determine whether the macroecological patterns of the influence of species introductions on size distributions hold for individual size distributions (ISDs) at local scales. We use a recently compiled dataset of fish communities in the highly invaded (6 native vs. 11 non-native) Verde River watershed, central Arizona, USA, to i) compare the statistical moments of ISDs between native and non-native species pools, and ii) relate biological and environmental covariates to the univariate moments of local ISDs and the multivariate community structure (i.e., accounting for size structure and abundance across guilds) of local fish assemblages.
4. Using a resampling approach on data pooled across sites, we found that ISDs of native and non-native species pools were significantly different. Notably, non-natives had smaller mean body size than natives across all guilds and within invertivore and omnivore guilds, but were significantly larger within the invertivore-piscivore guild. By modeling ISDs at the site-level as a function of potential biological and environmental covariates, we found that non-native

dominance within sites had the same general effects on ISDs as expected from differences between species pools. These results suggest that the effects of non-native introductions on ISDs in the Verde basin are probably additive, with less evidence for a role of species interactions in structuring size distributions. However, a constrained ordination analysis revealed that neither biological nor environmental predictors explained significant variation in multivariate community size and trophic structure.

5. Our results support macroecological findings and theory that suggests successful non-native species occupy the margins of size distributions, ultimately resulting in a shift in ISDs. Community-wide and guild-specific shifts in size distributions can have multiple impacts on ecosystem functioning, and our results provide a baseline for generating size-based predictions of non-native species impacts in riverine environments. However, these size-based predictions must be considered in light of other important traits such as trophic structure, which had no consistent relationship with non-native dominance in this study.

INTRODUCTION

Species introductions are nearly ubiquitous in freshwater ecosystems and are a leading form of global environmental change (Ricciardi 2007). Despite substantial research dedicated to better understanding the population-level effects of single-species introductions, we know less about ecosystem-level consequences such as the disruption of energy and nutrient cycling through food webs (Strayer 2010; Cucherousset & Olden 2011). Given that many freshwaters face multispecies introductions, focusing on the ecosystem effects of multiple invaders may provide a cumulative understanding of non-native impacts not captured by single-species research (Rowe 2007). One promising approach to forecast the ecosystem-level consequences of non-native species in these highly invaded systems is to assess the net change they induce in functional trait distributions (Strayer 2012; Matsuzaki, Sasaki & Akasaka 2013).

Body size is a fundamental functional trait that determines the role of biota in ecosystem functioning (Peters 1983; Woodward *et al.* 2005; Hildrew *et al.* 2007). Central to the metabolic theory of ecology, many per capita rates of important ecosystem functions— including nutrient cycling, consumption, and production— scale predictably with an organism's body size (Brown *et al.* 2004). Likewise, non-metabolic functions like prey community structure and composition can also respond to the body size distribution of a focal species or community (Rudolf & Rasmussen 2013). Species removals ordered by body size are generally more detrimental to functioning than random community disassembly, as demonstrated in aquatic systems for sediment bioturbation (Solan *et al.* 2004), nutrient recycling (McIntyre *et al.* 2007), and primary production (Seguin *et al.* 2014).

From a food web perspective, changes in body size are meaningful both within and across trophic guilds (Cohen, Jonsson & Carpenter 2003). Different trophic guilds control different

ecological processes (e.g., herbivory and primary productivity, decomposition, secondary production) and the distribution of body size within each guild can alter the rate of that particular function. Similarly, Rudolf *et al.* (2014) demonstrated experimentally that both size and species identity provided complementary information in determining the functional diversity of communities. Moreover, changing the ratio of consumer to resource body size (i.e., changing body size differentially across trophic guilds) can have emergent effects on population dynamics, food web stability, and ecosystem functioning (Brose *et al.* 2006). Although body size and trophic position of freshwater fishes are highly correlated at the global scale (Romanuk *et al.* 2011) and thus likely provide redundant functional information, this relationship weakens at smaller scales (Jennings *et al.* 2001). Therefore, examining how species turnover influences body size distributions both within and across trophic guilds may begin to provide a cumulative understanding of how non-native organisms influence ecosystem functioning.

Multiple non-independent hypotheses have been proposed to explain variation in species-level body size distributions from local to global scales (Allen *et al.* 2006). Biotic interactions are expected to be more influential at smaller scales and environmental, energetic, or evolutionary constraints more important as scale increases (Allen *et al.* 2006). However, non-native fish introductions have confounded this expectation, significantly altering median species size globally and disrupting temperature-based predictions of body size along latitudinal gradients (i.e., Bergmann's rule; Blanchet *et al.* 2010). Species introductions also appear to be trophic-biased at regional to global scales. Eby *et al.* (2006) cautioned about the effects of increasing trophic levels through non-native introductions, whereas more detailed studies of the trophic structure of invaded freshwater communities often reveal that non-native introductions lengthen food chains by adding both high- and low-trophic species to food webs (Cucherousset *et al.*

2012; Sagouis *et al.* 2015). These large-scale studies focus on the species-level— where each species is represented by a single trait value. Instead, the individual size distribution (ISD) may be a more relevant metric to ecosystem functioning because it incorporates information on the size and abundance of individuals (White *et al.* 2007) that, when coupled with trophic information, can provide better insight on foodweb structure and function (Cohen *et al.* 2003).

Despite the potential importance to ecosystem functioning, we are unaware of a study that evaluates whether the macroecological patterns of non-native species effects' on ISDs hold at smaller scales. At mesoscales of management concern, non-native introductions can influence size distributions simply through their numerical addition to ISDs (e.g., Blanchet *et al.* 2010). Disproportionate additions of large-bodied sport fishes (e.g., Eby *et al.* 2006) or smaller-bodied bait and aquarium fishes (e.g., Strecker, Campbell & Olden 2011a) can change the mean, variance, and skewness of the ISD by numerically overwhelming the native species pool. Concurrent with these additive effects, non-native introductions can influence ISDs through antagonistic species interactions (Griffiths 2013; Quintana *et al.* 2015). Non-native predators feeding within their gape limitation may disproportionately prey on small-bodied individuals, increasing the mean and decreasing the skew of the local ISD (Griffiths 2013). Likewise, introduced competitors may force individuals to exploit different and new resource pools to avoid strong competition. Because these consumer-resource relationships are generally size-structured (Brose *et al.* 2006), this trophic dispersion may increase the size diversity of the community (i.e., increase the CV of the ISD) (Schoener 1974). Considering these hypotheses together, non-native introductions can influence ISDs in complex ways. Consequently, there remains the need to explore the overall relationship between non-native introductions and ISD patterns to identify potential mechanisms, and potential consequences, of ISD change.

It is important to consider the impacts of non-native introductions in the context of other natural or anthropogenic drivers (Rahel & Olden 2008). Metabolic and community ecology theories predict that environmental covariates— namely temperature (predicted negative effect on body size), habitat size (predicted positive effect), and environmental stability (predicted positive effect) — also strongly influence body size distributions, and these hypotheses have received varying empirical support in fish studies at global (Blanchet *et al.* 2010), regional (Griffiths 2013), and local (Jellyman, McHugh & McIntosh 2014) scales.

Here we examine the effects of species introductions on ISDs within and across trophic guilds and alongside environmental gradients in the Verde River watershed of central Arizona, USA. This watershed hosts a highly endemic native fish fauna and has been subjected to a century of non-native introductions. Some of these introduced species have documented impacts on individual native species, but the overall outcome of these introductions on community and ecosystem-level processes is poorly understood. We ask i) do the ISDs of total native and non-native species pools differ in the Verde River system, ii) are non-native species' effects on ISDs detectable at local scales and in the face of important environmental gradients, and iii) does non-native dominance have a consistent influence on the multivariate structure (i.e., simultaneously considering size structure and guild abundances) of desert fish communities? By analyzing patterns of body size and trophic trait distributions, we hope to generate hypotheses of the effects of species turnover on river ecosystem functioning that can guide future mechanistic research and conservation efforts.

METHODS

Fish Community Dataset

We employ a freshwater fishes dataset recently compiled by the Arizona Game and Fish Department's Research Branch. This dataset collates 2500 unique fish sampling efforts led by state, federal, or academic scientists, totaling ~408,000 individual fish, in central Arizona's Verde River watershed, a 17,333 km² subwatershed of the Lower Colorado River Basin.

We followed a series of decision rules to reduce this dataset to a suite of comparable sites. Sampling efforts had to employ backpack electrofishing methods, target fish communities (N species ≥ 2) in free flowing rivers and streams, include at least 30 individuals to adequately characterize size distributions, and were assumed to be spatially extensive enough to capture the local characteristics of the fish community. We retained only those samples collected after 1980, a demonstrated breakpoint between historical and contemporary fish community composition in the Lower Colorado River Basin (Olden & Poff 2005). Season was treated as an environmental factor in analyses, given that fish community structure may vary across seasons with changing fish ontogeny and life history events. Only the most recent sample was used in each spatially discrete sampling unit, the National Hydrography Dataset's (NHDPlus, version 2) reachcode unit. NHD reachcodes are variably-sized (100s of meters to several kilometers) stream reaches that encompass similar hydrogeomorphology and environmental conditions. We only considered fish species that occurred in at least 5% of the reachcodes in which backpack electrofishing was performed. Though potentially important in the context of native species conservation or early non-native species detection, rare taxa may disproportionately influence statistical analyses relative to their numerical contribution to ecosystem functioning. Eight sites with extremely high recorded abundance ($>1,000$ individuals) were not included in analyses.

As is typical with fish surveys, body size was not recorded for every fish captured in the Verde River dataset. Thus, we only retained sites in which for each species either (a) every individual

captured was measured, (b) at least 15 individuals were measured, and the lengths of individuals not measured were resampled from this distribution, (c) at least 30 individuals had been measured at that site and in that sampling season in the past, and the lengths of individuals not measured were resampled from this distribution, (d) more than 50% of individuals captured in that sampling event were measured, and the lengths of individuals not measured were given as the mean of this distribution, or (e) for small-bodied species, the lengths of individuals not measured were resampled from the study-wide distribution of that species body size. This final criterion was implemented for three native and three non-native small-bodied minnows (max length ≤ 100 mm) that were systematically under-measured as compared to larger-bodied taxa (on average 15% of the study-wide total measured for small-bodied species vs. 37% measured for large-bodied species). The mean of individual size distributions for these species did not vary across our environmental gradients of interest and their exclusion would have removed many sampling efforts representative of Verde River fish communities. In all, we retained 63 unique stream reaches (Fig. 1) containing ~16,000 individuals of 6 native and 11 introduced species.

We assigned trophic guilds to each individual in the dataset using recent diet analyses specific to Verde River fishes (Bonar *et al.* 2004) or those in the upper Gila River (Pilger *et al.* 2010), an environmentally and biologically similar system within the same basin. Together these studies gathered gut content information for thousands of individuals of each species in our analysis or their close congeners. Pilger *et al.* (2010) further differentiated diet information across juvenile, subadult, and adult individuals (defined by size classes) of most large bodied species. Therefore, for each individual we assigned a trophic guild based on diet information specific to their species and size class whenever possible. Individuals were either invertivores (invertebrate + fish diet items $> 75\%$ total diet content and fish diet items $< 15\%$ total diet content), invertivore-

piscivores (invertebrate + fish diet items > 75% total diet content and fish diet items > 15% total diet content), or omnivores (all others, often with a high percentage of plant and detrital diet items). Guilds were first assigned using data from Pilger *et al.* (2010) and cross-checked for discrepancies against Verde assemblage-specific gut content data (Bonar *et al.* 2004) and qualitative southwestern species descriptions (Sublette, Hatch & Sublette 1990) (Table 1).

Environmental Covariate Datasets

We used environmental data that were collated as part of the Lower Colorado River Basin Aquatic Gap Analysis Program (reviewed in Strecker *et al.* 2011b) for each spatially discrete NHD reachcode in our final fish community dataset. We used Shreve stream order, mean annual air temperature (°C), and spring (March to April) precipitation variability (CV) as proxies for gradients in ecosystem size, thermal environment, and environmental stability, respectively. Climate variables were calculated according to the upstream contributing watershed and were based on daily records from 1971 to 2000 (Strecker *et al.* 2011b). In a regional analysis of the Lower Colorado River Basin, Pool *et al.* (2010) found these environmental covariates to be important natural drivers of taxonomic and functional richness of stream fish communities. These covariates represent major hypotheses of environmental influences on body size distributions and were considered alongside our biological hypotheses.

Comparing Species Pools

We first tested for differences in the study-wide native and non-native species pools (ln-transformed as is appropriate for allometric analyses; Kerkhoff & Enquist 2009) by collating data across sites and comparing the distributions using permutation tests (Manly 1997; Anderson 2001). Permutation tests relax some of the assumptions of parametric statistical tests (e.g., normality) and permit comparisons of different moments of the distribution. Here we compare

the mean, variance (CV), and skewness of size distributions because each may incur different consequences for size-dependent ecosystem functioning. For each guild and the total community we ran separate permutation tests. To run each, we pooled native and non-native size data together, then randomly reassigned lengths from these pooled data to native and non-native distributions. The number of individuals sampled was equal across origins and represented the true observed minimum number of individuals for native or non-native species in that trophic guild (i.e., at least 600 individuals). We calculated the difference between the native and non-native moments of these randomly sampled distributions, and repeated this procedure 9,999 times. To calculate the probability that the observed native and non-native size differences were random, we compared the observed difference to the distribution of the 9,999 randomly sampled differences. Statistical significance was calculated as the number of random differences that were equal or more extreme than the observed difference divided by 10,000 (iterations).

Community Analysis

We examined the influence of non-native species on local ISDs alongside potential environmental covariates (temperature, ecosystem size, and environmental variability) using an information theoretic approach. We modeled site-scale univariate ISD moments within and across guilds as a function of environmental and biological covariates in a series of multiple linear regressions. We considered total species richness (as a proxy for competition in general), percent total non-native dominance by abundance (as a proxy for potential non-native competition), and percent piscivore non-native dominance (as a proxy for potential non-native predation). At the guild-level we considered richness and total non-native dominance within the guild as a proxy for potential competition, and community-level piscivore dominance again as a proxy for potential predation. Guild-level ISDs were only considered if >10 individuals

comprised the guild. From these covariate possibilities, we identified 30 candidate models to test. Models included all covariates alone, the full suite of either environmental or biological covariates, all possible pairs of environmental or biological covariates separately, and all possible pairs of one environmental and one biological covariate. This model list is not exhaustive; instead, we identified models that made ecological sense to avoid dredging and to avoid over-parameterization within models given our small sample size. We fit each model separately to the mean, CV, and skew of community- or guild-level ISDs using ordinary least squares regression. Model fit was evaluated from the log-likelihood using Akaike's Information Criterion corrected for small sample size (AICc), and all models with $\Delta\text{AICc} < 2.0$ were retained as possible best models (Burnham & Anderson 2002).

Multivariate Analysis

To assess the effect of non-native introductions on multivariate community structure we employed a recently developed method by De Cáceres, Legendre & He (2013) using the *vegclust* package in R (De Cáceres, Font & Oliva 2010). The authors explicitly developed this approach to simultaneously consider information on size distributions and biological group abundances (e.g., populations, species, or, in our case, guilds) when calculating dissimilarities between ecological communities. Their approach requires the creation of a cumulative abundance profile (CAP) of each guild at a site that assigns individuals to bins of minimum log-body size x when the individual's body size $\geq x$. We grouped individual into 0.5 log unit bins that spanned the total range of body size in our study (2.5—6.5). The dissimilarity metrics proposed by De Cáceres *et al.* (2013) are robust to bin size and we repeated our analyses with bin sizes of 0.25 and 1.0 log units with no qualitative changes in our results. We then compared the areal overlap of guild-level CAPs between sites to calculate their pairwise alias Bray-Curtis dissimilarities (De Cáceres

et al. 2013). We assessed the effects of the environmental and biological covariates (i.e., our hypothesized drivers above) on community structure dissimilarity by performing a distance-based redundancy analysis (dbRDA) —a form of constrained ordination for semi-metric dissimilarity coefficients (Anderson & Legendre 1999; De Cáceres *et al.* 2013)— on the resultant alias Bray-Curtis dissimilarity matrix. dbRDA first applies a principal coordinate analysis to the guild X size dissimilarity matrix, and then constrains the relationship between site coordinates in this ordination by our predictor variables using classic redundancy analysis. Seasonal effects were first partialled out of the analysis, and the dbRDA was performed with environmental (temperature, stream order, spring precipitation CV) and biological (total non-native dominance, non-native predator dominance, total richness) covariates. We tested the effectiveness of the constrained ordination as a whole, the significance of individual axes, and the significance of individual covariates in explaining community structure dissimilarity using permutational significance tests with 999 iterations. We also plotted the averages of community-level ISD moments (mean, CV, and skewness) on the constrained ordination plot using the *envfit* function, which correlates these moments to the ordination axes.

RESULTS

Comparing Species Pools

The ISDs of non-native species pool differed significantly from native species in most ways measured (Table 2; Fig. 2). Non-native species were smaller on average than native species across all guilds (herein, non-native moment vs. native moment: 68.7 vs. 75.2 mm) and within both invertivore (53.5 vs. 71.5 mm) and omnivore guilds (62.2 vs. 73.7 mm), but were significantly larger in the invertivore-piscivore guild (139.8 vs. 112.2 mm). The variance of non-native ISDs was significantly higher across and within all guilds except for omnivores (Table 2). Non-native and native ISDs exhibited significantly different, but positive, skewness at the

community-level (0.40 vs. 0.88) and within the omnivore guild (1.69 vs. 1.05). Native ISDs were only slightly negatively skewed within the invertivore guild (-0.12), whereas non-native invertivores were positively skewed (0.54). Invertivore-piscivores from both origins were negatively skewed (-0.35 vs -0.59) and were not significantly different from each other (resampling test $P = 0.41$).

Community Analysis

A suite of biological and environmental covariates were important in explaining variation in ISDs both within and across guilds. Variance explained by top models was generally highest for the mean (average $R^2 = 0.31$), then the CV (average $R^2 = 0.24$), and skewness (average $R^2 = 0.17$), of community and guild level ISDs. Top models ($\Delta AICc < 2.0$, likelihood > 0.5) and their results are presented in detail in Table 3. We found varying evidence for the hypothesized effects of non-native introductions and environmental covariates on ISDs.

Top models of the means of each guild and the community reflected relationships expected from the species pool comparison. Within group non-native dominance had negative effects on the means of the community and invertivore and omnivore guilds, and positive effects on the invertivore-piscivore guild. Non-native predator dominance had a positive effect on the community-level mean, which may simply reflect their additive effects, but also had a positive effect on the mean of the invertivore guild, which may indicate the effects of increased predation on small-bodied individuals. Species richness was also included with opposing effects in top models of the community (positive effect) and invertivore (negative effect) means.

Species richness was included in all top models of the CV of ISDs except for the omnivore guild. For some groups, CV was also influenced by non-native dominance (invertivore: positive effect;

omnivore: negative effect) or non-native predator dominance (community: negative effect). Environmental covariates were also included in some top models (temperature: community [negative effect]; order: community [positive effect], omnivore [positive effect]; environmental variability: invertivore-piscivore [negative effect]), though we had no specific *a priori* hypotheses of how environmental covariates would relate to CV.

Only the invertivore guild had top models of skewness with adjusted $R^2 > 0.15$. In this guild, skewness was a function of richness (positive effect), stream order (negative effect in one model), and season (positive effects of spring and summer and negative effects of winter in one model). No model explained greater than 0.5 percent of the variance in skewness in the omnivore guild. At the community level, non-native predator dominance had a negative effect on skewness (likely a result of their additive effects), as did temperature. Skewness within the invertivore-piscivore guild was a function of combinations of non-native dominance (positive effect), temperature (negative effect), order (positive effect), and richness (negative effect). The contrasting effects of non-native predators on skewness at the guild vs. community level makes biological sense. Non-native predators assume a piscivorous diet at earlier life stages and smaller body sizes than native predators (Table 1), shifting the left-skewed native invertivore-piscivore guild toward normality (i.e., decreasing negative skew), while adult non-native predators increase the relative abundance of large-bodied individuals at the community level, decreasing right (positive skew).

