RESEARCH ARTICLE

Diversity and Distributions  WILEY

# Diversity–production relationships of fish communities in freshwater stream ecosystems

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## Abstract

**Aim:** Ecological relationships between species richness and biomass production are increasingly thought to be pervasive across the globe. Yet, diversity–production relationships have not been explored extensively for freshwater fish communities even though fisheries production provides key services to humans. Our aim was to evaluate the diversity–production relationship of fish communities inhabiting freshwater streams across the Appalachian Mountain range and examine how diversity–production relationships varied across streams possessing different thermal signatures.

**Location:** Our study area included 25 freshwater stream ecosystems spanning from Vermont to North Carolina in the United States. Twenty sites were located in Maryland south to Tennessee and North Carolina, while five additional higher latitude sites were sampled in Massachusetts and Vermont.

**Methods:** We sampled the 25 study streams from June to September 2012 and collected fish population information to calculate biomass, species richness, the Shannon diversity index and annual production for each fish community. Linear mixed effects models were used to analyse the relationship between diversity indices and total community production. We also compared diversity and production relationships across other taxa.

**Results:** Across all streams, community fish production, biomass and P/B ratios ranged from 0.15–6.79 g m$^{-2}$ y$^{-1}$, 0.61–0.73 g m$^{-2}$ and 0.21–1.07 y$^{-1}$, respectively. Species richness had a significant positive effect ($p = .012$) on community fish production, while accounting for the thermal signature of the streams as a random effect and other habitat covariates. The Shannon diversity index did not have a significant effect ($p = .101$) on community production.

**Main conclusions:** The diversity–production relationship observed for stream fish communities was similar to other studies but demonstrated one of the highest slopes. Our results demonstrate that effects of biodiversity resonate to influence the production of fishes; thus, management of fisheries is more closely coupled to biodiversity than previously thought.

## 1 | INTRODUCTION

The general relationship between biological diversity and production rates is one of the most widespread and intriguing patterns in ecology (Loreau, 2000; Mittelbach et al., 2001). Research aimed at understanding this relationship has intensified (Colwell, 2009), particularly as anthropogenic activities have prompted erosions to biodiversity and productivity at all scales (Díaz et al., 2020; Hooper et al., 2005). Yet, despite widespread interest, the pervasiveness of diversity–production relationships remains uncertain, including how relationship strength may vary across different ecosystem types and taxa. For example, diversity–production relationships have been most commonly explored within temperate grassland environments where biomass production rates can be more easily quantified (Aoki, 2003; Tilman et al., 1996, 2001). In comparison, studies examining diversity–productivity links in aquatic ecosystems are rarer (Rypel & David, 2017), even though these ecosystems are predicted to suffer disproportionate species losses due to global environmental change (Ricciardi & Rasmussen, 1999).

Hypotheses regarding mechanistic drivers of the diversity–production relationship remain a particularly important but controversial topic (Mittelbach et al., 2001). Two prevailing hypotheses dominate the literature—niche complementarity and sampling effects (Loreau & Hector, 2001; Tilman, 1997). In the first, higher species richness is thought to promote enhanced niche differentiation and increased efficiency in resource use, especially if there is low niche overlap (Loreau & Hector, 2001; Tilman, 1997). In the second, having more species is hypothesized to increase the mathematical probability of having at least one or more extremely productive species (Huston, 1997; Loreau & Hector, 2001; Tilman, 1997). Additionally, there is evidence that diversity–production relationships can be nonlinear depending on scale and ecological dynamics (Aoki, 2003; Rypel & David, 2017). For example, unimodal relationships have been revealed in vascular plants, forests, and freshwater lakes (Dodson et al., 2000; de LaFontaine & Houle, 2007; Mittelbach et al., 2001). In freshwater streams, Cardinale et al. (2006) suggested stream diversity–production relationships may simply be a function of more frequent disturbance. However, this and most other work on the topic has focused on short-lived species (e.g. often primary producers), which likely respond rapidly to environmental change, and not on freshwater fish (Woods et al., 2020). Diversity–production relationships are rarely assessed in more long-lived animal assemblages (e.g. those that might be more resilient to single disturbance events), in part due to the difficulty in estimating production rates of these organisms (Dolbeth et al., 2012). Yet, these taxa are often comprised of species directly managed by human societies for ecological services (Cowx et al., 2010; Dalton et al., 1998), and thus, loss in production via diversity is of direct relevance to humans.

