Received: 18 September 2018 | Revised: 30 December 2018 | Accepted: 23 January 2019

DOI: 10.1111/gcb.14584

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Evaluating ecosystem effects of climate change on tropical island streams using high spatial and temporal resolution sampling regimes

Therese C. Frauendorf[1] | Richard A. MacKenzie[2] | Ralph W. Tingley III[3] | Abby G. Frazier[4] | Michael H. Riney[5] | Rana W. El-Sabaawi[1]

[1]Department of Biology, University of Victoria, Victoria, British Columbia, Canada

[2]Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, Hilo, Hawaii

[3]Missouri Cooperative Fish and Wildlife Research Unit, The School of Natural Resources, University of Missouri, Columbia, Missouri

[4]East-West Center, Honolulu, Hawaii

[5]Shasta Valley Resource Conservation District, Yreka, California

Correspondence
Therese Frauendorf, Department of Biology, University of Victoria, Victoria, British Columbia, Canada.
Email: tfrauend@uvic.ca

Funding information
USDA Pacific Southwest Research Station; USDA Washington Office

Abstract

Climate change is expected to alter precipitation patterns worldwide, which will affect streamflow in riverine ecosystems. It is vital to understand the impacts of projected flow variations, especially in tropical regions where the effects of climate change are expected to be one of the earliest to emerge. Space-for-time substitutions have been successful at predicting effects of climate change in terrestrial systems by using a spatial gradient to mimic the projected temporal change. However, concerns have been raised that the spatial variability in these models might not reflect the temporal variability. We utilized a well-constrained rainfall gradient on Hawaii Island to determine (a) how predicted decreases in flow and increases in flow variability affect stream food resources and consumers and (b) if using a high temporal (monthly, four streams) or a high spatial (annual, eight streams) resolution sampling scheme would alter the results of a space-for-time substitution. Declines in benthic and suspended resource quantity (10- to 40-fold) and quality (shift from macrophyte to leaf litter dominated) contributed to 35-fold decreases in macroinvertebrate biomass with predicted changes in the magnitude and variability in the flow. Invertebrate composition switched from caddisflies and damselflies to taxa with faster turnover rates (mosquitoes, copepods). Changes in resource and consumer composition patterns were stronger with high temporal resolution sampling. However, trends and ranges of results did not differ between the two sampling regimes, indicating that a suitable, well-constrained spatial gradient is an appropriate tool for examining temporal change. Our study is the first to investigate resource to community wide effects of climate change on tropical streams on a spatial and temporal scale. We determined that predicted flow alterations would decrease stream resource and consumer quantity and quality, which can alter stream function, as well as biomass and habitat for freshwater, marine, and terrestrial consumers dependent on these resources.

KEYWORDS

Hawaii, macroinvertebrate biomass, organic matter, precipitation gradient, resource quality, space-for-time substitution, streamflow

1 | INTRODUCTION

Climate change is threatening the ecosystems, yet our understanding of the effects of precipitation change on ecosystem structure and function remains limited. Temperature, atmospheric carbon dioxide, and precipitation are altered simultaneously by climate change, but the majority of studies focuses on the effects of increasing temperature, followed by changes in carbon dioxide (Bale et al., 2002; Rosenblatt & Schmitz, 2014). Current climate models project global and regional changes in precipitation quantity, variability, and timing (Chadwick, Boutle, & Martin, 2013; Donat, Lowry, Alexander, O'Gorman, & Maher, 2016; IPCC, 2014). However, most experimental studies emphasize the effects of changes in precipitation quantity, rather than changes in intensity, timing and frequency of precipitation events (Wu, Dijkstra, Koch, Peñuelas, & Hungate, 2011). In addition, studies measuring the impact of changes in precipitation related to climate change are primarily focused on terrestrial ecosystems, while studies in freshwater systems remain limited (Wu et al., 2011). However, the effects of changes in precipitation are especially important to understand in lotic systems, as precipitation is one of the main drivers of streamflow.

Changes in rainfall patterns driven by global climate change are likely to have severe impacts on stream structure and function. A recent model estimated that predicted changes in streamflow and warming are equally important risks to stream community composition in different ecoregions (Pyne & Poff, 2017). The magnitude, variation, and duration of streamflow are essential for the ecological integrity of stream systems (Jardine et al., 2015; Poff et al., 1997). Natural flow disturbances regulate habitat structure, population size, and species diversity (Lytle & Poff, 2004). It is highly likely that the projected changes in precipitation can simultaneously affect streamflow magnitude, timing, and variation. For example, projections indicate that in northern temperate regions, warming will cause snowmelt-driven streams to switch into rainfall-driven streams, shifting the timing and magnitude of peak flows from summer to winter (Zwiers, Schnorbus, & Maruszeczka, 2011). In many tropical regions, the frequency and intensity of flash flood events is expected to increase, but overall streamflow is predicted to increase or decrease depending on the region-specific precipitation projection (IPCC, 2012).

Studies on the effects of precipitation changes are concentrated in temperate ecosystems (Wu et al., 2011), yet tropical regions are expected to be one of the first to be impacted by climate change (Mora et al., 2013). In addition, tropical biomes are considered especially sensitive ecosystems to climate variability, because they are often already approaching ecological tipping points (Seddon, Macias-Fauria, Long, Benz, & Willis, 2016). Tropical islands, in particular, are at the forefront of changes in precipitation. In Hawaii, for example, studies have documented significant drying trends statewide since 1920 (Frazier & Giambelluca, 2017) with an increase in the number of dry days in the last 50 years (Chu, Chen, & Schroeder, 2010) and long-term stream gauging showing a 23% reduction in flow over the past 100 years (Bassiouni & Oki, 2013). However, the ecological response to these changes in flow is not well understood. One of the reasons for this paucity in both tropical and temperate systems is that streamflow, in particular flow variability, is difficult to experimentally manipulate in situ and the results are often measured over a short time frame (Poff et al., 2018).

Predicting long-term ecosystem responses to changes in precipitation and streamflow is uniquely challenging, because we lack the data required to mechanistically model ecosystem processes in most aquatic ecosystems. Such a challenge can only be currently met by observational studies that substitute spatial variations in environmental conditions for temporal variation. A space-for-time substitution is an experimental design where a spatial gradient mimics a projected or historical change over time. It is an innovative way to characterize ecological dynamics that occur over time-scales beyond the duration of conventional experiments, without compromising realism (Fukami & Wardle, 2005). They have accurately predicted approximately 72% of real time scenarios in terrestrial systems (Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013) and have been used for quantitative predictions in data-poor regions like the tropics (Lester, Close, Barton, Pope, & Brown, 2014). They allow us to examine impacts of changes in precipitation quantity and variability across terrestrial gradients. However, the utilization of space-for-time substitutions in aquatic ecosystems is rare (Thomaz et al., 2012), despite the presence of appropriate gradients (e.g., Strauch, MacKenzie, Giardina, & Bruland, 2015).

Here, we use a space-for-time substitution approach in order to investigate how tropical island stream ecosystems will respond to projected changes in precipitation. We utilize a rainfall gradient on Hawaii Island that mimics projected decreases in seasonal precipitation and increases in precipitation variability (Elison Timm, Giambelluca, & Diaz, 2015; Zhang, Wang, Hamilton, & Lauer, 2016). The mean annual rainfall (MAR) along a 20 km long stretch of the North Hilo coastline has a range of approximately 3,500–7,000 mm/year (Giambelluca et al., 2013), while mean annual temperature, riparian plant community structure, land use, soil type, and geologic age show little variation at similar elevations. The strong decline in rainfall across this MAR gradient results in concomitant declines in stream baseflow and flow stability (Strauch et al., 2015). The precipitation trend across these streams follows the historical trends and future projections of streamflow for high-gradient streams of the Hawaii islands (Bassiouni & Oki, 2013; Strauch et al., 2015). Therefore, the streams along the North Hilo coast offer an excellent model ecosystem to test hypotheses about the response of stream resource and consumer dynamics to projected changes in precipitation and flow.

The first objective of this study was to determine how basal resources and consumers in streams respond to predicted changes in flow during the dry season (May to September) in eight streams across our rainfall-flow gradient. First, we wanted to test if the rainfall pattern during our seasonal sampling was representative of long-term conditions along our gradient (Giambelluca et al., 2013) and test if those changes in rainfall led to the predictable changes in streamflow quantity and variability that have been established previously

(Strauch et al., 2015). We repeated this analysis for 3 years in order to assess interannual variability. Second, we tested how the resources and macroinvertebrate consumers responded to projected changes in flow. We predicted that climate-driven changes in flow would increase detrital resources (e.g., leaf litter) at the expense of autochthonous (e.g., macrophytes) resources, because reduced streamflow can increase detrital standing stocks (Jones, 1997). In other words, detrital resources will dominate toward the dry end of the gradient. Macrophytes are a higher quality food resource compared to leaf litter, because they have lower carbon:nitrogen ratios (Dodds et al., 2004). Therefore, with declines in resource quality and changes in flow, we hypothesized that invertebrate consumer biomass will decline. We also predicted that species with faster turnover rates would become dominant at the dry end of the gradient as a result of high-flow variability.

Our second objective was to determine the sensitivity of predictions generated from a space-for-time study to changes in the sampling scheme. When establishing a space-for-time substitution, studies need to balance the number of sites representing a gradient of interest and the frequency of sampling events (Gonzalez et al., 2016). In tropical stream ecosystems, there are considerable short-term temporal variations in precipitation and flow due to seasonal changes in rainfall (i.e., dry vs. wet season dynamics) or interannual variability that results from influences of El Niño and La Niña events. Sampling across seasons along the gradient helps frame forecasted changes in flow to the seasonal cycle, but there is often a logistical tradeoff between sampling frequently in time and sampling frequently in space. To answer this question in the context of climate change, we collected resources and macroinvertebrate consumers in four of the eight streams across the MAR gradient, monthly for 1 year. This created two sampling schemes, where one has a high spatial (8 streams) and lower temporal resolution (1 × per year for 3 years), which will be referred to as high spatial resolution (HSR); while the other has a high temporal (12× per year for 1 year) but lower spatial resolution (4 streams), which will be referred to as high temporal resolution (HTR). This allowed us to compare the resource and consumer response to flow change between the two sampling schemes and determine if the magnitude and variability in the response variables are similar between the HSR and HTR sampling.