Multivariate Analysis

Fish communities varied widely with respect to guild relative abundances and size structure (Fig. 3A,B). However, we found that environmental and biological drivers had little combined effect on this multivariate community structure (permutation test on global dbRDA model: *pseudo-*

$F_{(6,53)} = 1.3$; $P = 0.18$; conditioned variance [season effect]: 0.04; constrained variance [combined environmental and biological effect]: 0.13) (Fig. 3C). Only the first axis of the constrained ordination was significant ($pseudo-F_{(1,53)} = 5.2$; $P = 0.01$), though the second axis was marginally significant ($pseudo-F_{(1,53)} = 2.1$; $P = 0.11$). Regardless of their significance, these axes explained only 9.27% and 3.65% of the variance in community dissimilarity, respectively. Lastly, a permutational significance test of individual terms in the model indicated that only species richness ($pseudo-F_{(1,53)} = 2.3$; $P = 0.09$) and environmental variability ($pseudo-F_{(1,53)} = 2.9$; $P = 0.04$) were influential in the dbRDA.

DISCUSSION

The distribution of body size in ecological communities provides important insight into the functioning of ecosystems (Woodward *et al.* 2005), and changes in functional trait distributions can help identify the ecosystem-level effects of non-native species (Strayer 2012). This may be especially useful in highly invaded systems where the ecological role of any one non-native species is hard to isolate. At macroecological scales non-native introductions have increased the median of species-level size distributions (Blanchet *et al.* 2010), disproportionately favored large-bodied, high trophic level sport fishes (Eby *et al.* 2006; Blanchet *et al.* 2010), and promoted the trophic dispersion of food webs (Cucherousset *et al.* 2012). By analyzing ISDs of fish communities within a large dryland river we found mixed agreement with these macroecological patterns.

In concordance with others, we found that introduced game fishes (e.g., smallmouth bass, brown trout) increased the mean body size of upper trophic levels (i.e., invertivore-piscivore guild; Fig. 2, Tables 2,3) relative to the native roundtail chub, which switches from a piscivorous to an omnivorous diet through its ontogeny (Table 1). However, the overall mean of ISDs across all

guilds and within invertivore and omnivore guilds declined with non-native dominance, in contrast to the general expectation from macroecological patterns. Across major river basins, Blanchet *et al.* (2010: Fig. 1) found that non-native species size distributions were bimodal, with the smaller mode aligning well with native size distributions. The authors hypothesized that this first mode probably contained species of unintentional introduction, but we believe may also contain those species specifically introduced for biocontrol or as baitfishes in our system (e.g., Western mosquitofish, red shiner, fathead minnow). We found a similar bimodal overlap in our system within the omnivore guild, where small-bodied native and non-native omnivores shared similar ISDs but mainly native species (roundtail chub, desert sucker, Sonora sucker; though also non-native common carp) occupied a larger omnivore mode (Fig. 2). However, successful non-native invertivores and invertivore-piscivores appeared to fall out along the shoulders (lower and higher, respectively) of contemporary native ISDs (Fig. 2). Anecdotally, these smaller non-native invertivores share similar asymptotic body size with the declining, ESA-listed spikedace and the extirpated Sonoran topminnow (native invertivores), while larger non-native invertivore-piscivores may have similar ISDs to the long-extirpated Colorado pikeminnow in the Verde. Allen, Forsy & Holling (1999) found that the margins of body size distributions were hotspots for invasion and extinction for multiple taxa in transforming landscapes. The authors presumed that, for better or worse, species at the margins relied on resource pools at different spatial scales than the modal species, and therefore were first to be influenced by landscape change. Given the degree of hydrologic alteration and fragmentation in southwestern rivers (Sabo *et al.* 2010), this is a plausible hypothesis in our system.

We expected that non-native species would not only have additive effects on ISDs, but would also influence distributions through their interspecific interactions (Quintana *et al.* 2015). In

particular, we hypothesized that non-native predation would increase the mean body size and reduce the positive skew of their preys' ISD (by selectively feeding on smaller individuals within their gape limitation: Griffiths 2013), as well as reduce the variance (by narrowing the range of body sizes safe from predation: Quintana *et al.* 2015). In reality, our model selection results only provided evidence that non-native predators had a positive effect on the body size of potential invertivore prey, not on omnivores or on any other moments of the ISD (Table 3). We also expected that non-native competition would increase the CV of ISDs (Schoener 1974). We found some model support for this at the community level and within the invertivore guild. However, most top models of CV in all groups included species richness (total or guild level). The effect of richness could be a simple statistical result in which increasing diversity necessarily increases the variability of an entity, or could be a true biological result where increasing the number of species increases niche differentiation and the dispersion of body size to take advantage of unique resource pools. Comparisons to null expectations from Taylor's power law or experimental manipulations might disentangle these effects in future research. Taken together, our results suggest that in this study non-native species likely influenced ISDs more through their simple additive effects than through their potential interspecific interactions. Using a wide range of aquatic taxonomic datasets, Quintana *et al.* (2015) came to similar conclusions; interaction effects on size distributions were detectable but weak, indicating that other forces are structuring size distributions.

Our correlational, trait-based findings agree in part with the results of a more detailed stable isotope and growth modelling approach in a nearby Colorado River tributary (Walsworth *et al.* 2013). The authors of this study found that despite strong overlap in native and non-native isotopic niche space (i.e., strong potential for competition), native growth rates and demography

(i.e., species-specific size structure) were not influenced by the presence of non-native species. This result suggests that non-native effects on ISDs in this basin may be more dependent on their additive effects than on species interactions. Walsworth *et al.* (2013) also found that non-native species influenced the dispersion of trophic space, with some non-natives feeding at higher and lower trophic positions than native species, rather than shifting trophic structure in one particular direction. This is an important finding that coincides with others (Cucherousset *et al.* 2012; Sagouis *et al.* 2015).

Alternatively, non-native species truly may not have consistent effects on the multivariate size and trophic structure of local fish communities, as our results suggest. At small scales productivity, habitat size, disturbance, and the nature of species interactions can interact in complex ways to determine the length of food chains in aquatic systems (e.g., Takimoto *et al.* 2012). In particular, habitat complexity is expected to be important in dictating the size structure (i.e., the textural discontinuity hypothesis) and concomitantly the trophic structure of communities. The textural discontinuity hypothesis has proven important in dictating the size structure of coral reef fish communities (Nash *et al.* 2012), and is expected to be important at scales similar to those in which species interactions occur, potentially masking those biological effects (Allen *et al.* 2006, Fig. 1). Species richness and environmental variability were the only marginally significant predictors of multivariate structure in our own analysis, loading on the first and second constrained axes, respectively (Fig. 3). These variables are sometimes considered indicators or drivers of habitat complexity, respectively, but additional investigations are needed to more fully understand multivariate community structure in this system.

Conclusion

We found that non-native species have significantly altered the individual size distributions, but not necessarily the trophic structure, of fish communities in the Verde River system. At the scale of our analyses these effects appear mainly additive, with less evidence to suggest that predatory or competitive effects exacerbate change in size structure. In reality multiple environmental, ecological, and evolutionary mechanisms constrain size distributions at multiple scales. That we detected the effects of non-native species on size structure through this noise suggests that non-native species have important influences on size-dependent ecosystem functioning in the Verde River. Decreasing the mean size of invertivores and omnivores while increasing the mean of invertivore-piscivores may have substantial impacts on food web dynamics, energetic efficiency, and nutrient cycling, which can all propagate laterally and longitudinally to influence adjacent ecosystems. These findings will help generate hypotheses and guide mechanistic non-native species research in riverine environments and contribute to greater understanding of using functional traits as an intermediary to forecast global change effects on ecosystem functioning.

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TABLES

Table 1. Native and non-native species of the Verde River and their trophic guild assignments.

| Species | Max | Juvenile | Subadult | Adult | Source |
|--|-----|-------------|-------------|-------------|-------------|
| <i>Large-bodied native</i> | | | | | |
| Desert sucker (<i>Catostomus clarkii</i>) | 382 | Omni | Omni | Omni | P |
| Sonora sucker (<i>Catostomus insignis</i>) | 436 | Invert | Invert | Omni | P |
| Roundtail chub (<i>Gila robusta</i>) | 352 | Invert | Invert-Pisc | Omni | P; congener |
| <i>Small-bodied native</i> | | | | | |
| Longfin dace (<i>Agosia chrysogaster</i>) | 101 | - | - | Omni | P |
| Spikedace (<i>Meda fulgida</i>) | 58 | - | - | Invert | P |
| Speckled dace (<i>Rhinichthys osculus</i>) | 108 | - | - | Invert | P |
| <i>Large-bodied non-native</i> | | | | | |
| Yellow bullhead (<i>Ameiurus natalis</i>) | 250 | Omni | Omni | Invert-Pisc | P |
| Channel catfish (<i>Ictalurus punctatus</i>) | 520 | - | - | Omni | B;S |
| Smallmouth bass (<i>Micropterus dolomieu</i>) | 285 | Invert-Pisc | Invert-Pisc | Invert-Pisc | P |
| Green sunfish (<i>Lepomis cyanellus</i>) | 228 | - | - | Invert | B |
| Largemouth bass (<i>Micropterus salmoides</i>) | 102 | Invert-Pisc | Invert-Pisc | Invert-Pisc | P; congener |
| Rainbow trout (<i>Oncorhynchus mykiss</i>) | 408 | (Invert) | Invert | Invert | P;S |
| Brown trout (<i>Salmo trutta</i>) | 465 | (Invert) | Invert | Invert-Pisc | P;S |
| Common carp (<i>Cyprinus carpio</i>) | 617 | - | - | Omni | B;S |
| <i>Small-bodied non-native</i> | | | | | |
| Red shiner (<i>Cyprinella lutrensis</i>) | 86 | - | - | Invert | B |
| Mosquitofish (<i>Gambusia affinis</i>) | 58 | - | - | Invert | B |
| Fathead minnow (<i>Pimephales promelas</i>) | 70 | - | - | Omni | S |

Notes: Guilds were assigned according to quantitative diet analyses (B: Bonar et al. 2004; P: Pilger et al. 2010) or a qualitative natural history review of desert fishes (S: Sublette, Hatch, and Sublette 1990). When data were available, guild could potentially vary between size classes within a species. “-“ indicates size-specific diet were unavailable or diet is invariant across sizes. For two species we used congener data (roundtail chub ← headwater chub; largemouth bass ← smallmouth bass). Max length (mm) is the largest individual of that species measured in our final dataset.

Table 2. Comparison of statistical moments of native (*N*) and non-native (*NN*) ISDs at the watershed level

| | | All | Omnivore | Invertivore | Inv-Piscivore |
|--------------|-----------|--------------------|--------------------|-----------------------|------------------------------|
| Mean (mm) | <i>N</i> | 75.2 [73.7 — 75.9] | 73.7 [70.1 — 76.7] | 71.5 [70.8 — 72.2] | 112.2 [119.9 — 113.3] |
| | <i>NN</i> | 68.7 [67.4 — 70.1] | 62.2 [59.7 — 64.1] | 53.5 [52.5 — 54.6] | 139.8 [135.6 — 144.0] |
| CV | <i>N</i> | 0.12 [0.12 — 0.12] | 0.13 [0.13 — 0.14] | 0.08 [0.08 — 0.08] | 0.04 [0.04 — 0.04] |
| | <i>NN</i> | 0.14 [0.14 — 0.15] | 0.10 [0.09 — 0.11] | 0.13 [0.12 — 0.13] | 0.08 [0.08 — 0.09] |
| Skewness | <i>N</i> | 0.88 [0.82 — 0.95] | 1.05 [0.89 — 1.21] | -0.12 [-0.20 — -0.04] | <i>-0.59 [-0.70 — -0.48]</i> |
| | <i>NN</i> | 0.40 [0.34 — 0.46] | 1.69 [1.10 — 2.09] | 0.54 [0.46 — 0.62] | <i>-0.35 [-0.65 — -0.08]</i> |

Notes: All values are the observed statistical moments with bootstrapped 95% CIs. Italic results indicate the only comparison that was *not* statistically significant (invertivore-piscivore skewness; $P = 0.41$). All other comparisons were significant at $P = 0.0001$. All resampling tests were performed on log-transformed ISDs, but here mean length is presented untransformed for easier interpretation.

Table 3. Model selection results of analysis relating univariate statistical moments of community ISDs to potential environmental and biological drivers. + or – superscripts indicate the qualitative direction of the covariate’s effect on the response in that model.

| Response | Model | Adj. R² | ΔAICc | Likelihood |
|----------------------|--|---------------------------|--------------|-------------------|
| <i>Community</i> | | | | |
| Mean | Rich ⁺ + NN ⁻ + NNPred ⁺ | 0.26 | 0.0 | 1.0 |
| CV | Rich ⁺ + Temp ⁻ | 0.33 | 0.0 | 1.0 |
| | Rich ⁺ + Order ⁺ | 0.33 | 0.10 | 0.95 |
| | Rich ⁺ + NNPred ⁻ | 0.32 | 0.94 | 0.63 |
| Skew | Non-native Predator ⁻ + Temp ⁻ | 0.15 | 0.0 | 1.0 |
| <i>Invertivore</i> | | | | |
| Mean | Rich ⁻ + NN ⁻ + NNPred ⁺ | 0.34 | 0 | 1.0 |
| CV | Rich ⁺ + NN ⁺ | 0.24 | 0 | 1.0 |
| Skew | Rich ⁺ + Order ⁻ | 0.25 | 0 | 1.0 |
| | Rich ⁺ + Season ^(Sp. +, Sm. +, W. -) | 0.27 | 1.05 | 0.59 |
| <i>Omnivore</i> | | | | |
| Mean | NN ⁻ + Temp ⁻ | 0.43 | 0 | 1.0 |
| CV | NN ⁻ + Order ⁺ | 0.13 | 0 | 1.0 |
| | Order ⁺ | 0.09 | 0.80 | 0.67 |
| Skew | NA | - | - | - |
| <i>Inv-Piscivore</i> | | | | |
| Mean | NN ⁺ | 0.21 | 0 | 1.0 |
| | NN ⁺ + Temp ⁻ | 0.26 | 0.20 | 0.91 |
| | NN ⁺ + Order ⁻ | 0.24 | 0.65 | 0.72 |
| | Rich ⁺ + Temp ⁻ | 0.23 | 1.0 | 0.61 |
| CV | Rich ⁺ + EnvCV ⁻ | 0.24 | 0 | 1.0 |
| Skew | NN ⁺ | 0.11 | 0 | 1.0 |
| | Temp ⁻ + Order ⁺ | 0.13 | 1.05 | 0.59 |
| | Rich ⁻ + Order ⁺ | 0.13 | 1.16 | 0.56 |
| | Rich ⁻ + NN ⁺ | 0.13 | 1.25 | 0.54 |

Note: Candidate models with ΔAICc < 2.0, likelihood < 0.5, or Adj. R² < 0.05 are not included in this table. NA is

given if no candidate model met these criteria. Biological covariates include: **Rich** = community- or guild-level

richness; **NN** = community- or guild-level non-native dominance; **NNPred** = community-level non-native predator dominance. Environmental covariates include: **Temp** = mean annual air temperature at reachcode (proxy for water temperature); **Order** = Shreve stream order at reachcode (proxy for habitat size); **EnvCV** = precipitation variability at reachcode (proxy for environmental (in)stability); **Season** = season (Sp. = spring, Sm. = summer, W. = winter, F. = Fall) in which sampling occurred.

FIGURE CAPTIONS

Figure 1. A map of the Verde River watershed located in central Arizona, USA. Points represent the most recent community-level sampling efforts from discrete NHD+ reachcode units that

match our data requirements. Point size is proportional to the degree of community-level non-native dominance and the black rectangle represents approximate study area.

Figure 2. Density plots of captured native (grey fill) and non-native (dashed line) fishes' size distributions ($\ln[\text{individual body size}]$) in the Verde River Basin, Arizona, USA. The top-left panel is for all individuals. The other panels represent individuals within each trophic guild (omnivore, invertivore-piscivore, or invertivore). Table 2 summarizes statistical differences between native and non-native species for the first three moments (mean, CV, skewness) of the distributions.

Figure 3. dbRDA constrained ordination results. All panels represent the same analysis with objects and descriptor components plotted separately for easier viewing. **A)** Points are sampled fish communities and their pairwise distances in ordination space represent their alias Bray-Curtis dissimilarity based on community (guild X body size) structure. Point size represents community-level non-native dominance, with larger points having high non-native dominance. **B)** Guild abundances (black) and community-level size descriptors (grey) are correlated to the ordination axes to interpret structural differences between communities (*sensu* De Cáceres, Legendre & He 2013). For example, communities in the bottom left quadrant of the ordination tend to be dominated by invertivore-piscivores and have large mean body size, while communities in the upper right quadrant have highly variable, skewed ISDs and tend to be dominated by invertivores. **C)** The constraining predictor variables (black = biological, grey = environmental) explained little variation in community structure ($\text{pseudo-}F_{(6,53)} = 1.3, P = 0.18, \text{constrained variation} = 0.17$). Covariate correlations with constrained axes are plotted, but only the environmental variability and species richness terms were marginally significant in permutation testing.

FIGURES

Figure 1.

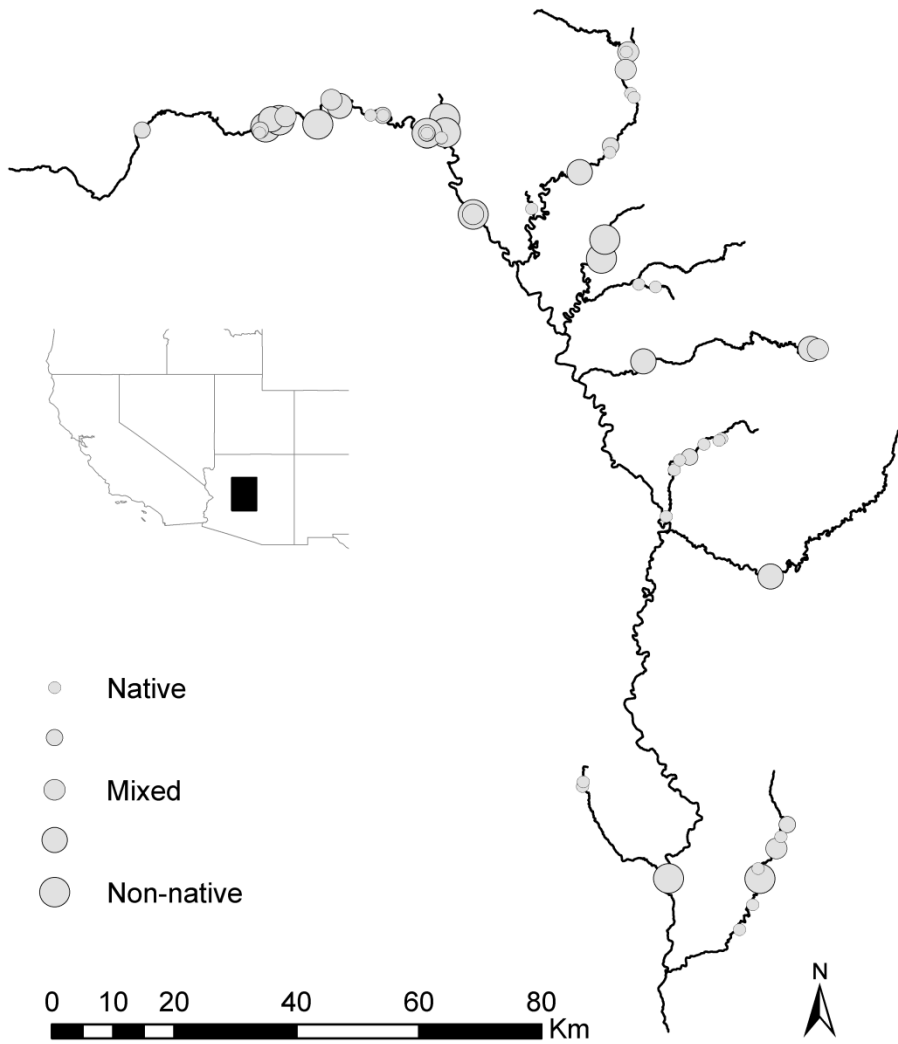


Figure 2.

