ECOLOGY

Precipitation and temperature drive continental-scale patterns in stream invertebrate production

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Secondary production, the growth of new heterotrophic biomass, is a key process in aquatic and terrestrial eco-systems that has been carefully measured in many flowing water ecosystems. We combine structural equation modeling with the first worldwide dataset on annual secondary production of stream invertebrate communities to reveal core pathways linking air temperature and precipitation to secondary production. In the United States, where the most extensive set of secondary production estimates and covariate data were available, we show that precipitation-mediated, low–stream flow events have a strong negative effect on secondary production. At larger scales (United States, Europe, Central America, and Pacific), we demonstrate the significance of a positive two-step pathway from air to water temperature to increasing secondary production. Our results provide insights into the potential effects of climate change on secondary production and demonstrate a modeling framework that can be applied across ecosystems.

INTRODUCTION

Secondary production is the generation of new heterotrophic biomass over time. It is a fundamental ecosystem process because it requires the consumption of basal energetic sources while sustaining consumers at higher trophic levels in both aquatic and terrestrial food webs (1–5). Secondary production can be used to assess higher-level responses to environmental change (6) and human perturbations (7, 8), including ecosystem services such as water filtration (9, 10) and fisheries production (11, 12). Understanding how secondary production may respond to climate change is therefore essential. Invertebrates are diverse and productive members of most food webs and comprise the majority of metazoan diversity globally. Previous research has characterized local-scale effects of temperature on individual invertebrate taxa (13–15), but the potential effects of continental- to global-scale shifts in temperature and precipitation on entire communities of invertebrate secondary producers are largely unknown (16).

Identifying drivers of annual community secondary production (ACSP), defined as the sum of annual production of all invertebrate populations within a community (17), is particularly challenging because individual- and species-level processes do not always scale up to the community level in a direct additive manner. Functional redundancy in the roles that species play within a food web can offset environmental perturbations via compensatory effects on overall production (18). For this reason, ACSP may be a more useful holistic indicator of the ecosystem-level effects of climate change than production rates of discrete taxa or functional groups. Unfortunately, studies of the effects of macroscale shifts in temperature and precipitation on ACSP, which are difficult to conduct in experimental settings, are rare [but see (19)].

Previous research in stream and river ecosystems provides a unique opportunity to further understand the linkages between ACSP and climate. When compared to other types of ecosystems, empirical studies of ACSP in streams and rivers are relatively common (20, 21). We leveraged this previous work by combining a literature review on freshwater ACSP with geospatial analysis, hydrologic modeling, and structural equation modeling (SEM) to test hypotheses linking air temperature and precipitation to ACSP in lotic ecosystems. Our ultimate goal was to build a systems-level framework that can be expanded or refined in future research and used to predict climate-driven changes in ACSP.

Our study focuses primarily on the effects of air temperature and precipitation on ACSP because both factors are closely linked to physicochemical conditions in freshwater ecosystems. Air temperature is a principal driver of water temperature in lotic systems (22), and water temperature stimulates in-stream primary production (23, 24); this two-step pathway may link air temperature to ACSP (25). Precipitation effects on ACSP may be mediated by hydrology, which is a key determinant of habitat stability for benthic invertebrates that reside on or within streambed substrates. Stable flows promote well-sorted substrates that support high invertebrate densities and allow extended growth periods (26, 27). In contrast, systems that experience extreme floods and/or droughts tend to have low secondary production (7, 28, 29).

We began this study with an extensive literature review of empirical measurements of ACSP in lotic ecosystems and associated in situ covariates, such as water temperature and channel substrate characteristics. We then used a geographic information system to append spatially derived covariates, including land use, elevation,

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slope, and local climate, to the ACSP data. Many environmental co-variates were available for study sites within the United States, but only climate and elevation data were consistently available for sites outside of the United States. New hydrologic variables, such as minimum 30-day stream flow (the minimum average discharge that persists for 30 consecutive days), were then calculated by using existing covariates as predictors in statistical models (see Materials and Methods) and appended to the covariate data for U.S. sites. By combining covariates from multiple sources, we were able to expand the number of variables and causal pathways that we tested in models of ACSP.