Relationships between fish species diversity or evenness and community production have not been extensively studied in streams, but studies suggest this relationship may be important. Rypel and David (2017) found direction and significance of the relationship between freshwater fish production and diversity was variable and scale dependent. Valentine-Rose et al. (2007) found strong positive relationships between species richness and community fish production in Caribbean tidal creeks; however, Watson and Balon (1984) found no correlation between species richness and production in tropical rain forest streams. Penczak (1981) found higher fish production in areas with lower species richness but pointed out that this relationship was not consistent across all sites sampled. Most importantly, these studies mostly took place in relatively large, open ecosystems where immigration and emigration effects of highly motile fishes are undoubtedly strong creating the potential for dilution effects, and highlighting the need for further research and examples on this topic to inform conservation.
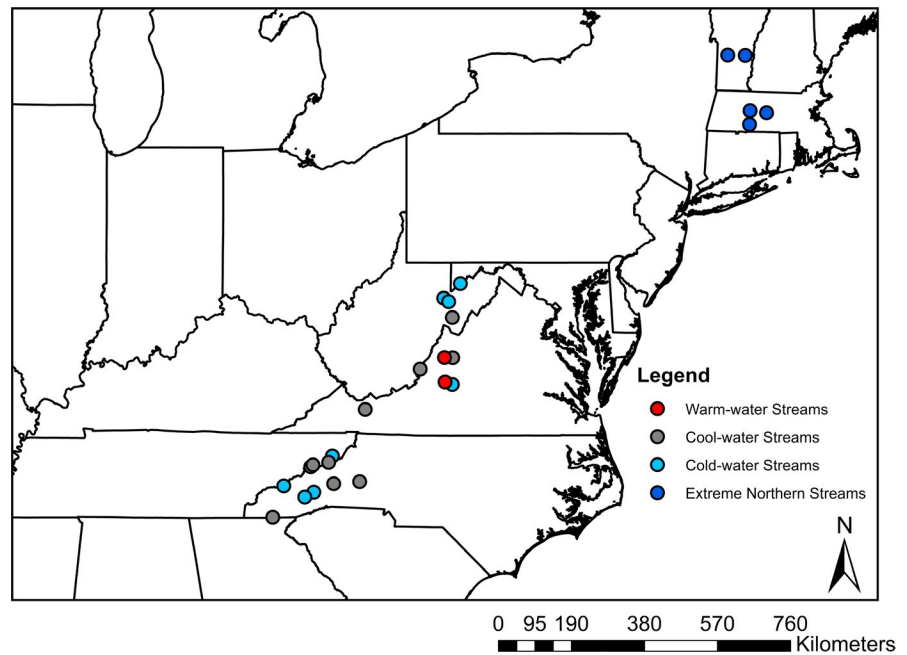
We studied fish diversity–production relationships in 25 Appalachian Mountain streams that fundamentally varied in their thermal and physical habitat characteristics. Community fish production across the streams was also variable exhibiting both relatively low and high total fish production (Myers et al., 2018). Here, our goals were to (1) calculate relationships between α-diversity (e.g. raw number of species—species richness and evenness—Shannon diversity index) and community fish production; (2) compare diversity–production relationships across stream thermal classes; and (3) compare coefficients from diversity–production relationships to previously published relationships for other taxa.

## 2 | METHODS

### 2.1 | Study area

A total of 25 freshwater stream ecosystems in the Appalachian Mountain Range (spanning Vermont to North Carolina, USA) were selected for study (Figure 1). We sampled twenty more southerly located sites (Maryland south to Tennessee and North Carolina) and five higher latitude sites (Vermont and Massachusetts). Sites were selected from a larger network of 204 southern Appalachian streams containing HOBO (Bourne, MA, USA) air and water temperature loggers that were deployed in 2010 by the United States Forest Service (USFS) Southern Research Station. Twenty streams (10% of the total) were selected for this study such that a latitude gradient was represented based on a stratified, random sample. The five northern sites located in Vermont and Massachusetts in the Connecticut River Watershed were selected a posteriori by the USFS Northern Research Unit to provide a comparison between distinct cold-water streams in the more northern and cold-water

**FIGURE 1** Twenty sampling locations classified as cold, cool, and warm water streams located across the Southern Appalachian Mountain Range in North Carolina, Tennessee, Virginia, West Virginia and Maryland sampled during summer 2012 and 5 northern sampling locations in Vermont and Massachusetts sampled during September 2012. The Vermont and Massachusetts sites have been slightly offset from the true location for better clarity



streams in the more southern Appalachian Range. Sites were 2nd- or 3rd-order tributaries located at mid-elevations (range = 71-1046 m; median elevation = 559 m) and characterized by dense canopy cover and cobble substrate.

Southern sites were a priori classified into three thermal classes all relative to high elevation Appalachian streams (i.e. cold-water streams, cool-water streams and warm-water streams) using a K-Means cluster analysis on the mean annual, mean summer, maximum summer and minimum summer water temperature data. The five northern streams in Vermont and Massachusetts were not included in the cluster analysis and were categorized as a separate group (i.e., extreme cold-water streams).

## 2.2 | Data collection

All data collection occurred from June–September 2012 except for field collection of air and water temperature data, which was continuously downloaded biannually following deployment. A random starting point upstream of the air and water temperature loggers was selected for each stream site. Using a systematic sampling design, ETS Electrofishing, LLC ABP-3Q-600-volt backpack electrofishing units were used to sample fish from two 50-metre stream reaches spaced 50 metres apart until depletion of the sampling area (e.g. 3–5 passes per reach). Block nets with 1/16'' mesh were placed downstream and upstream of each 50-metre reach to inhibit immigration and emigration of fishes within the sampling area. For all individuals captured, total lengths (mm) and weights (g) were measured. Subsamples of each species captured at each site were euthanized in tricaine methane sulfonate (MS-222) and frozen for examination and age estimation in the lab. Following Ketchen (1950) and Devries and Frie (1996) subsampling protocol, a fixed stratified subsample of approximately 10 individuals per species per length

group was collected. To reduce sampling bias, length–group intervals were relatively small (i.e. 30–40 mm, 40–50 mm, 50–60 mm; Devries & Frie, 1996).