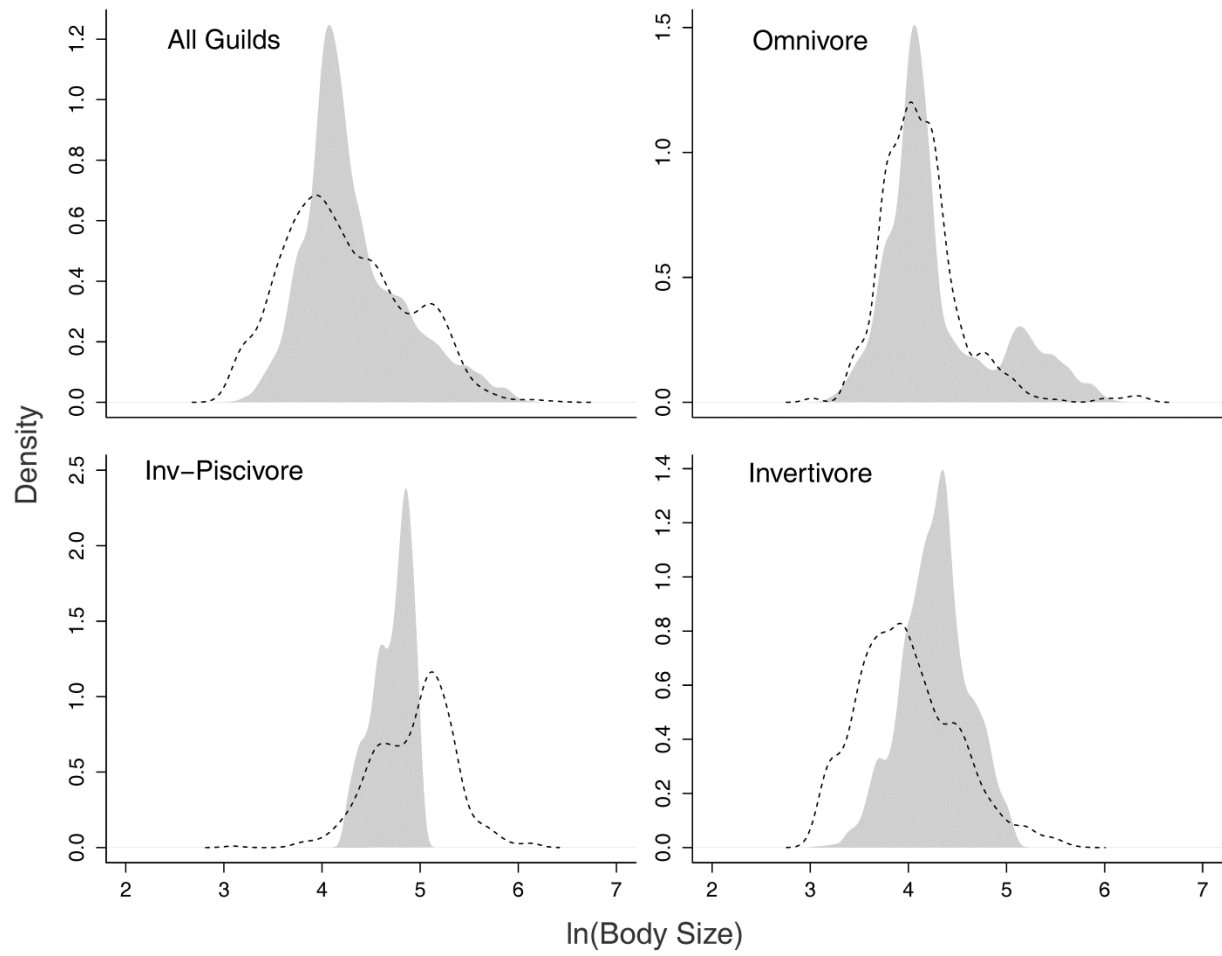
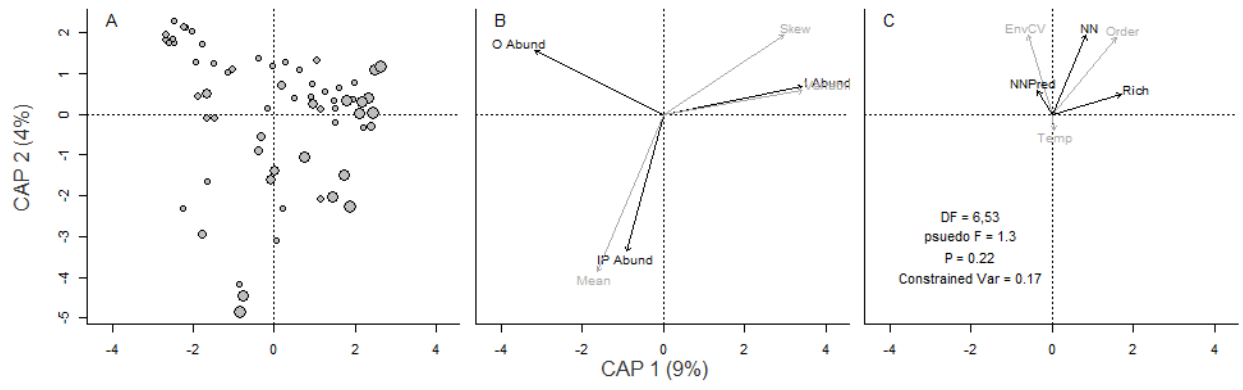


Figure 3.



Running Head: Body size, structure, and ecosystem function

Disentangling the influences of mean body size and size structure on ecosystem functioning

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ABSTRACT

1. Body size is an important functional trait that can be used to forecast individuals' responses to environmental change and their contribution to ecosystem functioning. However, information on the mean and variation of size distributions often confound one another when relating body size to functioning at the population level. Given that size-based metrics are increasingly used as indicators of ecosystem status, it is important to identify the specific aspects of size distributions that mediate ecosystem functioning.

2. Our goal was to simultaneously account for the mean, variance, and shape of size distributions when relating body size to aggregate ecosystem functioning.

3. We compared predictions from Jensen's inequality—the deterministic relationship between the average of a nonlinear function and the function of its average—to field survey results that related habitat-driven differences in size distributions to nutrient recycling by a non-native crayfish.

4. As predicted from Jensen's inequality, considering only the mean body size of populations overestimated aggregate population effects on ecosystem functioning. This bias declined with mean body size such that mean-field and variance-incorporating estimates of ecosystem functioning were statistically similar for populations at mean body sizes > 7.5 grams.

5. Although both true and Jensen-estimated biases of a mean-field approach declined with body size, the two metrics were significantly different at low mean body size. Size distributions were highly positively skewed at these low mean body sizes, and this skewness was tightly correlated with differences in the true and estimated bias.

6. Our findings support the prediction that variance around the mean can alter the relationship between body size and ecosystem functioning, especially at low mean body size. However, methods to account for mean-field bias performed poorly in samples with highly skewed distributions, indicating that changes in the shape of the distribution, in addition to the variance, may confound predictions from Jensen's inequality. Given that many functions of interest follow similar nonlinear allometric models, explicitly defining and experimentally or statistically isolating the effects of the mean, variance, and shape of size distributions is necessary to begin generalizing relationships between animal body size and ecosystem functioning.

Keywords: Verde River, Lower Colorado River Basin, *Orconectes virilis*, non-native, introduced, intraspecific variability, biodiversity-ecosystem function, non-linear averaging, aggregation bias

INTRODUCTION

Trait-based ecology holds considerable promise for forecasting the effects of global change on ecosystem functioning by scaling up the actions of individuals independent of their taxonomy (Luck *et al.* 2012). Across animal taxa, body size has long been considered a useful trait in determining species' responses to the environment, their ecological relationships, and their roles in ecosystem processes (Peters 1983; Woodward *et al.* 2005). The metabolic theory of ecology provides a mechanistic basis for the scaling relationships between body size and many system properties (Brown, Allen & Giloolly 2007), suggesting that body size may represent a universal trait to predict the effects of biological change on ecosystem functioning (Seguin *et al.* 2014).

Mean body size continues to be the primary currency by which studies have forecasted size-dependent, ecosystem-level impacts of extinctions, invasions, and compositional change (e.g., Solan *et al.* 2004; Larsen *et al.* 2005; McIntyre *et al.* 2007; Rudolf & Rasmussen 2013a; Seguin *et al.* 2014). However, individual variation (i.e., the frequency distribution of body size, herein size structure) across a population or community may have meaningful effects on ecosystem functioning that are masked by the averaging properties of mean trait values. Most ecosystem functions scale nonlinearly with body size following a power law function,

$$y = \alpha x^b \tag{1}$$

where x is body size, y is the per capita or population-level functional rate of interest, b is a scaling coefficient and α is a normalization constant. When $b \neq 1$, the function is nonlinear such that small and large organisms exhibit different functional rates per unit size. Thus, size distributions that are represented by the same mean body size but vary in the relative proportion of different organism size-classes may have varying effects on aggregate ecosystem functioning.

This prediction is formulated mathematically as Jensen's inequality, where for a nonlinear function $f(x)$ and distribution of x values with mean \bar{x} and nonzero variance, the average of the function, $\overline{f(x)}$, does not equal the function of the average, $f(\bar{x})$ (Ruel & Ayres 1999).

Despite recent research incorporating size structure in size-based investigations of ecosystem functioning (Toscano & Griffen 2012; Dangles *et al.* 2012; Norkko *et al.* 2013; Rudolf & Rasmussen 2013b), a perennial challenge involves the logistical constraints of experiments or natural field observations where size structure is often confounded with mean body size. For any function of interest that is predicted to scale allometrically (e.g., foraging rate, nutrient recycling, productivity), varying the distribution around the mean body size will deterministically alter the aggregate sum of that function at the population level following Jensen's inequality. Duursma & Robinson (2003) derived an approximation of the bias attributed to ignoring the variation around the mean for an allometric power law (i.e., tree stem mass \sim diameter at breast height) as

$$\text{Estimated Bias (\%)} = \frac{1}{2}[b(b - 1)]CV^2 \quad (2)$$

where b is the scaling coefficient of the power law and CV is the coefficient of variation of the size distribution. Accordingly, scientists studying the relationship between body size and ecosystem functioning may bias their estimates of the mean body size effect if variability also changes with their experimental design. This bias may be important given that both mean body size and size structure are subject to natural and human-induced variation across time and space, including ontogenetic shifts, phenotypic plasticity, climate change, and size selective harvesting. Paralleling recent calls to consider the importance of both inter- and intraspecific trait variability in community ecology (Violle *et al.* 2014), scientists now acknowledge the potential benefits of individual-level data in understanding the dynamics and functioning of ecosystems (e.g.,

Trebilco *et al.* 2013). Despite this recognition, research has not yet considered the importance of mean body size and size structure information simultaneously in explaining variation in consumer-driven ecosystem functioning.

Nutrient recycling is an important ecosystem function in which consumers can control resource dynamics by remineralizing nitrogen and phosphorus through excretion (Vanni 2002). Numerous studies have demonstrated that nutrient recycling can interact with traditional trophic controls of primary production in both experimental (Knoll *et al.* 2009; Kohler *et al.* 2011) and natural systems (Vanni *et al.* 2006), can rival atmospheric (Schindler, Knapp & Leavitt 2001) or watershed inputs of inorganic nutrients (Vanni *et al.* 2006), and can relieve and reverse nutrient limitation in some ecosystems (Allgeier, Yeager & Layman 2013; Atkinson *et al.* 2013).

Three decades of research demonstrate that, broadly, body size is important to nutrient recycling. Individual body size explains most variation in per capita nutrient excretion rates (Sereda, Hudson & McLoughlin 2008), though significant interspecific variability in this relationship may exist (Villegger *et al.* 2012). In aquatic systems, heterogeneous distributions of total consumer biomass can generate biogeochemical hotspots and hot moments — areas and times of elevated biogeochemical reaction rates (e.g., McClain *et al.* 2003; McIntyre *et al.* 2008; Atkinson *et al.* 2013). Species extinctions ordered by maximum body size had a larger effect on nutrient recycling than random extinction scenarios when population energy was conserved (McIntyre *et al.* 2007). Likewise, Hall *et al.* (2007) demonstrated that shifts in size structure impacted lake nutrient recycling, and models containing both total fish biomass and abundance best explained aggregate nutrient recycling (Verant *et al.* 2007). Size is clearly important to nutrient recycling, but the relative contributions of total mass, mean body size, and size structure are difficult to compare in these studies and poorly understood in general.

Here we deploy a field study to explore the relative contributions of mean body size and size structure to nutrient recycling by using a nonnative stream-dwelling crayfish (*Orconectes virilis* [Hagen, 1870]) as a case example. Nonnative crayfishes are known to exert major impacts on the structure and functioning of the recipient system (Twardochleb *et al.* 2013). The few studies available suggest crayfishes recycle nutrients at high N:P ratios relative to other taxa (Evans-White & Lamberti 2005; McManamay *et al.* 2011), likely because of the high P requirements of exoskeleton production for a frequently molting invertebrate (Habraken *et al.* 2015). Moreover, physical heterogeneity and ontogenetic preferences across longitudinal (i.e., riffle vs. run) and lateral (i.e., river thalweg vs. river bank) habitats provide large variation in total mass, mean body size, and size structure in crayfish populations. Given the potential importance of crayfish to nutrient cycles and the variation in their distribution in this system, we asked (1) what is the relative contribution of mean body size and size structure to observed differences in nutrient recycling across habitat types after accounting for total biomass, and (2) does the shape of size structure variation around the mean alter the bias in nutrient recycling estimates? Specifically, we expected that (1) ontogenetic preferences would generate dissimilar body size distributions (mean, variance, and shape) across habitat types, (2) that variance-induced bias in aggregate recycling estimates would be highest for populations/habitat types with smaller mean body sizes, and (3) only the variance— not the shape— of the distribution would be important for predicting bias (following the bias approximation presented by Duursma & Robinson [2003]).

METHODS

System Description

The Verde River is a large tributary (15,800 km²) in the Lower Colorado River Basin, Arizona, USA with a hydrologic regime controlled by a combination of perennial groundwater springs, cool wet winters (December - March), and warm wet summer monsoons (July - September) (Jaeger, Olden & Pellend 2014). The uppermost perennial section of the river (herein, 'upper Verde') runs 60 km from the run-of-river Sullivan Dam to its confluence with Sycamore Creek and maintained baseflows at 640 l/s during our study period (April-June). The Verde River is one of two designated Wild and Scenic Rivers in Arizona and is a historical stronghold of several federal or state-listed endemic species. However, a suite of human stressors and nonnative species serve as potential threats to this river ecosystem. The northern crayfish, *Orconectes virilis*, is native to the upper Midwest, USA and has been introduced widely across the Colorado River Basin (Martinez 2012), with common occurrences in the upper Verde River (Gibson & Olden 2014). Given that no crayfish species are native to Arizona and that nonnative crayfishes have large effects on ecosystem functioning (Twardochleb *et al.* 2013), *O. virilis* may play a novel and important functional role in the Verde and other southwestern rivers (e.g., Moody & Sabo 2013).

Individual Nutrient Recycling

We used standard incubations in the field to characterize nutrient excretion rates across a range of crayfish body sizes. We focus this analysis on ammonium (NH₄-N) recycling because nitrogen is historically limiting in similar Sonoran desert streams (Grimm & Fisher 1986), but results were qualitatively similar for phosphate (PO₄-P) recycling. Crayfish were captured by hand and placed individually in clear polyethylene bags filled with 250-500 mL of deionized water. Bags were incubated for 45 minutes in stream margins to maintain ambient water temperature and minimize stress. After the incubation crayfish were removed and measured (length [cm] and

mass [g]). Two water samples were drawn from the well-mixed bag, filtered (Whatman GFF 0.45 μm filter), and immediately frozen on dry ice for later analysis. Samples were analyzed for $\text{NH}_4\text{-N}$ using the colorimetric salicylate-hypochlorite method (Bower & Holm-Hansen 1980) on a flow injection analyzer (QuikChem 8000 Series, Lachat Instruments, Loveland, Colorado USA) at Northern Arizona University's Colorado Plateau Analytical Laboratory. N excretion rates were calculated for each sample after accounting for ambient nutrient concentrations in control bags. The per capita relationship between body size and nutrient recycling was modeled as a power law (Eq. 1) by regressing N ($\text{NH}_4\text{-N}$ $\mu\text{mol}/\text{individual}\cdot\text{hr}$) on individual mass (g) using nonlinear least squares.

Field Sampling and Characterizing Size Distributions

Stream habitat is longitudinally (riffle-run sequences) and laterally (mid-channel and stream bank) heterogeneous. Crayfish use this habitat differentially through their ontogeny to balance resource acquisition, predation risk, and life history requirements, generating spatial and temporal variation in local size distributions. We use this size variation as a natural experiment to examine the relative influences of mean body size and size structure on nutrient recycling.

Crayfish were surveyed in three riffles and three runs (channel units) at each of three 500-1000m reaches in the upper Verde River. Within each channel unit we sampled crayfish in mid-channel and bank areas (microhabitat units). In four randomly placed 1 m^2 quadrats in each microhabitat unit we disturbed the substrate to a depth of 15 cm for one minute and captured dislodged crayfish in a 2 m^2 , 500 μm mesh seine held downstream. The total length ($\pm 1 \text{ mm}$) and mass ($\pm 0.1 \text{ g}$) of all crayfish $> 45 \text{ mm}$ were recorded. Individuals of early molts that reached high abundance were grouped in like size classes and characterized by the average measured lengths

of at least 10 individuals. We used length and weight data from 443 individuals to define the length-weight relationship of the *O. virilis* population and estimated masses of individuals not directly weighed (Fig. S1).

Characterizing Size Distributions

Habitat-specific size descriptors were quantified by pooling all four quadrat samples, resulting in 36 final pooled samples: 9 per channel (riffle vs. run) X microhabitat (mid-channel vs. bank) unit combination. For each sample we calculated the mean body size (mass [grams]), CV of body size, skewness of the body size distribution, and total biomass of all individuals. We compared these moments individually across habitat types using 2-way analyses of variance (ANOVA).

We also summarized multiple aspects of size structure variation simultaneously using a multivariate ordination approach. The size structure of each sample was defined by its cumulative abundance profile (CAP): a stratification of the sample population into discrete size classes (by mass) where the proportion of individuals greater than or equal to the lower limit of the size class is reported for each size class (De Cáceres, Legendre & He 2013). The size structure of samples (i.e., shape of CAPs) can be compared using unconstrained, multidimensional scaling ordination methods that summarize dominant gradients of variation in the CAPs (De Cáceres, Legendre & He 2013). We calculated Bray-Curtis dissimilarity between samples' CAPs using the *vegdist* function in the *vegclust* R package (De Cáceres, Font & Oliva 2010) and ordinated this matrix into two dimensions using a principal coordinate analysis (PCoA). A permutational multivariate analysis of variance (Anderson 2001) and a test of multivariate dispersion were used to test for differences in the multivariate size structure between habitat types.

