

# Using a space-for-time substitution approach to predict the effects of climate change on nutrient cycling in tropical island stream ecosystems

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## Abstract

Climate change is expected to alter precipitation patterns worldwide, which can have direct effects on streamflow dynamics. In many tropical regions, climate-driven changes in rainfall are predicted to decrease streamflow and increase flash flooding, but the implications of these changes for stream ecosystem function are poorly understood. We used a rainfall gradient on Hawaii Island that mimics projected changes in rainfall and streamflow in order to estimate how climate change affects nutrient recycling. We measured per-capita excretion (nitrogen, phosphorus) and egestion rates of three dominant taxa (shrimp, caddisfly, midge) in eight streams along the gradient for 3 years. We scaled these rates to the population and community levels and measured nitrogen and phosphorus demand of the ecosystem to estimate if the relative contribution of nutrients supplied by invertebrates changes along the gradient. Across all three taxa, population egestion and excretion rates declined by 10-fold in drier streams. These declines were driven by lower population density, rather than differences in per-capita rates. Under the current climate scenario, community excretion supplied up to 70% of the nitrogen demand, which was 10-fold lower with projected changes in rainfall. Conversely, community excretion supplied up to 5% of the phosphorus demand, which did not vary across the rainfall gradient. This difference indicates that climate change may exacerbate nitrogen limitations in tropical island streams, and change the balance of nitrogen and phosphorus dynamics. Our study also demonstrates that space-for-time substitutions are a valuable tool to examine implications of climate change on ecosystem function in freshwater systems.

Climate models forecast regional and global changes in precipitation (IPCC 2014; Donat et al. 2016), which are predicted to alter structure and function of lotic ecosystems (Heino et al. 2009; Dudgeon 2014). The consequences of precipitation changes are important to understand in stream systems because precipitation is one of the main drivers of streamflow. Tropical regions often receive higher amounts of precipitation compared to their temperate counterparts, which can lead to more variable flow regimes (Lewis 2008; Feng et al. 2013). The Tropics are also expected to be one of the earliest regions to

deviate from the normal climate variability (Mora et al. 2013). Forecasted changes in precipitation have already been shown to alter the magnitude, timing, and variability of flow in tropical streams (Strauch et al. 2015), and each of these flow components are important for the integrity of stream ecosystems (Poff et al. 1997; Jardine et al. 2015). Recent studies have shown that these forecasted changes in streamflow can also alter ecosystem structure by decreasing abundance and biomass of fauna, and changing community composition in tropical island streams (Gutiérrez-Fonseca et al. 2018; Frauendorf et al. 2019). However, in tropical streams, implications of predicted changes in flow for stream ecosystem function (i.e., biological, geochemical, or physical processes) are still unknown.

Ecosystem function and structure are linked because the role of organisms in ecosystem processes depends on their traits, population characteristics, and community composition (Woodward et al. 2010b; El-Sabaawi 2017). In order to

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accurately forecast the effects of global change on ecosystem function, it is important to assess impacts of climate change across scales of ecological organization. For example, body size is an important trait for predicting the effects of biological change on ecosystem function (Fritschie and Olden 2016; Carlson and Langkilde 2017). However, studies have shown that population properties (e.g., density, size structure) also play an important role in altering ecosystem function (Jackson et al. 2017; Frauendorf 2019). In addition, the composition and structure of communities can be a key factor in influencing stream ecosystem function (Vanni et al. 2002; McIntyre et al. 2008). Therefore, the impacts of climate-driven changes in streamflow on ecosystem function need to be scaled from the individual to the ecosystem level, taking into account relevant variation at each level.

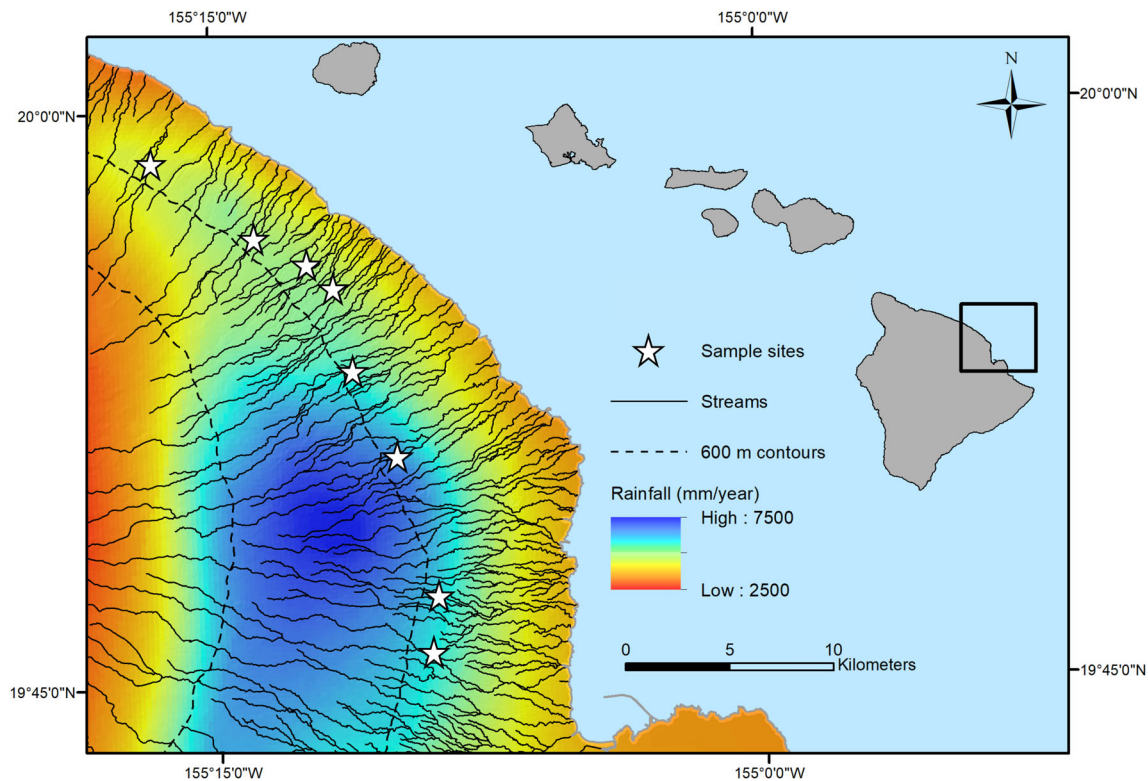
Nutrient cycling, defined as the flux of nutrients between biotic and abiotic compartments, is a critical component of ecosystem function in streams (Sterner and Elser 2002). Nutrient cycling can be affected by animals through direct (e.g., consumer-mediated recycling processes such as excretion, egestion) and indirect (e.g., grazing, soil compaction, bioturbation) pathways (Sterner and Elser 2002). Aquatic organisms sequester nutrients in their tissue because of growth and reproduction, and recycle nutrients back to the ecosystem through excretion (Atkinson et al. 2017). Excreted waste contains inorganic nutrients in the form of ammonium and phosphate that are readily available for primary producers (e.g., macrophytes, algae) and microbial communities (e.g., bacteria, fungi), supporting productivity at the base of the food web (Zimmer et al. 2006; Atkinson et al. 2017). Compared to excreted waste, egested material cannot be easily taken up by primary producers, but microbial breakdown and direct consumption of the egested material makes this waste product more accessible (Joyce et al. 2007; Halvorson and Atkinson 2019). Stream invertebrates can play a large role in nutrient cycling, as they often have large standing stocks, and their smaller size leads to larger mass-specific excretion rates compared to fish (Vanni 2002; Atkinson et al. 2017, 2019). For example, in a desert stream, invertebrate assemblages provide 70% of the nitrogen required by the stream biota (Grimm 1988). Body elemental composition, size, and diet of the consumer are important factors that determine the amount of nutrients excreted (Elser et al. 1996; Sterner and Elser 2002; Vanni et al. 2002), but these characteristics are sensitive to changes in environmental conditions (e.g., El-Sabaawi et al. 2012; Costello and Michel 2013; Griffiths and Hill 2014).