2 | MATERIALS AND METHODS

2.1 | Study sites and rainfall data

Streams along the north east coast of Hawaii Island are characterized by narrow gulches, riparian vegetation comprised of native ʻŌhiʻa trees (*Metrosideros polymorpha*), Uluhe fern (*Dicranopteris linearis*), and non-native strawberry guava (*Psidium cattleyanum*), and young geologic substrate that was formed from a similar aged lava flow (<100,000 years). The slopes of the streams are comparable along the gradient (Table 1, Strauch et al., 2015). Eight streams were selected along the rainfall gradient spanning a range of ~3,000 mm MAR (Honolii (HON), Kapue (KAP), Kolekole (KOL), Umauma (UMA), Manoloa (LOA), Makahiloa (MAK), Pahale (PAH),

TABLE 1 Physical characteristics of eight streams across the North Hilo rainfall gradient. Mean annual rainfall (MAR) was gathered from the Rainfall Atlas of Hawaii (Giambelluca et al., 2013). Baseflow (Q_{90}), median flow (Q_{50}), stormflow (Q_{10}), flow variability (Q_{10}/Q_{90}), flood intensity (peak flow/Q_{50}), as well as canopy cover and substrate composition were averaged for the sampling periods (May to September) across 3 years

	WET							DRY
Stream	HON	KAP	KOL	UMA	LOA	MAK	PAH	KAA
MAR (mm/year)	5,764	5,868	6,520	5,178	5,168	4,748	4,527	3,703
Elevation (m)	470	460	500	490	420	400	510	475
Mean slope (%)	6.2	6.7	6.1	8.5	8.8	8.8	8.9	9.9
Stream order	2	2	3	2	1	2	1	2
Canopy cover (%)	35.6	34.5	36.3	25.7	65.7	60.6	70.4	78.2
Flow metrics:								
Q_{10} (L s^{-1} km^{-2})	261.1	628.7	293.2	619.3	87.26	273.1	122.7	22.14
Q_{50} (L s^{-1} km^{-2})	53.07	57.22	46.77	42.09	10.59	16.52	4.11	0.18
Q_{90} (L s^{-1} km^{-2})	26.43	18.87	20.92	11.27	5.19	3.67	0.32	0.06
Flow variability	10.87	37.11	15.06	66.76	23.05	78.47	36,924	71,995
Flood intensity	24.17	59.47	34.26	225.6	230.6	422.6	1,117	402,819
Substrate comp. (%):								
Bedrock	33.3	76.7	54.2	0.6	3.3	11.9	76.7	73.1
Boulder	66.7	23.3	2.8	13.9	25	3.1	0	0
Cobble	0	0	20.4	48.2	63.3	37.5	0	14.9
Gravel	0	0	17.2	29	8.3	34.2	23.3	11
Sand	0	0	5.4	8.3	0	13.3	0	1.1

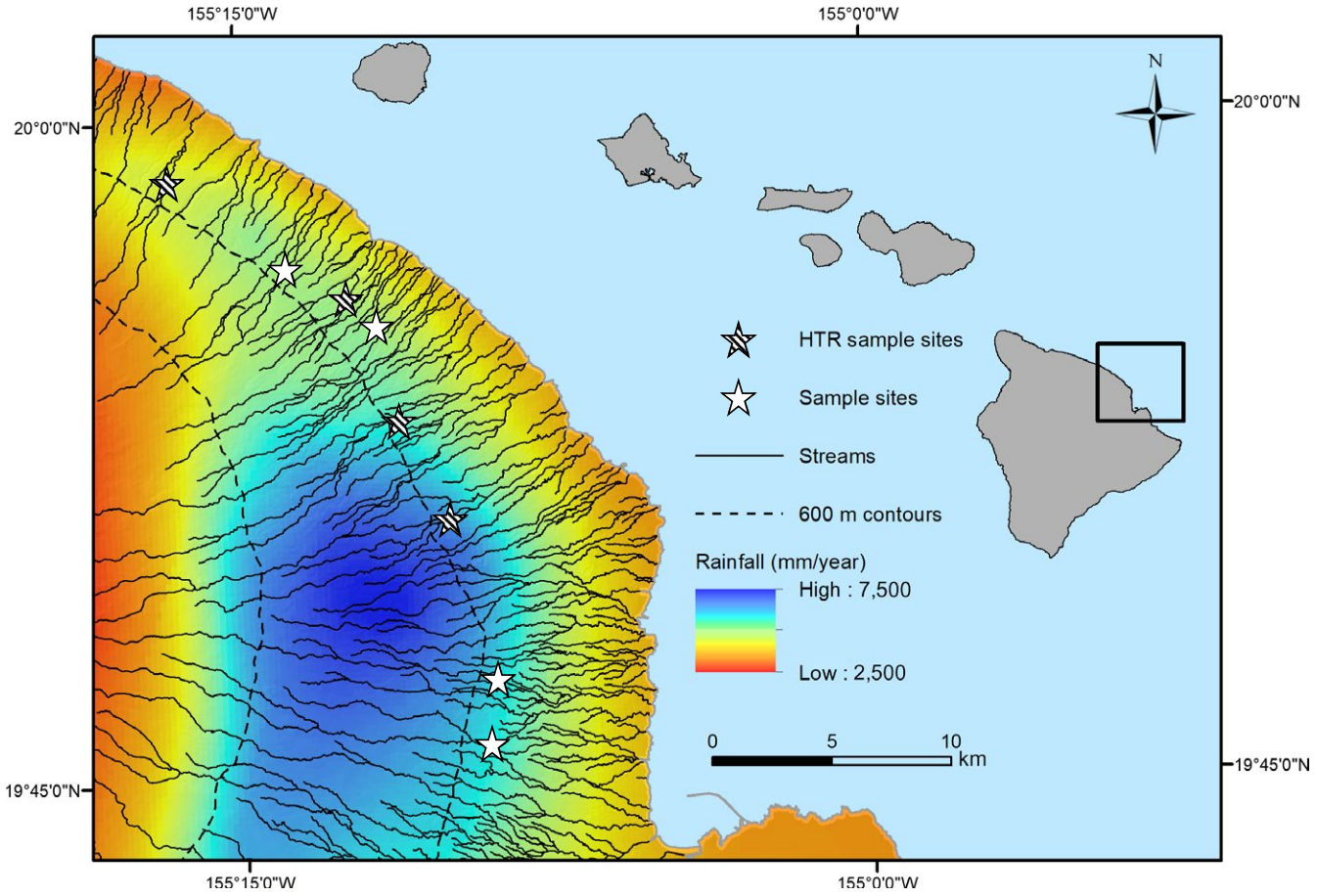

FIGURE 1 Eight sample stream sites (stars) located along the northeast coast of Hawaii Island with similar environmental characteristics except for the difference of ~3,000 mm mean annual rainfall. The striped stars indicate sites sampled at high temporal resolution (HTR). Data for this map were generated from the Rainfall Atlas of Hawaii (Giambelluca et al., 2013)

and Kaawalii (KAA)) for the HSR sampling scheme and sampled once during the dry season of 2015 and 2016 (Figure 1). In addition, four of the eight streams (KOL, UMA, MAK, and KAA) were selected for monthly sampling between April 2012 and March 2013 to represent the HTR sampling.

We attributed 30-year MAR estimates to all local catchments (see Tingley, Infante, MacKenzie, Cooper, & Tsang, 2018 for details on catchment delineation) within the study area by the Rainfall Atlas of Hawaii (Giambelluca et al., 2013). We then used an aggregation tool, described in Tsang, Wieferich, Fung, Infante, and Cooper (2014), to calculate the area-weighted average of rainfall in the upstream catchment of each sample site. Since both local and upstream rainfall influence the availability of fluvial habitat within the channel, we averaged upstream and local estimates of rainfall. In addition, we calculated 2012, 2015, and 2016 dry season rainfall using the same procedure. Monthly rainfall data were available for 2012 (Frazier, Giambelluca, Diaz, & Needham, 2016), while the 2015 and 2016 rainfall data were collected from all nearby stations and interpolated using an optimized Inverse Distance Weighted technique (see Longman et al., in press for method details). Rainfall totals were summed from May 1 through September 30 to obtain the dry season values for each year.

2.2 | Stream parameters

For each study stream, streamflow was compiled from a continuous dataset that uses in-stream data loggers to collect flow measurements at 15-min intervals (Strauch et al., 2015). Any interruptions in the continuous data set that resulted from logger malfunction or complete loss of logger due to strong flash flood events were supplemented with values from a distributed hydrology model (DHSVM), which was specifically developed for streams along the North Hilo coast (Povak et al., 2017). We calculated base- (Q_{90}), median- (Q_{50}), and storm flow (Q_{10}) based on mean daily flow and adjusted these values for the watershed area of each stream (L s^{-1} km^{-2}). From these values, flow variability (Q_{10}/Q_{90}) and flood intensity (peak flow/Q_{50}) were estimated. For HSR sampling, these flow variables were averaged from May through September of each year, while for the HTR sampling scheme flow variables were averaged across each month sampled.

Study reaches of each stream were dominated by riffle/run systems, and began and ended with large waterfall/plunge pool complexes. Since deep plunge pools are difficult to sample using the same methods and comprised only about 10% of the habitat, we focused our collections on riffle/run sites within a 100 m study

reach. All the sampling reaches were at similar elevation between sites (Table 1). For each HSR and HTR sampling event, we selected three random sites within the reach to obtain one collection of each resource and consumer variable and averaged these three replicates. In addition to these variables, percent substrate composition was visually estimated within a 0.1 m^2 sampling area and canopy cover was estimated using a densiometer at each of these three random locations. Resources and consumers were collected using the same methods for both HSR and HTR sampling schemes.

2.3 | Benthic and suspended resource biomass and composition

Benthic organic matter was collected at three random sites within the reach using a Surber sampler (250 μm mesh size, 0.1 m^2 sampling area). Samples were dried to a constant weight at 65°C (≥48 hr), combusted at 550°C for 3 hr, and reweighed to obtain ash-free dry mass (AFDM; Hauer & Lamberti, 2011). In 2012 and 2015, benthic samples were sorted into macrophyte, leaf litter, wood, seeds, grass, and miscellaneous (unidentified ≤1 mm detritus) categories before they were combusted to determine the dominant resource types. Suspended organic matter was collected using a drift net (250 μm mesh size, 0.1 m^2 sampling area) which was secured at the water surface for ~30 min during baseflow conditions. To estimate drift concentration (mg AFDM/L), volume of water passing through the net was calculated by accounting for water velocity across the net, area of submerged net, and time that the net was submerged.