Replicate water samples were collected upstream of the upper reach prior to sampling and were immediately placed on dry ice to ensure fast freezing and express shipped to The Coweeta Hydrologic Laboratory for analysis of water concentrations of ammonium, nitrite, nitrate, phosphorous, sulphate, potassium, calcium and magnesium using standard methods (USEPA, 1983a; USEPA, 1983b). Habitat data were recorded for the entire 150-m reach section using estimation methods outlined in the Basinwide Visual Estimation Technique, BVET (Dolloff, 1993). In addition to the BVET parameters, canopy cover was estimated in each habitat unit using a convex densiometer, and stream discharge was measured across two transects within the sampling reach using a Marsh-McBirney Flo-mate 2000 following standard procedures (Gore, 1996).

## 2.3 | Diversity and production calculations

Species richness was determined for each site as the total number of unique species, and mean species richness was calculated for the four site temperature classes (i.e. cold-, cool-, warm- and extreme cold-water). In addition, α-diversity was calculated using the Shannon diversity index (Colwell, 2009). We used species richness and the Shannon diversity index to investigate the production relationship with both the raw number of species present (i.e. species richness) and the evenness among species (i.e. Shannon diversity index; Colwell, 2009).

Sagittal otoliths were extracted from each retained specimen for estimation of age-at-capture and back-calculation of lengths at previous ages (Devries & Frie, 1996). Putative annual growth rings were counted under a microscope and interannual growth increments

measured by an experienced reader using a computer-based image analysis system interfaced with the microscope. Length-at-previous ages of all fish were calculated using the Fraser-Lee equation (Francis, 1990).

$$L_t = c + (L_c - c) \times (O_i/O_c).$$

where $L_t$ = back calculated length at ith annuli, $c$ = intercept constant, $L_c$ = length of fish at capture, $O_i$ = otolith radius at ith annuli, and $O_c$ = otolith radius at capture (DeVries & Fries, 1996; Francis, 1990). The intercept for each species was determined by plotting fish length as a function of otolith radius length (Francis, 1990). Finally, logarithmic or power growth functions (depending on the strength of the function fit) were used to predict the ages of measured fish of unknown age using total length data as a predictor.

Secondary production values for each species were estimated using the instantaneous growth rate method (Waters, 1977; Hayes et al., 2007). Age-specific growth (G) was calculated using the equation below.

$$G = ln(mean\,weight\,of\,age\,class_{x+1}) \div (mean\,weight\,of\,age\,class_x)$$

Age-specific biomass was calculated as the sum of the weights of all individuals sampled within that age class per unit area. Age-specific production was then estimated as the production of age-specific biomass and growth (Halyk & Balon, 1983; Rypel et al., 2015; Valentine-Rose et al., 2007, 2011). This method integrates the area under the traditional Allen curve with fish age classes on the x-axis and mean weight on the y-axis (Allen, 1951; Hayes et al., 2007). The formal equation used to calculate production was

$$P = \sum G\bar{B}$$

where $P$ = production, $B$ = arithmetic mean standing stock, and $G$ = instantaneous growth rate (i.e. $\ln\left(\frac{mean\,biomass\,at\,time\,t}{mean\,biomass\,at\,time\,t+1}\right)$ Rypel et al., 2015). Annual production (g m$^{-2}$ y$^{-1}$) for each species was calculated as the sum of production between each age class (Halyk & Balon, 1983), and whole community fish production was calculated by summing all individual species annual production values for the community (Halyk & Balon, 1983). The production to biomass (P/B) ratio for each species was calculated as annual production divided by mean annual biomass as an estimate of the estimated biomass turnover rate for that species in each stream (Hayes et al., 2007; Waters, 1977). Community P/B was calculated by dividing total community production by the total community biomass.

## 2.4 | Data analysis

First, an analysis of variance (ANOVA) with Tukey's post hoc comparisons was conducted to determine whether species richness varied significantly across the four temperature classes. We then investigated the potential relationship between diversity and community fish production using linear mixed effects models with penalized quasi-likelihood with community fish production as the dependent variable, species richness as the independent variable and stream thermal category as a random effect (Package MASS version 7.3-51.6; Venables & Ripley, 2002). We used penalized quasi-likelihood mixed effects models to account for community fish production having a log-normal distribution. In addition, we accounted for habitat covariates that were significantly correlated with the dependent variable, not multi-collinear and identified as influencing fish populations in the literature as additional independent variables: these included mean summer temperature (Rypel and David, 2017, Embke et al., 2019), dissolved oxygen (Cole & Pace, 1995; Ross et al., 2001) and calcium concentrations (Kwak & Waters, 1997). A parallel model was also run using the Shannon diversity index as the independent diversity variable. We calculated the variance inflation factor (VIF) for the 4 independent variables in both models to assess multicollinearity. All statistical analyses were conducted in R (R Core Team, 2017; version 3.6.3).