The importance of excreted nutrients in the broader nutrient cycle depends on the demand of the ecosystem and how much of this demand is supplied by consumers. Nutrient demand is defined as the amount of nutrients (i.e., nitrogen (N) and phosphorus (P)) required by the stream biota. If the supply of recycled nutrients is less than the demand, then recycled nutrients will be entirely consumed within the ecosystem. Conversely, if supply of recycled nutrients exceeds the

demand, then ecosystems can become net sources of nutrients that influence the productivity of adjacent ecosystems (Covino et al. 2018). Nutrient demand might also vary with climate change because it is the product of both abiotic (e.g., background nutrients, disturbance frequency, flow obstructions) and biotic (e.g., abundance, community composition of primary producers and microbes) factors (Allan and Castillo 2007).

Our goal is to explore how nutrient cycling in tropical island stream ecosystems might be altered under the projected climate-change scenario. To do so, we used a space-for-time approach, which exploits a natural gradient that mimics a forecasted change over time (Woodward et al. 2010b). In Hawaii, studies have forecasted a decline in rainfall and an increase in flash flooding in response to climate change. Indeed, studies have documented significant drying trends statewide since 1920 (Frazier and Giambelluca 2017), which have translated into declines in baseflow and increases in streamflow variability (Bassiouni and Oki 2013). These patterns are predicted to continue and intensify with climate change (Elison-Timm et al. 2015; Zhang et al. 2016). For our study, we sampled a rainfall gradient along the North Hilo coastline on Hawaii Island. The mean annual rainfall (MAR) decreases along the North Hilo coastline from approximately 7000–3500 mm yr<sup>-1</sup> (Giambelluca et al. 2013) within 20 km (Fig. 1), which corresponds to the forecasted climate-driven decline in rainfall (Elison-Timm et al. 2015; Zhang et al. 2016) and the resulting streamflow changes for Hawaii (Strauch et al. 2015). We and others have previously utilized this MAR gradient as a space-for-time substitution to investigate how predicted changes in precipitation alter stream ecosystem structure and to some extent function (Strauch et al. 2014; Riney 2015; Roberts et al. 2016; Tingley III 2017; Frauendorf et al. 2019). However, the implications for ecosystem function, such as nutrient recycling, remain unclear.

To address our goal, we quantified nutrient supply (N and P excretion; egestion) by dominant stream consumers and nutrient demand (N and P uptake) across eight streams along the North Hilo MAR gradient. We used these data to make predictions about the effects of climate change on stream ecosystem function in tropical streams. Previously, we showed that the decline in streamflow along the MAR gradient reduces the quality and quantity of benthic and suspended resources and changes benthic resource composition from being primarily macrophyte based (high quality) to leaf litter based (low quality; Frauendorf et al. 2019). Ecological stoichiometric theory predicts that because consumers have strict elemental homeostasis, decreases in food resource quality will force them to excrete less N and P in order to conserve their elemental composition (Sterner and Elser 2002). Therefore, we hypothesized that a reduction in food quality and quantity in drier and more hydrologically variable (i.e., increased flash flood frequency and intensity) streams will lower the excretion and egestion rates of individual invertebrates. Our previous work



**Fig. 1.** Eight stream sites (stars) located along the northeast coast of Hawaii Island with similar environmental characteristics except for the difference in mean annual rainfall. Average rainfall declines from ~7000 to 3500 mm per year along the coastline, mimicking projected effects of climate change on precipitation and streamflow. Data for this map were generated from the Rainfall Atlas of Hawaii (Giambelluca et al. 2013) and modified from Frauendorf et al. (2019).

showed that macroinvertebrate biomass also declines with decreasing streamflow (Frauendorf et al. 2019). As a result, we predicted that the concomitant declines in individual excretion and egestion rates, as well as population biomass, will cause an overall reduction in consumer-mediated recycling along the gradient. In contrast, we expected nutrient uptake to remain constant along the gradient, because losses in primary producers may be compensated by increases in microbial decomposers present with higher detrital resources. Since we expected nutrient demand to remain constant, but the nutrient supply by community excretion to decrease, we predicted that net export of nutrients would decline along the gradient as well. In other words, we predicted that climate change would increase the importance of consumer-mediated nutrient recycling within the stream reach, while decreasing the capacity of streams to export nutrients downstream.

## Methods

### Study system, rainfall, and streamflow parameters

Streams along the northeast coast of Hawaii Island are characterized by narrow gulches and young geologic substrate that was formed from a similar-aged lava flow (<100,000 yr) (Vitousek 1995). Besides the mean annual rainfall (MAR), characteristics like slope, elevation, mean annual temperature,

riparian vegetation, and soil age and type were all similar at each stream sampling site (Strauch et al. 2015). Eight streams were selected along the rainfall gradient spanning a range of ~3500 mm MAR (Honolulu (HON), Kapue (KAP), Kolekole (KOL), Umauma (UMA), Manoloa (LOA), Makahiloa (MAK), Pahale (PAH), and Kaawalii (KAA)) (Fig. 1).