Estimating Aggregate Nutrient Recycling and Quantifying Bias

For each sample we both estimated and calculated true aggregate areal nutrient recycling rates ($\mu\text{mol NH}_4\text{-N}$). We used a mean-field approach to estimate aggregate recycling rates by scaling the mean body size of each sample by the nutrient recycling model fitted above and multiplying by the total sample population. We repeated this process for every individual in the sample, rather than the mean, and summed across individuals to calculate the true aggregate recycling rate. Because we were interested in size structure effects and not total biomass effects, we standardized aggregate recycling rates by dividing each sample by its total biomass. The difference between the estimated and true aggregate recycling rate is considered the true bias of each sample,

$$\text{True Bias (\%)} = \frac{\text{True Recycling} - \text{Mean-field Recycling}}{\text{Mean-field Recycling}} \quad (3)$$

a consequence of not considering size structure variation around the mean. We also estimated the expected bias of each sample using the derivation of Duursma & Robinson (2003) for power laws (Eq. 2). Finally, we estimated a bias-corrected aggregate recycling rate by subtracting the product of the mean-field recycling estimate and the expected bias from the mean-field recycling estimate,

$$\text{Bias-corrected Recycling} = \text{Mean-field Recycling} - (\text{Mean-field Recycling} \times \text{Expected Bias}) \quad (4)$$

We took two steps to test our hypothesized relationships between size structure, aggregate recycling rates, and mean-field bias. First we compared the distributions of true, mean-field, and bias-corrected estimates of aggregate nutrient recycling between habitat types. This allowed us to qualitatively assess the importance of including variance information to predict ecosystem

functioning across populations with expected differences in size structure. Second, we plotted true and estimated bias against mean body size, CV, and skewness across all samples. Because we were interested in identifying general trends between these elements rather than defining quantitative relationships, we fit the data with loess smoothing and did not perform statistical analyses on regression models.

RESULTS

Per Capita Nutrient Recycling

Individual body size was significantly correlated with NH₄-N recycling by crayfish (Fig. 1), with NH₄-N decelerating with increasing body size (parameter estimate \pm standard error: $a = 2.88 \pm 0.49$, $b = 0.50 \pm 0.06$; $p < 0.001$). This decelerating relationship between body size and excretion rate is common among aquatic consumers. Though details are not presented in full here, the N:P excretion ratio of *O. virilis* (mean = 200) was similar to other crayfish species (Lessard-Pillon & McIntyre unpublished data; Evans-White & Lamberti 2005; McManamay *et al.* 2011) and high relative to other aquatic taxa.

Crayfish Size Distributions Across Habitats

Total biomass, mean body size, and size structure variability of crayfish varied differentially across stream habitat types (Table 1, Fig. 2, Fig. S2). We discarded four samples with low abundances ($N < 5$) for all analyses. Mean body size varied laterally (mean body size Mid = 5.5 g vs. Bank = 1.75 g: $F_{1,29} = 25.9$, $P < 0.001$) but not longitudinally (Riffle = 4.3 g vs. Run = 3.0 g: $F_{1,29} = 2.68$, $P = 0.11$). Total biomass varied both laterally (mean total biomass Mid = 31.1 g/m² vs. Bank = 56.0 g/m²: $F_{1,29} = 13.8$, $P < 0.001$) and longitudinally (Riffle = 31.15 g/m² vs. Run = 56.0 g/m²: $F_{1,29} = 9.08$, $P = 0.005$), but only the mid-channel x riffle unit was significantly lower

than the others when parsing apart habitat type differences with Tukey's HSD. CV also varied laterally (mean CV Mid = 1.07 vs. Bank = 1.79: $F_{1,29} = 26.9$, $P < 0.001$) but not longitudinally (Riffle = 1.37 vs. Run = 1.49: $F_{1,29} = 0.79$, $P = 0.38$). On average, distributions were right-skewed (skewness > 0), and skewness varied laterally (mean skewness Mid = 1.6 vs. Bank = 3.6: $F_{1,29} = 10.8$, $P = 0.003$) but not longitudinally (Riffle = 2.2 vs. Run = 2.98: $F_{1,29} = 1.50$, $P = 0.23$).

Size structure *per se* differed laterally (mid-channel vs. bank; perMANOVA *pseudo-F*_{1,31} = 13.8, $R^2 = 0.31$, $P = 0.001$) but not longitudinally (riffle vs. run; *pseudo-F*_{1,31} = 1.3, $R^2 = 0.03$, $P = 0.24$) (Fig. 2). Crayfish subpopulations in river banks were proportionally dominated by small-bodied juveniles (< 1 g) whereas large-bodied juveniles and adults (> 3 g) comprised a greater proportion of mid-channel subpopulations. Dispersion in ordination space (i.e., multivariate variability in CAPs) was not significantly different between habitat types ($F_{3,28} = 0.61$, $P = 0.61$; Fig 2b).

True and Estimated Aggregate Nutrient Recycling and Bias

The mean-field approach overestimated aggregate nutrient recycling (Fig. 3a) as predicted by Jensen's inequality for concave functions. Estimated bias ranged from 3.9 – 78.5% (mean \pm SD: 30.0 ± 18.9) whereas true bias was lower but still positive on average (range: -4.3 – 28.0%; 14.8 ± 7.0). As expected, both true and estimated bias decreased with mean body size across all samples (Fig. 3a). For the bias estimation according to Duursma & Robinson (2003) (see Eq. 2), this negative association is a direct consequence of a negative relationship between CV and mean body size (Fig. 4a). Decreasing important of variance around the mean is also conceptually supported by a second derivative of the power law function that approaches zero with increasing

mean body size (Fig. S3; *sensu* Inouye 2005). Consequently, differences in mean-field, bias-corrected, and true aggregate recycling rates were qualitatively greater in habitats with small mean body size (i.e., banks) than with large mean body size (mid-channels) (Fig. 3b). In habitats with large mean body size, mean-field approaches consistently overestimated true aggregate nutrient recycling, while correcting for bias following Eq. 2 consistently underestimated true functioning.

Although both true and estimated bias decreased with mean body size, these biases differed significantly at mean body sizes $< \sim 2.5$ g (Fig. 3a). Differences between true and estimated bias were as high as 52.6% in samples with low mean body size (1.6 g). At high CV values (i.e., low mean body sizes), size distributions were also very strongly positively skewed (Fig 4b).

Increasing skewness was correlated with increasing differences between true and estimated bias (Fig. 4c), suggesting that the shape of the size distribution may exacerbate bias induced by changing CV.

DISCUSSION

Functional trait ecology has emerged as a powerful arena to predict species distributions and subsequent ecosystem functioning in natural communities (Violle *et al.* 2014). Intraspecific variability is expected to be important in relating traits to these population-, community- and ecosystem-level processes, but to date we are unaware of an explicit accounting of the relative importance of mean body size and body size variation to animal-mediated ecosystem functioning. Consistent with predictions from Jensen's inequality, we found that variation around the mean reduced crayfish's contributions to nutrient recycling and that the relative importance of variance (i.e., bias) decreased with increasing mean body size. However, bias predictions from

Jensen's inequality diverged from reality as the shape of the size distribution became increasingly skewed.

Natural variation in nutrient recycling was generated by variable crayfish size distributions in the upper Verde River. Total biomass, mean body size, and size structure all varied laterally and longitudinally across unique habitat types. *O. virilis* in this lower portion of the Colorado River Basin reached substantially higher total biomass (mean = 41.8 vs. 15.8 g/m²), abundance (13.5 vs. 9.3 individuals/m²), and mean body size (3.1 vs. 2.0 g) than the same species invading the upper basin (Martinez 2012). After controlling for total biomass, we found that true aggregate ammonium recycling was highest among habitats with low mean body size and high CV — i.e., banks (mean ± SD umol NH₄-N/m²*hr: 1.90 ± 0.44) vs. the mid-channel (1.28 ± 0.51).

Comparing true recycling rates to the mean-field approach (i.e., true bias) allowed us to then separate the importance of variance from the mean. Variance dampened aggregate recycling at a given mean (i.e., positive mean-field bias), but the importance of variation decreased with increasing body size. This declining relationship can be attributed specifically to the negative relationship between the CV and mean of body size in this study (Fig. 4a); following Eq. 2, bias increases with the square of CV for power laws. Power law functions also generally become increasingly linear with increasing body size (i.e., second derivative approaches zero; Fig. C1), reducing the importance of variation around the mean (Ruel & Ayres 1999; Inouye 2005) independent of mean-CV relationships.

When mean body size > 2.5 g, both true and estimated bias (Eq. 2) generally agreed on the degree of mean-field overestimation in functioning (i.e., overlapping confidence intervals, Fig. 3a). However, these bias calculations departed at low mean body size where true bias was

significantly lower than that estimated from Eq. 2. We suspect that this difference is due to the increasing skewness of crayfish size distributions at high CV and low mean body size. Positive relationships between CV and skew are common for the log-normal and Weibull-like functions that often define body size frequency distributions, and in fact this relationship saturates such that there can be high variability in skewness within a very narrow range of CV for these particular distributions (Vargo, Pasupathy & Leemis 2010). Higher-order moments like skewness were not accounted for in the Taylor series expansion of Duursma & Robinson's (2003) bias estimate but are potentially important and could be incorporated with higher-order expansion in future research.

Overall, we found distinct effects of the mean, variance, and shape of body size distributions on ecosystem functioning that were masked when considering only the mean. In the least, these effects of higher-order moments may be considered statistical nuisances that must be accounted for when studying the relationship of true interest: between mean body size and ecosystem functioning. On the other hand the mean, variance, and shape of body size distributions may respond distinctly to separate ecological and evolutionary pressures at different spatiotemporal scales. For example, predation pressure (Palkovacs *et al.* 2009), climate warming (Ohlberger 2013), and size-selective harvesting (Coltman *et al.* 2003) can select for smaller mean body size in a population over time while life history cycles influencing the variance and shape of the distribution remain unchanged (e.g., cohort recruitment, seasonal ontogenetic shifts, and mortality). When environmentally-induced changes in size structure moments are decoupled, differentiating the roles of the mean, variance, and shape on ecosystem functioning may be of ecological, rather than just statistical, interest.

‘Functioning’ is broadly defined in ecology, and the effects of mean body size and size structure may follow different patterns for functions that are not distinct allometric rates of energy or material processing (e.g., prey community diversity and composition). Body size often relates to these functions according to discrete breaks or thresholds in body size rather than following a continuous allometric relationship. For example, body size alone could not predict basal ecosystem multifunctionality in aquatic invertebrate communities because individuals of different size classes interacted with lower trophic levels in fundamentally different, non-scalable ways (i.e., size-dependent foraging preferences: Rudolf & Rasmussen 2013b). Moreover, changing animal behaviors may alter nonlinear body size-function relationships, and deterministic predictions from Jensen’s inequality may not perform realistically in such situations (Inouye 2005; Benedetti-Cecchi 2005). How mean body size versus size structure affects these types of functions requires additional investigation. Benedetti-Cecchi (2003) provides guidance on experimentally isolating the effects of the variance and mean of ecological processes, but we are unaware of a study that has extended this framework to body size-ecosystem functioning relationships.

Conclusion

Here we presented an example of how the mean and size structure can be confounded when explaining ecosystem functioning and highlight mathematical and experimental methods from related ecological fields to partition these effects (Ruel & Ayres 1999; Benedetti-Cecchi 2003; Duursma & Robinson 2003; Inouye 2005). By doing so, we found that not accounting for variance can severely overestimate ecosystem functioning, especially at low mean body sizes, and that simultaneous changes to the shape of the size distribution confound straightforward methods to account for this mean-field bias. Ecologists are increasingly interested in using size-

based indicators to gauge ecosystem status, and both mean body size and size structure-based metrics have been proposed or are in operation (Shin *et al.* 2005; Petchey & Belgrano 2010). Yet the decision on which metric to use and how to set its reference condition is somewhat arbitrary and generally does not account for how size descriptors differentially reflect ecosystem functioning (Jennings & Dulvy 2005). We hope that explicitly defining and isolating the effects of the mean, variance, and shape of size distributions on ecosystem functioning in future basic research can lead to a better understanding of the size metrics appropriate for monitoring the functioning and health of ecosystems.

DATA ACCESSIBILITY

Data will be archived digitally for public access on the Olden lab Figshare account.

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SUPPORTING INFORMATION

The following Supporting Information is available for this article online.

Figure S1

Length-weight relationship of *O. virilis* measured in this study

Figure S2

Habitat-specific plots of crayfish size distributions

Figure S3

Second derivative of per capita body size-ammonium recycling model

TABLES

Table 1. Habitat differences in *O. virilis* total biomass and size structure metrics.

| Response and Predictor | <i>F</i> | df | <i>P</i> | Habitat Type Means | | | |
|-----------------------------------|----------|-------|----------|--------------------|------------|----------|-------------|
| | | | | Mid Run | Mid Riffle | Bank Run | Bank Riffle |
| Mean Body Size (g) | | | | 4.4 (ab) | 6.6 (a) | 1.5 (c) | 2.0 (bc) |
| Channel (Riffle vs. Run) | 2.7 | 1, 29 | 0.110 | | | | |
| Microhabitat (Bank vs. Mid) | 25.9 | 1, 29 | < 0.001 | | | | |
| Total Biomass (g/m ²) | | | | 42.6 (ab) | 19.6 (b) | 69.3 (a) | 42.7 (ab) |
| Channel (Riffle vs. Run) | 9.1 | 1, 29 | 0.005 | | | | |
| Microhabitat (Bank vs. Mid) | 13.8 | 1, 29 | < 0.001 | | | | |
| Coefficient of Variation | | | | 1.1 (b) | 1.0 (b) | 1.9 (a) | 1.72 (a) |
| Channel (Riffle vs. Run) | 0.8 | 1, 29 | 0.380 | | | | |
| Microhabitat (Bank vs. Mid) | 26.9 | 1, 29 | < 0.001 | | | | |
| Skewness | | | | 2.1 (ab) | 1.2 (b) | 3.9 (a) | 3.3 (ab) |
| Channel (Riffle vs. Run) | 1.5 | 1, 29 | 0.230 | | | | |
| Microhabitat (Bank vs. Mid) | 10.8 | 1, 29 | 0.003 | | | | |

Notes: Mean body size and biomass differences were analyzed with ANOVA on square root- transformed data.

Interactive effects were not significant for either response so we report the results of the most parsimonious, main effects-only models. Reported habitat type means are untransformed, and corresponding letters indicate significant differences according to Tukey's posthoc HSD (on square root transformed data).

FIGURE CAPTIONS

Figure 1. $\text{NH}_4\text{-N}$ per capita recycling rates increased with individual body size following a monotonically decreasing power function ($\text{NH}_4\text{-N} = 2.88 * \text{Mass}^{0.50}$).

Figure 2. Differences in crayfish size structure between river habitat types. **(a)** The degree of overlap in samples' cumulative abundance profiles (CAP) can be used to calculate a multivariate dissimilarity matrix between samples' size structure. Average CAPs for each habitat type are presented here, with lateral habitat differences represented by color (black vs. grey) and longitudinal differences represented by line style (solid vs. dashed). **(b)** There were significant differences in size structure laterally through streams (black vs. grey) but not longitudinally (circles vs. squares).

Figure 3. A) The relationship between mean site body size and the true (dashed) vs estimated (solid) bias when using the mean-field approach. Bias values near 0 indicate that the mean-field approach and the true/estimated approach yield similar aggregate ecosystem functioning results. Positive bias values indicate that the mean-field approach overestimates aggregate functioning. Grey shading indicates 95% confidence intervals around each loess-smoothed model. B) Differences in true, mean-field, and estimated bias-corrected aggregate nutrient recycling across habitat types. Aggregate recycling was standardized by the total biomass of the sample. For clarity this plot displays bank and mid-channel differences for riffle units only. Results for runs were qualitatively similar.

Figure 4. Relationships between (A) mean body size and CV, (B) CV and skew, and (C) skew and differences in true and estimated bias for $\text{NH}_4\text{-N}$ per capita recycling rates across all samples. Grey shading indicates 95% confidence intervals around each loess-smoothed model.

FIGURES

Figure 1.

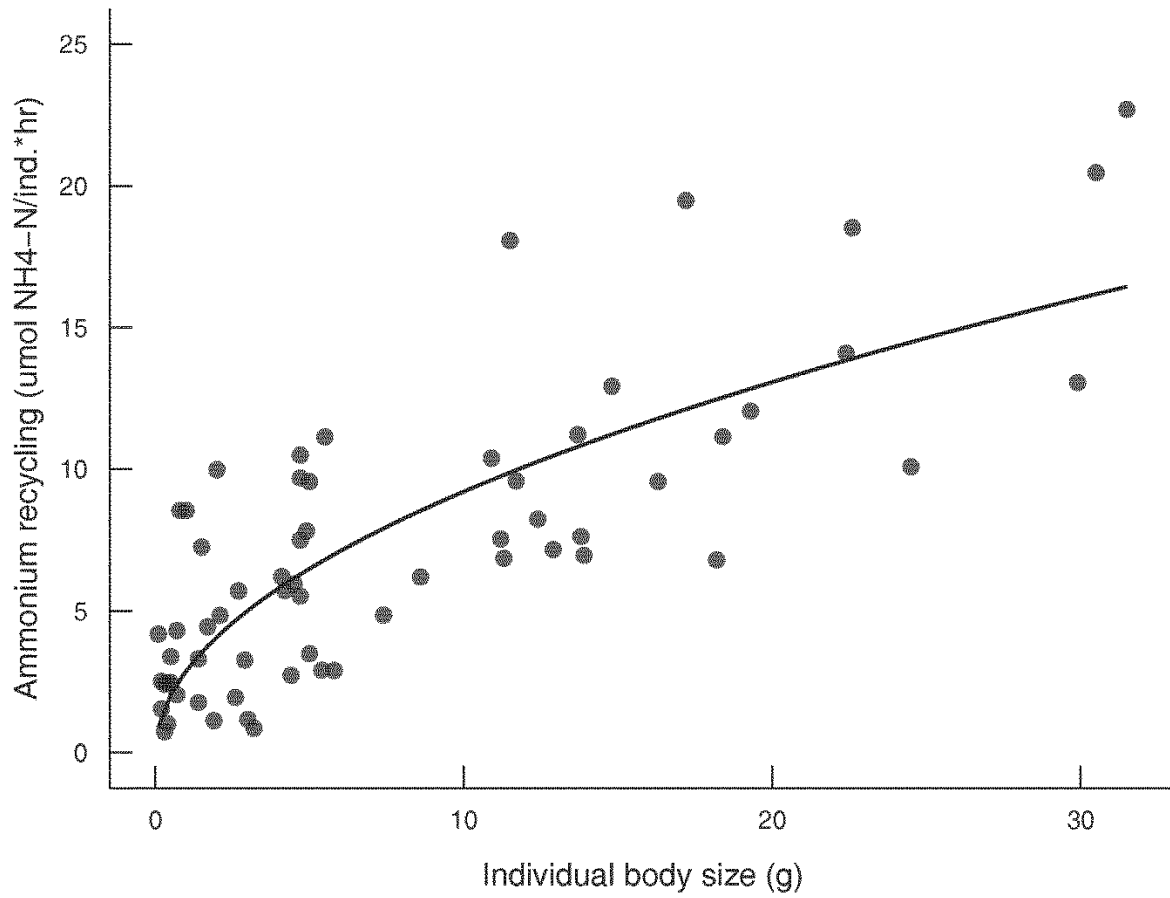


Figure 2.