Links between climate and ACSP were then tested with a combination of traditional univariate regression analysis and SEM. The latter approach was central to our study because SEMs can be used to evaluate cause-and-effect relationships among discrete variables (30), can explicitly account for covariation among variables, and can simultaneously test systems-level hypotheses that are expressed as complex networks of interrelationships among variables (31). Development of SEMs of ACSP constitutes a significant advance, relative to previous reviews of aquatic secondary production (1, 32), because it allows us to evaluate multiple drivers of ACSP within a single integrative framework. In addition, this study demonstrates a novel yet general approach to integrate meta-analysis of published results, covariate data that were mined from independent sources and appended to published data, and statistical modeling (univariate regression and SEM) for the purpose of deriving greater insight from published information and creating new conceptual understanding of connections among suites of environmental and biotic variables.

Before model building and testing, we outlined an a priori hypothesis or "metamodel" (30) of systems-level links between major climate variables and ACSP (Fig. 1). Habitat stability and water temperature were predicted to be proximal drivers of ACSP. Hydrology (28), channel substrate (33), and land cover (34) were predicted to drive habitat stability. Air temperature (22), canopy shading (35), and stream channel size (36) were predicted to influence water temperature. Precipitation, latitude, and elevation were predicted to act as distal effects on ACSP, mediated through their effects on temperature and riparian vegetation.

Models were tested at two distinct spatial scales. First, we modeled ACSP at the continental scale, using only U.S. study sites. This allowed us to test complex cause-and-effect relationships using the full suite of environmental covariates that was assembled for U.S. sites. Second, we developed simpler ACSP models at a larger scale that included sites from Europe, Central and South America, and New Zealand. These inclusive models were constrained by the smaller number of environmental covariates that were available at all study sites, but they did allow us to test the generality of some key results from the U.S. models.

RESULTS AND DISCUSSION

Among all U.S. samples, ACSP spanned four orders of magnitude [35 to 612,231 mg ash-free dry mass (AFDM) m^{-2} year^{-1}] and was strongly positively skewed [median, 9991; coefficient of variation (CV), 0.41; see Fig. 2A, inset]. A nearly identical distribution of ACSP was observed at the global scale (median, 9982; CV, 0.42; see Fig. 2B, inset). In U.S. streams, univariate regression analyses detected significant positive effects of mean annual water temperature, basin area, minimum 30-day flow, and percent urban development on

ACSP (Table 1), consistent with hypothesized links A, B, E, F, and H in Fig. 1. A significant negative effect was also detected for percent forest cover, as predicted by link C in the metamodel. Of the univariate relationships, water temperature had the strongest overall effect on ACSP (standardized effect size β = 0.39).

Nine covariates and 14 path links were retained in the final SEM for U.S. streams (Fig. 2A and Table 2). Of these, some paths were simple and predictable, such as the strong effect of air temperature on water temperature (37), the effects of latitude and elevation on air temperature, and the effect of precipitation on minimum 30-day discharge. However, other paths were more complex. For instance, the total effect of precipitation on water temperature included two paths: a direct positive link from precipitation to water temperature and a negative indirect link that was mediated by forest cover (precipitation → forest cover → water temperature; see Fig. 2A). This indirect effect of precipitation on water temperature may be attributed to wetter regions having comparatively dense forests with larger canopies and more extensive shading (38, 39) or enhanced evaporation (40).

The U.S. SEM confirmed many of the hypothesized pathways in the metamodel (Fig. 1), most notably the direct influence of base flow stability and water temperature on ACSP. Significant indirect effects of climate (air temperature and precipitation), the physical landscape (catchment elevation and basin area), and land cover (impervious surface area and forest cover) on ACSP were mediated through their direct effects on water temperature and base flow stability. The final inclusive SEM complimented the U.S. model by confirming that air temperature and precipitation have consistent, predictable effects on ACSP that are mediated by their direct effects on water temperature (Fig. 2B).

The positive effect of water temperature on ACSP in the U.S. and global models is perhaps intuitive, but our quantitative results raise pressing theoretical questions and can help to reconcile conflicting results from previous site-specific studies. The metabolic theory of ecology (MTE) predicts that standing stock biomass should decrease with increasing temperature, while the production-to-biomass (P:B) relationship should increase with temperature, resulting in no net change in secondary production (41). Some empirical support for this prediction is provided by observational meta-analyses (32) and controlled in situ stream warming experiments (16), but other studies have documented net positive effects of temperature on body size, growth rates, and total production (1, 25). Our results, which constitute the most comprehensive meta-analysis to date, indicate that the relationship between temperature and ACSP is net positive. Given that the MTE assumes constant resource supply, we posit that the mechanism responsible for the observed positive relationship between water temperature and ACSP may be a temperature-mediated increase in basal resources (42). Thus, we suggest that closer examination of the effect of basal resources on ACSP should be a priority area in future research (43–45).