Benthic biofilm was collected using a modified Loeb sampler (Loeb, 1981) and scrubbing between 1 and 7 subsamples from one rock area, which were homogenized into one sample. A subsample of the slurry was filtered through a glass-fiber filter and combusted to approximate total biofilm biomass (mg AFDM/m^2). To estimate the photosynthetic component, an additional subsample of slurry was filtered and standard EPA methods were used to calculate chlorophyll *a* (mg Chl *a*/m^2) concentrations (Arar & Collins, 1997. In addition, for the HTR sampling scheme only, annual net benthic primary production (mg Chl *a* m^{-2} $year^{-1}$) was calculated by summing the average differences between each month for 1 year.

2.4 | Macroinvertebrate biomass and composition

We focused on macroinvertebrates, because they are a major component of animal biomass in streams and they are critical for ecosystem function (Wallace & Webster, 1996). In addition, macroinvertebrates are often the first organisms to respond to environmental stress and therefore used as biotic indicators of stream health (Feld & Hering, 2007). Many species have adapted to the predictability of natural flow regimes and prolonged deviations may threaten the local persistence of species and even entire communities (Poff et al., 2018; Poff & Ward, 1989). Macroinvertebrates were sampled at three random locations within each stream reach with a Surber net and preserved in 70% ethanol. Invertebrates were counted, measured to the nearest millimeter, and identified to the lowest feasible taxonomic level, generally genus. Biomass of macroinvertebrate taxa that represented >1% of the total abundance in each stream was calculated using our own length–mass relationships (Table S1) with methods adapted from Benke, Huryn, Smock, and Wallace (1999).

2.5 | Statistical analyses

Generalized linear models were run to determine the relationships between rainfall, streamflow metrics, resource quantity and quality, and invertebrate biomass, using the "lme4" and "pscl" (to extract R^2 values) packages from the statistical program R (Bates, Maechler, Bolker, & Walker, 2015; Jackman, 2017). To explore how flow drives changes in resources and consumers, we first had to select an appropriate flow predictor variable since median flow, flow variability, and flood intensity were all strongly correlated with baseflow (R^2 of Q_{90} vs. Q_{50} = 0.88, Q_{10}/Q_{90} =0.92, peak flow/Q_{50} = 0.88, analyses not shown). We chose baseflow (Q_{90}) as the main flow predictor variable, because it is a more direct driver of resources and consumers in streams than median flow (Pyrce, 2004). Our choice was confirmed in an exploratory analysis where we used the "relaimpo" package in R (Grömping, 2006) to estimate the relative importance of each of the flow variables to changes in resource and consumer biomass (using the following linear model (lm): resource or consumer biomass ~baseflow + flow variability + flood intensity; lm resource: R^2 = 0.63, p = 0.002; lm consumer: R^2 = 0.68, $p \leq 0.001$). We found that baseflow was the main driver of both resource and consumer biomass changes (61%–72%) followed by flow variability and flood intensity.

To address the potential temporal pseudo replication in our HTR sampling scheme (i.e., repeated monthly measurements within one stream), we ran generalized mixed effect models with months as a random factor to determine the relationship between flow and the response variables (Bolker et al., 2009). For the HSR sampling scheme, we ran generalized linear models separately for each of the 3 years. Based on the distribution of the data and the model fit (residual and Q-Q plots), we selected the Gaussian, Gamma, or Gamma (link = log) family for our generalized models. The parameters and output of each model are reported in Table S2.

For each sampling scheme (i.e., HTR, HSR), we plotted the macroinvertebrate community data (based on abundance) across streams in a NMDS plot using the "vegan" package in R (Oksanen et al., 2017). If the stress value of the plots were ≤0.2, we used the "clustsig" package (Whitaker & Christman, 2014) to determine any clusters in the data and ran an analysis of similarity (ANOSIM) to establish if these clusters were significantly different ($p \leq 0.05$). Finally, we performed a SIMPER test with the "vegan" package to determine which species were driving these significant differences.

3 | RESULTS

3.1 | Rainfall and stream parameters

Rainfall during the dry season (May to September) generally related with the 30-year MAR and streamflow (Figure 2). The total rainfall

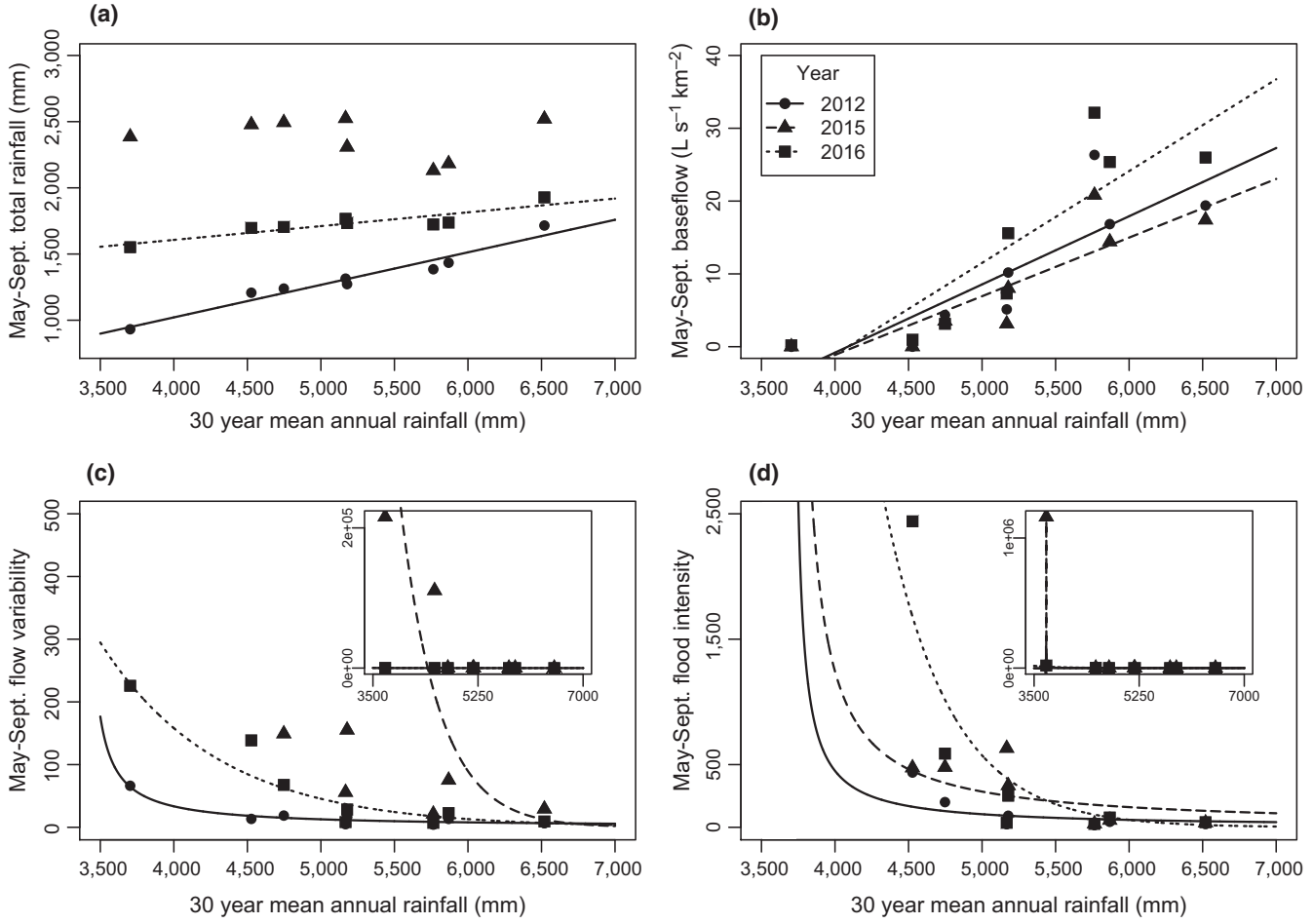

FIGURE 2 Rainfall and streamflow variables of eight sites (one point per stream) across the three sampling years. The 30-year mean annual rainfall average related to the total rainfall during the sampling period in years 2012 and 2016 (a). Baseflow (b; Q_{90}) increased with rainfall; while streamflow variability (c; Q_{10}/Q_{90}) and flood intensity (d; peak flow/Q_{50}) exponentially declined with rainfall. Lines indicate the significant model output of each relationship ($p \leq 0.05$)

during the dry season sampling period in 2012 (lm: $R^2 = 0.95$, $p < 0.001$) and 2016 (lm: $R^2 = 0.79$, $p = 0.003$) followed the same general upward trend as the long-term rainfall (Figure 2a). The year 2012 was the eighth driest in 60 years (NOAA, 2013), while 2015 had statewide the highest dry season rainfall in 30 years (NOAA, 2017). Baseflow (Q_{90}) increased with seasonal rainfall in 2012 (lm: $R^2 = 0.72$, $p = 0.008$), 2015 (lm: $R^2 = 0.76$, $p = 0.005$), and 2016 (lm: $R^2 = 0.76$, $p = 0.005$) (Figure 2b), a trend that was mirrored by median- (Q_{50}) and storm flow (Q_{10}, Table 1). On the other hand, streamflow variability (Figure 2c; Q_{10}/Q_{90}) and flood intensity (Figure 2d; peak flow/Q_{50}) exponentially decreased with increasing seasonal rainfall in 2012 (generalized linear model (glm): $R^2 = 0.78$, $p = 0.005$; $R^2 = 0.96$, $p = 0.022$, respectively), 2015 (glm: $R^2 = 0.99$, $p = 0.002$; $R^2 = 0.98$, $p = 0.019$, respectively), and 2016 (glm: $R^2 = 0.81$, $p = 0.002$; $R^2 = 0.91$, $p = 0.001$, respectively).

Canopy cover decreased with increasing baseflow (lm: $R^2 = 0.70$, $p = 0.010$), likely because higher flow creates wider streams, decreasing canopy cover. Substrate type within the streams varied across the streamflow gradient (Table 1). The driest and wettest sites were mostly composed of bedrock and boulder, while intermediate flow sites had smaller substrate present (e.g., sand, gravel, cobble). These substrate patterns are expected, because strong flash floods at dry sites and higher flow in wet streams scour smaller substrate to downstream areas.