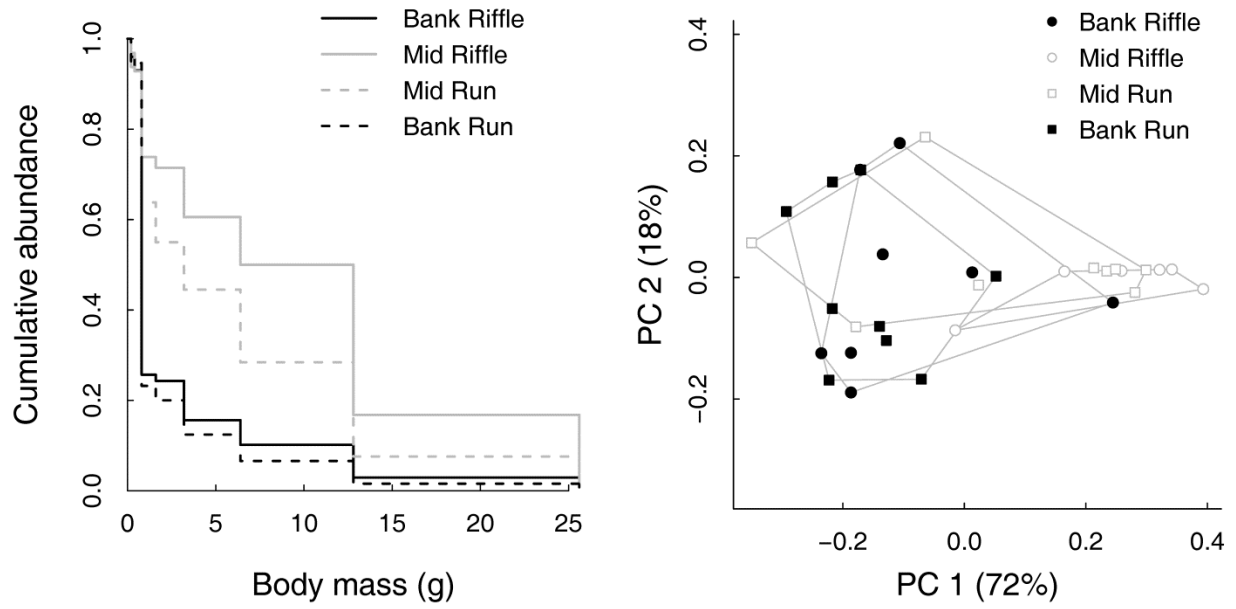


Figure 3.

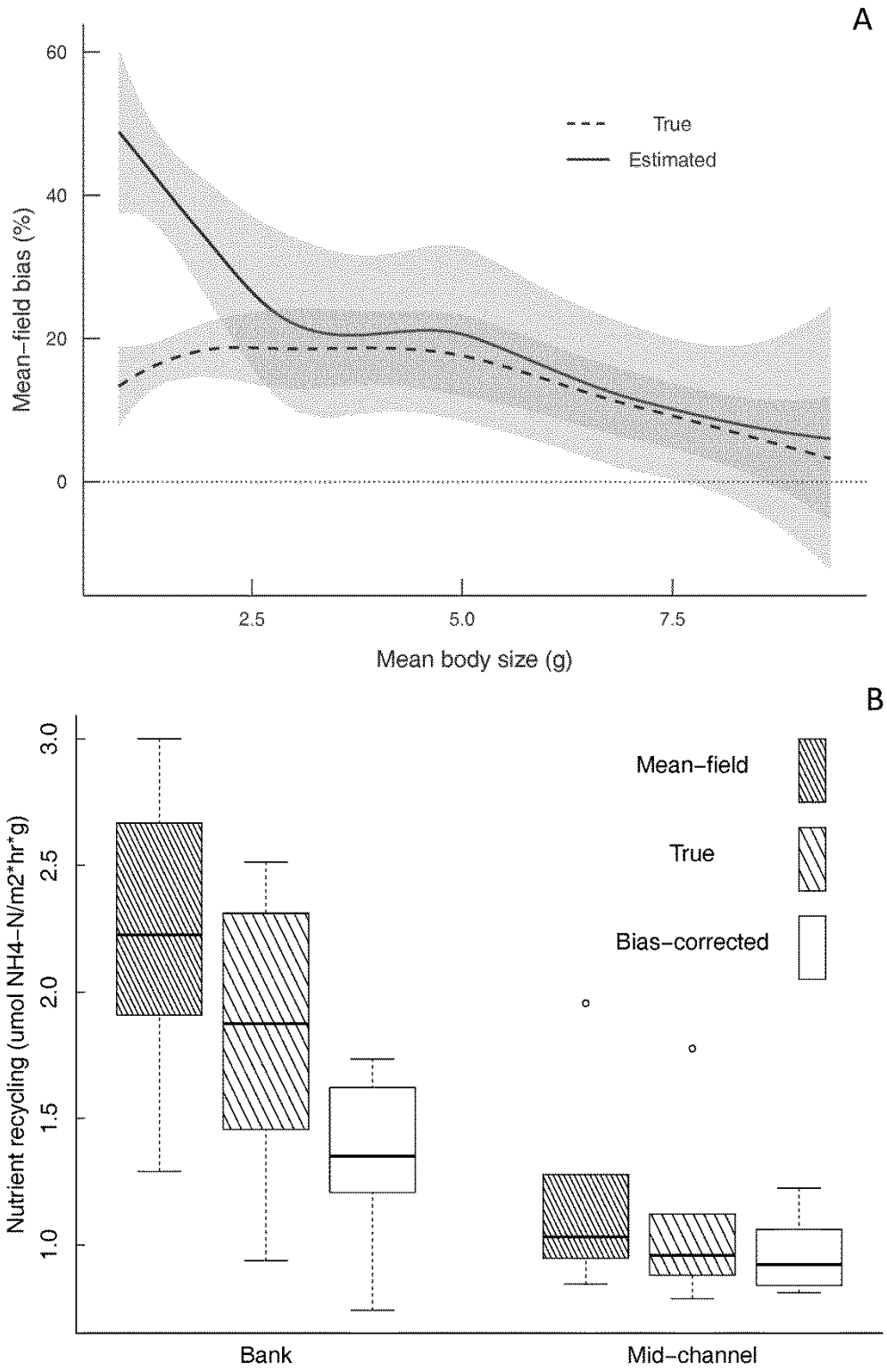
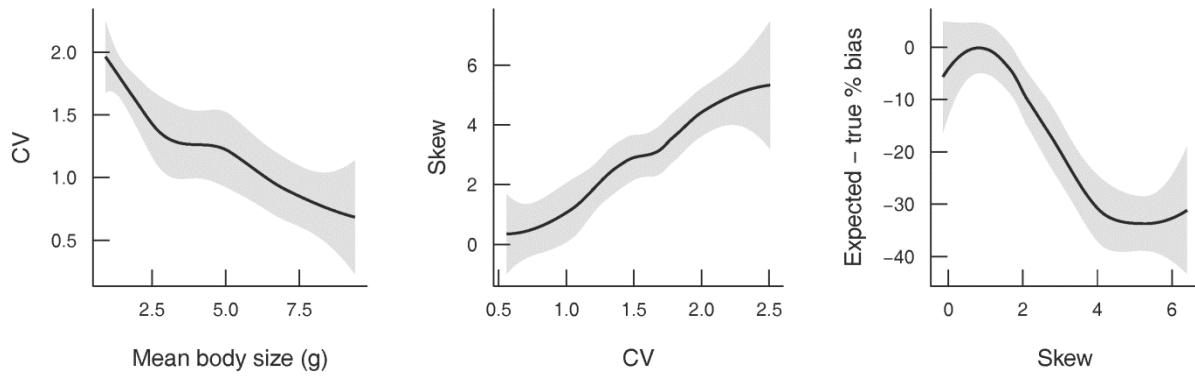
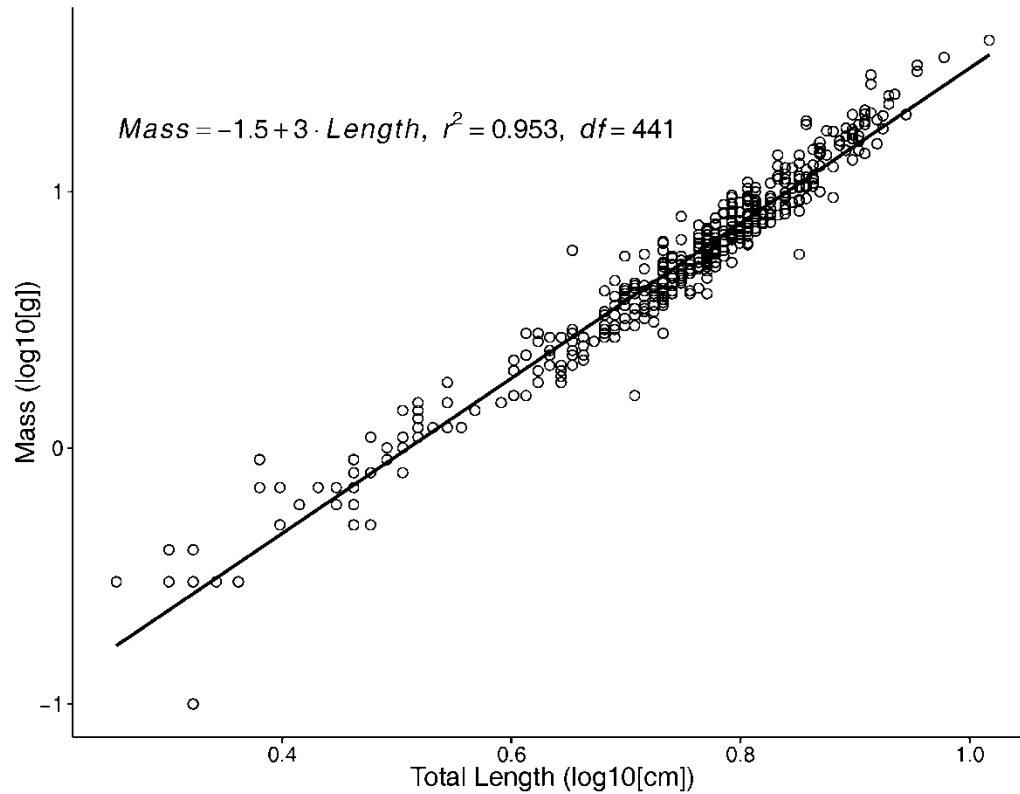


Figure 4.



SUPPORTING INFORMATION

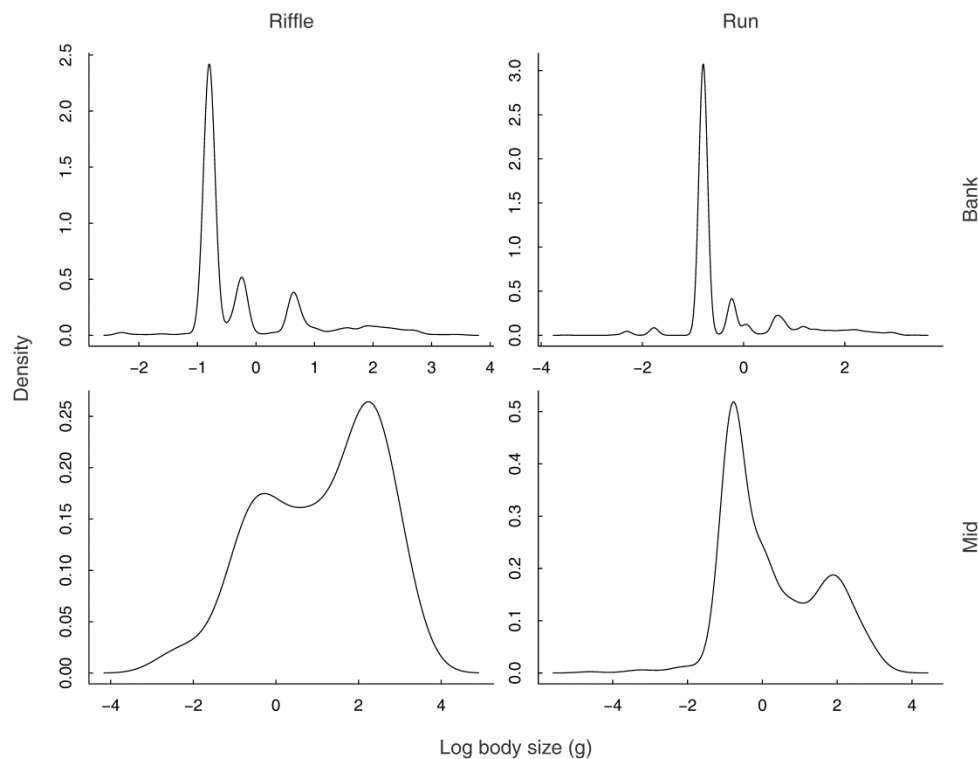
Figure S1. Weight-length regression model for *Orconectes virilis* in the upper Verde River, Arizona, USA. Each point is an individual crayfish measured in the field. Methods following Froese (2005).



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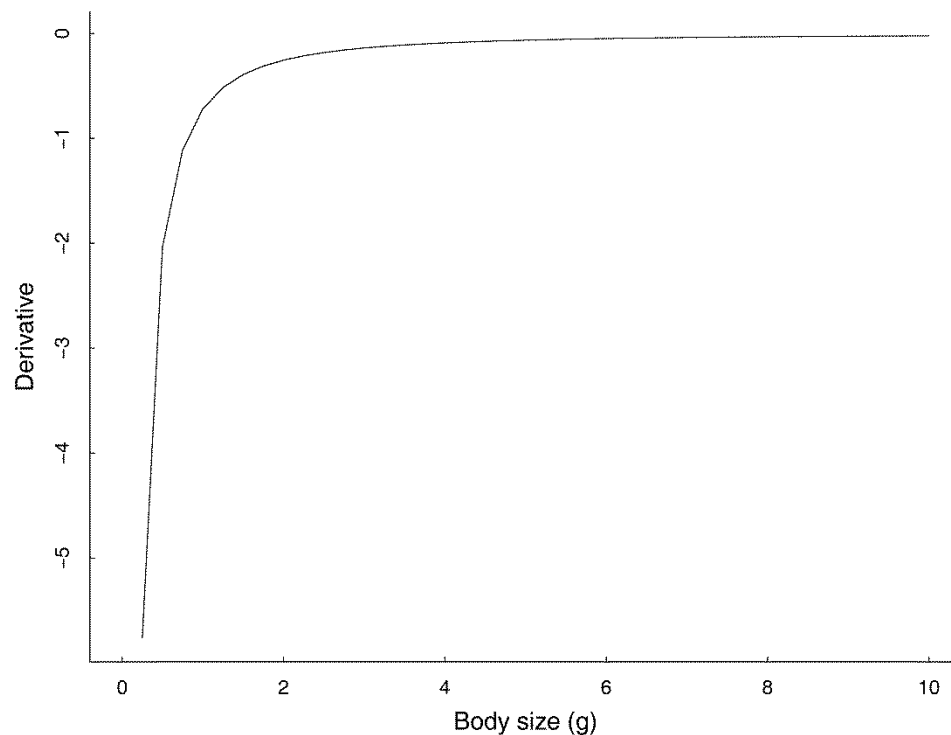
Figure S2. Habitat-specific kernel density estimates of crayfish body size in this study pooled in Riffle (left column) and Run (right column) by bank (top row) and mid-channel (bottom row) habitat types. Data here are log-transformed for better visualization, though log-transforming skewed size distributions can either reveal or generate multimodality in the data (Wyszomirski 1992). We employed the multivariate method of De Cáceres, Legendre & He (2013) to quantify size distribution dissimilarities (alias Bray-Curtis) between plots to capture simultaneous differences in the mean, variance, and shape of distributions.



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Figure S3. The second order derivative of the power law relationship between body size and per capita ammonium recycling rate ($\mu\text{mol NH}_4\text{-N}/\text{individual}\cdot\text{hr}$). Following Ruel and Ayres (1999) and Inouye (2005), the second order derivative of the function provides an approximation of the importance of the variance of a process around the mean, with a non-zero variance indicating that variance will bias functioning estimated by the mean-field approach. This is a useful qualitative method to detect the potential importance of the variance, but does not provide an explicit estimate of mean-field bias.



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Running Head: Species turnover, body size, and ecosystem functioning

Estimating the effects of species turnover on nutrient recycling requires species-specific allometric models

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ABSTRACT

1. Non-native species introductions are a ubiquitous form of global environmental change, but the impacts of multiple species introductions on ecosystem functioning remains poorly understood. In highly invaded systems, one promising approach to forecast the effects of multispecies introductions on ecosystem functioning is to quantify introduced species' effects on functional trait distributions. Here we use Monte Carlo simulations parameterized by field data to estimate the trait-based (body size) effects of shifts from native to non-native fish communities on consumer-mediated nutrient recycling.
2. Such an approach assumes that functional traits provide a common currency to relate individuals to ecosystem functioning. Though body size is traditionally thought to control most variation in per capita rates of nutrient recycling, a number of studies demonstrate significant interspecific variability in this allometric relationship. We modeled per capita N and P excretion rates as species-specific or global functions of individual body size and used both to forecast the effects of non-native species on nutrient recycling.
3. Using a species-specific model we found that non-native dominated communities excreted N at similar rates as native-dominated communities, but P at significantly lower rates. The resultant difference in the N:P ratio (native mean \pm SD = 12.2 ± 2.53 ; non-native = 46.8 ± 9.04) was surprisingly large, generally independent of body size, and potentially important for aquatic microbial communities in this system. By contrast, the global model incorporating body size but not taxonomy did not capture this significant N:P difference (native = 22.3 ± 1.35 ; non-native = 24.9 ± 1.33).
4. Our results demonstrate that non-native introductions may have substantial impacts on ecosystem functioning that can be forecast by trait-based approaches. However, using

body size as a sole trait currency to reduce the complexity of ecosystems may mask important interspecific variation in functional roles.

Keywords: allometry, scaling, Colorado River Basin, disassembly, reassembly, response-effect framework, biodiversity-ecosystem functioning, biogeochemical hotspots, ecological stoichiometry, Redfield ratio

INTRODUCTION

Rapid global climate change, environmental disturbance, and human-assisted invasions have reduced biodiversity worldwide (Sax & Gaines 2003). At local scales, however, native extirpations and non-native introductions have variably increased, decreased, or maintained species richness, depending on the alternative rates of species gains and losses (Engelhardt *et al.* 2010). Biotic communities mediate the flows of energy and materials through ecosystems, and biodiversity generally positively impacts these processes (Cardinale *et al.* 2012). However, both the diversity and composition of communities matter in controlling ecosystem rates (Hooper & Vitousek 1997), raising the question: how does species turnover impact ecosystem functioning? To answer this question, ecologists are increasingly interested in identifying functional traits that quantify organisms' responses to and effects on ecosystem processes, independent of their taxonomic identity (Lavorel & Garnier 2002). Ecologists can use such functional traits to scale up an organism's effects on ecosystem processes by coupling integration equations (which multiply trait values by the abundance of organisms that possess them) with statistical models (which quantify the relationship between trait values and per capita contributions to ecosystem functioning) (Violle *et al.* 2007; Garnier *et al.* 2004; Kerkhoff & Enquist 2006). This functional trait approach offers a common currency to examine the ecosystem-level effects of variation in community composition (Suding *et al.* 2008). Moreover, it provides an explicit framework to assess the impacts of species turnover on ecosystem functioning by assessing the degree to which native extirpations and non-native introductions have altered functional trait distributions of biotic communities (Strayer 2012). Studies taking this approach have drawn different conclusions about the degree of functional redundancy and divergence associated with species turnover (e.g., Forsy & Allen 2002; Matsuzaki, Sasaki & Akasaka 2013), but it remains difficult

to translate such effects into their ecosystem-level consequences without knowing the mechanistic relationship between the given functional traits and per capita contributions to ecosystem functioning.

Body size may provide a mechanistic functional trait to determine the roles of individuals and species turnover in ecosystem functioning (Peters 1983; Woodward *et al.* 2005; Hildrew *et al.* 2007). Body size constrains important ecosystem functions associated with metabolic processes (e.g., nutrient cycling, consumption, production: Brown *et al.* 2004), dictates species interactions in food webs (Brose *et al.* 2006), and controls ecosystem engineering (Solan *et al.* 2004). Species removals ordered by body size are generally more detrimental to functioning than random community disassembly, as demonstrated in aquatic systems for sediment bioturbation (Solan *et al.* 2004), nutrient recycling (McIntyre *et al.* 2007), and primary production (Seguin *et al.* 2014). The potential scaling relationship between body size and multiple ecosystem functions is important given the push to move beyond single processes to characterize non-native species' overall effect on ecosystem functioning (Gutierrez, Jones & Sousa 2014).