Basal resources are likely to improve systems-level models of ACSP because food quality and quantity are already known to be fundamental determinants of individual growth (46–48) and of ACSP (49) in aquatic ecosystems. For instance, allochthonous leaf litter has low nutritional value, relative to autochthonous material, but can account for >90% of the annual variation in secondary production within temperate streams because it is so abundant (45, 50, 51). Allochthonous material was not included in our models because it was not measured at most study sites (see data file 2). However,
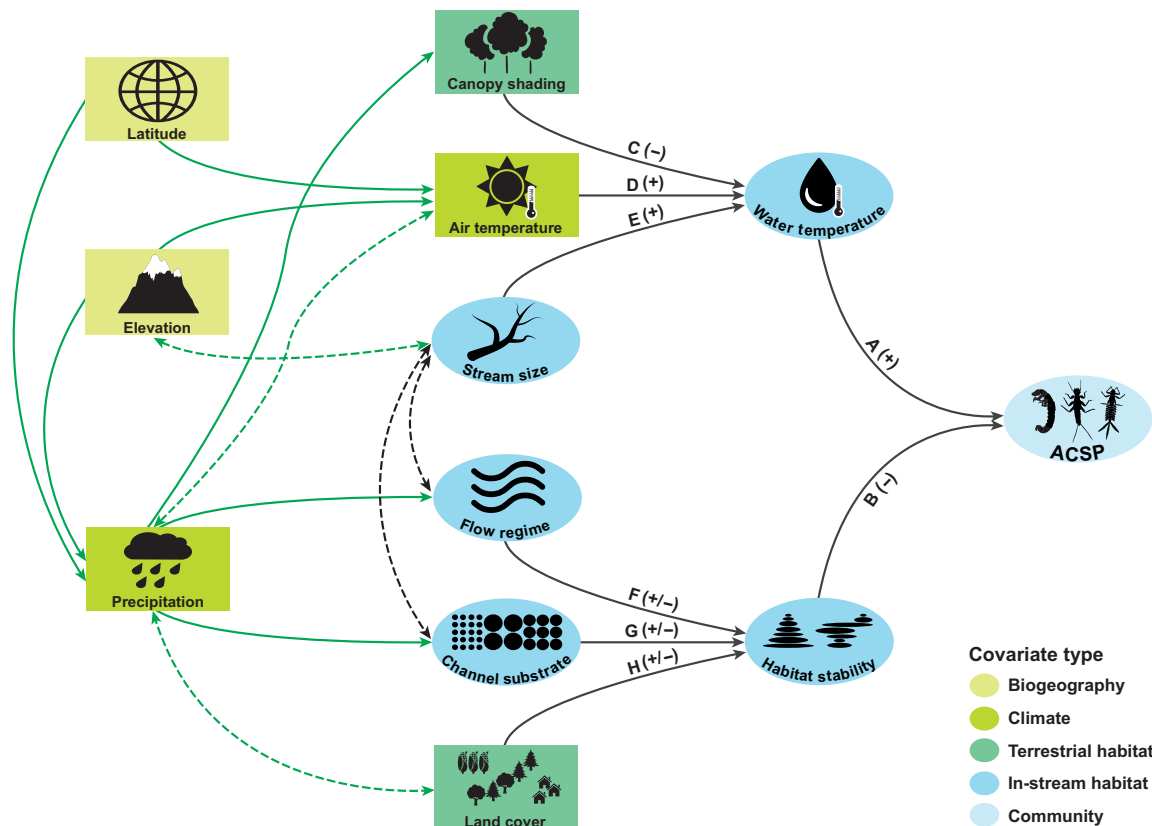
Fig. 1. Conceptual diagram or metamodel of major hypothesized influences on ACSP. Covariates that are external to stream ecosystems (i.e., exogenous variables) are indicated by rectangles. Covariates that are direct measures of in-stream conditions or processes (i.e., endogenous variables) are indicated by ovals. Each covariate is also recognized as one of five color-coded types (see inset key): biogeography, climate, terrestrial habitat, in-stream habitat, and community. Solid black arrows depict known causal effects among covariates. Arrow labels correspond to exemplar references [A (*23, 25*), B (*26, 27*), C (*35, 94*), D (*22, 95*), E (*36, 96*), F (*7, 28*), G (*29, 33*), H (*34, 97*)]. Parenthetic signs next to black arrow labels indicate that the relationship is expected to be positive (+), negative (−), or variable (+/−). Solid green arrows depict fundamental relationships that are expected but not explicitly documented here (e.g., the negative relationship between latitude and air temperature). Dashed arrows depict hypothesized covariation among variables.

