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REPORT

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# Resource quantity and quality co-limit consumer production in forest streams

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## Abstract

Ecological theory predicts that consumers should be co-limited by resource quantity and quality, given widespread consumer-resource nutritional imbalances. We used 25 estimates of annual community secondary production (ACSP) of stream macroinvertebrates to assess the relative roles of basal resource quantity (leaf litter standing stock [LLSS]) and quality (% nitrogen and % phosphorus of leaf litter) in modulating patterns of production in forest streams. We also tested the effects of hypothesized indirect drivers (stream discharge and inorganic nutrient concentrations) on basal resource quality and quantity and secondary production. In the top model for ACSP, LLSS, and %P together explained 59% of its variation, providing strong evidence of co-limitation by both resource quantity and quality. Mean annual stream discharge and stream water P concentration explained 75% and 43% of variation in LLSS and %P, respectively. Together, stream discharge and stream water P concentration explained 77% of the variation in ACSP, demonstrating a critical link between hypothesized indirect and direct (basal resources) drivers and ACSP. Our results are the first to demonstrate co-limitation of ACSP and highlight several mechanisms by which drivers of anthropogenic global change, such as altered precipitation (stream discharge) and eutrophication, influence the productivity of animal communities in stream ecosystems.

**KEYWORDS**
co-limitation, Coweeta Hydrologic Laboratory, ecological stoichiometry, nitrogen, phosphorus, secondary production

## INTRODUCTION

Secondary production, or the formation of heterotrophic biomass through time, is an important ecosystem function that represents a principal pathway in the fate and transformation of organic matter in food webs (Benke, 1993). Studies from both terrestrial and aquatic systems have reported positive relationships between resource abundance (or productivity) and secondary productivity of entire consumer assemblages (McNaughton et al., 1989; Wallace et al., 2015), which is expected given that energy limitation of consumer trophic levels is a foundational concept in ecology. At the same time, elemental (nitrogen [N] and phosphorus [P]) imbalances

  

between consumers and resources are common (Elser et al., 2000; Lemoine et al., 2014) and variation in the P content of food resources has been linked to patterns of secondary production in stream ecosystems (Demi et al., 2018). Per the growth rate hypothesis (Elser et al., 2003), P-limitation specifically should be common for many fast-growing consumers given that a high concentration of P-rich ribosomal RNA is needed to support the rapid protein synthesis associated with fast growth.

Despite acknowledgement of the importance of both diet quantity and quality, the relative roles of various drivers of secondary production remain poorly understood in many ecosystems, constraining our knowledge of how ecosystems respond to environmental change. In this context, the co-limitation hypothesis has gained increased attention over recent decades (Marcarelli et al., 2011; Sperfeld et al., 2016). Co-limitation of consumers by resource quantity and quality is a cornerstone of ecological stoichiometry theory (Sterner & Elser, 2002) and the central concept of the threshold elemental ratio (Sterner, 1997). Though demonstrated at the individual level (Halvorson et al., 2017; Prater et al., 2024), simultaneous co-limitation by resource quantity and quality (nutrient content) remains untested with respect to rates of annual community secondary production (hereafter ACSP).

Here, we investigate the potential for co-limitation of secondary production by resource quantity and quality by synthesizing data from three multiyear N and P enrichment experiments in small, detritus-based, forest stream ecosystems (see Cross et al., 2006; Davis et al., 2010; Demi et al., 2018). The forest streams manipulated in these studies are ideal systems for addressing the importance of resource quantity and quality for secondary production because: (1) their food webs are almost entirely reliant on autumn-shed leaf detritus (Wallace et al., 1999), which has characteristically low N and P content compared to detritivores (Cross et al., 2003; Martinson et al., 2008), (2) increased N and P availability stimulates microbial biomass thereby increasing detrital nutrient content and reducing nutrient imbalances for consumers (Danger et al., 2013; Evans-White & Halvorson, 2017; Manning et al., 2015), and (3) increases in resource nutrient content are not accompanied by increased resource quantity, as in autotroph-based food webs. We hypothesized that variation in secondary production would be best described by patterns of leaf litter standing stock (hereafter LLSS) and P content, consistent with co-limitation by basal resource quantity and nutrient quality. We also investigated the relative role of several predicted indirect drivers of secondary production, namely, mean annual stream discharge and stream water N and P concentrations. We expected that stream discharge and stream water P concentrations would be significant drivers of secondary production based on the known effects of discharge on LLSS (Wallace et al., 2015) and stream water P on litter P content (Demi et al., 2018; Prater et al., 2015).