Finally, we compared our diversity–production relationship with previously quantified and extractable diversity–production relationships occurring at the community level for other taxa. We selected papers based on the following criteria: (1) represented a different taxa or ecosystem, and (2) data on production and diversity were extractable. The slope and strength (i.e. $R^2$) of the relationship between log-transformed community fish production and species richness in this study were compared to selected studies on various taxa. However, because production can vary inter-specifically to a wide degree based on life histories, for example growth rate and body size (Boudreau et al., 1991), diversity–production relationships were standardized by calculating a relative production value for each ecosystem in relation to the maximum production estimate found reported for that ecosystem. Thus, for each individual community, the percentage of potential maximum production across all communities of that ecosystem type was plotted against species richness, which yielded a standardized set of diversity–production relationships across different taxa.

## 3 | RESULTS

### 3.1 | Diversity and allocation of production

Fish community abundance (Figure S1), biomass (Figure S1), production (Figure S1) and P/B ratio (Figure S1) varied across the study area. Across all streams, mean community fish production, biomass and P/B were 2.32 g m$^{-2}$ y$^{-1}$ (± 1.84 SD, range: 0.15–6.79 g m$^{-2}$ y$^{-1}$), 3.47 g m$^{-2}$ (± 2.56 SD, range: 0.61–10.73 g m$^{-2}$) and 0.96 y$^{-1}$ (±0.34 SD, range: 0.56–1.81 y$^{-1}$), respectively. Species richness varied across the four stream temperature classes with the northern, extreme cold-water streams having the lowest species richness ($N = 5$, richness range: 1–9 species) compared to the colder water streams ($N = 8$, richness range: 2–11 species), cooler water streams (stream $N = 10$, richness range: 2–16 species), and warmer water streams (stream $N = 2$, richness range: 19–22 species; Figure S2). Warm-water streams had significantly higher species richness compared

to cold-water ($p = .01$), cool-water ($p = .03$), and northern, extreme cold-water ($p = .004$) streams based on Tukey's post hoc comparisons of the means, while mean species richness at the cold-water, cool-water, and the northern, extreme cold-water streams did not differ statistically (i.e. $p = .33$ for extreme cold-water vs. cool-water, $p = .89$ for cold-water vs. cool-water and $p = .71$ for extreme cold-water vs. cold-water streams).

Species dominance in terms of abundance, biomass and annual production varied across the streams. Blacknose Dace (*Rhinichthys atratalus)* occurred at the most sites (17) but only had the highest abundance at one site (Table 1). Brook Trout (*Salvelinus fontinalis)* and Mottled Sculpin (*Cottus bairdii*) occurred at the same number of sites (13) and had the second and third overall highest abundance and production excluding Central Stoneroller (*Campostoma anomalum)*, which had the highest annual production of the top 10 most dominant species across all sites (Table 1). Bluehead Chub (*Nocomis leptocephalus)*, Brook Trout and Rainbow Trout (*Oncorhynchus mykiss)* had the highest mean annual production rates (0.97, 0.89 and 0.70 g m$^{-2}$ y$^{-1}$, respectively) compared to the other top 10 most occurring species (Table 1). Additionally, salmonids (Salmonidae), cyprinids (Cyprinidae) or cottids (Cottidae) had the highest relative production at each site with all communities sampled dominated by species from one of these three fish families.

## 3.2 | Diversity-production relationship

Both species richness and the Shannon diversity index exhibited a significant positive effect on community fish production, while incorporating a random effect of site thermal class (i.e. extreme cold, cold, cool, and warm; Figure 2) alone. While controlling for other habitat covariates in the model, we found for every one unit increase in species richness community fish production increases by 0.057 g m$^{-2}$ y$^{-1}$ ($p = .012$) (Table 2). In contrast, the Shannon diversity index did not have a significant effect on community fish production when accounting for the random effect of thermal class of the site

and other habitat covariates ($p = .101$; Table 2). In general, species richness had both a stronger positive relationship ($R^2 = .723$) with annual community fish production than evenness ($R^2 = .498$), represented by the Shannon diversity index (Figure 2), and a significant effect when important habitat covariates were accounted for in the models (Table 2).

## 3.3 | Cross-ecosystem comparison

For seven studies for which appropriate data were available (including the present study), the slope of the diversity–production relationship was positive (Table 3). The present study had a higher coefficient of determination ($R^2 = .57$) compared to a study on fish communities in Bahamian tidal creeks ($R^2 = .46$; Valentine-Rose et al., 2007). The diversity–production relationship in two grassland studies had the other highest $R^2$ values ($R^2 = .52$ and $R^2 = .53$, respectively), while two studies on diversity-production relationships for birds in deciduous forests, birds in grassland and desert habitats, and herbaceous communities in the Arctic tundra to deserts in North America having the lowest $R^2$ values ($R^2 = .15$, $R^2 = .31$, $R^2 = .02$, respectively; Table 3; Gough et al., 1994; Hurlbert, 2004). The present study and the study conducted on fish communities in Bahamian tidal creeks had the highest slopes of standardized diversity–production relationships (3.65 and 3.15, respectively; Valentine-Rose et al., 2007; Table 3, Figure 3).