3.2 | Resource availability

Benthic and suspended resources increased with baseflow (Figure 3). Benthic organic matter standing stocks increased tenfold with increasing baseflow in 2015 (lm: $R^2 = 0.90$, $p = 0.001$) and in 2016 (lm: $R^2 = 0.77$, $p = 0.004$) (Figure 3a). However, this pattern was not significant for the HTR sampling scheme (Figure 3b; generalized linear mixed model (glmm): $p = 0.068$). Suspended material (g AFDM/day) was 40× greater at higher baseflow for both HSR (Figure 3c; glm 2012: $R^2 = 0.62$, $p = 0.052$; glm 2015: $R^2 = 0.62$, $p = 0.031$; and lm 2016: $R^2 = 0.79$, $p = 0.003$) and HTR (Figure 3d; glmm: $R^2 = 0.29$, $p = 0.004$) sampling schemes.

Macrophyte and miscellaneous organic material (unidentified ≤1 mm detritus) were the most abundant resources in high-flow

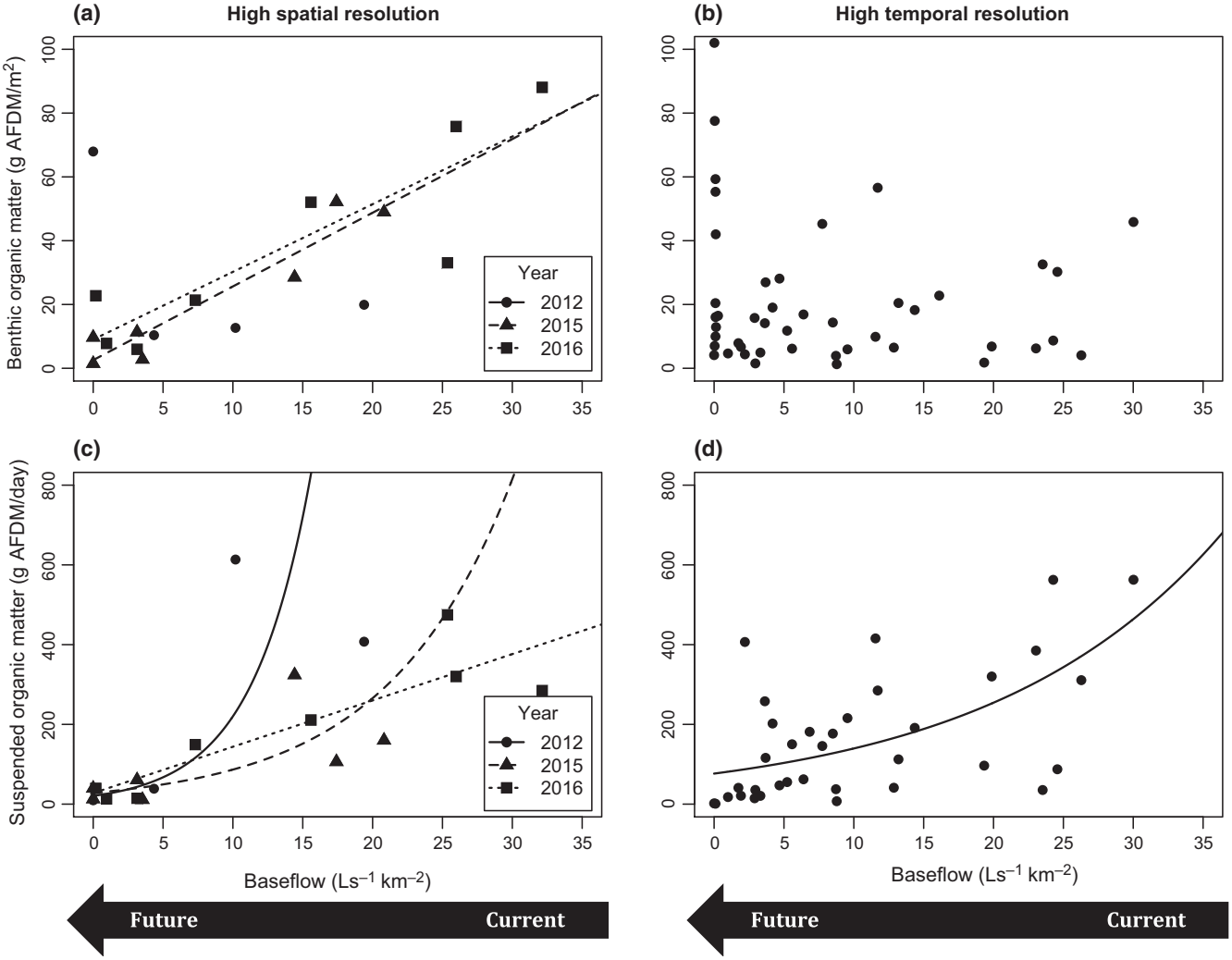

FIGURE 3 Responses of stream resource quantity to predicted decreases in base flow when sampling under higher spatial (a and c; up to eight streams per year) and temporal (b and d; four streams per month, 12 months) resolution. Benthic organic matter (a; g Ash-free dry mass (AFDM)/m^2) increased significantly with baseflow across years. However, this pattern was not significant within the year 2012 (b). Suspended material (g AFDM per day) increased with base flow across years (c) and within the year (d). Lines indicate the significant model output of each relationship ($p \leq 0.05$)

streams, while in low-flow streams leaf litter and miscellaneous organic material dominated (Table S3). Since macrophytes and leaf litter were the two most abundant resource types, we calculated their percent contribution to the total benthic resource availability and regressed the percentages against baseflow (Figure 4). Macrophyte presence increased up to 80% with higher baseflow for HSR (Figure 4a; lm 2012: $R^2 = 0.97$, $p = 0.016$; lm 2015: $R^2 = 0.88$, $p = 0.002$) and HTR (Figure 4b; glmm: $R^2 = 0.34$, $p = 0.001$) sampling. Macrophytes consisted mostly of two native feather moss species (*Glossadelphus zollingeri* and *Eurhynchium mulleri*). Percent leaf litter, on the other hand, exponentially declined with increasing baseflow for HSR (Figure 4c; glm 2012: $R^2 = 0.98$, $p = 0.009$; glm 2015: $R^2 = 0.99$, $p < 0.001$) and HTR (Figure 4d; glmm: $R^2 = 0.22$, $p = 0.007$).

Benthic biofilm did not vary across our sites, but net primary production was greater in high-flow streams. We saw no patterns with the photosynthetic (Chl *a*) and non-photosynthetic (AFDM) component of biofilm across the rainfall gradient on a monthly basis within the year (HTR glmm: $p = 0.83$, $p = 0.47$, respectively) or across sampling years (HSR lm 2012: $p = 0.53$, $p = 0.26$; glm 2015: $p = 0.39$, $p = 0.23$; and lm 2016: $p = 0.27$, $p = 0.19$). However, net benthic primary production was tenfold higher with increases in flow within the year 2012 (lm: $R^2 = 0.99$, $p = 0.003$).

3.3 | Macroinvertebrate biomass and composition

Invertebrate biomass increased on average by 35× with baseflow with both sampling schemes (Figure 5). In 2012, invertebrate biomass increased by 28× during the wet season (October to April) and by 42× during the dry season. The increases in 2012 (annual glmm: $R^2 = 0.73$, $p < 0.001$, dry season glm: $R^2 = 0.74$, $p = 0.028$), 2015 (glm: $R^2 = 0.74$, $p = 0.014$), and 2016 (glm: $R^2 = 0.61$, $p = 0.024$) biomass along the gradient were driven by an increase

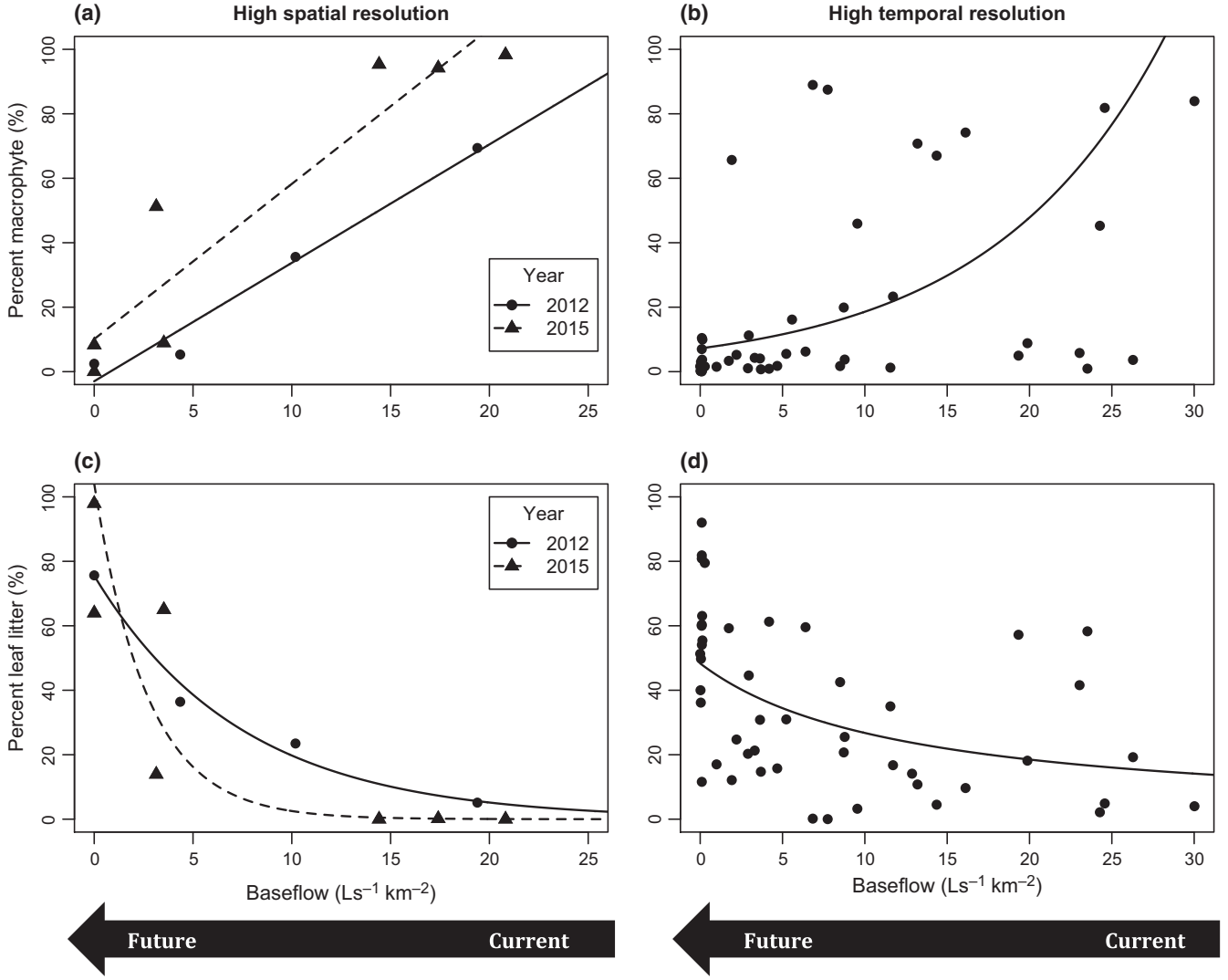

FIGURE 4 High spatial (a and c; up to eight streams per year) and high temporal (b and d; four streams per month, 12 months) sampling of percent availability of dominant stream resource types across base flow. Macrophyte presence increased with higher baseflow across years (a) and within the year 2012 (b), while percent detritus decreased with increased baseflow across years (c) and within the year (d). Lines indicate the significant model output of each relationship ($p \leq 0.05$)

in caddisfly and midge biomass in wetter streams (see Table S4 for detail).