# METHODS

## Study sites and data collection

Our study combines previously published data from three separate reach-scale nutrient-enrichment experiments conducted at the Coweeta Hydrologic Laboratory (CHL) in Macon County, North Carolina, USA (Appendix S1: Figure S1). Detailed site descriptions can be found in the original papers (see Cross et al., 2006; Davis et al., 2010; Demi et al., 2018). The timing and duration of each study is summarized in Appendix S1: Table S1. Collectively, these studies provide 25 unique estimates of ACSP, collected from seven streams, which are accompanied by estimates of mean annual discharge and stream water N (dissolved inorganic N [DIN] = $NO_3^-$ + $NH_4^+$) and P (soluble reactive P [SRP]) for each sample year. A detailed account of mean nutrient concentrations and annual discharge from each stream during each year of study can be found in Appendix S1: Table S1. Accompanying 21 of these production estimates are estimates of mean LLSS and nutrient content (%N and %P) estimated from monthly benthic samples (Appendix S1: Table S1). In each study, experimental nutrient enrichment was achieved by the continuous, simultaneous addition of DIN and SRP to each stream (except for a concurrently measured reference stream during the Cross et al. (2006) and Davis et al. (2010) studies) for multiple years, following a year of pre-enrichment monitoring under reference conditions. Detailed descriptions of the enrichment methodology used in the different experiments can be found in the original papers (see Cross et al., 2006; Davis et al., 2010; Demi et al., 2018). The specific concentrations and ratios of inorganic N and P that were added varied among streams and experiments, and when combined with ambient nutrient concentrations in reference streams or years resulted in a wide range of mean N (13–798 μg $L^{-1}$ DIN) and P (2–117 μg $L^{-1}$ SRP) concentrations and N:P (2–128) ratios (Appendix S1: Table S1). All ACSP estimates presented are from mixed-substrate habitat (mixture of boulders, cobble, and finer sediments) and therefore exclude estimates from bedrock habitat, which makes up a smaller proportion of the total benthic habitat (Cross et al., 2006; Davis et al., 2010). Estimates of ACSP and mean LLSS were calculated from monthly benthic samples following protocols first described by Lugthart and Wallace (1992) and

summarized by both Cross et al. (2006) and Demi et al. (2018). Methods for calculating annual secondary production of individual populations are described in the original papers (Cross et al., 2006; Davis et al., 2010; Demi et al., 2018). Leaf litter nutrient content was determined from monthly samples of leaf litter and is reported as %N and %P of dry mass (see Cross et al., 2003; Demi et al., 2018 for additional details). Discharge was determined from rating curves developed for each stream that related continuous measurements of water level from pressure transducers to manual measurements of discharge under different flow conditions. Estimates of secondary production from 2003 to 2005 were not accompanied by estimates of litter %N, %P, or LLSS as those data were not collected in two streams during that time frame and thus were not included in the analysis of direct drivers (basal resource quantity and quality).