## 4 | DISCUSSION

Improved understanding of diversity–production relationships is important for conservation science at all scales (Isbell et al., 2011). This need is clear for freshwater stream ecosystems where biodiversity is increasingly threatened by myriad human activities (Duarte et al., 2006; Warren & Burr, 1994). In this study, species richness

**TABLE 1** Summary of ranges and means (in parentheses) for species abundance (number of individuals), biomass (g m$^{-2}$), annual production (g m$^{-2}$ y$^{-1}$), P/B ratio (y$^{-1}$) and occurrence for the 10 most common species across the 25 stream locations ranging from Vermont to North Carolina sampled in June–September 2012

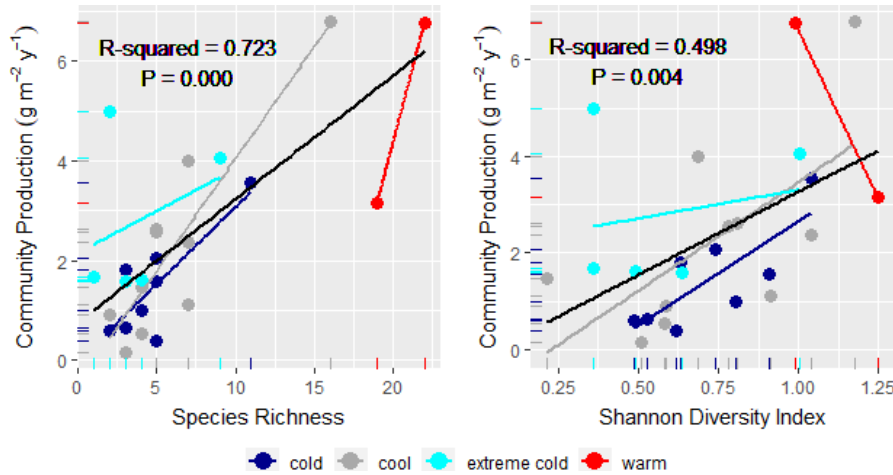| Species | Abundance (N) | Biomass (g m$^{-2}$) | Production (g m$^{-2}$ y$^{-1}$) | P/B (y$^{-1}$) | # of sites present |
|---|---|---|---|---|---|
| *Rhinichthys atratalus* Blacknose Dace | 4–400 (66) | 0.08–4.18 (0.68) | 0.01–2.25 (0.40) | 0.34–0.75 (0.79) | 17 |
| *Salvelinus fontinalis* Brook Trout | 3–275 (68) | 0.02–4.38 (1.05) | 0.00–1.68 (0.89) | 0.52–1.31 (0.92) | 13 |
| *Cottus bairdii* Mottled Sculpin | 6–130 (66) | 0.05–1.97 (0.86) | 0.003–1.56 (0.48) | 0.06–0.75 (0.59) | 13 |
| *Oncorhynchus mykiss* Rainbow Trout | 2–185 (77) | 0.02–2.65 (1.04) | 0.00–1.42 (0.70) | 0.002–1.30 (1.10) | 9 |
| *Nocomis leptocephalus* Bluehead Chub | 36–154 (96) | 0.66–1.56 (1.08) | 0.15–1.84 (0.97) | 0.45–1.15 (0.94) | 6 |
| *Clintostomus funduloides* Rosyside Dace | 2–168 (45) | 0.02–0.98 (0.43) | 0.00–0.74 (0.18) | 0.20–0.80 (0.47) | 8 |
| *Campostoma anomalum* Central Stoneroller | 1–285 (68) | 0.12–4.38 (1.15) | 0.00–3.74 (0.84) | 0.03–0.64 (0.45) | 5 |
| *Semotilus atromaculatus* Creek Chub | 2–87 (26) | 0.04–1.93 (0.56) | 0.00–1.26 (0.28) | 0.08–1.04 (0.70) | 8 |
| *Rhinichthys cataractae* Longnose Dace | 1–64 (21) | 0.01–0.65 (0.30) | 0.00–0.48 (0.14) | 0.14–0.56 (0.57) | 9 |
| *Thorburnia rhothoeca* Torrent Sucker | 1–84 (26) | 0.06–1.14 (0.38) | 0.00–0.84 (0.21) | 0.51–0.81 (0.53) | 6 |