Macroinvertebrate community composition changed significantly across the streams, even though richness did not (glm: $p = 0.20–0.60$). The NMDS plots had stress values of 0.15 and we therefore ran a cluster analysis and ANOSIM on both sampling schemes. Invertebrate taxa did not cluster significantly for the HSR sampling (Figure 6a), while HTR had three significant clusters (Figure 6b; $R = 0.48$, $p = 0.001$). The three clusters in the HTR NMDS plot separated low, intermediate, and high-flow sites (Figure 6b). Macroinvertebrate communities were 23%–38% dissimilar (SIMPER) between the driest stream and the other paired sites (Table S5). Higher abundances of snails, mosquitoes, and copepods at the driest sites contributed to 26%–70% of that difference, while higher abundance of caddisflies and damselflies in the wetter streams contributed to 29%–70% of the difference.

4 | DISCUSSION

Climate models project increases in precipitation extremes and decreases in total MAR for many areas of Hawaii (Zhang et al., 2016). Our study is unique because it attempts to quantify the effects of both of these climate variables on stream structure simultaneously, by using a natural rainfall gradient as a space-for-time substitution. Flow patterns along this gradient have been previously studied and are thought to mimic the predicted effects of climate change (Strauch et al., 2015), providing an important opportunity to test the effects of climate-driven changes in flow on stream ecosystems. In addition, we compared HSR and HTR sampling efforts within the space-for-time substitution model and determined that there are few differences between the results of the two sampling schemes. Both sampling designs indicated that resource quantity and quality and consumer biomass in tropical island streams generally declined

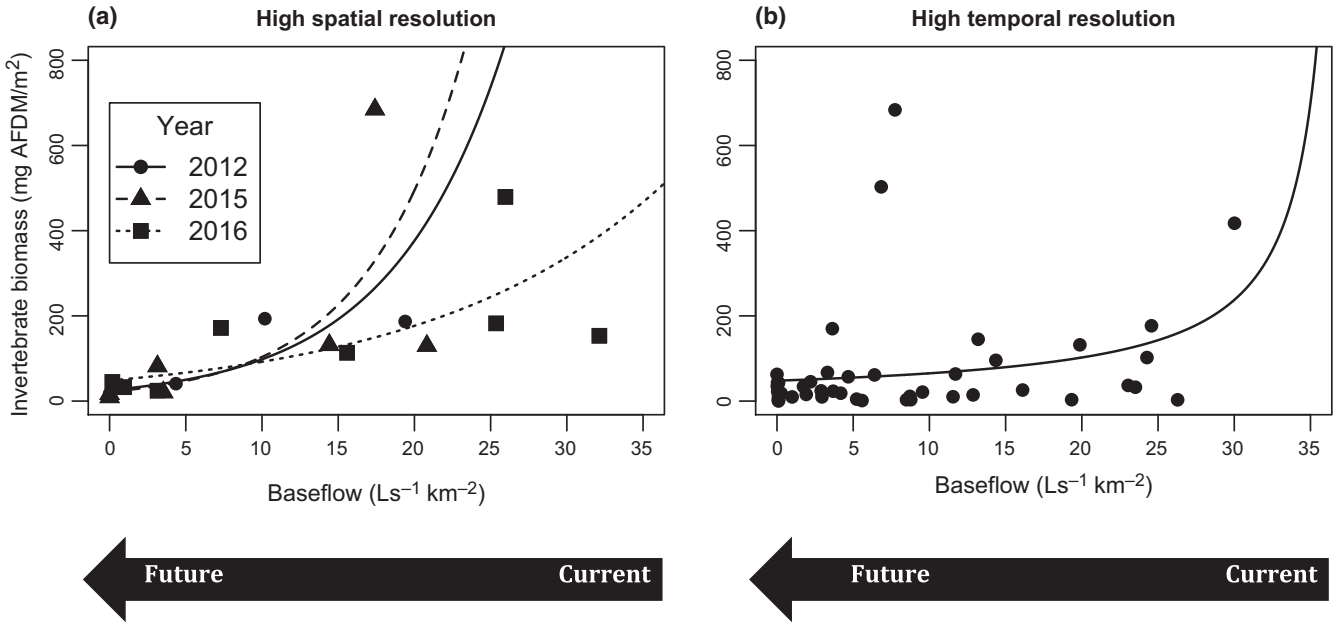

FIGURE 5 Stream invertebrate biomass (mg ash-free dry mass (AFDM) per m^2) across baseflow sampled under high spatial (a; up to eight streams per year) and temporal (b; four streams per month, 12 months) resolution. Invertebrate biomass increased with higher baseflow across years and within the year 2012. Lines indicate the significant model output of each relationship ($p \leq 0.05$)

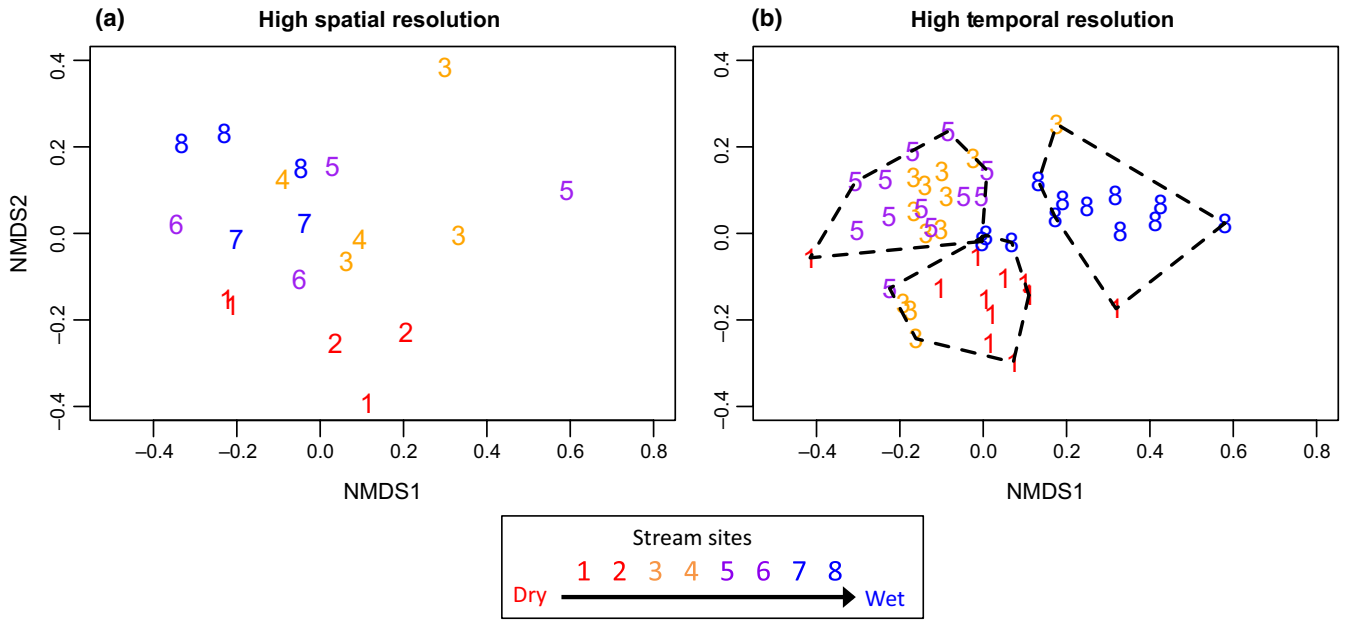

FIGURE 6 Ordination plots of invertebrate taxa when using the high spatial (a; n = 2 or 3 years) and high temporal (b; n = 12 months) sampling scheme, where each point represents one stream, sampled at one time point. Streams are labeled from low (1) to high (8) flow using average annual flows (1. KAA, 2. PAH, 3. MAK, 4. LOA, 5. UMA, 6. HON, 7. KAP, 8. KOL). The stress value for each plot was 0.15. The driest and wettest sites separated out significantly from the intermediate flow streams with high temporal resolution sampling, but this separation was not significant with high spatial resolution sampling [Colour figure can be viewed at wileyonlinelibrary.com]

by at least tenfold with predicted changes in streamflow. In addition, macroinvertebrate composition switched to species with higher turnover rates. Not only are many of the variables we measured related with streamflow, several of these relationships are exponential, suggesting rapid changes in ecological parameters in response to changes in precipitation. These results provide important insight into the effects of climate change on these vulnerable tropical island ecosystems and improve our understanding of how to apply a space-for-time substitution more effectively when estimating climate change impacts.

Benthic and suspended resource availability declined with decreasing streamflow. A 40-fold decline in suspended organic material

can have a stark impact on filter feeding species like endemic shrimp, which depend on suspended resources for more than 30% of their diet (Riney, 2015). In addition, decreases in flow have shown to reduce the quality of the suspended material (Atkinson, Golladay, Opsahl, & Covich, 2009), which can have further implications for these native filter feeders. Benthic resource availability declined with changes in flow as well; a trend that is supported by studies that investigate the relationship of flow and resource availability in temperate (Jones, 1997) and tropical (MacKenzie, Wiegner, Kinslow, Cormier, & Strauch, 2013) streams. These declines in benthic resources are driven by reduced macrophyte biomass in drier systems.