## Data analysis

We used multiple regression in a linear mixed-effects model framework to assess the relative roles of hypothesized indirect (discharge, DIN, and SRP) and direct drivers (LLSS and litter %N and %P) in modulating patterns of ACSP, as well as the production of primary consumers only and of leaf-shredding macroinvertebrates (hereafter shredders) only. Additionally, we used linear mixed-effects models to examine links between our hypothesized direct and indirect drivers of secondary production, including relationships between litter %P and mean SRP concentration, litter %N and mean DIN concentration, and mean LLSS and stream discharge. In all models, stream was included as a random effect to account for nonindependence of the multiple estimates of secondary production from each of the seven study streams. All indirect and direct drivers were modeled as fixed effects. We tested and compared model fits by calculating pseudo $R^2$ estimates, where $R^2_m$ (marginal CV) represents the variance explained by fixed effects, and $R^2_c$ (conditional CV) represents variance explained by the entire model, including fixed and random effects (Harrison et al., 2018; Nakagawa et al., 2017). We standardized all predictor variables as *z*-scores by subtracting the mean and dividing by the SD to facilitate comparison of effect sizes among predictor variables. We based our interpretation of evidence for co-limitation on comparisons of models using corrected Akaike information criterion for small sample sizes ($AIC_c$; Harrison et al., 2018). Models with $\Delta AIC_c$ scores of 2 or less, relative to the model with the lowest $AIC_c$ score, are considered top competing models for each set of drivers. Additional evaluation of model performance is informed by comparisons of calculated $R^2_m$ among top models, as identified by relative $AIC_c$ scores. We assessed the relative importance of drivers via comparisons of relative effect sizes (parameter estimates) of fixed effects within models. Mixed-effects models were executed using the R package *lme4* (Bates et al., 2024) and $AIC_c$ and pseudo $R^2$ values were calculated using the R package *MuMIn* (Bartoń, 2023). Data were $\log_e$-transformed as necessary to conform to assumptions of linearity, homogeneity of variance, and normality of residuals.

Lastly, we generated response-surface plots to provide graphical evaluation of co-limitation of ACSP based on Sperfeld et al. (2016) and Halvorson et al. (2017). Response surfaces were generated using the "Tps" function from the R package fields (Nychka, 2023), which both interpolated and extrapolated ACSP values using a kriging function. The surface plots were subsequently generated using the "geom_raster" and "geom_contour" functions in the R package *ggplot2* (Wickham, 2016). All analyses were performed using the R statistical environment (version 4.4.2; R Core Team, 2024). All data and R code for the linear mixed-effects models and surface plots are accessible via Dryad and Zenodo (Demi et al., 2025a, 2025b).

# RESULTS

Among our hypothesized indirect drivers of secondary production, discharge had a negative effect, while SRP and DIN had positive effects on ACSP (Table 1, Appendix S1: Figure S2), and shredder (Appendix S1: Table S2) and primary consumer (Appendix S1: Table S3) production. The three top-performing models of ACSP, based on $AIC_c$ scores, were the SRP + discharge, SRP-only, and full model (SRP + DIN + discharge) of indirect drivers (Table 1). In the discharge + SRP model, the fixed effects collectively explained 77% of variation in, and had similar relative effects on, ACSP (Table 1). In the SRP-only model, SRP concentrations explained 32% of the variation in ACSP. The next-best model included all three terms as fixed effects and explained 78% of variation in production estimates among the streams, though the relative effects of mean annual discharge and SRP were 2.6× and 2.0× greater, respectively, than that of DIN in this model (Table 1). The two remaining indirect drivers alone explained between 20% (DIN) and 30% (discharge) of variation in ACSP (Table 1).

For primary consumer production, $AIC_c$ scores identified four top candidate models, all of which included SRP as a fixed effect (Appendix S1: Table S2). Of these candidate models, the SRP + discharge and full model had the

**TABLE 1** Linear mixed-effects model results (standardized parameter estimates and SE, $n = 25$; also shown are the multiple model-support criteria we used to rank model fits [marginal $R^2_m$, conditional $R^2_c$, and corrected Akaike information criterion, $AIC_c$]) for annual community secondary production based on proposed indirect drivers, which include stream water dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) concentrations and mean annual discharge ($Q$).