using a subset of U.S. studies that measured both allochthonous organic material and ACSP (*n* = 41), we detected a strong positive univariate relationship between coarse particulate organic matter (CPOM) and ACSP ($r^2 = 0.279$, $P < 0.001$). Notably, CPOM accounted for more of the variation in ACSP than water temperature and habitat stability combined (in the U.S. SEM; see Fig. 2A). We are therefore confident that additional information on basal resources and the mechanisms that link them to climate (*52–55*) will enhance our ability to predict ACSP in changing climates.

Hydrology also stood out as a key regulator of ACSP. Results from U.S. streams indicated that discharge magnitude during dry or low flow periods (i.e., minimum 30-day flow) has a significant positive effect (β = 0.24) on ACSP (Fig. 2A and Table 1). While this is consistent with previous site-specific findings that environmental stability increases in-stream production (*56–58*), our study is the first to demonstrate this relationship at the continental scale. Hydrologic stability, as one dimension of environmental stability in lotic ecosystems, is known to have a significant effect on secondary production (*59–62*), particularly in drought-prone systems (*63*). However, the effect of hydrology did not extend to measures of flooding or "flashiness." These factors are important to invertebrates in some lotic ecosystems (*26, 58, 64*), but they did not have a significant effect on ACSP in our analyses. This may be due to variation

among communities in the response to flashiness, where naturally flashy streams are inhabited by organisms with adaptive traits that convey resilience (*59, 65*).

One notable difference between the U.S. and inclusive models was a significant positive effect of absolute latitude on ACSP; this link between latitude and ACSP, which was independent of a latitudinal effect on temperature, was detected in the inclusive model but not in the final U.S. model. The difference may be an artifact of the truncated range of latitudes among U.S. streams relative to the global range. However, it may also indicate that additional information on benthic community structure is needed to understand ACSP at global scales. Links between benthic diversity, biomass (*66, 67*), and secondary production (*68, 69*) have been documented in freshwater ecosystems, and benthic invertebrate diversity is known to vary with latitude (*70, 71*). Incorporating new dimensions of community structure, such as diversity and standing stock biomass, may therefore help to explain the effect of latitude on ACSP.