Previous studies along this rainfall gradient have established that flow patterns along the gradient mimic the forecasted effects of climate change and showed that changes in rainfall and flow alter the structure of streams. Decreases in MAR result in concomitant declines in stream baseflow and flow stability (Strauch et al. 2015), which mimic the historical trends reported from streams in the Hawaiian islands (Bassiouni and Oki 2013). Declines in streamflow along this gradient have decreased the amount of particulate organic carbon (Strauch et al. 2018), and benthic and suspended resource quantity and quality (Frauendorf et al. 2019). As a result, the endemic and dominant shrimp in these streams have a smaller average body size and are in poorer condition in streams with lower baseflow (Tingley III 2017). Overall, invertebrate biomass was 35-fold lower in drier streams, which was apparent in both seasonal and inter-annual sampling regimes (Frauendorf et al. 2019). For this study, we sampled across three dry seasons (May–September of 2014, 2015, 2016) to document how changes in flow would impact nutrient

dynamics and to test how stable these patterns are when taking interannual variation into account.

Tropical streams have dry and wet season precipitation cycles. Since we sampled during the dry season only, we began by comparing how well rainfall and streamflow patterns during a sampling season reflected broader patterns along the gradient. In other words, we wanted to ensure that flow variation among the sites in the dry season reflected long-term patterns. These patterns have already been verified for 2015 and 2016 (Frauendorf et al. 2019), and therefore only needed to be confirmed for the 2014 sampling year. The 30-yr mean annual rainfall (MAR) and the seasonal rainfall data of each sampling year were calculated by using the Rainfall Atlas of Hawaii (Giambelluca et al. 2013) to average the area-weighted upstream and local rainfall of the catchment for each sample site (Frauendorf et al. 2019). 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). 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, we estimated flow variability ( $Q_{10}/Q_{90}$ ) and flood intensity (peak flow/ $Q_{50}$ ). These flow variables were then averaged from May through September of each year.

### Consumer excretion, egestion, and tissue composition

Individual excretion rates of the three dominant consumer taxa were measured across the full range of the observed size distributions in each of the eight study streams. Shrimp (*Atyoida bisulcata*), caddisflies (*Cheumatopsyche analis*), and midges (Chironomidae) were the three dominant consumers that represented in total between 70% and 98% of the animal biomass in each of the streams (estimated from Tingley III 2017; Frauendorf et al. 2019). Each individual (20 individuals per species, per stream, per year) was placed in a sealable container filled with a known volume of filtered stream water (scaled to the size of the organism). We added 3–5 control containers per species and sampling event, which were filled with the same amount of filtered stream water, but did not hold an organism. Containers were positioned in stream water to maintain similar temperature and incubated between 30 and 90 min. At the end of the incubation, the individual was removed and the water sample was filtered through a  $0.7 \mu m$  pore sized glass fiber filter to separate any material egested. Water samples were immediately put on ice until nutrients were analyzed. After euthanasia, the standard body length of each invertebrate was measured (to the nearest 0.01 mm), the gut was removed, and the remaining tissue was dried and analyzed for the carbon (C) and nitrogen (N) content using a Carlo Erba NA1500 CHN analyzer. From these data, we calculated molar tissue C:N ratios to examine elemental homeostasis of invertebrates across the gradient.

We measured ammonium concentration of the excretion water samples for all 3 years, but only determined the phosphate and nitrate concentrations in 2014 and 2015. We measured ammonium concentrations with a Turner Design Trilogy fluorometer following methods described by Holmes et al. (1999), with modifications by Taylor et al. (2007). Phosphate concentration was determined by using the ammonium molybdate method and a Shimadzu spectrophotometer (Strickland and Parsons 1972; Parsons et al. 1984). Finally, nitrate concentrations of the water samples were estimated by the University of Hilo Analytical Lab, using the cadmium reduction method with a Lachat Quikchem flow injection analyzer. Per-capita excretion rates ( $\mu g N$  or  $P$  individual $^{-1} hr^{-1}$ ) were calculated by subtracting the background nutrient concentration from the final, and adjusted for the volume of water in the container and incubation time. Mass-specific excretion rates ( $\mu g N$  or  $P$   $hr^{-1} mg$  of ash-free dry mass  $[AFDM]^{-1}$ ) were then estimated by dividing per-capita excretion rates by the individual's mass (AFDM was estimated from length-mass regressions extracted from Frauendorf et al. (2019) and Tingley III (2017). The excretion rates of the 20 individuals were then pooled to obtain an average per-capita and mass-specific excretion rate per site and year.

Population excretion rates ( $\mu g N$  or  $P$  population $^{-1} m^{-2} hr^{-1}$ ) are defined as the amount of N and P excreted by all individuals within a population (El-Sabaawi et al. 2015). Consequently, population excretion is the product of per-capita excretion and the density of the population. Since per-capita excretion often scales allometrically with body size (Sternler and Elser 2002), the size distribution of a population can also influence population excretion (Fritschie and Olden 2016). Thus, we first ran a linear model for each taxon to determine if per-capita excretion related to body size. If an allometric relationship was present, we calculated population excretion ( $R$ ) using the following equation adapted from Frauendorf (2019):

$$R = \int E_{(z)} P_{(z)} N dz, \quad (1)$$

where  $E_{(z)}$  is the per-capita excretion rate at a given size  $z$ ,  $P_{(z)}$  is the proportion of individuals in the population with the size  $z$ , and  $N$  is the population density. If there was no allometric relationship present, we simply multiplied the average per-capita excretion rates by the population density for each taxon and site:

$$R = EN \quad (2)$$

Densities and size distributions were obtained from Frauendorf et al. (2019) for the caddisflies and midges, and from Tingley III (2017) for the shrimp. Both studies collected these data from the same sampling streams, season, and years, with the exception of the shrimp. Shrimp density and size

distribution sampling only overlapped during the dry season of 2014. However, the same study found little difference in shrimp density and size between years along this rainfall gradient (Tingley III 2017). Lastly, we calculated the community excretion rate ( $C$ ,  $\mu\text{g N or P m}^{-2} \text{ hr}^{-1}$ ), defined as the amount of N and P excreted by all the populations in a community, by summing the population excretion rates from the three dominant taxa in our streams:

$$C = R_{\text{Shrimp}} + R_{\text{Caddisfly}} + R_{\text{Midge}} \quad (3)$$

During 2014 and 2015, filters from the individual excretion trials with the egested material were dried, weighed, ashed at  $550^{\circ}\text{C}$ , and reweighed to obtain an estimate of the amount of particles egested per individual ( $\mu\text{g AFDM}$ ). This estimate was adjusted by the incubation time ( $\mu\text{g AFDM/hr}$ ), and any weight from the control container filters was subtracted from these estimates. Due to the small amount of egested material, we were not able to obtain midge egestion rates.