Our results suggest that climate change will tip the balance between autochthonous and allochthonous resources in tropical stream ecosystems. Lower light availability (i.e., high canopy cover) and higher frequency of scouring events (Kohler et al., 2012; Salas & Dudgeon, 2003) likely decreased macrophyte biomass and periphyton production toward the drier end of the gradient. Evidence suggests that tropical stream consumers rely more strongly on autochthonous resources compared to their temperate counterparts (Neres-Lima et al., 2016). An over tenfold decline in macrophytes and periphyton resources can therefore have stark consequences for higher trophic levels. In addition, consumers may utilize certain macrophyte types (e.g., moss) not only for direct consumption, but also for shelter and refugia during high-flow events (Jansson, Nilsson, & Malmqvist, 2007).

Our study suggests that extended low-flow periods associated with declines in rainfall are likely to increase allochthonous resources in tropical streams. Leaf litter accumulation increased toward the drier end of our flow gradient (Figure 4c,d; Table S3). This result was further highlighted by increased detrital storage during 2012, which was one of the driest years in the past 60 years (NOAA, 2013). Increases in allochthonous resource availability with climate-driven changes in flow have recently been reported in high-elevation temperate streams as well (Larson, Poff, Atkinson, & Flecker, 2018). However, it is important to note that the contribution of macrophytes to total resource biomass is larger in high-flow streams (maximum 49.12 mg AFDM/m^2) than the contribution of leaf litter in low-flow streams (up to 9.48 mg AFDM/m^2, Table S3). This results in the overall decline in available benthic resources at the drier end of the gradient, despite the increase in allochthonous resources. The shift from a macrophyte to detrital dominated carbon system decreases resource quality (i.e., low C:N macrophytes to high C:N detritus), which can increase consumer feeding rates in order to maintain a similar nutritional intake (Jochum et al., 2017). Therefore, declines in both resource quantity and quality can adversely impact consumer biomass.

As predicted, we found a consistent decrease in invertebrate biomass with projected declines in flow rates and increases in flow variability, suggesting that climate change will affect the standing stocks of these important stream consumers. Previous studies have shown that flow alterations triggered by climate change can decrease invertebrate abundance by predictive models (Kakouei et al., 2018) and long-term monitoring of two Costa Rican streams (Gutiérrez-Fonseca, Ramírez, & Pringle, 2018). In our study, we found that both abundance and biomass of invertebrates declined up to 20× and that caddisflies and midges were the dominant invertebrate taxa that drove these changes in biomass and abundance (Table S4). In comparison, two studies conducted on Maui Island, Hawaii, found a 44%–60% decline in invertebrate abundance and biomass as a result of flow reduction by river dams, but did not attribute the decline to certain taxa (Gorbach, Shoda, Burky, & Benbow, 2014; McIntosh, Schmitz, Benbow, & Burky, 2008). In addition, a congruent study along this rainfall gradient shows that the endemic shrimp, *Atyoida bisulcata*, has lower average biomass in streams with low baseflow (Tingley, 2017). We speculate that the drop in consumer biomass results from both direct (i.e., scouring from increased flood intensity and flow variability) and indirect (i.e., lower food resource availability and quality) effects of changes in flow. We encourage future studies to investigate the relative contribution of each effect on invertebrate biomass.

While we did not see dramatic changes in invertebrate richness along the gradient, we saw a shift toward species that tolerate flow variability and changes in resource quantity and quality. Caddisflies and damselflies dominated invertebrate communities at the wet end of the gradient, while snails, mosquitoes and copepods were more abundant at the dry end. This pattern suggests that climate change will shift community composition toward organisms with shorter life histories. Studies from semi-arid boreal ecosystems have shown that macroinvertebrate community composition changes with elevated numbers of drying (Eady, Hill, & Rivers-Moore, 2014) and extreme hydrological events (Sarremejane et al., 2018). Increases in magnitude and variation in streamflow can lead to species with shorter larval life cycles, smaller body size, and low oxygen tolerance (Bunn & Arthington, 2002; Poff & Ward, 1989). In addition, a mesocosm study demonstrated that functional redundancy in macroinvertebrate communities increases with habitat contraction and fragmentation (Boersma, Bogan, Henrichs, & Lytle, 2014), indicating that predicted decreases in flow may not only affect stream structure, but also function (Boersma et al., 2014; Pyne & Poff, 2017).

Downscaled climate projections for Hawaii and other parts of the Tropics indicate that certain regions will likely experience simultaneous declines in precipitation quantity and increases in extreme events (Elison Timm et al., 2015; Rauscher, Kucharski, & Enfield, 2010; Zhang et al., 2016). Our results raise the question whether changes in flow rates or flow variability are the main driver of resource and consumer patterns along our gradient. Previous studies have shown that declines in flow (Northington & Webster, 2017) and increases in variability (Ohlberger et al., 2018) can each affect stream resources and consumers separately. However, our rainfall gradient presented us with the unique opportunity to estimate ecosystem effects of flow magnitude and variation alteration combined. Our preliminary models speculate that the decline in flow is the strongest driver of decreases in resource and consumer biomass (61%–72%) compared to increased flow variability and flood intensity (see Section 2.5). However, further flow manipulation studies are necessary to tease apart how much each flow variable drives

the predicted changes in resources and consumers. Overall, we conclude that predicted declines in streamflow quantity and changes in variability will result in decreased freshwater resource and invertebrate biomass, which can have negative repercussions for higher trophic levels such as predatory fish, birds, and mammals that rely on this important food resource.

Globally, extreme precipitation events have increased and are projected to continue to intensify in the future (IPCC, 2013). However, it is necessary to recognize that the projections for total precipitation change vary across regions, and a large amount of uncertainty still exists for the tropics and subtropics, both in models and observationally constrained datasets (Bador, Donat, Geoffroy, & Alexander, 2018; Kent, Chadwick, & Rowell, 2015). For example, recent evidence shows that there has been little change in total precipitation in wet regions of the world, although these results were less robust for tropical regions (Donat, Lowry, Alexander, O'Gorman, & Maher, 2017). On the other hand, regional calculations for Meso-America (Rauscher et al., 2010) and Central America (Diffenbaugh & Giorgi, 2012) project a reduction in precipitation. In addition, the downscaled projections available for the Hawaiian Islands vary spatially, depending on local air temperature, evapotranspiration, ocean water surface temperature, and wind speed and direction (Zhang et al., 2016). While there are uncertainties and variation in estimates of total precipitation change across the Tropics, declines have been projected in several cases and the implications of our results can be applied to other tropical areas where similar precipitation projections have been made.

The HSR sampling scheme allowed us to evaluate interannual variability, while HTR sampling efforts demonstrated little differences in patterns within the year. We were able to capture a relatively dry, extremely wet, and an average rainfall year with the HSR sampling regime, which allowed us to evaluate if resource and consumer patterns are altered by extreme years. The seasonal rainfall patterns of 2012 and 2016 were strongly related with the 30-year long-term rainfall trend, but this relationship did not hold up during the extremely wet season in 2015. This is likely because the drier end of the gradient received an increased number of short but extreme rainfall events, inflating the average rainfall estimates in these areas. However, the flow pattern of 2015 was similar to 2012 and 2016, because baseflow estimates avoid the artificial inflation by extreme flood events. Since baseflow is a direct driver of stream resources and consumer, we saw little difference in the ecological response patterns (biomass and composition) between the 2015 and the 2012/2016 years. This agreement indicates that this space-for-time substitution is a robust sampling model that can be useful in quantifying long-term responses, even in years that involve extreme events. The HTR sampling regime also demonstrated that there was little difference in the resource and consumer response patterns between the months. Nevertheless, when averaged, the resource and consumer biomass patterns were stronger during the dry season (e.g., invertebrate biomass 28× decline in wet vs. 42× in dry season, analyses not shown), which mimicked the overall biomass patterns we observed in the eight streams sampled for the HSR along our rainfall gradient. This indicates that the flow variability within the year (HTR) simulates the flow range along our rainfall gradients (HSR).

There was little difference in the direction and strength of the resource and consumer response pattern to variation in flow between the two sampling schemes, suggesting that both schemes provide similar predictions about how climate change will affect tropical communities. Baseflow and resource and consumer response variables had very similar ranges between the HTR and HSR sampling schemes, indicating the difference between monthly sampling events (e.g., wet vs. dry season) mirrored interannual variation in rainfall events (e.g., El Niño-Southern Oscillation). The only difference between the two schemes was in the response of community composition to changes in flow. The HTR sampling scheme detected a significant separation of communities between wet, dry, and intermittent streams, indicating that there are significant shifts in macroinvertebrate community composition with changes in flow. These patterns did not significantly cluster out with the HSR sampling scheme (Figure 6a), although the wet, dry, and intermittent streams grouped similar to HTR sampling. The lack of separation is likely because there were only two to three points per stream for the HSR sampling regime. Therefore, the HTR sampling captured the community structure more effectively and we suggest using this method when answering consumer and resource composition questions. However, overall, we deem both sampling strategies comparable when answering ecosystem questions where a space-for-time substitution approach is appropriate.

Although using a space-for-time substitution approach to estimate effects of climate change can have some drawbacks, it has been a valuable tool when used in the right context. Space-for-time substitutions have the benefit of capturing long-term environmental responses within a reasonable sampling time scale without losing realism. However, there are three main criticisms of this method: site and species histories can vary or are unknown, biotic and abiotic factors vary along the spatial gradient, and the spatial variability may not represent the temporal variability (Fukami & Wardle, 2005; Johnson & Miyanishi, 2008). Since our predictive rainfall gradient was formed along a short distance (~20 km) and from the same lava flow, it presented us with the unique opportunity to have similar site and species history. In addition, we reported many of the biotic and abiotic factors to ensure they are not a cofactor driving our results. By comparing our two sampling regimes (HTR vs. HSR), we were able to conclude that the spatial variability generally represented the temporal variability well. In addition, a recent long-term study (15 years) in Costa Rica, where the projected changes in precipitation variability aligned with ours, reported similar declines in macroinvertebrate abundance (Gutiérrez-Fonseca et al., 2018). We conclude that a space-for-time substitution approach is a valuable tool to assess climate impacts on the whole ecosystem if the limitations of the approach are addressed by the study design. We encourage other climate studies to include landscape gradients to address anthropogenic impacts in a timely manner.