Moving forward, an obvious goal should be to increase the explained variation in ACSP. Coefficients of determination for ACSP were <0.25 in both the U.S. and global SEMs (Fig. 2)—a strong indication that some key variables were not included in the models. Here, our goal was to advance conceptual understanding of the systems-level drivers of ACSP by identifying causal pathways that link climate
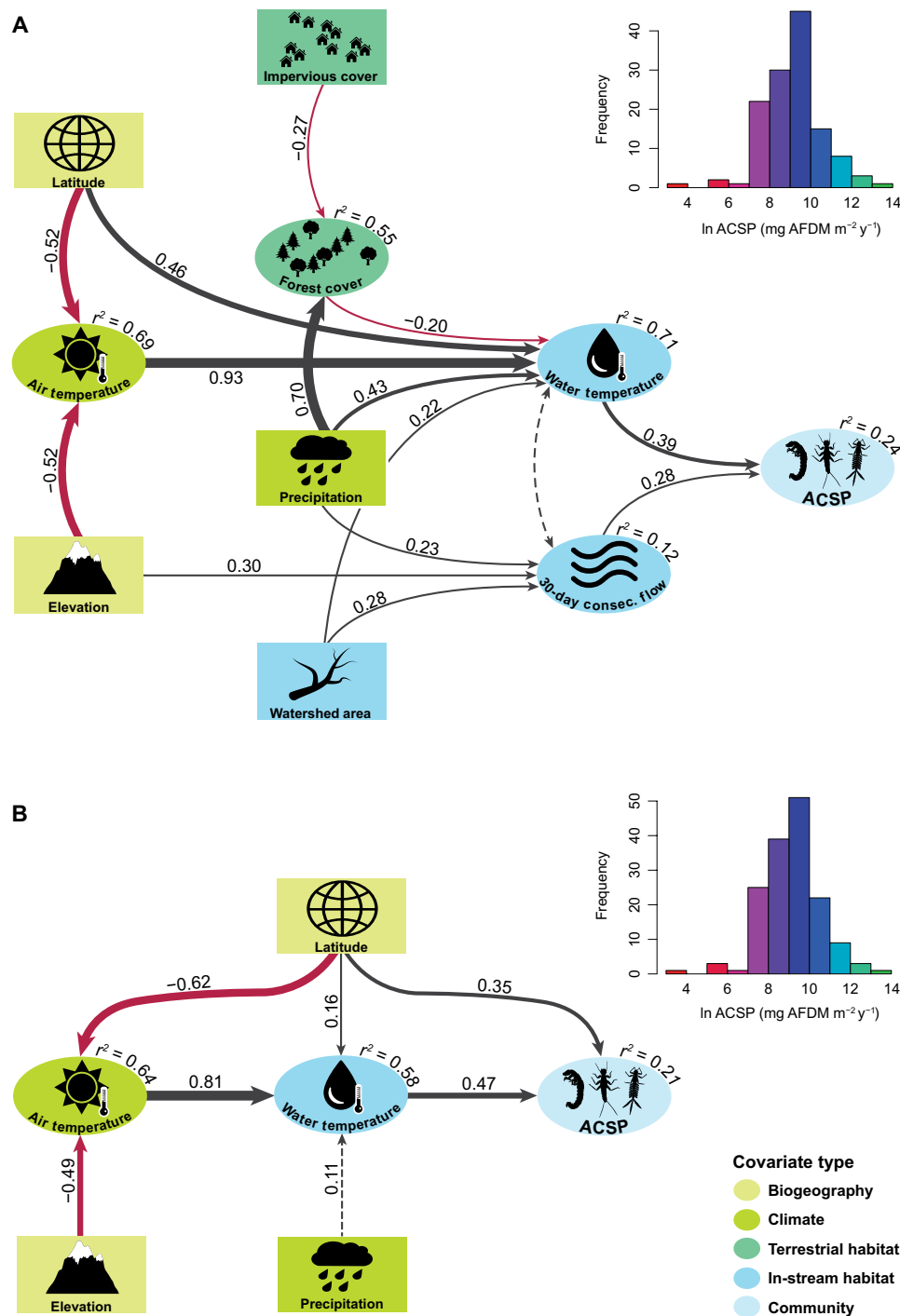
Fig. 2. SEMs of ACSP in streams and rivers. Models include an SEM for the U.S. (**A**) and for global streams and rivers (**B**). Exogenous variables are indicated by rectangles, and endogenous variables are represented by ovals. Coefficients of determination (r^2) are shown for all endogenous variables, and standardized path coefficients are shown for all modeled relationships. Positive and negative effects among variables are depicted by black and red arrows, respectively, with arrow widths proportional to effect sizes (i.e., path coefficients). In the U.S. model, significant covariance between mean annual water temperature ("Water temperature") and the minimum average discharge that persists for 30 consecutive days ("30-day consec. flow") is depicted by a dashed double-headed arrow. In the global model, the dashed arrow between mean annual precipitation ("Precipitation") and mean annual water temperature indicates a nominally significant ($P = 0.09$) effect; all other relationships in the U.S. and global models are significant at $P = 0.05$. Both the U.S. and global models satisfied each of the three model fit criteria, with significant χ^2 P values (U.S. = 0.06; global = 0.63), standardized root mean squared residuals (U.S. = 0.06; global = 0.02), and comparative fit index values (U.S. = 0.97; global > 0.99). Inset histograms show the distribution of natural log (ln)–transformed ACSP at U.S. and global scales. Covariate types are as shown in Fig. 1.

Table 1. Comparison of effect sizes in univariate regression models of ACSP in U.S. streams. Unstandardized regression slopes (*b*) and standardized slopes (β) are each reported with 95% confidence intervals (shown in parentheses) as well as sample sizes (*n*) and coefficients of determination (r^2). Covariates shown in bold text have slopes (95% confidence intervals) that exclude zero and are therefore considered statistically significant.