| | Parameter estimates (SE) | | | | | | |
|---|---|---|---|---|---|---|---|
| Model | Intercept | DIN | SRP | $Q$ | $R^2_m$ | $R^2_c$ | $AIC_c$ |
| SRP + $Q$ | 9.195 (0.052) | ... | 0.323 (0.053) | −0.315 (0.053) | 0.766 | 0.766 | 16.3 |
| SRP | 9.118 (0.131) | ... | 0.267 (0.050) | ... | 0.324 | 0.818 | 17.1 |
| DIN + SRP + $Q$ | 9.195 (0.243) | 0.123 (0.065) | 0.243 (0.065) | −0.324 (0.049) | 0.777 | 0.777 | 18.6 |
| DIN + SRP | 9.112 (0.132) | 0.078 (0.072) | 0.217 (0.066) | ... | 0.315 | 0.844 | 19.2 |
| DIN + $Q$ | 9.170 (0.092) | 0.237 (0.069) | ... | −0.307 (0.089) | 0.504 | 0.666 | 26.3 |
| DIN | 9.100 (0.169) | 0.242 (0.062) | ... | ... | 0.199 | 0.825 | 25.0 |
| $Q$ | 9.161 (0.131) | ... | ... | −0.223 (0.121) | 0.294 | 0.515 | 33.0 |

highest proportion of variance explained by the fixed effects, at 68% and 72%, respectively (Appendix S1: Table S2). The $R^2_m$ for the remaining models, including other top competing models, ranged from 0.52 (DIN + SRP) to 0.20 (discharge). For the SRP + discharge model, SRP had a 1.2× greater effect on primary consumer production than discharge. In the full model, discharge had a 1.1× greater effect than SRP and a 2.2× greater effect than DIN on primary consumer production. For shredders, the three top models included those containing SRP + discharge, all three predicted drivers, and SRP + DIN (Appendix S1: Table S3). Among these models, the fixed effects explained between 73% and 79% of variation in shredder production. Discharge consistently had the strongest effect (1.6× to 2.1× greater than SRP; 1.5× to 3.3× greater than DIN) among predictors in all three models (Appendix S1: Table S3).

We predicted that discharge and both DIN and SRP concentrations would indirectly affect ACSP via their effects on LLSS and litter N and P content. Our second set of linear mixed-effects models confirmed strong relationships between two hypothesized pairs of indirect and direct drivers: a negative relationship between mean annual discharge and LLSS ($R^2_m = 0.75$, $R^2_c = 0.89$; Figure 1A) and a positive relationship between SRP concentrations and leaf litter %P ($R^2_m = 0.43$, $R^2_c = 0.84$; Figure 1B).

Annual community (Table 2), shredder (Appendix S1: Table S4) and primary consumer (Appendix S1: Table S5) production were all positively influenced by both resource quantity and leaf litter %P, and weakly negatively related to leaf litter %N. For ACSP, the top two models, based on $AIC_c$, included the LLSS + litter %P model, which explained 59% of variation in production. In this model, LLSS had a 1.5× greater effect on ACSP than litter %P (Table 2). All three direct drivers were included in the second model, in which the fixed effects collectively explained 62% of variation in ACSP. The relative effect sizes of LLSS and %P were 3.1× and 2.7× greater, respectively, than that of leaf litter %N (Table 2). In individual models, the three direct drivers alone explained between 8% (%N) and 46% (LLSS) of variation in ACSP as fixed effects (Table 2).

The two competing top models of primary consumer production were the full model and the %P + LLSS model, in which the fixed effects explained 51% and 42% of the variation in production, respectively (Appendix S1: Table S4). In the full model, leaf litter %P and LLSS had a similar effect on production, which for both was 1.6× greater than that of leaf litter %N. In the %P + LLSS model, LLSS had a 1.5× greater effect on production than litter %P. For shredders, the top model, based on $AIC_c$, was the %P-only model, which explained only 24% of the variation in production (Appendix S1: Table S5). In the second-best model ($\Delta AIC_c = 3$), which included %P and LLSS, the effect of leaf litter %P on production was 4.6× greater than that of LLSS, indicating a weak LLSS effect. Although the %P-only model was the top model based on $AIC_c$, the LLSS-only model explained the most variation (49%) in shredder production.

Finally, we visualized the relative strength of resource quantity and quality in limiting macroinvertebrate production using response-surface plots. Plots using both indirect (Figure 1C) and direct (Figure 1D) drivers showed that the highest rates of ACSP were predicted to occur in streams with low mean annual discharge (= high LLSS) and high mean annual SRP concentration (= high %P content of leaf litter), though these conditions were not explicitly targeted in any of the experiments.