**FIGURE 2** Community production (g m$^{-2}$ y$^{-1}$) as a function of species richness (left) and the Shannon diversity index (right). The black solid line represents the overall regression based on all 25 sites while the coloured lines represent the regression of the cold-water streams (8 sites), cool-water streams (10 sites), extreme cold-water streams (5 sites) and warm-water streams (2 sites). Site points and regression lines are colour coded based on the thermal groupings (light blue = extreme cold-water streams, dark blue = cold-water streams, grey = cool-water streams and red = warm-water streams)

| Linear mixed model results | | | |
|---|---|---|---|
| **Fixed effects** | **Value** | **Std. Error** | **p-value** |
| a. Model: Production ~SR + temp +DO + CA ~1| thermal class | | | |
| Intercept | −0.714 | 2.829 | .804 |
| Species richness (SR) | 0.057 | 0.021 | .012[a] |
| Mean summer temperature (°C; temp) | 0.087 | 0.137 | .533 |
| Dissolved oxygen (DO) | −0.115 | 0.062 | .081 |
| Calcium concentration (CA) | 0.028 | 0.028 | .325 |
| b. Model: Production ~ SD + temp +DO + CA ~1| thermal class | | | |
| Intercept | −4.416 | 2.602 | .108 |
| Shannon diversity index (SD) | 0.724 | 0.417 | .101 |
| Mean summer temperature (°C; temp) | 0.258 | 0.126 | .056 |
| Dissolved oxygen (DO) | −0.101 | 0.065 | .135 |
| Calcium concentration (CA) | 0.006 | 0.030 | .848 |

**TABLE 2** Linear mixed model results for community production as a function of two diversity metrics, that is species richness (a) and the Shannon diversity index (b), three important habitat variables and stream thermal class (random effect)

[a]Denotes significant p-value at the .05 α level.

varied substantially over the spatial scale of the study area thereby providing a unique opportunity to address the potential link between fish diversity and community fish production. Fish species richness and diversity indices were strongly and positively correlated with total community fish production, suggesting that fish communities with higher diversity often have higher overall fisheries productivity. Species richness had a significant effect on community fish production across both models; however, community fish production was not significantly related to the Shannon diversity index when we accounted for other important covariates. These findings suggest evenness may play less of a role in driving total community fish production compared to sheer richness alone. Raw species richness and community fish production also had a stronger correlation than the highest correlated temperature variable (mean summer water temperatures; $R^2$ = .723; $R^2$ = .559, respectively).
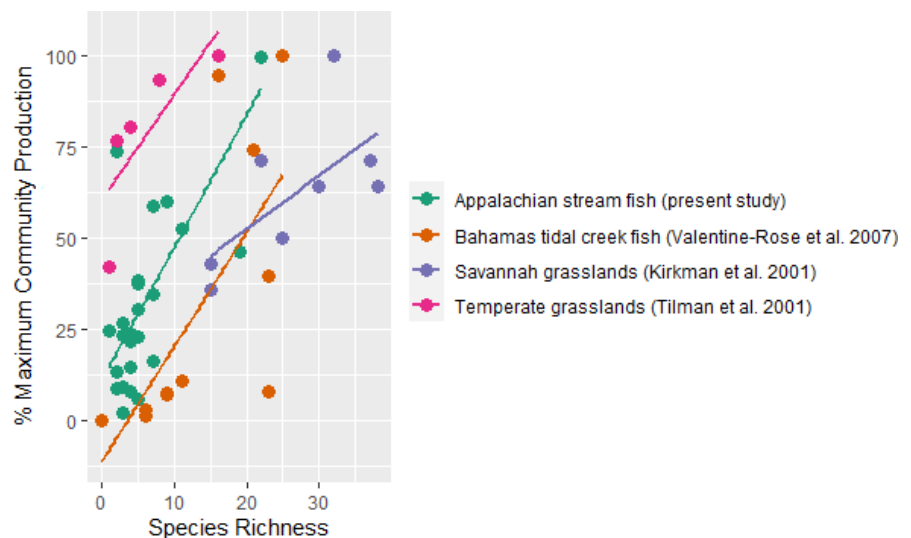
Niche complementarity is one of two common hypothesized mechanisms for stable species coexistence and increased productivity (Lehman & Tilman, 2000; Loreau & Hector, 2001; Tilman, 1997). For example, interspecific differences in resource requirements by species (e.g. food resource and habitat preferences) are well-known drivers of niche differentiation (Mulder et al., 2001). Thus, a larger number of species would be predicted to increase efficiency of species energy acquisition (Kaspari et al., 2000; Loucks, 1970; Paine, 1966). In Appalachian Mountains streams, primary food sources and spatial and temporal habitat preferences of fishes vary distinctly across ecosystems and genera. For example, Central Stonerollers graze algae from boulder and cobble habitats (Fowler & Taber, 1985), while Brook Trout are drift feeders on aquatic and terrestrial insects (Allan, 1981). Mottled Sculpin are benthic insectivores inhabiting run and riffle habitat (Jenkins & Burkhead, 1993;

**TABLE 3** Summary of published diversity–production coefficients of determination ($R^2$), associated *p*-value and the equation of the line for the normalized relationship between species richness and community production for various taxa including the present study