However, body size may not provide a common currency of ecosystem functioning across all species. Rudolf *et al.* (2014) recently demonstrated experimentally that the size structure and taxonomic composition of predator communities had interactive effects on ecosystem functioning; neither predator identity nor body size alone explained the resultant multivariate structure of invertebrate prey communities. These differences may reflect species' differences in foraging behavior that ultimately dictate consumptive and non-consumptive effects on the prey community. Beyond behavioral differences, metabolically-constrained functions may also show interspecific variability in the relationship between body size and ecosystem functioning. Despite an average scaling coefficient of $B = 0.75$, metabolically-constrained processes relate to body

size according to power law relationships with coefficients ranging from $B = 0.20$ to $B = 1.20$, depending on the species, function, and environmental conditions (Savage *et al.* 2004). It is unclear, however, if failing to account for these interspecific differences in a quest for general body size—functioning relationships leads to biased estimates of ecosystem functioning when scaling from individuals to ecosystems.

Size—functioning scaling issues are particularly applicable to consumer-mediated nutrient recycling, where consumers control resource dynamics by remineralizing nitrogen and phosphorus to basal autotrophs and heterotrophs (Vanni 2002). In some systems consumer-mediated nutrient recycling can interact with top down trophic effects on basal production (e.g., Knoll *et al.* 2009; Vanni *et al.* 2006), rival the magnitude of extrinsic nitrogen and phosphorus inputs (e.g., Schindler, Knapp & Leavitt 2001; Vanni *et al.* 2006), relieve nutrient limitation (e.g., Allgeier, Yeager & Layman 2013; Atkinson *et al.* 2013), and generate biogeochemical hotspots (e.g., McIntyre *et al.* 2008; Atkinson *et al.* 2013). Single invasive species (e.g., non-native loricariid catfishes) have had large effects on nutrient cycling in stream systems (Capps & Flecker 2013), but the potential effects of multiple invasions and extirpations has not been assessed.

Such an assessment is potentially stymied by intraspecific variability in body size—nutrient recycling scaling. Body size has long been appreciated in controlling consumer-mediated rates of nutrient recycling (Kitchell *et al.* 1979; Vanni 2002) and indeed explained most of the variation in nutrient recycling in a recent re-analysis of nutrient recycling studies (Sereda, Hudson & McLoughlin 2008). However, ecological stoichiometry indicates that other factors should interact with body size to determine the overall rates and ratios of nutrient recycling (Vanni 2002). Notably, the stoichiometry of an individual's diet and its own body tissue should

influence nutrient excretion of homeostatic organisms (Schindler & Eby 1997). Empirical studies have provided mixed support for diet or body stoichiometry effects on nutrient recycling (e.g., Sereida, Hudson & McLoughlin 2008; McManamay *et al.* 2011; Small *et al.* 2011). In some instances accounting for broad taxonomic relationships (e.g., family) improves models of nutrient excretion (McManamay *et al.* 2011), perhaps because these taxonomic groups account for physiological similarities not captured by diet or body content metrics. By contrast, a recent exploration of 18 European fishes revealed large interspecific differences in the magnitude and direction of body size—nutrient recycling scaling, and these differences were not explained by quantitative phylogenetic relationships (Villegier *et al.* 2012). In such instances, information on body size and taxonomic identity best predicted ecosystem functioning (Allgeier *et al.* 2015).

Here we examine the utility of using body size as a common currency to understand the effects of species turnover on ecosystem functioning. Specifically, we combine experimental incubations, fish community field sampling, and species turnover simulations to compare consumer-mediate nutrient recycling between native- and non-native dominated, and freshwater fish communities in the Verde River watershed of central Arizona, USA. The Verde River is one of two designated Wild and Scenic Rivers in the state and is a historical stronghold for the highly endemic, highly endangered fish fauna of the Lower Colorado River Basin. However, a century of intentional and unintentional fish introductions have resulted in the establishment of at least non-native species in the Verde River watershed. This is a common issue in the western United States, where over 50% of river kilometers contain non-native species (Schade & Bonar 2005). Given that Sonoran desert streams are generally N-limited (Grimm & Fisher 1986), large changes in consumer-mediated nutrient recycling due to shifts in fish community structure may have important implications for basal productivity. To estimate potential shifts in ecosystem

functioning in the Verde River system we ask i) is the relationship between body size and nutrient recycling consistent across origin, family, trophic guild, and the whole species pool, ii) do native, non-native and contemporary mixed communities differ in their aggregate rates and ratios of nutrient recycling, and iii) does the use of more or less general functional trait models alter conclusions about the effects of species turnover on ecosystem functioning?

METHODS

Fish Community Sampling

In May-June 2012 fish communities were sampled in 25 lotic sites in the upper Verde watershed (Fig. 1; Gibson *et al.* 2015). At each site researchers designated a ~100 m reach enclosing 1-2 pool-riffle-run sequences, closed the ends of the reach with block nets, and sampled the fish community using 2-pass depletion backpack electroshocking. Each fish, or a subset of fish for very abundant species, were measured (total length, cm), weighed (g), and released.

Nutrient Recycling Modeling

We used standard incubations in the field to characterize individual fish excretion rates of ammonium ($\text{NH}_4\text{-N}$: herein N), phosphate ($\text{PO}_4\text{-P}$: herein P), and the N:P ratio. Fish were captured by backpack electroshocking in 7 sites in the upper Verde watershed (Fig 1) and held in a run-of-river holding pen with natural cover and food sources for c. 15 minutes to acclimatize to capture. Individuals were then transferred to clear polyethylene bags filled with deionized water of varying volumes (500 mL to 15 L), depending on the size of fish. Bags containing individual fish were incubated for 45 minutes in stream margins to maintain ambient water temperature and minimize stress. After the incubation fish were removed and measured (length [cm] and mass [g]). Two water samples were drawn from the well-mixed bag, filtered (Whatman GFF 0.45 μm filter), and immediately frozen on dry ice for later analysis. Samples were analyzed for N using

the colorimetric salicylate-hypochlorite method (Bower & Holm-Hansen 1980) or the colorimetric molybdate method (Murphy & Riley 1958) for P on a flow injection analyzer (QuikChem 8000 Series, Lachat Instruments, Loveland, Colorado USA) at Northern Arizona University's Colorado Plateau Analytical Laboratory. N and P excretion rates were calculated for each sample after accounting for ambient nutrient concentrations in control bags. The per capita relationship between body size and nutrient recycling was modeled as a linearized power law by regressing log-nutrient (nutrient $\mu\text{mol}/\text{individual}\cdot\text{hr}$) or log-N:P ratio on log-individual mass (g) using nonlinear least squares. To test the generality of the body size-nutrient recycling relationship, analyses of covariance (ANCOVA) were performed with species, trophic guild, family, or origin (native vs. non-native) as a potential categorical covariate in the model. General trophic guilds were assigned to species according to Olden *et al.* (2006). These guild assignments do not take into account potential ontogenetic shifts in species' diets (e.g., Pilger *et al.* 2012). Models were compared with one another and with a global size-nutrient recycling model (i.e., no categorical covariate) in an information criterion framework. Aikake's Information Criterion corrected for small sample size (AICc) was calculated from the log likelihood of each model and the model with the lowest AICc score was considered the model best supported by the data, though any with $\Delta\text{AICc} < 2.0$ are considered candidate top models. Body size may act as a universal trait predicting nutrient recycling by fishes in this system if the global model is considered the best fit, whereas additional trait-based information may be necessary if any other models receive more support in the model selection approach.

We also compared the log-transformed N:P ratio of nutrient recycling between species, guilds, families, and origin, using separate Welch's one-way analyses of variance (ANOVA-like procedure assuming unequal variances). The N:P ratio determines the quality of inorganic

nutrient recycling and can be extremely important in determining community composition and dynamics of microbial communities (Tilman, Kilham & Kilham 1982). Grouping the data to compare N:P across factor levels ignores within group variation in body size, but the ratio of N:P is often less variable across a range of body sizes than the raw magnitudes of N or P excretion alone (e.g., Allgeier *et al.* 2015). We withheld common carp and rainbow trout data from these analyses (at the species level and each higher level group of which they were members) because their small sample sizes ($N < 10$) may unduly influence analyses.

Simulating Species Turnover and Aggregate Nutrient Recycling

Contemporary rates of aggregate N, P, and N:P recycling were calculated for each of the 25 sites by applying species-specific recycling models to the observed fish community data. Then for each site we used a Monte Carlo procedure to simulate alternative community size structures (i.e., body size distributions) under theoretical native or non-native species-only scenarios. By comparing aggregate rates of nutrient recycling under each scenario, we were able to estimate broad-scale changes in ecosystem functioning as a consequence of shifts from native- to non-native-dominated communities. We also compared simulation outcomes calculated from global vs. species-specific per capita recycling models to understand if generalized trait-based models of ecosystem functioning (i.e., using body size as a universal predictor of per capita recycling) significantly alters predictions about the ecosystem effects of community change.

For a more resolved view of Verde trophic structure that accounted for ontogenetic shifts in diet, we assigned observed individuals to invertivore, invertivore-piscivore, or omnivore trophic guilds according to their taxonomic identity and body size (*sensu* Fritschie & Olden *in review*), relying on extensive species- and size-specific diet data for this species pool (Pilger *et al.* 2010; Bonar *et al.* 2004). We then calculated the energy contained in each guild at a site by summing

across individuals, where the energy level of an individual of mass M is $E = M^{0.75}$ (Brown *et al.* 2004). Conserving energy across simulated community structures reflects expectations from the metabolic theory of ecology (Ernest *et al.* 2003) and has been used in probabilistic simulation modeling of fish communities and nutrient recycling (e.g., McIntyre *et al.* 2007). Moreover, conserving the trophic structure of the community reflects the expectation that energetic compensation during species turnover is likely to occur between individuals sharing common resource pools (McIntyre *et al.* 2007). For each simulation at each site we reallocated the observed energy of each guild to individuals drawn from a pool of individuals of that guild and of either native or non-native origin. We sampled individuals from an extensive dataset of Verde River fish community sampling efforts (~16000 individuals; Fritschie & Olden *in review*) that represent the watershed-wide abundances and body size frequency distributions of all native and non-native species in this study. We allowed all species from the regional pool to be sampled at a site, given that few major permanent barriers to dispersal exist, that non-native species are widespread in this system, and that native species once were (Rinne 2012). After simulated reassembly, aggregate recycling (N, P) was calculated based on both species-specific and global N and P recycling models, and the N:P ratio was then calculated from these estimates. Simulations for each unique combination of site, origin, and model type were repeated 999 times to form a distribution of potential aggregate nutrient recycling values. The final simulated dataset included 999 aggregate N, P, and N:P values for each model (species-specific vs. global) for each origin (native vs. non-native) at each site (25 sites; Figs. A1-A3).

Comparing Simulation Results

Because baseline conditions (i.e., total energy) varied between sites, we calculated the dimensionless log response ratio (LRR; Hedges, Gurevitch & Curtis 1999) between non-native

and native nutrient recycling (or global and species-specific models) within sites. LRRs were then summarized across sites to evaluate the average effects of non-native vs. native communities (or global vs. species-specific models) on nutrient recycling. Effect size comparisons are common in ecology and meta-analysis and were recently used to compare the effects of simulated native and non-native species on fish community functional trait diversity across Japanese ecoregions (Matsuzaki, Sasaki, & Akasaka 2013). LRRs were calculated as

$$LRR = \ln \left(\frac{\bar{X}_1}{\bar{X}_2} \right),$$

where \bar{X}_i is the mean of the simulated N,P or N:P distribution for native or non-native (and global or species-specific models) groups at a single site. Non-native species or global model means were always in the numerator of our calculations. Thus, positive or negative LRR can be interpreted as systematically higher or lower nutrient recycling values for non-native species (global models), whereas mean differences that overlap zero indicate no effect of non-native species (global models) on nutrient recycling relative to the ‘control’ groups (native species or species-specific recycling models). Rather than perform analyses of statistical significance on simulated data, and particularly data with unequal variances for global vs. species-specific model output, we summarized the mean \pm standard error of LRR across sites and interpret general trends in the directionality and magnitude of these effect sizes.

RESULTS

Nutrient Recycling Models

Despite having the most parameters, the species-specific ANCOVA with an interaction term performed best for all three response variables (Table 1). Support for all other candidate models for all response variables were weak ($\Delta AICc > 2.0$, likelihood < 0.0001), and models with body

size alone were always ranked within the bottom two models (Table 1). Variance explained was high for the best model of N recycling (adjusted $R^2 = 0.94$), and varied little across models (lowest adjusted $R^2 = 0.93$). Variance explained was more variable across models of P (top model adjusted $R^2 = 0.78$; bottom model adjusted $R^2 = 0.67$), and much lower overall for N:P (top model adjusted $R^2 = 0.38$; bottom model adjusted $R^2 = 0.05$).

The interaction term in all species-specific top models indicated that species had significantly different slopes and intercepts for body size-nutrient recycling relationships (Table 2; Fig. 2). However, species models without this interaction term (i.e., only account for different species-specific intercepts, not slopes) explained similar levels of variance as the top model, but were still not considering competitive top models according to the AICc approach. The global model (body size alone) had a scaling coefficient (0.74 ± 0.03 standard error) extremely close to the 0.75 predicted from metabolic theory (Savage *et al.* 2004), but there was greater variation among species-specific parameters (lowest = 0.50 ± 0.12 ; highest = 1.07 ± 0.06). Global P scaling was lower than predicted from metabolic theory alone (0.62 ± 0.02) and species-specific variation around this global rate was even larger (lowest = 0.14 ± 0.34 ; highest = 1.06 ± 0.26). The N:P ratio increased with body size in the global model ($B = 0.11 \pm 0.03$), but variance explained by this model was low (adjusted $R^2 = 0.05$; Fig. 2). Species-specific N:P scaling estimates were variable with both positive and negative values, but most either had SEs overlapping zero or were significant but low (< 0.33 or > -0.33). Notable exceptions include N:P scaling estimates for green sunfish (0.89 ± 0.14) and fathead minnow (0.53 ± 0.36). Table 2 indicates species-specific parameter estimates that are significantly different than longfin dace, the first factor level alphabetically in the analysis. ANCOVA does not calculate significance values for all pairwise species comparisons or species vs. global model comparisons.

Significant differences in the average N:P ratio existed across origin ($t_{285.8} = -4.2$, $P = <0.001$), guilds ($F_{4,118.4} = 18.8$, $P = <0.001$), families ($F_{4,85.4} = 16.8$, $P = <0.001$), and species ($F_{10,115.9} = 1.5$, $P = <0.001$). We had no *a priori* expectations of differences between particular groups, so we analyzed N:P distributions plotted across groups (Figure 3) rather than perform post hoc means comparisons to identify statistically different groups. All native species recycled N:P at or near the Redfield ratio (native mean = 15.3), as did smaller-bodied non-native cyprinids (red shiner mean = 11.9; fathead minnow mean = 14.5) and the only poeciliid (western mosquitofish mean = 13.4). By contrast, the remaining non-native species recycled N:P at a much higher ratio (yellow bullhead mean = 31.2; smallmouth bass mean = 75.6; green sunfish mean = 34.4). Non-native common carp and rainbow trout were not included in formal means comparisons because of their small sample sizes, but also excreted N:P at a higher ratio than all natives (means = 61.4 and 54.6, respectively). Of these non-native species with high average N:P ratios, the N:P ratio increased significantly with body size for green sunfish ($b \pm SE = 0.89 \pm 0.14$) and common carp (0.23 ± 0.14), and decreased significantly for smallmouth bass (-0.24 ± 0.12).

Comparing Simulation Results

Non-native communities reduced the magnitude of P recycling relative to native communities across model types, but the negative effect of non-natives on P was much more pronounced in species-specific (LRR mean \pm SE: -1.3 ± 0.2) than in global (-0.11 ± 0.02) models (Fig. 4a). By contrast, simulated non-native communities had miniscule negative or no effect (i.e., SEs overlapped zero) on the overall magnitude of N recycling as compared to native communities, depending on the model type used (global = -0.005 ± 0.002 ; species-specific = 0.01 ± 0.05 ; Fig. 4a). By contrast, The effect of little change in N recycling with species turnover but decreases in

P recycling was a net positive LRR for N:P ratios (Fig. 4a). Positive LRRs were modest for global models (0.12 ± 0.02) and large for species-specific models (1.3 ± 0.13).

Discrepancies in non-native/native LRRs indicated that global vs. species-specific models provided conflicting estimates of aggregate nutrient recycling (Fig. 4b). Global models modestly underestimated aggregate N recycling, and this was equally true for both native (-0.08 ± 0.03) and non-native (-0.1 ± 0.03) species (Fig 4b). By contrast, global models consistently overestimated P recycling for non-native species (0.5 ± 0.08) and underestimated it for native species (-0.7 ± 0.11), resulting in underestimates of N:P for non-native communities (-0.6 ± 0.09) and overestimates for native communities (0.6 ± 0.09). Overall, both global and species-specific models suggest that switching to non-native dominated communities increases the N:P ratio of aggregate nutrient recycling (Fig. 5). However, global models only indicate modest shifts from native (mean N:P = 22.3) to non-native (mean N:P = 24.9) communities, while species-specific models indicate much larger shifts (native N:P = 12.2; non-native N:P = 46.8). Unsurprisingly, mean contemporary estimates of N:P recycling for assemblages of mixed origin fall out between these native and non-native extremes (Fig. 5; global contemporary N:P = 23.8; species-specific contemporary N:P = 37.9).

DISCUSSION

By coupling species-specific models of nutrient recycling with simulations based on real community composition and size structure data, we found that transitioning from native- to non-native dominated fish communities can increase the N:P ratio of consumer-mediated nutrient recycling more than threefold on average in the Verde River system. Changing the ratio of aquatic resources may have significant consequences for basal primary producer coexistence and

functioning (Tilman, Kilham & Kilham 1982). Consumer-mediated nutrient recycling has relieved or reversed nutrient limitation (Allgeier, Yeager & Layman 2013; Atkinson *et al.* 2013), altered algal community composition (Attayde & Hansson 2001), and promoted primary production (Schindler, Knapp & Leavitt 2001) in diverse aquatic systems from coral reefs to alpine lakes. Future work is needed to assess whether the stoichiometric effects of species turnover that we calculated ultimately translate into lower trophic level impacts in this system.

Differences in N:P recycling ratios in native and non-native communities were driven primarily by differential excretion of P. Non-native species had little effect on aggregate N recycling relative to native scenarios (Fig. 4a), and this was true for both species-specific (i.e., top model according to AICc) and global models (i.e., most general model). Both global and species-specific models explained similar amounts of variation in per capita N excretion ($R^2 \sim 0.94$) and the SEs of the global model' and many species' N scaling coefficients overlapped the $3/4$ scaling predicted from the metabolic theory of ecology (Savage *et al.* 2004). By contrast, the species-specific model of P excretion explained more variation than the global model ($R^2 = 0.78$ vs. $R^2 = 0.67$); supported by the fact that individual species' P scaling coefficients were much more variable than N coefficients and not consistently overlapping 0.75 (Table 2), and average N:P ratios (summarizing across body sizes) differed significantly across origin, trophic guild, families, and species (Fig. 4). The cumulative effects of these differences on aggregate P recycling were large, with non-native communities excreting substantially less aggregate P and thus substantially higher N:P than simulated native communities (Figs. 4a,5). Because the general global model masked significant interspecific (and inter-origin) differences in the slopes and intercepts of P recycling, global models detected only modest differences in N:P recycling between native and non-native communities (Figs.4-5).

That predominantly higher trophic level non-native fishes (yellow bullhead, green sunfish, smallmouth bass, rainbow trout) have the highest average N:P excretion ratios in this system was not expected. The N:P ratio of nutrient recycling is in part a function of the nutrient mass balance of an individual and its diet (Elser & Urabe 1999; though see Moody *et al.* 2015; Allgeier *et al.* 2015). Following this stoichiometric prediction, predators are generally assumed to excrete at low N:P because they consume relatively P-rich animals, rather than detritus or plant material (Schindler & Eby 1997). However, in the Verde River many of the available prey species are small-bodied cyprinids, a family that often has high N:P body content relative to other fishes, especially centrarchids (Sterner & George 2000). This discrepancy between high prey and low predator N:P content may exacerbate the differential assimilation of P vs. N of the predator, leading to high N:P excretion. Another possible explanation is that non-native species adapted to cooler temperate rivers than their invaded range in warmer dryland rivers may have faster growth rates, and thus larger P demands. Higher N:P excretion by larger-bodied non-native fishes is a striking pattern with important ecosystem implications that will require further energetic and stoichiometric studies to understand.