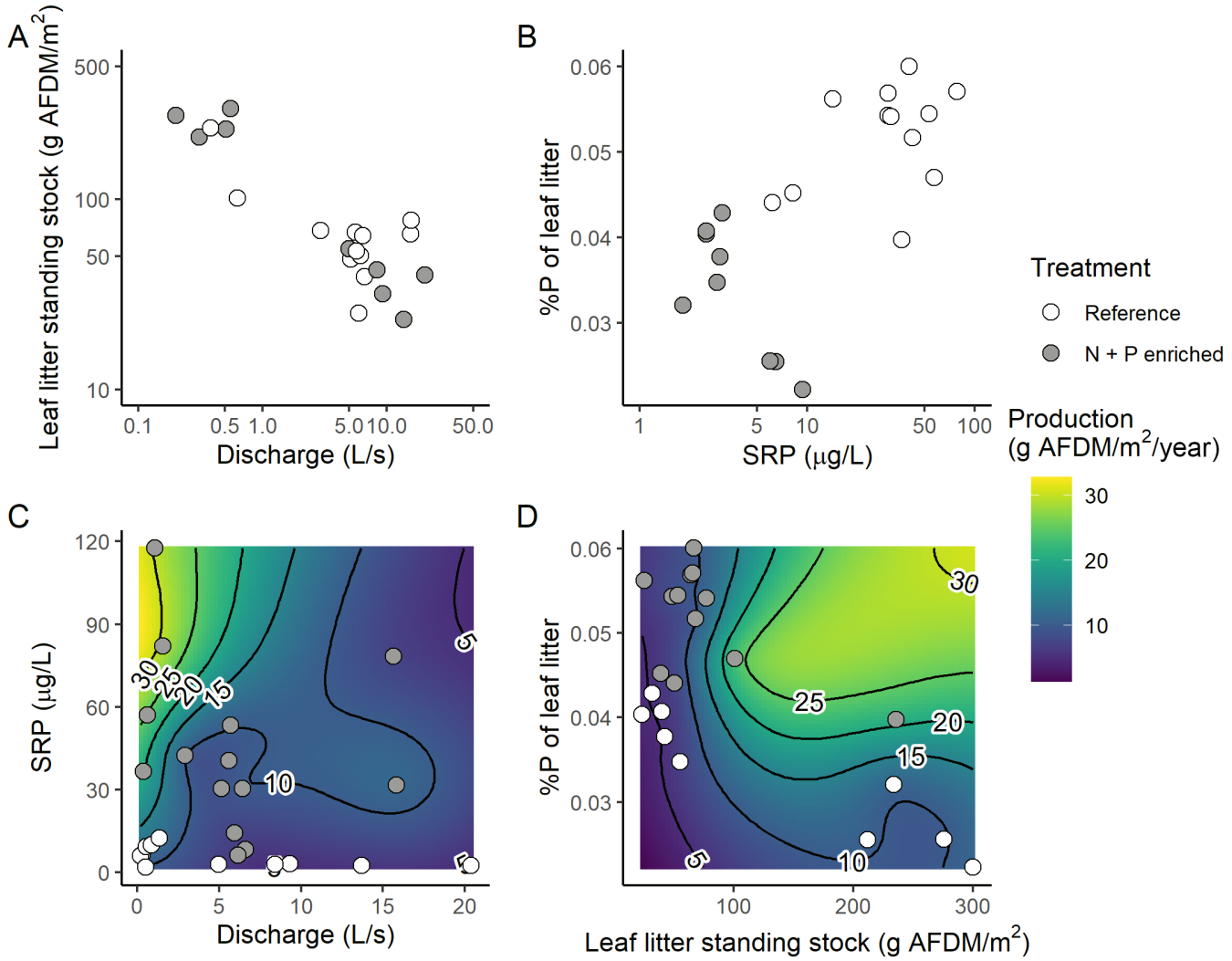


**FIGURE 1** Relationships between hypothesized indirect and direct drivers of annual community secondary production, including discharge and leaf litter standing stock biomass (A; $R^2_m = 0.75$, intercept: 4.877 [±0.168], discharge: −0.491 [±0.087]) and soluble reactive phosphorus (SRP) and %P of leaf litter (B; $R^2_m = 0.43$, intercept: 0.029 [±0.004]; P: 0.006 [±0.001]) as well as surface plots indicating co-limitation of production by hypothesized indirect drivers (SRP and discharge, C) and direct drivers (leaf litter standing stock biomass and %P, D). For panels A and B, axes are $\log_{10}$-scaled in correspondence with variables that were $\log_e$-transformed for data analysis. Contour labels indicate predicted rates of total production in grams of ash-free dry mass per square meter per year. Plotted points in panels (C) and (D) indicate measured values of predictor variables from each sample year. $n = 21$ in panels (A), (B), and (D) and $n = 25$ in panel (C).

## DISCUSSION

We found that both the quantity and P content of leaf litter strongly limited annual secondary production in these small forest stream ecosystems. Our results, which indicate simultaneous energy (resource quantity) and nutrient (P) limitation of secondary production, are consistent with predictions rooted in ecological stoichiometry and co-limitation theory. Our analysis is the first to extend such a result from individual consumers (Halvorson et al., 2017; Prater et al., 2024) to biomass production of entire consumer assemblages in natural ecosystems. Although our analysis indicates that the highest rates of secondary