ACKNOWLEDGEMENTS

We are grateful to J. Akau, M. Apwong, A. Char, P. Foulk, T. Froese, K. Harms, E. Lapoint, L. Low, P. Marques, E. Salmin, and A. Strauch for their assistance with data collection. We thank P. Selmants, J. Richardson, F. Juanes, and two anonymous reviewers for the valuable advice and suggestions during the development of this manuscript. We also thank the Aquatic Landscape Ecology lab at Michigan State University for analytical support. Kamehameha Schools-Bishop Estates facilitated access to many of the study sites, with special thanks given to J. Wong, K. Duarte, and I. Lindsey for their assistance. Funding for this project was provided by the USDA Washington Office and the Pacific Southwest Research Station.

ORCID

Therese C. Frauendorf https://orcid.org/0000-0003-3524-5297
Abby G. Frazier https://orcid.org/0000-0003-4076-4577

REFERENCES

Arar, E. J., & Collins, G. B. (1997). *Method 445.0: In vitro determination of chlorophyll a and pheophytin a in marine and freshwater algae by fluorescence*. Washington, DC: United States Environmental Protection Agency, Office of Research and Development, National Exposure Research Laboratory.

Atkinson, C. L., Golladay, S. W., Opsahl, S. P., & Covich, A. P. (2009). Stream discharge and floodplain connections affect seston quality and stable isotopic signatures in a coastal plain stream. *Journal of the North American Benthological Society*, *28*(2), 360–370. https://doi.org/10.1899/08-102.1

Bador, M., Donat, M. G., Geoffroy, O., & Alexander, L. V. (2018). Assessing the robustness of future extreme precipitation intensification in the CMIP5 ensemble. *Journal of Climate*, *31*(16), 6505–6525. https://doi.org/10.1175/JCLI-D-17-0683.1

Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., … Whittaker, J. B. (2002). Herbivory in global climate change research: Direct effects of rising temperature on insect herbivores. *Global Change Biology*, *8*(1), 1–16. https://doi.org/10.1046/j.1365-2486.2002.00451.x

Bassiouni, M., & Oki, D. S. (2013). Trends and shifts in streamflow in Hawai'i, 1913–2008. *Hydrological Processes*, *27*(10), 1484–1500. https://doi.org/10.1002/hyp.9298

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48.

Benke, A. C., Huryn, A. D., Smock, L. A., & Wallace, J. B. (1999). Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the Southeastern United States. *Journal of the North American Benthological Society*, *18*(3), 308–343. https://doi.org/10.2307/1468447

Blois, J. L., Williams, J. W., Fitzpatrick, M. C., Jackson, S. T., & Ferrier, S. (2013). Space can substitute for time in predicting climate-change effects on biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(23), 9374–9379. https://doi.org/10.1073/pnas.1220228110

Boersma, K. S., Bogan, M. T., Henrichs, B. A., & Lytle, D. A. (2014). Invertebrate assemblages of pools in arid-land streams have high functional redundancy and are resistant to severe drying. *Freshwater Biology*, *59*(3), 491–501. https://doi.org/10.1111/fwb.12280

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., & White, J.-S.-S. (2009). Generalized linear mixed models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*(3), 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bunn, S. E., & Arthington, A. H. (2002). Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, *30*(4), 492–507. https://doi.org/10.1007/s00267-002-2737-0

Chadwick, R., Boutle, I., & Martin, G. (2013). Spatial patterns of precipitation change in CMIP5: Why the rich do not get richer in the tropics. *Journal of Climate*, *26*(11), 3803–3822. https://doi.org/10.1175/JCLI-D-12-00543.1

Chu, P.-S., Chen, Y. R., & Schroeder, T. A. (2010). Changes in precipitation extremes in the Hawaiian Islands in a warming climate. *Journal of Climate*, *23*(18), 4881–4900. https://doi.org/10.1175/2010JCLI3484.1

Diffenbaugh, N. S., & Giorgi, F. (2012). Climate change hotspots in the CMIP5 global climate model ensemble. *Climatic Change*, *114*(3), 813–822. https://doi.org/10.1007/s10584-012-0570-x

Dodds, W. K., Martí, E., Tank, J. L., Pontius, J., Hamilton, S. K., Grimm, N. B., … Gregory, S. (2004). Carbon and nitrogen stoichiometry and nitrogen cycling rates in streams. *Oecologia*, *140*(3), 458–467. https://doi.org/10.1007/s00442-004-1599-y

Donat, M. G., Lowry, A. L., Alexander, L. V., O'Gorman, P. A., & Maher, N. (2016). More extreme precipitation in the world's dry and wet regions. *Nature Climate Change*, *6*(5), 508–513. https://doi.org/10.1038/nclimate2941

Donat, M. G., Lowry, A. L., Alexander, L. V., O'Gorman, P. A., & Maher, N. (2017). Addendum: More extreme precipitation in the world's dry and wet regions. *Nature Climate Change*, *7*(2), 154–158.

Eady, B. R., Hill, T. R., & Rivers-Moore, N. A. (2014). Shifts in aquatic macroinvertebrate community structure in response to perenniality, southern Cape, South Africa. *Journal of Freshwater Ecology*, *29*(4), 475–490. https://doi.org/10.1080/02705060.2014.910146

Elison Timm, O., Giambelluca, T. W., & Diaz, H. F. (2015). Statistical downscaling of rainfall changes in Hawai'i based on the CMIP5 global model projections: Downscaled Rainfall Changes in Hawai'i. *Journal of Geophysical Research: Atmospheres*, *120*(1), 92–112. https://doi.org/10.1002/2014JD022059

Feld, C. K., & Hering, D. (2007). Community structure or function: Effects of environmental stress on benthic macroinvertebrates at different spatial scales. *Freshwater Biology*, *52*(7), 1380–1399. https://doi.org/10.1111/j.1365-2427.2007.01749.x

Frazier, A. G., & Giambelluca, T. W. (2017). Spatial trend analysis of Hawaiian rainfall from 1920 to 2012. *International Journal of Climatology*, *37*(5), 2522–2531. https://doi.org/10.1002/joc.4862

Frazier, A. G., Giambelluca, T. W., Diaz, H. F., & Needham, H. L. (2016). Comparison of geostatistical approaches to spatially interpolate month-year rainfall for the Hawaiian Islands. *International Journal of Climatology*, *36*(3), 1459–1470. https://doi.org/10.1002/joc.4437

Fukami, T., & Wardle, D. A. (2005). Long-term ecological dynamics: reciprocal insights from natural and anthropogenic gradients. *Proceedings of the Royal Society of London B: Biological Sciences*, *272*(1577), 2105–2115.

Giambelluca, T. W., Chen, Q., Frazier, A. G., Price, J. P., Chen, Y.-L., Chu, P.-S., … Delparte, D. M. (2013). Online rainfall atlas of Hawai'i. *Bulletin of the American Meteorological Society*, *94*(3), 313–316. https://doi.org/10.1175/BAMS-D-11-00228.1

Gonzalez, A., Cardinale, B. J., Allington, G. R. H., Byrnes, J., Endsley, K. A., Brown, D. G., … Loreau, M. (2016). Estimating local biodiversity change: A critique of papers claiming no net loss of local diversity. *Ecology*, *97*(8), 1949–1960. https://doi.org/10.1890/15-1759.1

Gorbach, K. R., Shoda, M. E., Burky, A. J., & Benbow, M. E. (2014). Benthic community responses to water removal in tropical mountain streams. *River Research and Applications*, *30*(6), 791–803. https://doi.org/10.1002/rra.2679

Grömping, U. (2006). Relative importance for linear regression in R: The package relaimpo. *Journal of Statistical Software*, *17*(1), 1–27.

Gutiérrez-Fonseca, P. E., Ramírez, A., & Pringle, C. M. (2018). Large-scale climatic phenomena drive fluctuations in macroinvertebrate assemblages in lowland tropical streams, Costa Rica: The importance of ENSO events in determining long-term (15y) patterns. *PLoS ONE*, *13*(2), e0191781. https://doi.org/10.1371/journal.pone.0191781

Hauer, F. R., & Lamberti, G. A. (2011). *Methods in stream ecology*. San Diego, CA: Academic Press.

IPCC. (2012). *Managing the risks of extreme events and disasters to advance climate change adaptation: Special report of the Intergovernmental Panel on Climate Change*. In C. B. Field, V. Barros, T. F. Stocker, D. Qin, D. J. Dokken, K. L. Ebi, M. D. Mastrandrea, K. J. Mach, G.-K. Plattner, S. K. Allen, M. Tignor, & P. M. Midgley (Eds.). Cambridge, UK, and New York, NY: Cambridge University Press.

IPCC. (2013). *Climate change 2013: The physical science basis. Contribution of Working Group I to the fifth assessment report of the Intergovernmental Panel on Climate Change*. In T. F. Stocker, D. Qin, G.-K. Plattner, M. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, & P. M. Midgley (Eds.). Cambridge, UK and New York, NY: Cambridge University Press.

IPCC. (2014). *Climate change 2014: Synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. In Core Writing Team, R. K. Pachauri, & L. A. Meyer (Eds.). IPCC, Geneva, Switzerland. Cambridge: Cambridge University Press.

Jackman, S. (2017). pscl: Classes and methods for R developed in the political science computational laboratory (version 1.5.2). Retrieved from https://github.com/atahk/pscl/

Jansson, R., Nilsson, C., & Malmqvist, B. (2007). Restoring freshwater ecosystems in riverine landscapes: The roles of connectivity and recovery processes. *Freshwater Biology*, *52*(4), 589–596. https://doi.org/10.1111/j.1365-2427.2007.01737.x

Jardine, T. D., Bond, N. R., Burford, M. A., Kennard, M. J., Ward, D. P., Bayliss, P., … Bunn, S. E. (2015). Does flood rhythm drive ecosystem responses in tropical riverscapes? *Ecology*, *96*(3), 684–692.