### Nutrient uptake

We measured uptake using an instantaneous nutrient release method adapted from Covino et al. (2010) in each of the eight streams along the gradient. We released a conservative tracer ( $\text{NaCl}$ ) and measured the time and change in specific conductivity over a 100-m long reach. The change in conductivity over time curve was then integrated to calculate the exact flow for the reach. Based on this flow rate, the appropriate reach length and salt and nutrient concentrations were calculated to ensure that the nutrient residence time (18–25 min) and concentrations ( $5 \text{ g NaCl L}^{-1} \text{ s}^{-1}$ ,  $300 \text{ mg KH}_2\text{PO}_4\text{-P L}^{-1} \text{ s}^{-1}$ ,  $200 \text{ mg KNO}_3\text{-N L}^{-1} \text{ s}^{-1}$ , and  $100 \text{ mg NH}_4\text{Cl-N L}^{-1} \text{ s}^{-1}$ ) were constant across the streams. Sodium chloride acted as the conservative tracer to account for any non-biological nutrient loss, while ammonium chloride, potassium nitrate, and potassium phosphate are biologically active and are taken up by microbial and plant communities. After the salts were dissolved and released at the top of the reach, 30 filtered water samples spanning the breakthrough curve were collected at the bottom of the reach. Samples were placed on ice until the nutrient analyses, which followed the methods described above. Nutrient uptake rates ( $\mu\text{g N or P m}^{-2} \text{ hr}^{-1}$ ) were then calculated by taking the slope of the difference between the initial and final nutrient concentration to conservative tracer ratio of each of the 30 collected samples (Covino et al. 2010). We calculated percent contribution of excreted nutrients to the demand across the flow gradient by dividing the community excretion rate by the nutrient uptake of the stream and multiplying the result by 100.

### Statistical analysis

To explore how flow drives changes in nutrient dynamics, we selected baseflow ( $Q_{90}$ ) as the main flow predictor variable, because previous research along this rainfall gradient shows

that baseflow is the strongest driver of resource and consumer dynamics (Frauendorf et al. 2019). In addition, we used the “relaimpo” package in R (Grömping 2006) to estimate the relative importance of each flow variable (i.e., baseflow, flow variability, flood intensity) to changes in excretion and uptake. We confirmed that baseflow was the main driver of population excretion and nutrient uptake (55–93%), followed by flow variability (4–25%) and flood intensity (3–20%) (Supporting Information, Table 1).

Generalized linear models were run to determine the relationships between the rainfall and streamflow as predictor variables, and population density, average population size, and nutrient metrics (excretion and uptake) as response variables, using the “lme4” and “pscl” (to extract  $R^2$  values) packages from the statistical program R (Bates et al. 2015; Jackman 2017). For each relationship, we ran our linear models separately for each sampling year to examine inter-annual variation. We did not run a linear model for 2014, since we sampled only three streams along the gradient, but we added the data points to the graphs for qualitative comparisons with 2015 and 2016. We examined the distribution of the response variables using density, residual, and QQ plots, and used this information to select the family of our generalized models. Since most of our data were exponential, we chose the Gamma family for log normal data distributions. In some cases where the data had a strong positive skew, we added a log link function to the Gamma family. The parameters and output of each model are reported in Supporting Information, Tables 2–6.

## Results

### Rainfall and stream parameters

Total rainfall during the 2014 dry season increased along the MAR gradient as expected and was comparable to the other 2 years ( $R^2$  (pseudo  $R^2$ ) = 0.7771,  $E$  (estimate) = 0.1198,  $SE$  (standard error) = 0.0262,  $t$  ( $t$ -value) = 4.5730,  $p$  ( $p$ -value) = 0.0038, Supporting Information, Fig. 1 and Table 2). The year 2015 had the highest rainfall in 30 years (NOAA 2017) with 1000 mm more rainfall during the dry season compared to 2014 and 2016. As expected, baseflow ( $Q_{90}$ ) exponentially increased with rainfall along the gradient in 2014 ( $R^2$  = 0.6295,  $E$  = 0.0046,  $SE$  = 0.0014,  $t$  = 3.1820,  $p$  = 0.0190). Streamflow variability ( $Q_{10}/Q_{90}$ ) and flood intensity (peak flow/ $Q_{50}$ ) were inversely related to rainfall in 2014 ( $(Q_{10}/Q_{90})$ :  $R^2$  = 0.9914,  $E$  = -0.0036,  $SE$  = 0.0008,  $t$  = -4.6510,  $p$  = 0.0035; (peak flow/ $Q_{50}$ ):  $R^2$  = 0.8995,  $E$  = -0.0032,  $SE$  = 0.0006,  $t$  = -5.4770,  $p$  = 0.0015). Overall, baseflow, flow variability, and flood intensity patterns during the 2014-sampling season were similar to the patterns in 2015 and 2016 (Supporting Information, Fig. 1).

Baseflow background nutrients across streams and years ranged between  $4\text{--}9 \mu\text{g N L}^{-1}$  for ammonium,  $2\text{--}19 \mu\text{g N L}^{-1}$  for nitrate, and  $4\text{--}7 \mu\text{g P L}^{-1}$  for phosphate (Table 1).

**Table 1.** Physical characteristics of 8 streams across the North Hilo rainfall gradient. Mean annual rainfall (MAR) was generated from the Rainfall Atlas of Hawaii (Giambelluca et al. 2013). Baseflow ( $Q_{90}$ ) and background nutrients ( $\mu\text{g}$  molar nitrogen (N) or phosphorus (P)  $\text{L}^{-1}$ ) were averaged for the sampling periods (May–September) across the 3 years.

| Stream        | WET   |       |       |      | DRY  |      |      |      |
|---------------|-------|-------|-------|------|------|------|------|------|
|               | HON   | KAP   | KOL   | UMA  | LOA  | MAK  | PAH  | KAA  |
| MAR           | 5764  | 5868  | 6520  | 5178 | 5168 | 4748 | 4527 | 3703 |
| $Q_{90}$      | 22.36 | 15.50 | 17.56 | 8.65 | 4.53 | 2.56 | 0.32 | 0.06 |
| $\text{NH}_4$ | 6     | 9     | 4     | 4    | 7    | 6    | 5    | 5    |
| $\text{NO}_3$ | 14    | 2     | 13    | NA   | 18   | 10   | 19   | 18   |
| $\text{PO}_4$ | 4     | 5     | 4     | 6    | 7    | 5    | 6    | 7    |

Ammonium and nitrate were not related to baseflow ( $\text{NH}_4$ :  $E = 0.0143$ ,  $\text{SE} = 0.0699$ ,  $t = 0.2050$ ,  $p = 0.8442$ ;  $\text{NO}_3$ :  $E = -0.1191$ ,  $\text{SE} = 0.1516$ ,  $t = -0.7850$ ,  $p = 0.4678$ ), but phosphate slightly decreased with increases in flow ( $R^2 = 0.6020$ ,  $E = -0.1008$ ,  $\text{SE} = 0.0335$ ,  $t = -3.0120$ ,  $p = 0.0236$ ).