Hypothesized effect	Covariate	*n*	*b*	β	r^2
Temperature	Mean annual air temperature	128	1.32 (−0.11 to 2.75)	0.16 (−0.01 to 0.34)	0.02
	Mean annual water temperature	**107**	**1.32 (0.74 to 1.90)**	**0.39 (0.22 to 0.57)**	**0.15**
Canopy shading	**% Forest cover in catchment**	**128**	**−0.56 (−1.06 to −0.06)**	**−0.19 (−0.37 to −0.02)**	**0.03**
Stream size	**Basin area**	**128**	**0.10 (0.02 to 0.19)**	**0.21 (0.03 to 0.38)**	**0.03**
	Mean annual discharge	102	0.04 (−0.03 to 0.11)	0.10 (−0.08 to 0.27)	<0.01
Hydrology	Flashiness	124	−0.23 (−0.64 to 0.19)	−0.10 (−0.27 to 0.08)	<0.01
	CV discharge	124	−0.20 (−0.86 to 0.45)	−0.06 (−0.24 to 0.13)	0.01
	Minimum 30-day consecutive flow	**124**	**1.36 (0.39 to 2.33)**	**0.24 (0.07 to 0.42)**	**0.05**
Channel substrate	Average sediment size (unweighted)	88	−0.10 (−0.22 to 0.02)	−0.17 (−0.38 to 0.04)	0.02
	Average sediment size (weighted)	88	−0.12 (−0.24 to 0.00)	−0.20 (−0.41 to 0.01)	0.03
Land cover	Impervious surface in basin	124	3.24 (−0.19 to 6.67)	0.16 (−0.01 to 0.34)	0.02
	% Medium density urbanization in catchment	**128**	**3.39 (1.11 to 5.68)**	**0.25 (0.08 to 0.42)**	**0.06**
	% Crop cover in catchment	128	0.86 (−0.46 to 2.18)	0.11 (−0.06 to 0.29)	0.01

to ACSP; we did not seek to maximize explained variation in ACSP per se. The SEM allowed us to test the hypothesized linkages among variables (Fig. 1) in a critical and explicit way. Nevertheless, future progress will benefit from the addition and testing of new covariates and links between climate and ACSP.

Basal resource availability was previously noted as a priority research topic. Another focus area should be the role of anthropogenic stressors on ACSP. Previous research has reported a positive relationship between some land-use activities and ACSP that covaries with watershed area (72). Consistent with this earlier finding, we detected a positive relationship between watershed area and ACSP. However, when impervious surface area and agricultural land use were added to preliminary SEMs, we were unable to detect a significant influence of either variable on ACSP. The apparent lack of a strong land-use effect on ACSP may be a sampling artifact, as many of the study sites were located at field stations where human impacts were likely minimal. For example, 64% of all streams in the U.S. database were entirely unaffected by row-crop agriculture and only 7% of the U.S. streams flowed through watersheds, where row-crop agriculture accounted for >10% of internal land use. Thus, the current ACSP database may be ill suited to evaluate land-use effects, leaving a key information gap to be filled.

Despite the limitations of the ACSP models, our results have clear implications for ecosystem function in the face of climate change. Climate models predict that over the next century, average air temperatures will continue to rise (73) and precipitation patterns will shift markedly (74, 75). Our models suggest that these changes will

have cascading effects on ACSP mediated through water temperature and discharge during dry periods. For instance, the SEMs predict that warming temperatures will tend to increase ACSP. However, the frequency and severity of low flow events are expected to increase in many ecosystems as subhumid regions transition to semiarid climates (75–77). If these systems are populated by invertebrates that lack physiological or life history traits that allow them to persist under drought conditions, temperature-driven increases in ACSP are likely to be offset by increased mortality or diminished recruitment.

In conclusion, we suggest that four key areas of research should now be pursued to advance understanding of ACSP. First, new ACSP data from undersampled regions are needed to determine whether the results presented here are applicable in other parts of the globe. Second, a better understanding of the roles that basal resources or other bottom-up trophic constraints play in regulating ACSP and how these basal factors are affected by climate is needed. Third, the effects of anthropogenic stressors should be incorporated in systems-level models. Fourth, the general ACSP results should be tested using habitat-specific production estimates (3, 60, 62), paying special attention to account for differential effects on specific invertebrate traits or functional groups (78, 79). Addressing each of these needs will be a challenging and labor-intensive process, but we have shown that an enhanced understanding of the complex mechanisms that drive ACSP at continental to global scales is achievable when the efforts and data of many ecologists are integrated within an appropriate modeling framework.

Table 2. Direct and total effects of each driver on ACSP in the U.S. and global models. Total effects are calculated as the sum of the direct and indirect effects of the predictor on the response variable.