production are likely to occur when resource quantity and quality (%P) are high, these conditions never occurred simultaneously during any year of this study. Furthermore, because increases in leaf litter P (and N) content are a function of increased microbial activity, it may be unlikely that very high %P and standing stocks of leaf litter will co-occur, as elevated microbial activity results in more rapid decomposition of leaf litter and lower annual mean LLSS (Rosemond et al., 2015).

Energy limitation of consumers is a foundational concept in ecology and is consistent with the results of this study and others that report a positive relationship

**TABLE 2** Linear mixed-effects model results ($n = 21$) for annual community secondary production based on proposed direct drivers, which include leaf litter %N (N), %P (P), and leaf litter standing stock (LLSS).

| Model | Parameter estimates (SE) | | | | $R^2_m$ | $R^2_c$ | $AIC_c$ |
|---|---|---|---|---|---|---|---|
| | Intercept | N | P | LLSS | | | |
| P + LLSS | 9.062 (0.075) | ... | 0.253 (0.064) | 0.387 (0.076) | 0.586 | 0.729 | 15.4 |
| N + P + LLSS | 9.062 (0.074) | −0.110 (0.073) | 0.292 (0.065) | 0.339 (0.078) | 0.618 | 0.770 | 17.2 |
| P | 9.062 (0.190) | ... | 0.291 (0.059) | ... | 0.236 | 0.911 | 20.0 |
| N + P | 9.062 (0.171) | −0.117 (0.074) | 0.324 (0.062) | ... | 0.252 | 0.900 | 21.2 |
| LLSS | 9.062 (0.072) | ... | ... | 0.291 (0.073) | 0.455 | 0.476 | 22.0 |
| N + LLSS | 9.062 (0.072) | −0.008 (0.091) | ... | 0.287 (0.091) | 0.456 | 0.75 | 25.5 |
| N | 9.062 (0.109) | −0.117 (0.095) | ... | ... | 0.081 | 0.355 | 29.3 |

Abbreviation: $AIC_c$, corrected Akaike information criterion.