Small-bodied non-native fishes had similar N:P ratios to all native species, so why wasn't there greater overlap in aggregate N:P for native and non-native communities? Aggregate nutrient recycling at the community level proved to be a complex function of trophic structure, size structure, size-recycling relationships, and species' relative abundances (see also McIntyre *et al.* 2007,2008; Small *et al.* 2011; Allgeier *et al.* 2014,2015a,b), even in these simplified simulated communities. In our simulations we drew from a watershed-wide dataset of empirical surveys that represent the actual relative abundances and size distributions of native and non-native species in this watershed. Higher trophic level non-native species like the centrarchids are not as

numerically abundant as smaller-bodied non-native species (e.g., red shiner) in this dataset. Using this dataset in a recent study (Fritschie & Olden *in review*), we found that non-native introductions decreased the mean body size of the fish assemblage as a whole, the invertivore guild, and the omnivore guild, while increasing the mean body size of the invertivore-piscivore guild. The net decrease in whole assemblage body size might suggest nutrient recycling rates would increase with non-native dominance, given energetic conservation. However, the magnitude of N excretion did not change between native and non-native communities, despite similar N scaling coefficients between species of different origin (and the exact same scaling relationship for the global model). Instead, non-native P and N:P recycling largely reflected the rates and ratios of stoichiometrically unique species. Similarly, Small *et al.* (2011) found that a non-dominant (numerical or biomass) cyprinid accounted for a substantial portion of the P recycling in a tropical stream because it uniquely integrated terrestrial resources and thus excreted at extremely different N:P than the rest of the assemblage.

Taxonomic identity contains no *a priori* information about the roles of individuals in ecosystems and must be coupled with some degree of trait information to make ecological predictions (Rudolf *et al.* 2014; Raffaelli 2007). In an attempt to forego the constraints of taxonomy, functional trait frameworks (McGill *et al.* 2006) and body size frameworks in particular (Woodward *et al.* 2005; Brose *et al.* 2006) have been proposed to understand individual's interactions and roles in ecosystems. Beyond basic ecology, such frameworks can be useful in forecasting the ecological effects of changes in community structure, including those changes induced by native species extirpations () and non-native species introductions (Strayer 2012; Forsy & Allen 2002; Matsuzaki, Sasaki & Akasaka 2013). These approaches require that functions can be related to traits in a generalizeable way across taxa, or at least that scaling

differences can be accounted for with easily obtainable information. Given consumer-mediated nutrient recycling's theoretical adherence to aspects of metabolic theory and ecological stoichiometry (Schindler & Eby 1997; Allen and Gillooly ; Algeier *et al.* 2015) we expected that size—recycling relationships would be fairly well generalized across taxa and could be used to estimate functional change induced by transitions from native to non-native communities. By contrast, generalized models grossly underestimated the striking change that non-native species induced in the stoichiometry (N:P ratio) of nutrient recycling. Our study joins a growing body of literature that emphasizes the utility and importance of a balanced taxonomic and trait-based approach in understanding the role of individuals in ecosystems.

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DATA AVAILABILITY

Upon acceptance of this manuscript excretion modeling data will be available at the Olden lab account on Figshare.

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SUPPORTING INFORMATION

Supporting Information A.

Simulated distributions of aggregate N, P, and N:P for native or non-native species using global or species-specific models across 25 sites

TABLES

Table 1. Model selection results for nutrient recycling rates/ratios. Models included a body size covariate alone, or body size with an interactive (*) or additive (+) ecological factor (Species, Family, Guild, Origin). Models are listed from best- to worst-performing in this candidate model set according to ΔAICc values, where $\Delta\text{AICc} > 2.0$ indicates model performance was worse than top model. ΔAICc , variance explained (Adj. R^2), and relative likelihood are given.

| Response | Model | Adj. R^2 | ΔAICc | Likelihood |
|---|---------------------|------------|---------------------|------------|
| NH ₄ ⁺ Recycling | Body Size * Species | 0.94 | 0.0 | 1.0 |
| | Body Size + Species | 0.94 | 28.9 | - |
| | Body Size * Guild | 0.93 | 41.2 | - |
| | Body Size * Family | 0.93 | 49.8 | - |
| | Body Size + Family | 0.93 | 52.7 | - |
| | Body Size + Guild | 0.93 | 59.1 | - |
| | Body Size * Origin | 0.93 | 67.7 | - |
| | Body Size | 0.93 | 69.5 | - |
| | Body Size + Origin | 0.93 | 70.1 | - |
| PO ₄ ³⁻ Recycling | Body Size * Species | 0.78 | 0.0 | 1.0 |
| | Body Size + Species | 0.77 | 4.4 | - |
| | Body Size + Family | 0.75 | 22.3 | - |
| | Body Size + Guild | 0.75 | 25.1 | - |
| | Body Size * Family | 0.75 | 27.6 | - |
| | Body Size * Guild | 0.75 | 30.5 | - |
| | Body Size * Origin | 0.74 | 39.6 | - |
| | Body Size + Origin | 0.69 | 89.1 | - |
| | Body Size | 0.67 | 110.0 | - |
| NP Ratio | Body Size * Species | 0.38 | 0.0 | 1.0 |
| | Body Size * Guild | 0.30 | 18.4 | - |
| | Body Size + Species | 0.30 | 24.9 | - |
| | Body Size + Guild | 0.27 | 26.9 | - |
| | Body Size * Family | 0.26 | 37.2 | - |
| | Body Size * Origin | 0.25 | 37.5 | - |
| | Body Size + Family | 0.25 | 38.0 | - |
| | Body Size + Origin | 0.12 | 85.8 | - |
| | Body Size | 0.05 | 111.0 | - |

Table 2. Species-specific nutrient recycling parameters ($y = \log(a) + bx$) from best-fit ANCOVA models for each nutrient recycling rate/ratio, and the global models across all individuals.

| Species | Descriptors | | | | NH ₄ ⁺ Recycling | | PO ₄ ³⁻ Recycling | | NP Ratio | |
|---------------------|-------------|----|----|----|--|--------------------|---|--------------------|--------------|--------------------|
| | ID | N | G | F | log(a) (±SE) | b (±SE) | log(a) (±SE) | b (±SE) | log(a) (±SE) | b (±SE) |
| <i>Global Model</i> | 356 | | | | 1.29 (0.03) | 0.74 (0.01) | -1.45 (0.08) | 0.62 (0.02) | 2.73 (0.08) | 0.11 (0.03) |
| <i>Native</i> | | | | | | | | | | |
| Longfin dace | AGCH | 30 | O | CY | 1.19 (0.07) | 0.72 (0.07) | -1.73 (0.14) | 0.95 (0.13) | 2.87 (0.16) | -0.14 (0.16) |
| Desert sucker | CACL | 33 | HD | CA | 2.03 (0.40) | 0.55 (0.09) | -0.56 (0.79) | 0.49 (0.18) | 2.59 (0.85) | 0.05 (0.19) |
| Sonora sucker | CAIN | 21 | HD | CA | 1.4 (1.28) | 0.71 (0.22) | -2.49 (2.54) | 0.92 (0.43) | 3.89 (2.73) | -0.21 (0.47) |
| Roundtail chub | GIRO | 21 | O | CY | 1.84 (0.33) | 0.61 (0.07) | 0.16 (0.66) | 0.42 (0.14) | 1.68 (0.71) | 0.19 (0.15) |
| Speckled dace | RHOS | 36 | I | CY | 1.38 (0.08) | 0.69 (0.08) | -1.41 (0.16) | 0.88 (0.15) | 2.80 (0.17) | -0.19 (0.16) |
| <i>Non-native</i> | | | | | | | | | | |
| Yellow bullhead | AMNA | 24 | IP | IC | 1.50 (0.48) | 0.71 (0.11) | -2.30 (0.99) | 0.79 (0.23) | 3.96 (1.07) | -0.12 (0.25) |
| Common carp | CYCA | 5 | O | CY | 1.84 (0.31) | 0.65 (0.06) | -1.28 (0.61) | 0.42 (0.13) | 3.12 (0.65) | 0.23 (0.14) |
| Red shiner | CYLU | 35 | O | CY | 1.21 (0.11) | 0.79 (0.10) | -1.53 (0.29) | 1.06 (0.26) | 2.82 (0.31) | -0.34 (0.28) |
| W. mosquitofish | GAAF | 43 | I | PO | 1.08 (0.07) | 0.50 (0.12) | -1.49 (0.13) | 0.48 (0.21) | 2.63 (0.16) | -0.03 (0.26) |
| Green sunfish | LECY | 36 | IP | CE | 0.37 (0.15) | 1.07 (0.06) | -1.21 (0.36) | 0.27 (0.13) | 1.29 (0.38) | 0.89 (0.14) |
| Smallmouth bass | MIDO | 34 | P | CE | 2.17 (0.22) | 0.55 (0.06) | -3.05 (0.43) | 0.79 (0.11) | 5.22 (0.47) | -0.24 (0.12) |
| Rainbow trout | ONMY | 7 | IP | SA | 2.04 (3.77) | 0.54 (0.76) | -3.54 (7.49) | 0.86 (1.51) | 5.58 (8.07) | -0.32 (1.63) |
| Fathead minnow | PIPR | 34 | O | CY | 1.71 (0.17) | 0.67 (0.17) | -0.49 (0.33) | 0.14 (0.34) | 2.20 (0.35) | 0.53 (0.36) |

Notes: Guilds (G) are: O = Omnivore, HD = Herbivore-Detritivore, I = Invertivore, IP = Invertivore-Piscivore, P =

Piscivore. Families (F) are: CY = Cyprinidae, CA = Catostomidae, IC = Ictaluridae, PO = Poeciliidae, CE =

Centrarchidae, SA = Salmonidae. Species (ID) are: AGCH = longfin dace, AMNA = yellow bullhead, CACL =

desert sucker, CAIN = Sonora sucker, CYLU = red shiner, GAAF = Western mosquitofish, GIRO = roundtail chub,

LECY = green sunfish, MIDO = smallmouth bass, PIPR = fathead minnow, RHOS = speckled dace. Bolded

parameter estimates indicate scaling coefficients whose 95% CIs do not overlap 1 (N,P rates) or 0 (N:P ratio).

FIGURE CAPTIONS

Figure 1. Locations of fish community sampling efforts (Gibson et al 2015; grey circles) and per capita nutrient recycling measurements (this study; black crosses) in streams of the upper Verde River watershed in central Arizona, USA.

Figure 2. Log-log plots of the allometric relationships between body size and nutrient recycling (N, P, or N:P) for 356 individuals sampled in the field. Columns display the same data grouped by increasingly more resolved levels of organization (Global → Origin → Guild → Family → Species). Codes to species abbreviations can be found in Table 2.

Figure 3. N:P ratios of individuals grouped by different levels of biological organization (a: Origin, b: Family, c: Guild, d: Species). Grouping individuals ignores variation induced by changes in body size, but coefficients of body size—N:P relationships were small or overlapping zero for most species (Table 2) and body size explained little variation in N:P for most groups (Table 1). Explanations of group abbreviations can be found in Table 2, and species are color coded in panel d according to their origin (blue = native, grey = non-native). Whiskers identify the maximum/minimum point within 1.5 * interquartile range distance to the median.

Figure 4. Average LRR across sites for a) non-native/native or b) global/species-specific effect sizes on simulated aggregate N, P, and N:P recycling. In panel a) LRRs are presented for both global (grey) and species-specific models, and positive values indicate that non-native species had higher average nutrient recycling rates or ratios than native species. In panel b) LRRs are presented for both native and non-native scenarios, and positive values indicated that global models estimated higher average nutrient recycling rates or ratios than species-specific models. Points are means and whiskers are \pm 95% CI.

Figure 5. Differences in simulated aggregate N:P recycling ratios between native (blue) and non-native (grey) scenarios. The magnitude of estimated differences varied between global (left) and species-specific modeling approaches. Dashed lines represent the mean contemporary N:P ratios estimated for the 25 sampled sites using species-specific (black; mean = 37.9) or global (gray; mean = 23.8) models. Whiskers identify the maximum/minimum point within 1.5 * interquartile range distance to the median.

FIGURES

Figure 1.

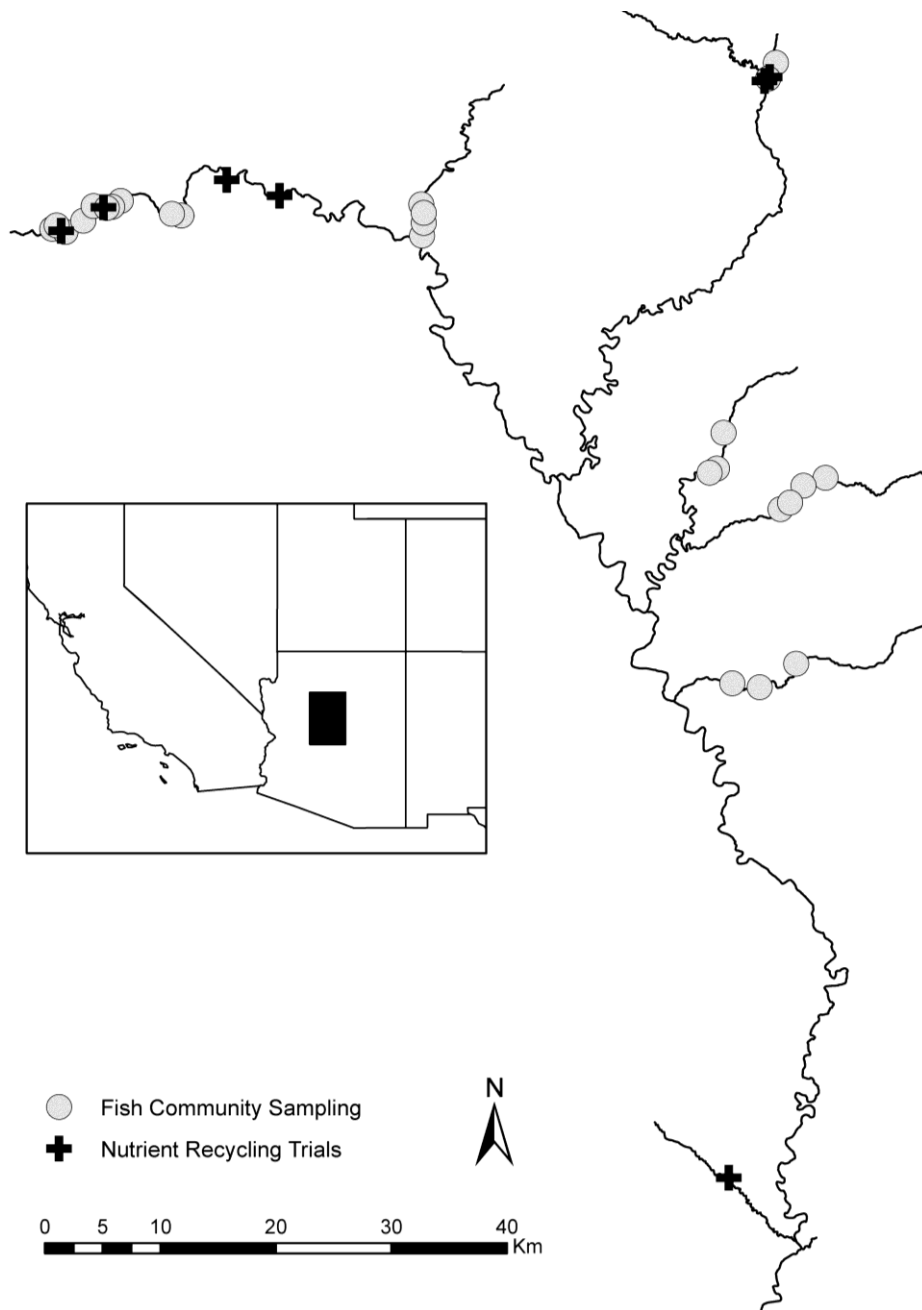


Figure 2.

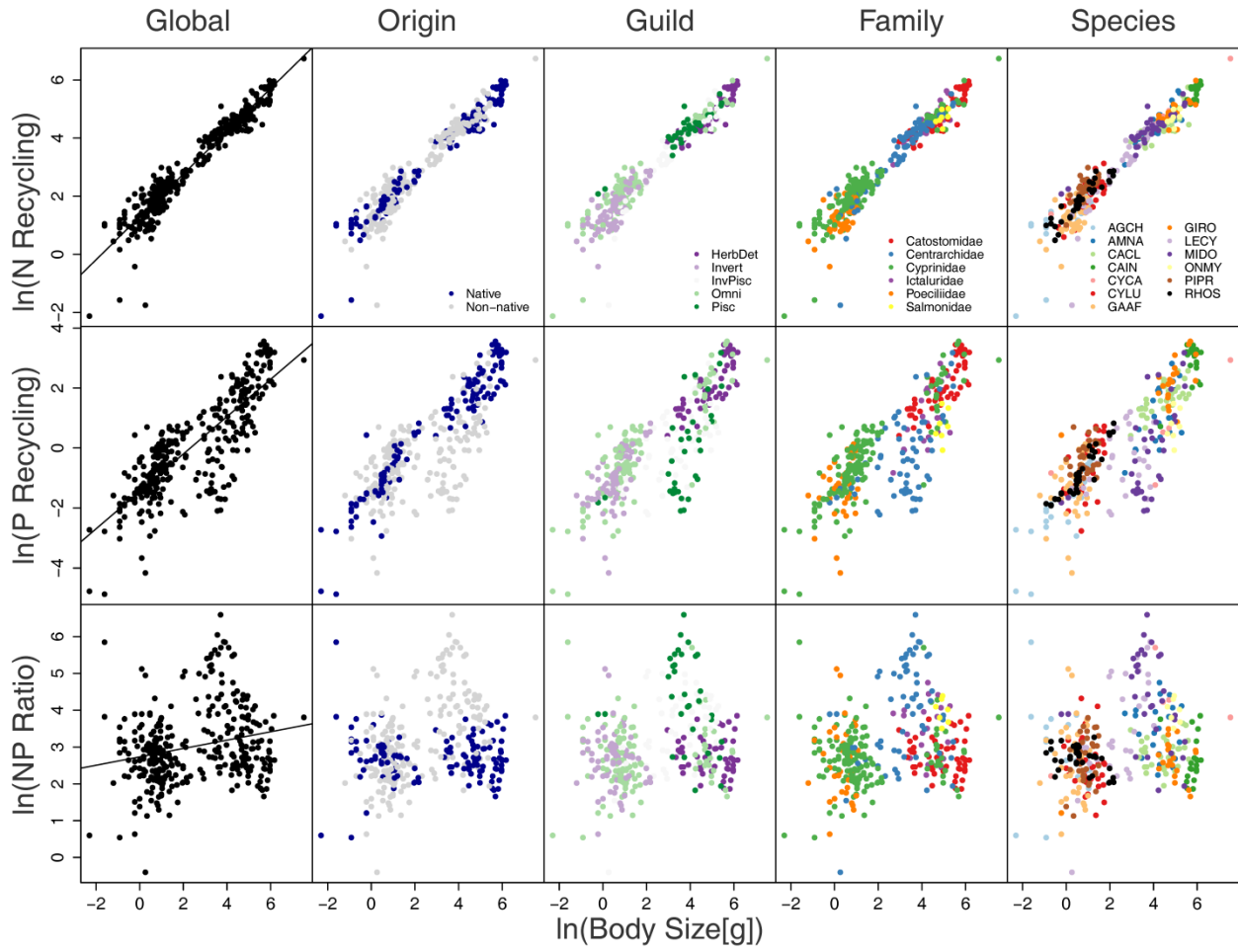


Figure 3.