| Study ecosystem and taxa | N | $R^2$ | p-value | Normalized Equation | Reference |
|---|---|---|---|---|---|
| Appalachian streams from Vermont to North Carolina; freshwater fish | 25 | .57 | .004 | % max production = 3.65 (species richness) + 11.12 | Present study |
| Bahamas tidal creek; fish communities | 34 | .46 | .02 | % max production = 3.15 (species richness)−11.13 | Valentine-Rose et al., 2007 |
| Ethiopian desert lake habitat-total lake, reservoir and river ecosystem trophic groups; phytoplankton, zooplankton and fish | 13 | .45 | Not provided, but significant | [a] | Aoki, 2003 |
| Minnesota temperate grassland; vascular plants | 147 | .52 | <.001 | % max production = 2.88 (species richness) + 60.67 | Tilman et al., 2001 |
| Sandhills to wetlands–South-eastern U.S. savanna grassland; vascular plants | 6 | .53 | .03 | % max production = 1.47 (species richness) + 23.22 | Kirkman et al., 2001 |
| Deciduous forests in North American; birds | 1,184 | .15 | Not provided, but significant | [a] | Hurlbert, 2004 |
| Desert or grasslands in North America; birds | 658 | .31 | Not provided, but significant | [a] | Hurlbert, 2004 |
| Arctic tundra to deserts in North America; herbaceous plant communities | 36 | .02 | <.01 | [a] | Gough et al., 1994 |

[a]Denotes information that was unavailable or could not be extracted.

**FIGURE 3** Percentage of maximum community production as a function of species or taxa richness across 4 different ecosystem types (Appalachian streams, Bahamas tidal creeks, savannah grasslands and temperate grasslands) from published studies summarized in Table 3. We only included studies in this figure that we could confidently extract the relevant data



Rohde & Arndt, 1981), while Blacknose Dace are generalists that consume a diverse range of prey (Johnson & Johnson, 1982). As implied by Tilman et al. (2001), production increases when a particular combination of species that are utilizing all the resources available in the system are present. Consequently, when fish species combine within communities to utilize a larger variety of resources and habitats, total stream fish production may increase. However, at higher individual (and perhaps species) densities, competition for resources will intensify, which could ultimately limit productive capacity at a certain tipping point (Huston, 1997).

Another potential mechanism for the positive correlation between community fish production and species richness is simple probability. That is, increasing species richness increases the probability that one or more extremely productive species will colonize a community and contribute differentially to high community production rates (Huston, 1997; Nijs & Roy, 2000; Srivastava & Lawton, 1998). In these streams, fish species richness had a stronger correlation with community production and explained a larger amount of the variation in production (Figure 2); however, the Shannon diversity index, which accounts for both species richness and evenness, did not exhibit a significant effect on community production when accounting for habitat covariates (Table 2). Our data showed the higher latitude cold-water streams tended to have lower evenness but consistently average to higher community production
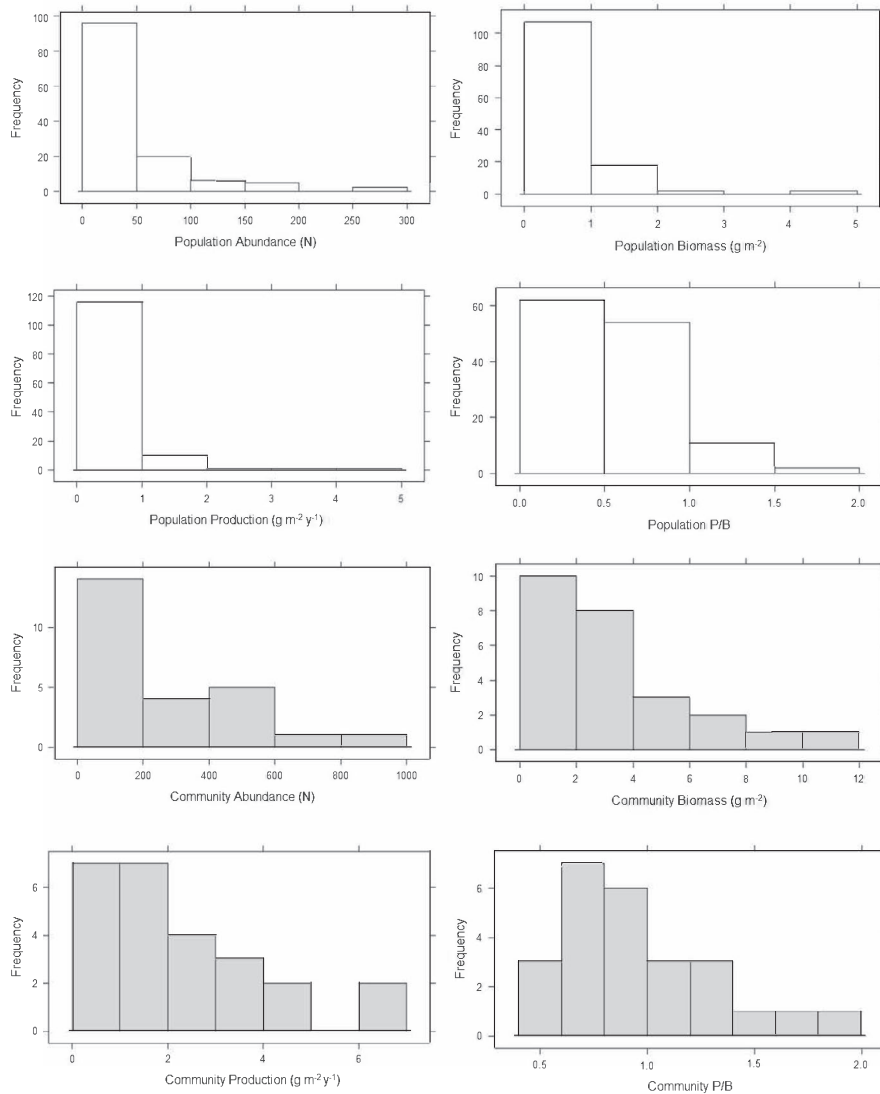
**FIGURE 4** Relative frequency histograms of individual fish population abundance (N), production (g m$^{-2}$ y$^{-1}$), biomass (g m$^{-2}$) and annual P/B, and fish community abundance, production, biomass and annual P/B for the 25 sampled streams across the Appalachians