between secondary production and basal resource quantity (McNaughton et al., 1989; Wallace et al., 2015). For example, Patrick et al. (2019) found a strong positive association between basal resource quantity and ACSP in a continental-scale analysis of stream ecosystems. The authors argued that warmer temperatures and increased flow stability support greater basal resource quantity, highlighting an important link between ACSP and key climatic factors (temperature and precipitation) over large spatial scales. Our analysis of secondary production in small forest streams also revealed an important role for stream discharge in modulating patterns of macroinvertebrate production because higher mean annual discharge reduces LLSS. Indeed, discharge was included in two of the top three models of ACSP, two of the top four models of primary consumer production, and each of the top three models of shredder production. In each case, models that included discharge explained a greater proportion of variance in secondary production than those that did not. Moreover, we argue that much of the random (stream) effect in our models can be explained by variation in discharge among streams, given that mean annual discharge varied by almost 2 orders of magnitude among the study sites (Appendix S1: Table S1) and because the inclusion of discharge (or LLSS) in models typically reduced the additional variance explained by the random effect (i.e., the difference between $R^2_c$ and $R^2_m$), sometimes to zero. Although other studies have reported strong relationships between basal resource quantity and other stream flow metrics, such as maximum stream flow, flow stability, and seasonality (Patrick et al., 2019; Wallace et al., 1995), mean annual discharge explained 75% of the variation in mean annual LLSS in our study and was included in many of the top models of indirect drivers of ACSP, primary consumer, and shredder production.

Our analysis also revealed an important role for resource quality, particularly P content, in driving rates of secondary production in these forest stream ecosystems, as leaf litter %P was included in all top models of ACSP, primary consumer, and shredder production. In models that included both %P and %N, the %P of leaf litter consistently had a greater relative effect on patterns of secondary production, indicating that P content is likely the primary component of resource quality that limits secondary production in these streams. This result is consistent with foundational concepts of ecological stoichiometry theory, which posits that the high C:P ratio of vascular plant detritus relative to detritivore demand (Cross et al., 2003) results in strong consumer P-limitation. Estimates of leaf litter %P among our study streams were positively related to stream water SRP concentrations and are likely driven by microbially induced shifts (i.e., higher fungal biomass) in resource nutrient content (Manning et al., 2015). Interestingly, leaf litter %N effects on secondary production were generally negative. However, we argue that this is likely an artifact of our experimental design, given that low DIN additions were paired with high SRP during some of the enrichment experiments (Demi et al., 2018), as well as the primacy of P-limitation of these food webs, rather than an indication of inhibition of consumers by elevated resource N content. Lastly, though we tested effects of only two aspects of resource quality, %P and %N content, other diet components, such as total lipid or fatty acid content, may also be important controls on consumer ingestion, growth, and survival rates (Torres-Ruiz et al., 2007; Twining et al., 2021). However, given the prevalence of limited P availability in undisturbed habitats, the low P content of detritus, and the essential role of P in building biomass, it is not surprising that we found litter P content to be a strong predictor of secondary production.

Identification of key indirect drivers of secondary production, and their links to resource quantity and quality, provides valuable insight into how this important ecosystem process may respond to continued anthropogenic forcing in a variety of ecosystems. For example, increased variability in precipitation (the primary driver of stream discharge), resulting from anthropogenic climate change, is predicted to reduce detrital quantity in streams (Catalan et al., 2023) and alter, and in some cases reduce, terrestrial primary productivity in some biomes (Ritter et al., 2000). Moreover, the effects of human activities on global patterns of nutrient availability (Peñuelas et al., 2013) further modify basal resource quantity and quality in many ecosystems via shifts in basal resource productivity, residence times, and edibility (Du et al., 2020; Rosemond et al., 2015). In aquatic ecosystems supported by living autotroph biomass (as opposed to detritus) increased nutrient availability may increase both the quantity and quality of basal resources, leading to greater effects on consumer production than those reported here. A notable exception is when nutrients stimulate unpalatable autotrophs such as some cyanobacteria, leading to reduced quality and quantity of food for consumers. Additionally, whether N or P are limiting is likely to vary among ecosystems and as a function of the sources and magnitude of anthropogenic nutrient loading (Du et al., 2020; Peñuelas et al., 2013). Although the magnitude and direction of effects of altered precipitation and nutrient availability on basal resources are likely to differ among ecosystems, this study demonstrates that subsequent changes to basal resource quantity and quality may affect the productivity of consumer assemblages in predictable ways.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Demi et al., 2025a) are available in Dryad at https://doi.org/10.5061/dryad.m63xsj4d3. Code (Demi et al., 2025b) is available in Zenodo at https://doi.org/10.5281/zenodo.14775265.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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