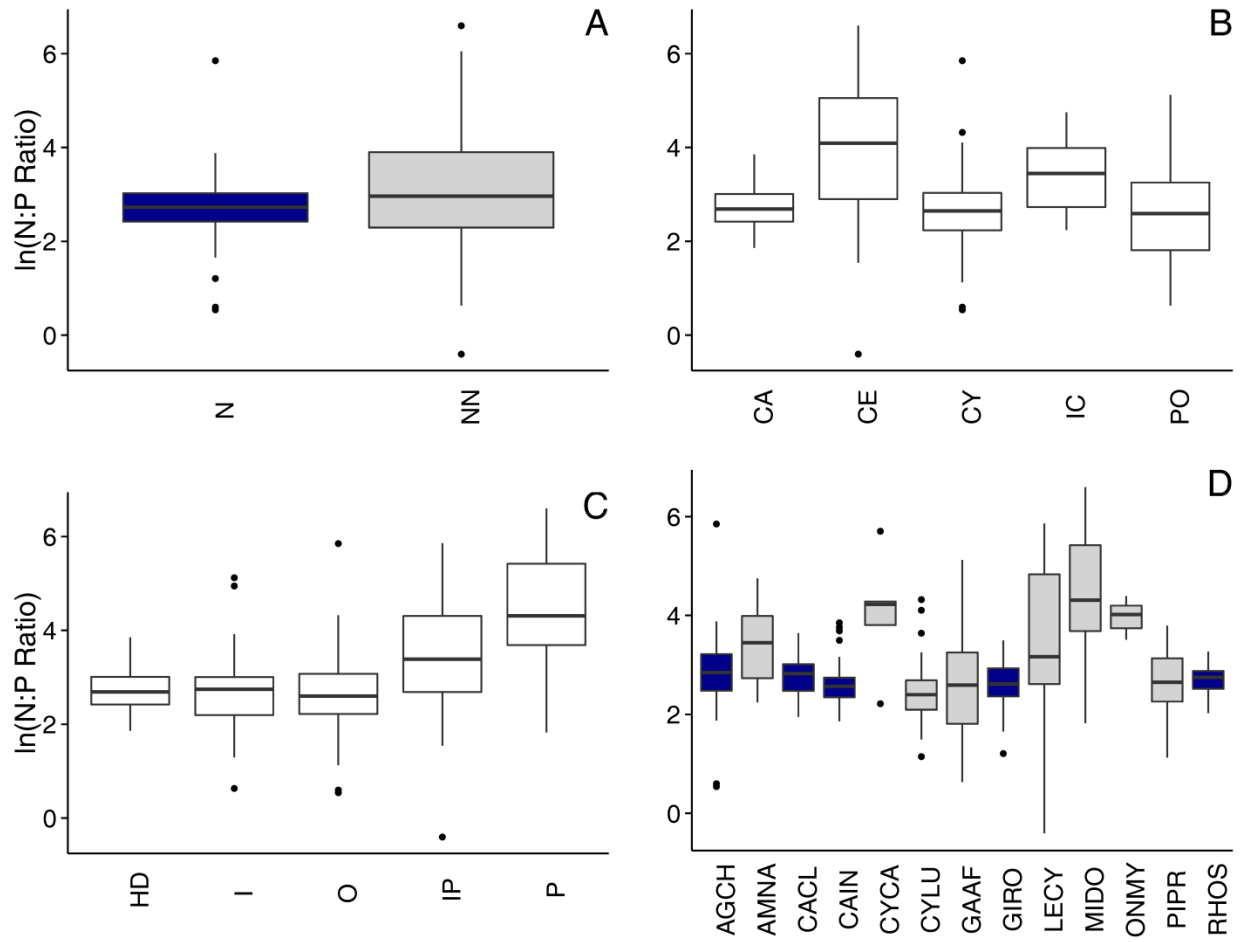


Figure 4.

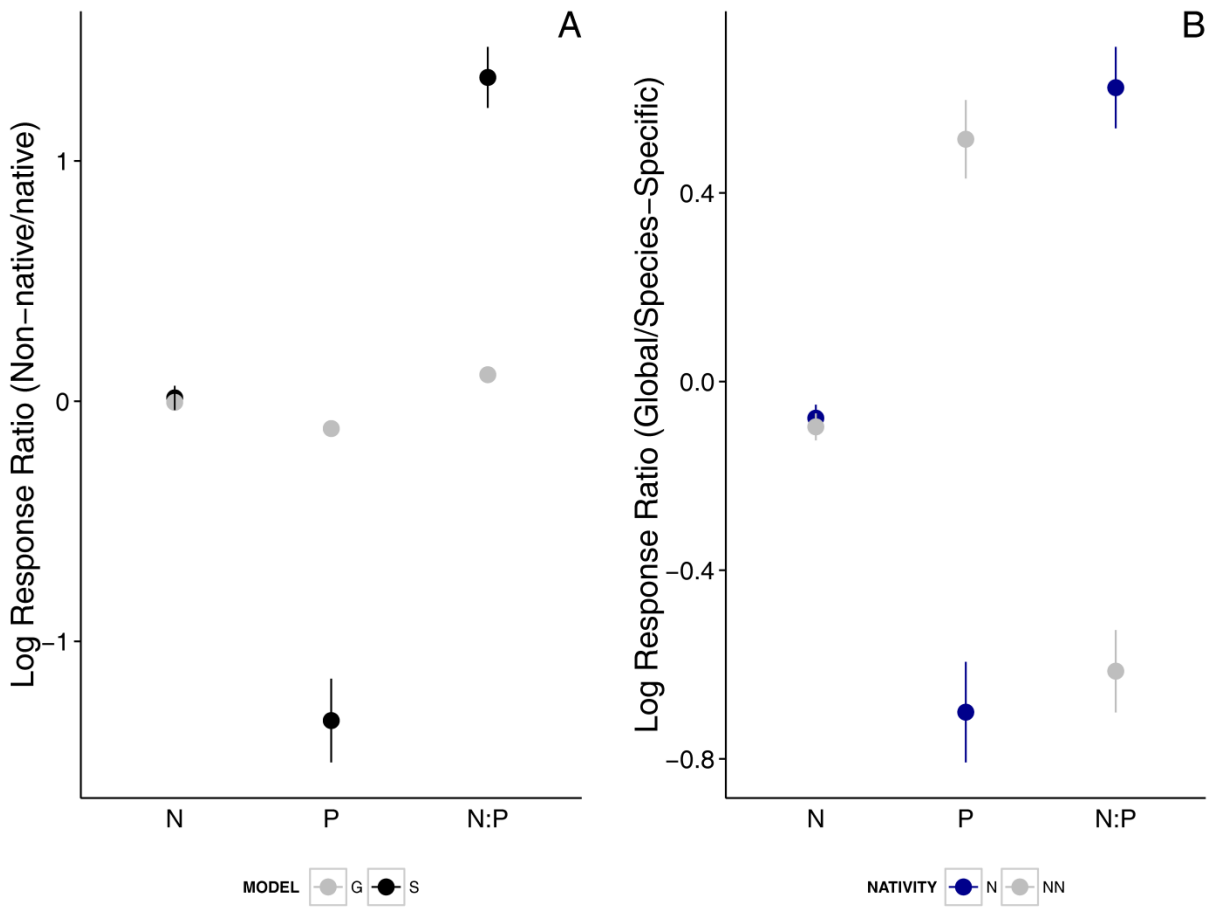
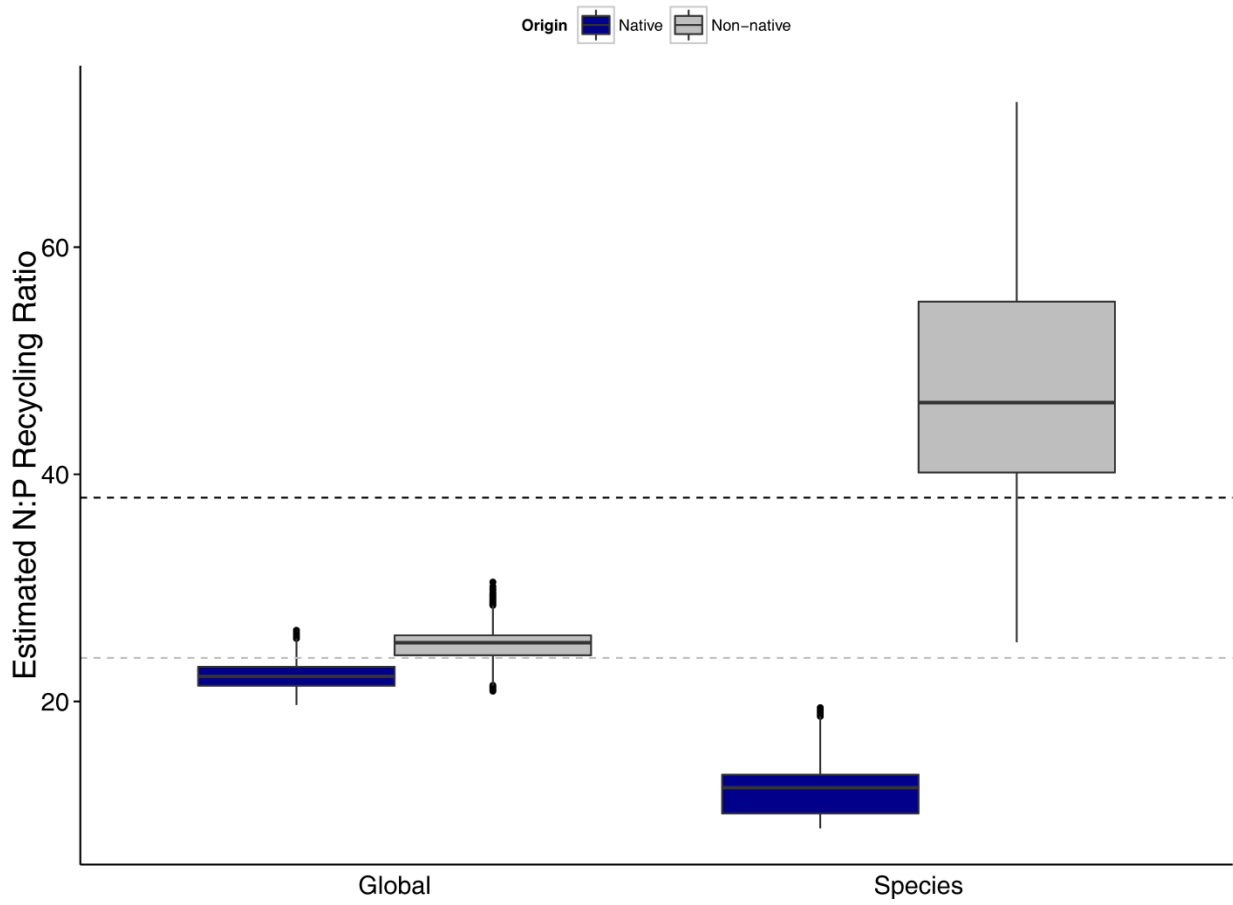


Figure 5.



SUPPORTING INFORMATION

Supporting Information A. Comparison of native and non-native simulated distributions of N, P, and N:P for each site, using either species-level or global models of nutrient recycling.

Figure A1. Observed and simulated aggregate rates of NH_4 recycling. At each site native and non-native communities were assembled 999 times each, with body size distributions constrained by the community-level energy of the observed fish community at that site. Species-specific or global models relating body size to nutrient recycling were used to scale up the body size distributions of each simulation to an aggregate rate of nutrient recycling for that simulated community. Here we present the nutrient recycling distributions for each of the 999 simulations of native (grey) vs. non-native (black) species pools, and using either species-specific (solid lines) or global (dashed lines) models. Means of these distributions were compared using log response ratios (LRRs) as described in the *Methods* section of the text. LRRs are calculated within sites, providing a dimensionless metric to summarize across sites. Thus, here the x and y scales of each panel vary for better visual differentiation of site-level data. Variance differences of each distribution are a consequence of both the sampled size range of individuals in the simulation and the degree of variation in the size—recycling model coefficients (i.e., global models are represent by a single coefficient set, whereas species-specific model has 12 coefficient sets). Large differences in distribution variances precluded the use of parametric significance tests to compare LRRs. Observed rates of nutrient recycling for each site are shown by vertical red lines (species-specific model: solid; global model: dashed) for comparison.

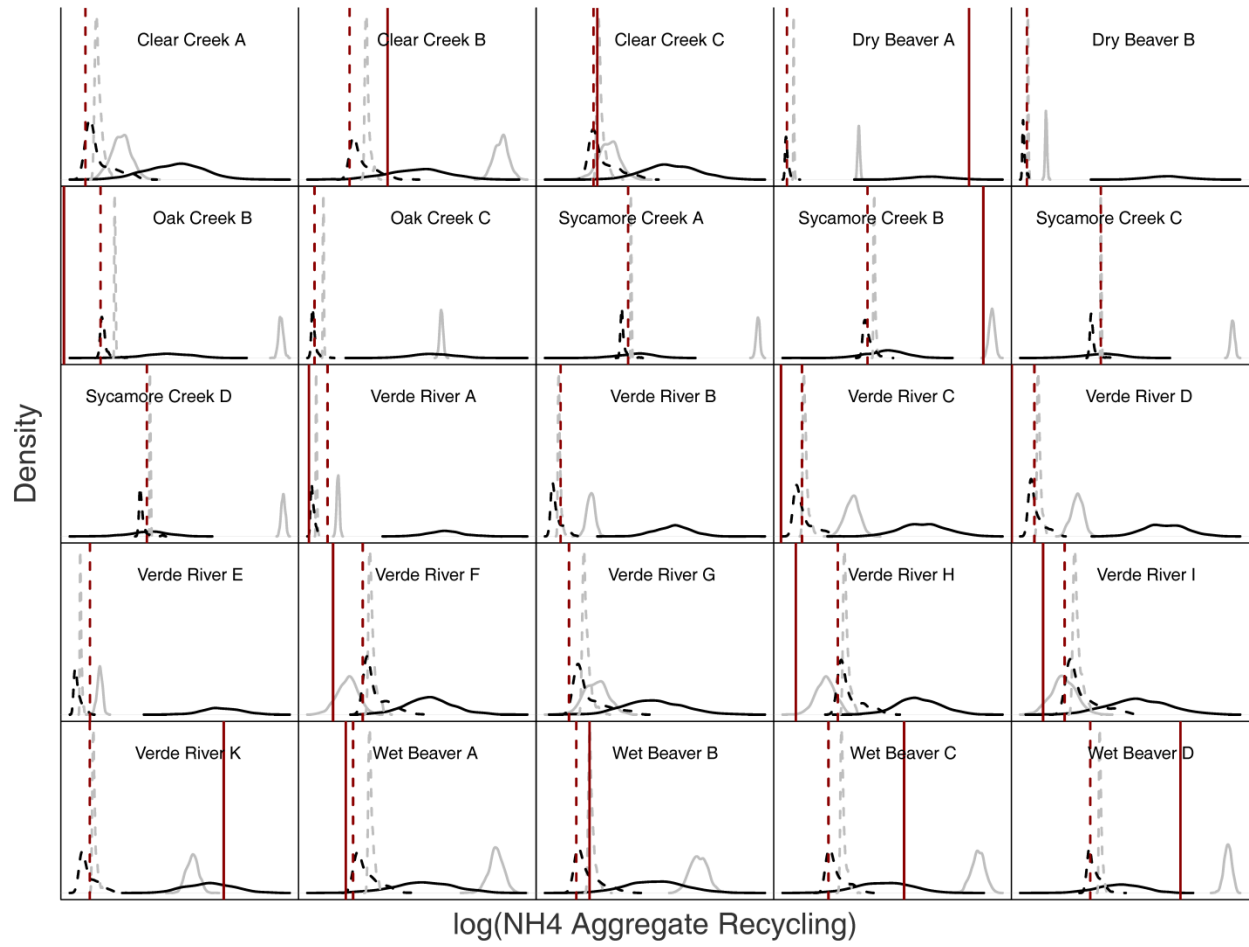


Figure A2. Observed and simulated aggregate rates of PO_4 recycling. Figure is as described above (Fig. A1).

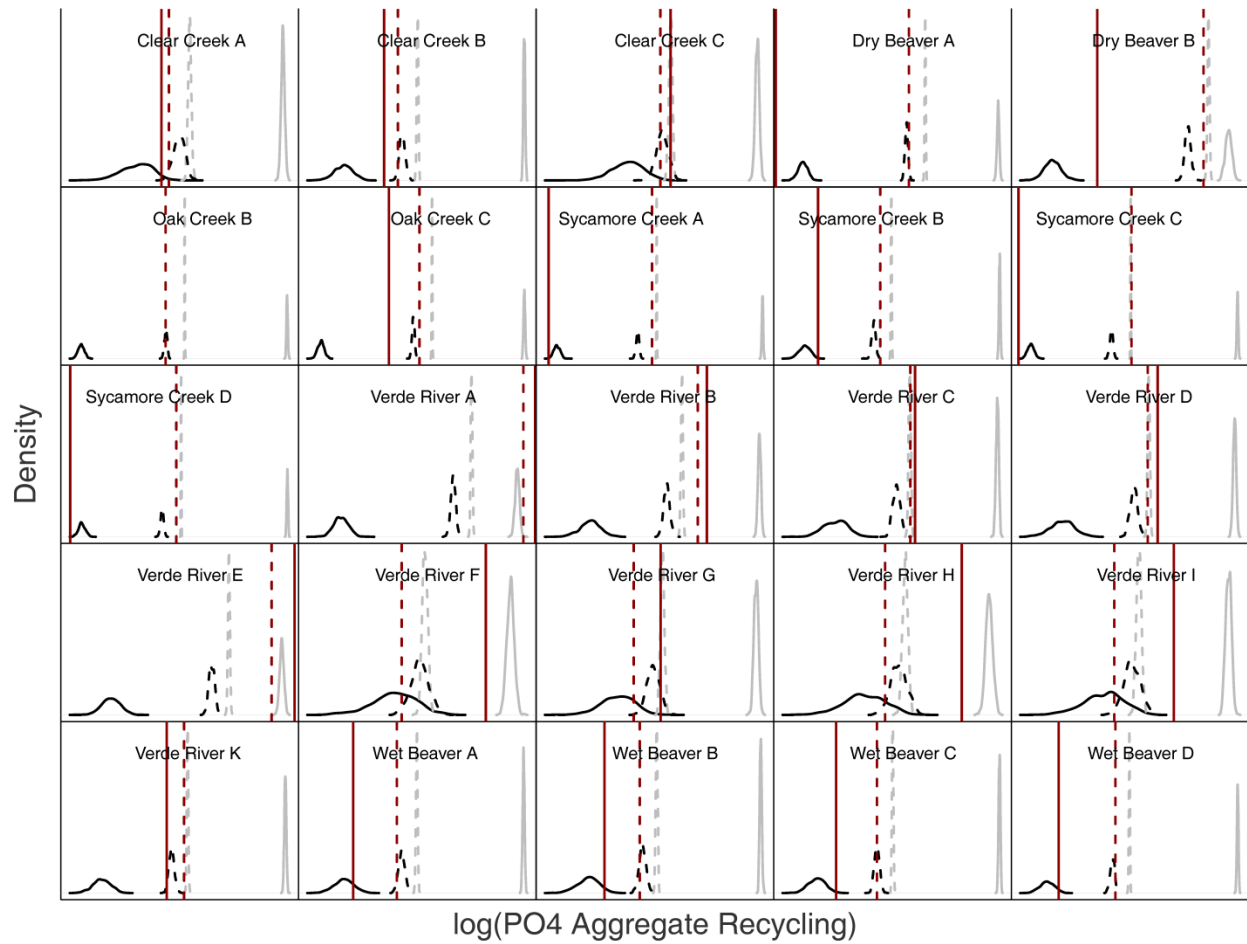


Figure A3. Observed and simulated aggregate N:P ratio of recycling. Figure is as described above (Fig. A1).