#### Individual responses along the rainfall gradient

Contrary to our predictions, per-capita and mass-specific excretion rates showed weak trends across the streamflow gradient (Fig. 2, Supporting Information, Figs. 2 and 3, and Table 3). Shrimp per-capita ammonium excretion rates increased with baseflow in 2015 ( $R^2 = 0.6975$ ,  $E = 0.3242$ ,  $\text{SE} = 0.0955$ ,  $t = 3.3960$ ,  $p = 0.0193$ ) and 2016 ( $R^2 = 0.8138$ ,  $E = 0.2419$ ,  $\text{SE} = 0.0472$ ,  $t = 5.1210$ ,  $p = 0.0022$ ) (Fig. 2a). Shrimp per-capita phosphate and nitrate excretion rates, as well as all caddisfly and midge per-capita excretion rates, remained relatively constant across the gradient (Fig. 2 b,c, Supporting Information, Figs. 2 and 3, Table 3). Per-capita phosphorus excretion ranged between 0.01 and 1.39  $\mu\text{g P hr}^{-1}$  for shrimp (Supporting Information, Fig. 2a), 0.03–0.27  $\mu\text{g P hr}^{-1}$  for caddisflies (Supporting Information, Fig. 2b), and 0.01–0.13  $\mu\text{g P hr}^{-1}$  for midges (Supporting Information, Fig. 2c). Shrimp excreted on average 0.15  $\mu\text{g NO}_3\text{-N hr}^{-1}$  per-capita, which did not vary significantly with baseflow (Supporting Information, Fig. 3a). We did not detect any nitrate excreted from caddisflies and midges (detection limit: 0.07  $\mu\text{M}$ ). Mass-specific ammonium and phosphate excretion did not show a significant pattern across the streamflow gradient (Fig. 2d–f; Supporting Information, Figs. 2d–f and 3b). The exception was midge mass-specific phosphate excretion in 2015, which was lower with larger baseflow ( $R^2 = 0.7947$ ,  $E = 0.0152$ ,  $\text{SE} = 0.0051$ ,  $t = 2.9910$ ,  $p = 0.0300$ ; Supporting Information, Fig. 2f). This was caused by higher variability in mass-specific excretion during the wet year in 2015. Lastly, the nitrate mass-specific excretion rates of shrimp also did not vary with baseflow (Supporting Information, Fig. 3b).

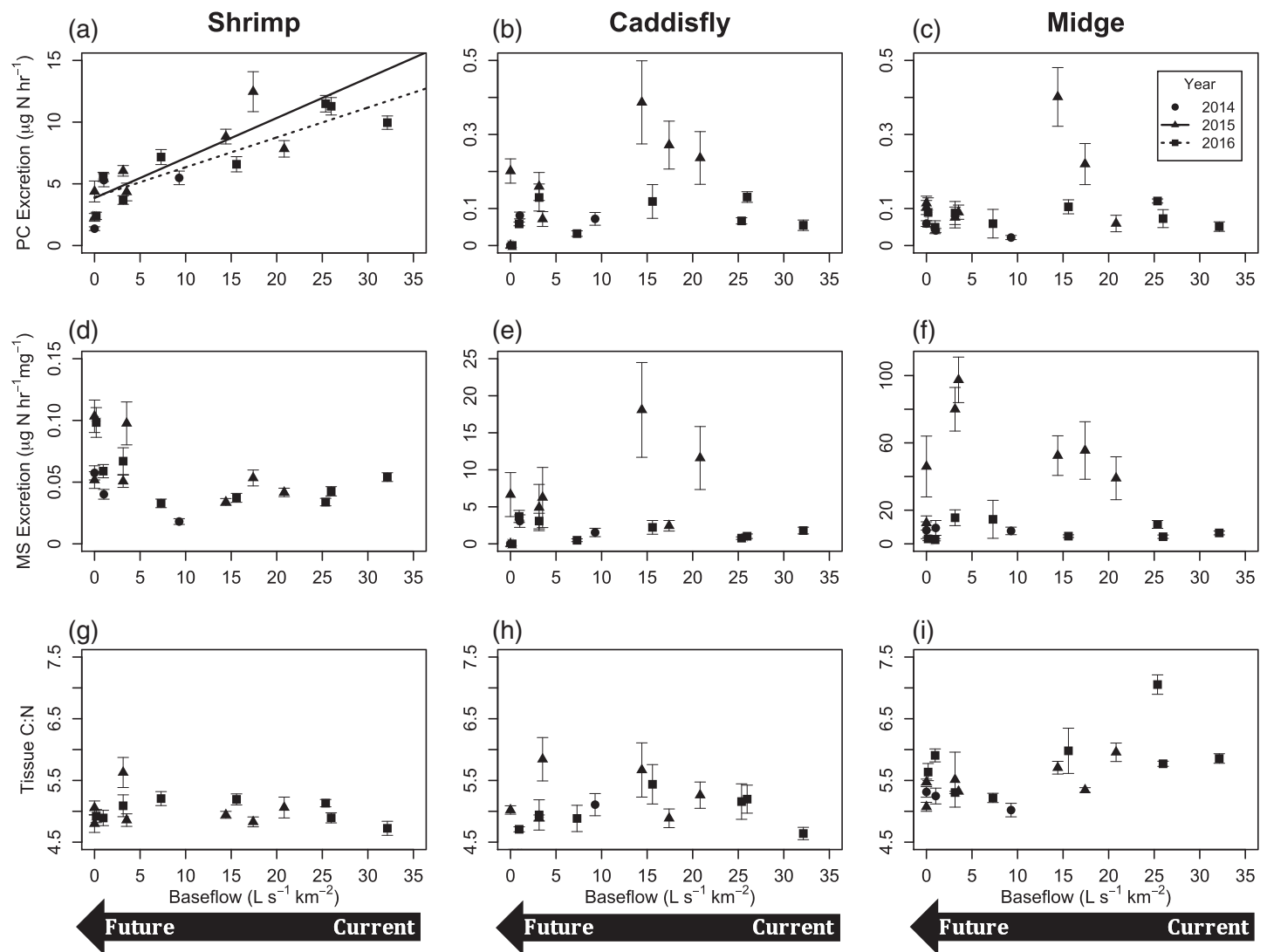
Likewise, C:N in the tissues of the three dominant taxa showed little variation across baseflow (Fig. 2g–i). Shrimp C:N ratios ranged from 4.12 to 5.62, caddisfly ratios ranged

between 4.30 and 5.84, while midge C:N ratios ranged from 5.02 to 7.05, without a consistent pattern with baseflow.