Jochum, M., Barnes, A. D., Ott, D., Lang, B., Klarner, B., Farajallah, A., … Brose, U. (2017). Decreasing stoichiometric resource quality drives compensatory feeding across trophic levels in tropical litter invertebrate communities. *The American Naturalist*, *190*(1), 131–143. https://doi.org/10.1086/691790

Johnson, E. A., & Miyanishi, K. (2008). Testing the assumptions of chronosequences in succession. *Ecology Letters*, *11*(5), 419–431. https://doi.org/10.1111/j.1461-0248.2008.01173.x

Jones, J. B. (1997). Benthic organic matter storage in streams: Influence of detrital import and export, retention mechanisms, and climate. *Journal of the North American Benthological Society*, *16*, 109–119. https://doi.org/10.2307/1468243

Kakouei, K., Kiesel, J., Domisch, S., Irving, K. S., Jähnig, S. C., & Kail, J. (2018). Projected effects of climate-change-induced flow alterations on stream macroinvertebrate abundances. *Ecology and Evolution*, *8*(6), 3393–3409. https://doi.org/10.1002/ece3.3907

Kent, C., Chadwick, R., & Rowell, D. P. (2015). Understanding uncertainties in future projections of seasonal tropical precipitation. *Journal of Climate*, *28*(11), 4390–4413. https://doi.org/10.1175/JCLI-D-14-00613.1

Kohler, T. J., Heatherly, T. N., El-Sabaawi, R. W., Zandonà, E., Marshall, M. C., Flecker, A. S., … Thomas, S. A. (2012). Flow, nutrients, and light availability influence Neotropical epilithon biomass and stoichiometry. *Freshwater Science*, *31*(4), 1019–1034. https://doi.org/10.1899/11-141.1

Larson, E. I., Poff, N. L., Atkinson, C. L., & Flecker, A. S. (2018). Extreme flooding decreases stream consumer autochthony by increasing detrital resource availability. *Freshwater Biology*, *63*(12), 1483–1497. https://doi.org/10.1111/fwb.13177

Lester, R. E., Close, P. G., Barton, J. L., Pope, A. J., & Brown, S. C. (2014). Predicting the likely response of data-poor ecosystems to climate change using space-for-time substitution across domains. *Global Change Biology*, *20*(11), 3471–3481. https://doi.org/10.1111/gcb.12634

Loeb, C. (1981). An in-situ method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. *Limnology and Oceanography*, *26*(2), 394–399.

Longman, R. J., Frazier, A. G., Newman, A. J., Giambelluca, T. W., Schanzenbach, D., Kagawa-Viviani, A., … Clark, M. P. (in press). High-resolution gridded daily rainfall and temperature for the Hawaiian Islands (1990–2014). *Journal of Hydrometeorology*.

Lytle, D. A., & Poff, N. L. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, *19*(2), 94–100. https://doi.org/10.1016/j.tree.2003.10.002

MacKenzie, R. A., Wiegner, T. N., Kinslow, F., Cormier, N., & Strauch, A. M. (2013). Leaf-litter inputs from an invasive nitrogen-fixing tree influence organic-matter dynamics and nitrogen inputs in a Hawaiian river. *Freshwater Science*, *32*(3), 1036–1052. https://doi.org/10.1899/12-152.1

McIntosh, M. D., Schmitz, J. A., Benbow, M. E., & Burky, A. J. (2008). Structural and functional changes of tropical riffle macroinvertebrate communities associated with stream flow withdrawal. *River Research and Applications*, *24*(8), 1045–1055. https://doi.org/10.1002/rra.1104

Mora, C., Frazier, A. G., Longman, R. J., Dacks, R. S., Walton, M. M., Tong, E. J., … Giambelluca, T. W. (2013). The projected timing of climate departure from recent variability. *Nature*, *502*(7470), 183–187.

Neres-Lima, V., Brito, E. F., Krsulović, F. A., Detweiler, A. M., Hershey, A. E., & Moulton, T. P. (2016). High importance of autochthonous basal food source for the food web of a Brazilian tropical stream regardless of shading. *International Review of Hydrobiology*, *101*(3–4), 132–142. https://doi.org/10.1002/iroh.201601851

NOAA (2013). *State of the climate: Drought for annual 2012*. National Centers for Environmental Information. Retrieved from https://www.ncdc.noaa.gov/sotc/drought/201213#hi-usapi-sect

NOAA. (2017). *Media advisory: Wet season rainfall outlook for the state of Hawaii (media advisory)*. Honolulu, HI: National Oceanic and Atmospheric Administration. Retrieved from http://www.prh.noaa.gov/hnl/hydro/pages/MediaAdvisory2017-18HawaiiWetSeasonOutlook.pdf

Northington, R. M., & Webster, J. R. (2017). Experimental reductions in stream flow alter litter processing and consumer subsidies in headwater streams. *Freshwater Biology*, *62*(4), 737–750. https://doi.org/10.1111/fwb.12898

Ohlberger, J., Buehrens, T. W., Brenkman, S. J., Crain, P., Quinn, T. P., & Hilborn, R. (2018). Effects of past and projected river discharge variability on freshwater production in an anadromous fish. *Freshwater Biology*, *63*(4), 331–340. https://doi.org/10.1111/fwb.13070

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., …Wagner, H. (2017). Vegan: Community ecology package (version 2.4-4). Retrieved from https://CRAN.R-project.org/package=vegan

Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegaard, K. L., Richter, B. D., … Stromberg, J. C. (1997). The natural flow regime. *BioScience*, *47*, 769–784. https://doi.org/10.2307/1313099

Poff, N. L., Larson, E. I., Salerno, P. E., Morton, S. G., Kondratieff, B. C., Flecker, A. S., … Funk, W. C. (2018). Extreme streams: Species persistence and genomic change in montane insect populations across a flooding gradient. *Ecology Letters*, *21*(4), 525–535. https://doi.org/10.1111/ele.12918

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*(10), 1805–1818. https://doi.org/10.1139/f89-228

Povak, N. A., Hessburg, P. F., Giardina, C. P., Reynolds, K. M., Heider, C., Salminen, E., … MacKenzie, R. A. (2017). A watershed decision support tool for managing invasive species on Hawai'i Island, USA. *Forest Ecology and Management*, *400*, 300–320. https://doi.org/10.1016/j.foreco.2017.05.046

Pyne, M. I., & Poff, N. L. (2017). Vulnerability of stream community composition and function to projected thermal warming and hydrologic change across ecoregions in the western United States. *Global Change Biology*, *23*(1), 77–93. https://doi.org/10.1111/gcb.13437

Pyrce, R. (2004). Hydrological low flow indices and their uses (WSC no. 04–2004). Peterborough: Watershed Science Centre.

Rauscher, S. A., Kucharski, F., & Enfield, D. B. (2010). The role of regional SST warming variations in the drying of Meso-America in future climate projections. *Journal of Climate*, *24*(7), 2003–2016.

Riney, M. (2015). *The impacts of stream flow rates on food resource quality and diets of native endemic atyid shrimps (Atyoida bisulcata) in Hawaiian streams*. Hilo, HI: University of Hawaii at Hilo.

Rosenblatt, A. E., & Schmitz, O. J. (2014). Interactive effects of multiple climate change variables on trophic interactions: A meta-analysis. *Climate Change Responses*, *1*, 8. https://doi.org/10.1186/s40665-014-0008-y

Salas, M., & Dudgeon, D. (2003). Life histories, production dynamics and resource utilization of mayflies (Ephemeroptera) in two tropical Asian forest streams. *Freshwater Biology*, *48*(3), 485–499.

Sarremejane, R., Mykrä, H., Huttunen, K.-L., Mustonen, K.-R., Marttila, H., Paavola, R., … Muotka, T. (2018). Climate-driven hydrological variability determines inter-annual changes in stream invertebrate community assembly. *Oikos*, *127*(11), 1586–1595. https://doi.org/10.1111/oik.05329

Seddon, A. W. R., Macias-Fauria, M., Long, P. R., Benz, D., & Willis, K. J. (2016). Sensitivity of global terrestrial ecosystems to climate variability. *Nature*, *531*(7593), 229. https://doi.org/10.1038/nature16986

Strauch, A. M., MacKenzie, R. A., Giardina, C. P., & Bruland, G. L. (2015). Climate driven changes to rainfall and streamflow patterns in a model tropical island hydrological system. *Journal of Hydrology*, *523*, 160–169. https://doi.org/10.1016/j.jhydrol.2015.01.045

Thomaz, S. M., Agostinho, A. A., Gomes, L. C., Silveira, M. J., Rejmánek, M., Aslan, C. E., & Chow, E. (2012). Using space-for-time substitution and time sequence approaches in invasion ecology. *Freshwater Biology*, *57*(11), 2401–2410. https://doi.org/10.1111/fwb.12005

Tingley, R. W. III (2017). Conserving streams with changing climate: A multi-scaled research framework to consider current and future condition of Hawaiian stream habitats. Dissertation, Michigan State University, East Lansing, MI.

Tingley, R. W., Infante, D. M., MacKenzie, R. A., Cooper, A. R., & Tsang, Y.-P. (2018). Identifying natural catchment landscape influences on tropical stream organisms: Classifying stream reaches of the Hawaiian Islands. *Hydrobiologia*, *826*(1), 67–83. https://doi.org/10.1007/s10750-018-3726-5

Tsang, Y.-P., Wieferich, D., Fung, K., Infante, D. M., & Cooper, A. R. (2014). An approach for aggregating upstream catchment information to support research and management of fluvial systems across large landscapes. *SpringerPlus*, *3*(1), 589. https://doi.org/10.1186/2193-1801-3-589

Wallace, J. B., & Webster, J. R. (1996). The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, *41*(1), 115–139. https://doi.org/10.1146/annurev.en.41.010196.000555

Whitaker, D., & Christman, M. (2014). Clustsig: significant cluster analysis (version 1.1). Retrieved from https://CRAN.R-project.org/package=clustsig

Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J., & Hungate, B. A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Global Change Biology*, *17*(2), 927–942. https://doi.org/10.1111/j.1365-2486.2010.02302.x

Zhang, C., Wang, Y., Hamilton, K., & Lauer, A. (2016). Dynamical downscaling of the climate for the Hawaiian Islands. Part II: Projection for the late twenty-first century. *Journal of Climate*, *29*(23), 8333–8354.

Zwiers, F. W., Schnorbus, M. A., & Maruszeczka, G. D. (2011). *Hydrologic impacts of climate change on BC water resources: Summary report for Campbell, Columbia and Peace River watersheds (Summary Report)*. Pacific Climate Impacts Consortium. Victoria, BC: University of Victoria.

SUPPORTING INFORMATION

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

How to cite this article: Frauendorf TC, MacKenzie RA, Tingley RW III, Frazier AG, Riney MH, El-Sabaawi RW. Evaluating ecosystem effects of climate change on tropical island streams using high spatial and temporal resolution sampling regimes. *Glob Change Biol.* 2019;25:1344–1357. https://doi.org/10.1111/gcb.14584