SEM model	Predictor	Response	Direct	Total effect
U.S. model	Water temperature	ACSP	0.39	0.39
	30-day consecutive flow	ACSP	0.28	0.28
	Precipitation	ACSP		0.18
	Air temperature	ACSP		0.36
	Impervious cover	ACSP		0.02
	Watershed area	ACSP		0.16
	Mean elevation	ACSP		−0.10
	Absolute latitude	ACSP		−0.01
	Forest cover	ACSP		−0.08
Global model	Absolute latitude	ACSP	0.35	0.19
	Air temperature	ACSP		0.38
	Mean elevation	ACSP		−0.19
	Precipitation	ACSP		0.05
	Water temperature	ACSP	0.47	0.47

MATERIALS AND METHODS

We used the following workflow: (i) perform a literature review of invertebrate ACSP studies; (ii) append environmental covariates to the ACSP data assembled in the literature review; (iii) use univariate regression to test significant relationships between key covariates and ACSP; and (iv) use SEM to identify causal pathways within networks of interacting covariates, thereby distinguishing direct from indirect drivers of ACSP (*31*). SEM analyses were conducted at two scales: streams throughout the United States and a global analysis of streams distributed across six continents (fig. S1). By first analyzing U.S. streams, we were able to use a large standardized set of environmental covariates in critical testing of the metamodel (Fig. 1). The global-scale analysis was limited by a reduced number of covariates, but it allowed us to examine the generality of some key pathways in the U.S. model.

Literature review

Potential sources of ACSP data were first identified through an ISI Web of Science search (keywords "stream OR streams OR creek OR lotic AND benthic OR benthos OR invertebrate OR macroinvertebrate AND production") that returned 468 sources (peer-reviewed publications, government reports, or indexed theses). Each of these publications was then checked for compliance with three a priori criteria: (i) Data were exclusive to within-channel ACSP and did not include estimates of floodplain production; (ii) samples were inclusive of all locally occurring taxa and did not focus on a discrete subset of taxa or functional feeding groups; and (iii) ACSP estimates were inferred from repeat samples collected throughout the year [e.g., size frequency or cohort methods (*17*)], rather than P:B relationships (*80*). However, ACSP estimates inferred from P:B relationships were acceptable when used solely to "fill in" production estimates for rare or low biomass taxa that could not be partitioned into distinct size classes or cohorts. This screening process reduced the initial list of 468 publications to 56, most of which included ACSP estimates for multiple sites; from

the final 56 publications, we obtained 164 site-specific estimates of ACSP. Most study sites are located in the contiguous United States (*n* = 137; fig. S1A), with others in Europe (fig. S1B), Iceland, Costa Rica, Panama, Chile, and New Zealand (sites not shown in fig. S1). Complete citation information for all sites retained in this study are listed in data file S1. Before analyses, all ACSP estimates were standardized to units of milligrams AFDM per square meter per year (mg AFDM m^{-2} year^{-1}), using conversion factors by Waters (*81*), and then natural log–transformed to improve normality.

Environmental covariates

To test the hypothesized relationships shown in the metamodel (Fig. 1), we appended a suite of environmental covariates, as well as author-reported total invertebrate biomass and density estimates, to each of the 164 ACSP study sites. These covariates included location information (longitude and latitude), water quality parameters (e.g., water temperature, pH, and conductivity), physical habitat characteristics (e.g., stream channel dimensions and substrate particle size), and climate conditions (air temperature and precipitation). Whenever possible, covariate values were obtained from the original literature sources or from companion studies that were conducted at the same study sites. Complete descriptions of all covariates in the ACSP database are listed in table S1 and detailed methods used to obtain them are provided in the Supplementary Materials. Availability of covariate data was variable, with many more covariates accessible for U.S. sites than non-U.S. sites. Two versions of the ACSP database were therefore prepared: a U.S.-only database with a large selection of covariates for each of the 137 U.S. sites (see data file S2) and a global-scale database inclusive of all 164 study sites but with a limited number of covariates for each site (see data file S3). Many of the covariates in the U.S. database were not represented in the metamodel (Fig. 1); these were included in the compiled database to provide a ready data source for testing hypotheses not considered here.

Hydrologic modeling

Hydrologic indices were independently predicted for each U.S. site, using time series of daily discharge records from the U.S. Geological Survey (USGS) Water Services portal (https://waterservices.usgs.gov), and appended to the ACSP dataset. We began by selecting a national sample of flow gauges from the USGS Geospatial Attributes of Gages for Evaluating Streamflow database [GAGES II; Falcone *et al.* (*82*)] that featured (nearly) continuous discharge records from 1970 through the present day; this duration allowed robust characterization of contemporary flow dynamics while maximizing the number and spatial distribution of gauges used to develop hydrologic models. We then removed gauges with upstream impoundments of >50 Ml (megaliters) km^{-2} (impoundment volume scaled by watershed area), as these sites may be more strongly influenced by dam release operations than natural precipitation and land-use factors (*83*). This screening process resulted in a sample of 2568 gauges.