#### Population responses along the rainfall gradient

The density of all three dominant taxa increased with baseflow, and body size of shrimp was higher in wetter streams (Fig. 3, Supporting Information, Table 4). The average body size of shrimp was significantly larger with elevated flow ( $R^2 = 0.639$ ,  $E = 3.7690$ ,  $\text{SE} = 1.1580$ ,  $t = 3.2550$ ,  $p = 0.0173$ ), as was the shrimp population size distribution (Fig. 3a). However, there were little differences in the size distributions for caddisfly and midge populations across the MAR gradient (Fig. 3b,c). Overall, per-capita N and P excretion scaled with body size for shrimp ( $p$ -values between <0.001 and 0.057, respectively), but not for caddisflies ( $p$ -values between 0.18 and 0.82) or midges ( $p$ -values between 0.26 and 0.76). Densities of all three taxa increased exponentially with streamflow in 2015 and 2016 (Fig. 3d–f). Shrimp densities doubled in wetter streams (2015:  $R^2 = 0.8328$ ,  $E = 0.0767$ ,  $\text{SE} = 0.0175$ ,  $t = 4.3870$ ,  $p = 0.0071$ ; 2016:  $R^2 = 0.6998$ ,  $E = 0.0507$ ,  $\text{SE} = 0.0146$ ,  $t = 3.4630$ ,  $p = 0.0134$ ), while the densities of caddisflies were up to 2000 $\times$  higher (2015:  $R^2 = 0.5182$ ,  $E = 0.1813$ ,  $\text{SE} = 0.0503$ ,  $t = 3.6070$ ,  $p = 0.0154$ ; 2016:  $R^2 = 0.5026$ ,  $E = 0.0797$ ,  $\text{SE} = 0.0355$ ,  $t = 2.2470$ ,  $p = 0.0066$ ) and midges up to 100 $\times$  (2015:  $R^2 = 0.5448$ ,  $E = 0.0773$ ,  $\text{SE} = 0.0257$ ,  $t = 3.0060$ ,  $p = 0.0299$ ; 2016:  $R^2 = 0.8568$ ,  $E = 0.0622$ ,  $\text{SE} = 0.0110$ ,  $t = 5.6350$ ,  $p = 0.0013$ ). Therefore, density of the dominant taxa and shrimp body size were lower with projected climate-driven changes in streamflow.

As we predicted, population excretion rates generally increased exponentially with elevated streamflow (Fig. 3g–i). Shrimp ammonium (Fig. 3g), phosphate (0.01–64.4  $\mu\text{g P m}^{-2} \text{hr}^{-1}$ , Supporting Information, Fig. 4a), and nitrate (0.01–104.3  $\mu\text{g N m}^{-2} \text{hr}^{-1}$ , Supporting Information, Fig. 4d) population excretion were all significantly and positively related to baseflow (Supporting Information, Table 4). Midge and caddisfly ammonium population excretion was also significantly higher in wetter streams, but the phosphate population excretion of both taxa showed no significant trends across the gradient (midge: 1.7–52.5  $\mu\text{g P m}^{-2} \text{hr}^{-1}$ ; caddisfly:



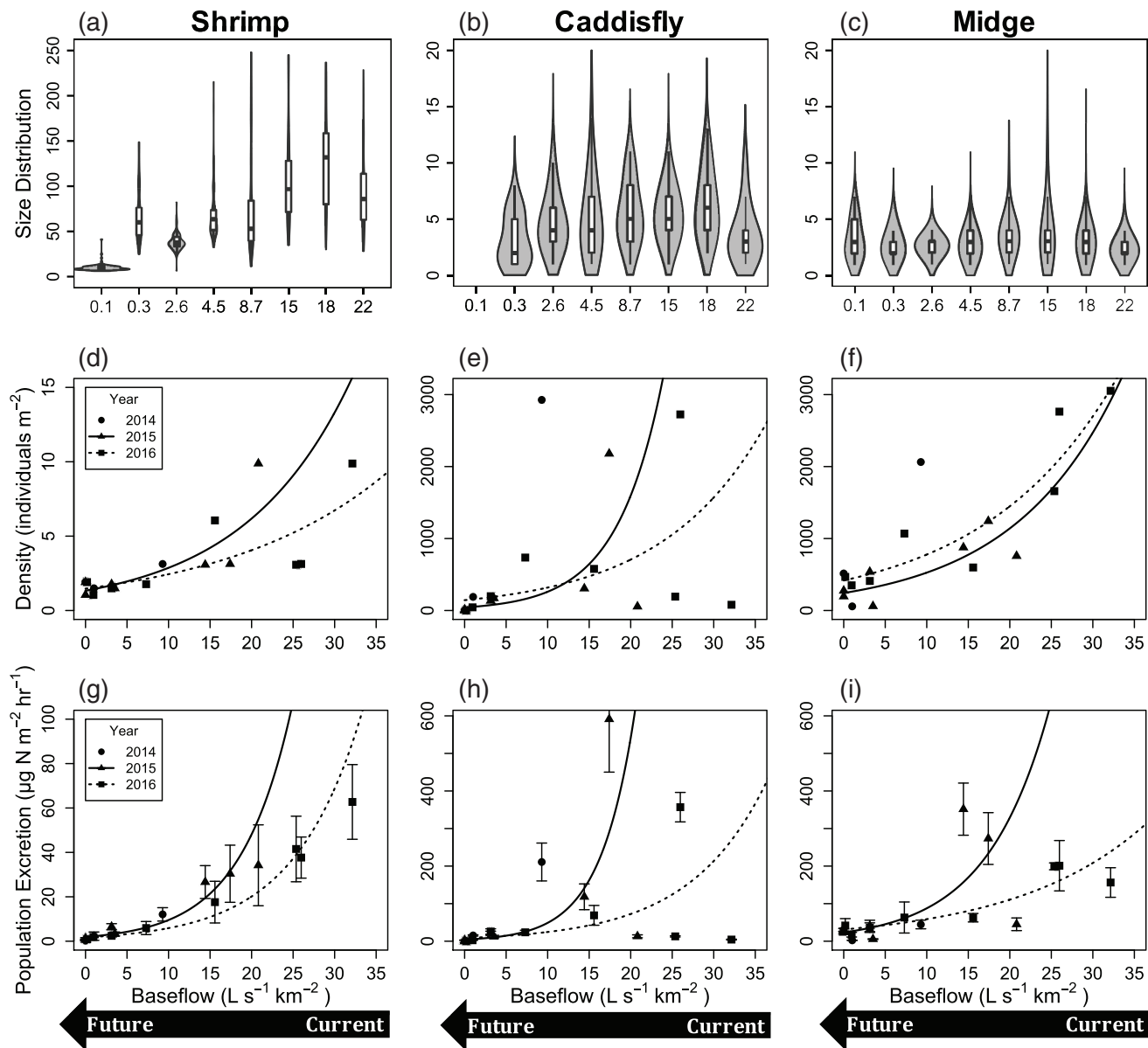
**Fig. 2.** Per-capita ammonium excretion rates increased with baseflow for shrimp (**a**) in 2015 and 2016, but not mass-specific excretion (**d**). Per-capita and mass-specific excretion did not vary appreciably across the gradient for caddisflies (**b,c**) or midges (**e, f**). Tissue chemistry also did not vary for shrimp (**g**), caddisflies (**h**), and midges (**i**). Each point represents the average of 20 individuals per taxon (with standard error) in one stream per sampling year. Lines denote significant model output of each relationship ( $p \leq 0.05$ , see text for modeling details). The x-axes represent baseflow ( $Q_{90}$ ) averaged for May–September, while block arrows indicate the direction of predicted declines in baseflow with climate change.