compared to the cool and lower latitude cold-water sites (Figures S1 and S2). Thus, community production at these sites was dominated by a few species rather than all species contributing similar amounts of production. Indeed, simple frequency histograms of production and biomass both across and within sites revealed a dominance of right-skewed log-normal distributions (Figure 4), further illustrating that most fish species contribute relatively little to total community fish production. These observations align with the lack of a significant model using the Shannon diversity index (which does account for evenness) as a independent variable. Taken together, our results suggest the theory of probability is a more plausible mechanism in generating the positive correlation between fish diversity and community production in stream ecosystems. Ultimately, the importance of each potential mechanism to the observed fish diversity–production relationship is beyond the scope of this study. However, multiple mechanisms influencing the diversity–production relationship have been documented in other taxa and is consistent with the concept that diversity–production patterns can be variable across an array of taxa and environments with varying disturbances (Cardinale et al., 2006; Waide et al., 1999).

## 4.1 | Literature comparisons

Species diversity and ecological productivity frequently are positively correlated but tend to be highly variable (Rypel & David, 2017; Tilman et al., 2001; Valentine-Rose et al., 2011; Waide et al., 1999; Zak et al., 2003). The diversity–production relationship for stream fish communities in this study was comparable to that of other taxa. However, this relationship may not be general to other assemblage and habitat types and should therefore be investigated on a case-by-case basis (Nijs & Roy, 2000; Solimini et al., 2003; Tilman et al., 2001). Coefficients of determination for the diversity–production relationships in this study were oftentimes greater than other studies demonstrating a similar positive correlation (Table 3). In fact, this Appalachian stream fish diversity–production relationship was similar in positive correlation and in slope to the diversity–production relationships of Minnesota, U.S. temperate grassland plants (Tilman et al., 1996), Ethiopian desert lake ecosystem (Aoki, 2003), sandhills-to-wetlands savanna grasslands in south-eastern U.S. (Kirkman et al., 2001), temperate North American deciduous forest birds and desert/grassland birds (Hurlbert, 2004), and coastal marine fish

communities (Valentine-Rose et al., 2007; Table 3). Yet, while there was surprising congruence among standardized diversity-production relationships, these trends are scale-dependent (Aoki, 2003; Rypel & David, 2017). For example, diversity–production relationships can also be characterized by negative or unimodal relationships (Mittelbach et al., 2001). Nonetheless, a highly salient result from this study was that the fish diversity–production relationship for Appalachian streams had one of the highest correlation coefficients and slopes compared to that of other taxa (Table 3, Figure 3). Thus, a link appears to exist between fish species richness and production similar to that found for plant, bird, and coastal marine fish communities (Hurlbert, 2004; Tilman et al., 1996; Valentine-Rose et al., 2007, 2011). Although we compared our results to a small set of other studies highlighting 7 different taxa or ecosystem types, we conclude a larger scale, comprehensive comparison among diversity–production relationships across ecosystems is warranted. Debate remains over whether diversity drives productivity or productivity drives diversity (Gross & Cardinale, 2007; Mittelbach et al., 2001). Regardless, this study highlights a significant positive link and suggests an importance for conserving biodiversity to aide fisheries production.

## 5 | CONCLUSIONS

The link we established between biodiversity and fish production is extremely important for fisheries management and conservation. Our results support predictions from theoretical work and field studies from other taxa. Perhaps most importantly, the pattern challenges traditional notions of fisheries management, in particular those aimed at augmenting production directly through stocking (Holmlund & Hammer, 1999; Arlinghaus & Mehner, 2005). Nonnative Rainbow Trout have been stocked in southern Appalachian streams for many decades (Strange & Habera, 1998). Current populations are well established and naturally reproducing with potential consequences on the native fish assemblages; however, stocked Rainbow Trout did not have significant effects on catch, species richness, and the Shannon diversity index on nongame fish assemblages in similar southern Appalachian streams in North Carolina (Weaver & Kwak, 2013). Alternatively, our work suggests that an approach based on diversity–production relationships may be a more efficient and natural method for managing diverse fish populations (Sass et al., 2017). In conclusion, negative impacts to biodiversity (e.g. through human activities) that affect "non-managed species" may have the potential to cascade through food webs to impact other charismatic or managed species and hinder progress towards management and conservation goals.

## CONFLICT OF INTEREST
The authors declare no conflict of interest.

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**BIOSKETCH**

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**SUPPORTING INFORMATION**

Additional supporting information may be found online in the Supporting Information section.