Random forest models were then developed for a set of hydrologic indices, incorporating four of five hydrologic components: flow magnitude, frequency, duration, and rate of change (*84*). We began with models of 12 hydrologic indices that are broadly representative of perennial streams in a variety of conditions (*85, 86*). Flow magnitude was characterized by variability, skewness, two measures of spread, and median annual maximum flow. Flow frequency was characterized by low flow pulse percentage, frequency of low flow events, and two measures of high flood pulse percentage. Flow duration was characterized by the 30-day minimum and maximum daily discharge. Rate of change was characterized by hydrologic flashiness (*87*). Following Carlisle *et al.* (*88*), random forest models (500 iterations per model) were built for each flow index using the randomForest library in R (*89*). Each random forest model was parameterized with a suite of predictor variables representing precipitation, underlying geology, and land use, but excluding predictor variables that were subsequently used in SEMs of secondary production (forest cover, watershed size, and impervious surface in the upstream watershed). Random forest model fit differed among hydrologic indices, and we focused on those models that explained ≥45% of the variance in their respective indices. These included flashiness, high flow pulse percentage (i.e., number of daily values within a time series) exceeding the daily median by ×7 (HighFlowPulse7) and ×3 margins (HighFlowPulse3), minimum consecutive 30-day flow, low flow pulse percentage, and variation in daily flow. The final six random forest models were then used to predict flow indices at each of the stream sites included in the U.S.ACSP database.

Data analyses

A subset of 13 covariates (see Table 1), each representative of a hypothesized ACSP driver as shown in Fig. 1, was first selected for univariate regression analyses of U.S. streams. Associations between these covariates and ACSP were then independently tested with regression models of the general form ACSP = $b \times C + Y$, where C is the covariate of interest, b is a coefficient (i.e., regression model slope) relating C to ACSP, and Y is an intercept term. Natural log transformations were used to improve normality for covariates with skewed distributions. In cases where C was a categorical variable (e.g., stream order), b was calculated for each categorical level in comparison to a baseline level. For example, the stream order baseline was first-order (i.e., the smallest) streams. Thus, b for second-order streams was the difference between first- and second-order streams.

Because measurement units differed among covariates, standardized regression model parameter estimates were calculated [β (*90*)] to facilitate direct comparisons among covariates. Coefficients of determination (r^2) were also calculated for each regression model to estimate the variation in ACSP explained by the respective covariate.

Next, SEM was used to confront the ACSP metamodel (Fig. 1) with the empirical ACSP and covariate data (table S1). This allowed us to (i) assess the complete graphical network of hypothesized interactions and relationships, with the directions of links (i.e., paths) in the SEM diagram indicating causal influences, and (ii) test the overall fit of the network (*31, 91*). Separate models were fit to the U.S. and global databases, with the former used to test the complete network of interrelationships among covariates shown in Fig. 1 and the latter testing for generality of the U.S. results at the global scale. At each of the two scales, an iterative process of testing and linking covariates, consistent with the hypotheses outlined in the metamodel, was used to produce a final SEM of ACSP. Three indices of model fit were used with conventional significance thresholds—the χ^2 P value (χ^2 $P > 0.05$), the standardized root mean squared residual (SRMR ≤ 0.08), and the comparative fit index (CFI ≥ 0.95)—to assess the overall fit of each SEM (*92*). All SEM procedures were conducted with the lavaan library in R (*93*). Code to build the final U.S. and global models is provided in data file S4.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/5/4/eaav2348/DC1

Supplementary Materials and Methods

Fig. S1. Maps of study sites included in the ACSP database.

Table S1. Data dictionary for variables included in the secondary production database for U.S. streams.

Data file S1. Citation records for all studies included in the ACSP database.

Data file S2. Complete secondary production and covariate data for all U.S. streams.

Data file S3. Secondary production and covariate data for the global streams database.

Data file S4. R code to build the U.S and global SEM models.

References (*98–102*)

REFERENCES AND NOTES

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Science Advances

Precipitation and temperature drive continental-scale patterns in stream invertebrate production

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