$0.64\text{--}178.6 \mu\text{g P m}^{-2} \text{ hr}^{-1}$ ; Supporting Information, Fig. 4b,c, Table 4). Based on our results, we expect population excretion to exponentially decline with climate-driven changes in rainfall, but these effects will be stronger for nitrogen compared to phosphorus.

### Community and ecosystem responses along the rainfall gradient

Midge population excretion rates supplied on average 60% of ammonium and 55% of phosphate to community excretion. Caddisfly populations contributed on average 30% to the ammonium and 41% to the phosphate community excretion, while shrimp contributed only 10% and 4%, respectively. However, these relative contributions varied across baseflow.

Midges contributed up to 99% in the driest and wettest streams along the gradient, while caddisflies supplied up to 80% to the community excretion of intermediate flow streams. Meanwhile, the relative contribution of shrimp population excretion significantly increased with baseflow ( $\text{NH}_4$ : up to 37%,  $R^2 = 0.3687$ ,  $E = 0.0499$ ,  $\text{SE} = 0.0183$ ,  $t = 2.7210$ ,  $p = 0.0158$ ;  $\text{PO}_4$ : up to 39%,  $R^2 = 0.8477$ ,  $E = 0.3046$ ,  $\text{SE} = 0.0512$ ,  $t = 5.9440$ ,  $p = 0.0006$ ). Since shrimp were the only taxon that had measurable excreted nitrate, they were the predominant contributor to the nitrate community excretion. As predicted, nitrogen recycled by the invertebrate community increased exponentially with baseflow, while nutrient uptake did not vary with streamflow. Community ammonium (Fig. 4a) and nitrate ( $0.01\text{--}104.3 \mu\text{g N m}^{-2} \text{ hr}^{-1}$ , Supporting

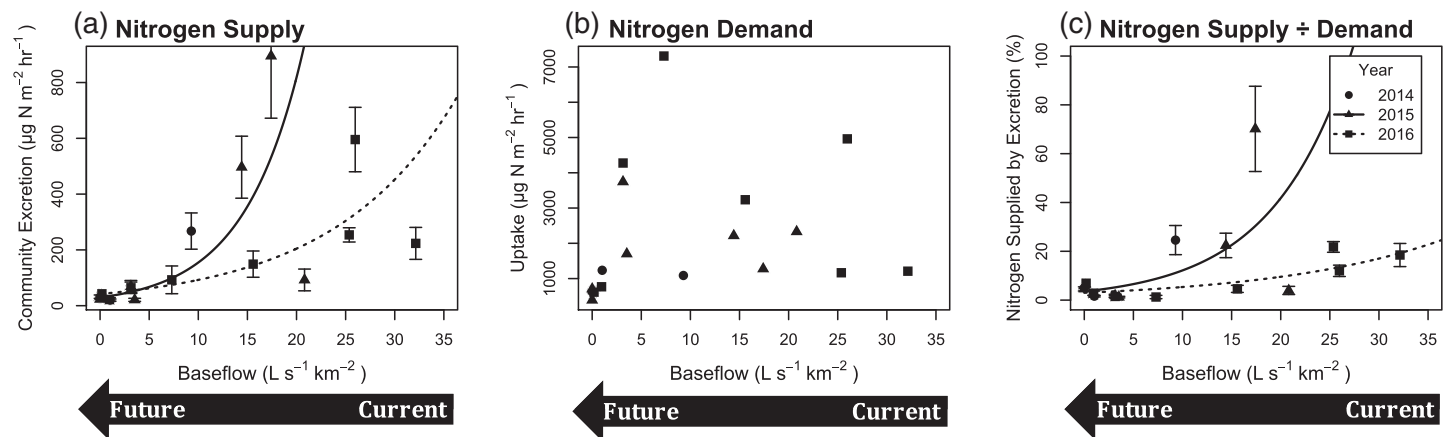


**Fig. 3.** The violin plots (a–c) display the size distribution of the three dominant taxa across baseflow, where the width of the shaded area indicates the frequency of a particular size class. The average size of shrimp (a; mg AFDM for 2014 only) populations increased significantly with higher baseflow, while the average size of caddisfly (b; mm body length average for 2014–2016) and midge populations (c; mm body length for 2014–2016) did not vary across flow. Density (d–f) and population-level ammonium excretion (g–i) of all three taxa generally increased exponentially with higher baseflow streams. Each point represents the average of 20 individuals per taxon (with standard error) in one stream per sampling year. Lines denote significant model output of each relationship ( $p \leq 0.05$ , see text for modeling details). The x-axes represent baseflow ( $Q_{90}$ ) averaged for May–September, while block arrows indicate the direction of predicted declines in baseflow with climate change.

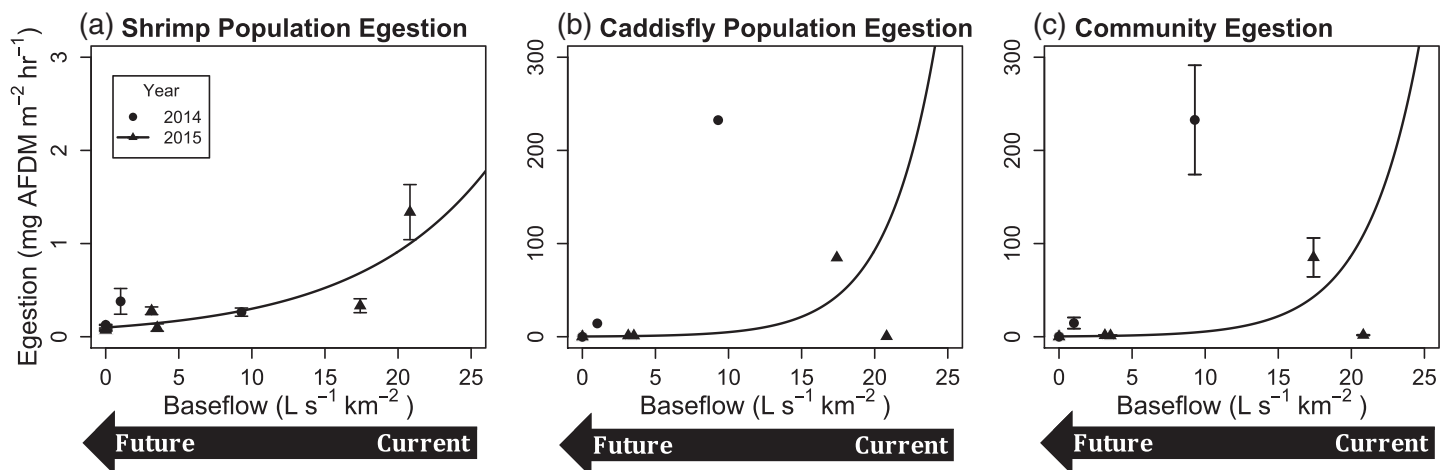
Information, Fig. 5d) excretion rates showed a significant positive relationship with streamflow (Supporting Information, Table 5), yet this pattern was not significant for phosphate ( $6.72\text{--}231.3 \mu\text{g P m}^{-2} \text{ hr}^{-1}$ ; Supporting Information, Fig. 5a).

Ecosystem uptake rates for ammonium (Fig. 4b) were variable across streams and years, and did not show a consistent pattern with baseflow (Supporting Information, Table 5). However, phosphate ( $636\text{--}5621 \mu\text{g P m}^{-2} \text{ hr}^{-1}$ , Supporting

Information, Fig. 5b) and nitrate ( $265\text{--}8992 \mu\text{g N m}^{-2} \text{ hr}^{-1}$ , Supporting Information, Fig. 5e) uptake was higher in high flow streams in 2015 ( $\text{PO}_4$ :  $R^2 = 0.7789$ ,  $E = 212.84$ ,  $\text{SE} = 50.710$ ,  $t = 4.1970$ ,  $p = 0.0085$ ;  $\text{NO}_3$ :  $R^2 = 0.7475$ ,  $E = 330.65$ ,  $\text{SE} = 85.940$ ,  $t = 3.8480$ ,  $p = 0.0120$ ). The relative amount of nitrogen supplied to the streams by invertebrates was positively related with baseflow, supporting our predictions. Invertebrate communities contributed between 1.6% and 6.9% of



**Fig. 4.** Ammonium supplied by community excretion (a) increased exponentially in streams with higher baseflow, while nitrogen demand (b) did not change. Therefore, the percent of nitrogen supplied by excretion (c) increased by 10-fold as streams increased in baseflow. Each point represents the average of 20 individuals per taxon (with standard error) in one stream per sampling year. Lines denote significant model output of each relationship ( $p \leq 0.05$ , see text for modeling details). The x-axes represent baseflow ( $Q_{90}$ ) averaged for May–September, while block arrows indicate the direction of predicted declines in baseflow with climate change.



**Fig. 5.** Population (a,b) and community egestion (c) increased exponentially with baseflow. Each point represents the average of 20 individuals per taxon (with standard error) in one stream per sampling year. Lines denote significant model output of each relationship ( $p \leq 0.05$ , see text for modeling details). The x-axes represent baseflow ( $Q_{90}$ ) averaged for May–September, while block arrows indicate the direction of predicted declines in baseflow with climate change.

ammonium to the nutrient uptake in drier streams, but this number increased 10-fold in streams with higher baseflow (Fig. 4c; 2015:  $R^2 = 0.5469$ ,  $E = 0.1234$ ,  $SE = 0.0421$ ,  $t = 2.9310$ ,  $p = 0.0326$ ; 2016:  $R^2 = 0.6025$ ,  $E = 0.0577$ ,  $SE = 0.0214$ ,  $t = 2.6940$ ,  $p = 0.0358$ ). Although percent phosphorus and nitrate supplied by invertebrates increased 10-fold with streamflow as well (Supporting Information, Fig. 5c,f, respectively), the relative contribution of excretion to the demand was comparatively small ( $PO_4$ : 0.4–4.4%;  $NO_3$ : 0.1–1.7%). In 2015, these small increases were significant for nitrate ( $R^2 = 0.9994$ ,  $E = 0.3430$ ,  $SE = 0.0686$ ,  $t = 5.0040$ ,  $p = 0.0041$ ), but not for phosphate (Supporting Information, Table 5).

#### Egestion rates along the rainfall gradient

Individual, population, and community egestion rates followed similar trends across the rainfall gradient compared to excretion rates (Fig. 5). Per-capita egestion rates ranged between 0.001 and 0.854 mg AFDM  $hr^{-1}$  for shrimp and between 0.001 and 2.25 mg AFDM  $hr^{-1}$  for caddisflies, while mass-specific egestion ranged between 0.02 and 6.58 mg AFDM  $hr^{-1} g^{-1}$  for shrimp and between 9.92 and 233.2 mg AFDM  $hr^{-1} g^{-1}$  for caddisflies. Per-capita and mass-specific egestion rates did not differ with changes in baseflow (Supporting Information, Table 6). However, population (Fig. 5a,b; shrimp:  $R^2 = 0.8322$ ,  $E = 0.1112$ ,  $SE = 0.0305$ ,  $t = 3.6400$ ,  $p = 0.0220$ ; caddisfly:  $R^2 = 0.9810$ ,  $E = 0.2935$ ,  $SE = 0.0474$ ,  $t = 6.1860$ ,  $p = 0.0035$ )

egestion rates were significantly higher with elevated baseflow. Community level egestion (Fig. 5c) mimicked the significant changes in population excretion rates ( $R^2 = 0.7948$ ,  $E = 0.2752$ ,  $SE = 0.0436$ ,  $t = 6.3100$ ,  $p = 0.0032$ ) in 2015, and these differences were driven almost exclusively by changes in caddisfly egestion. These significant relationships were dependent on the inclusion of one point, but outlier analyses did not support removing that point.

## Discussion

Climate change is a prominent and growing threat to freshwater ecosystems. Several climate models have projected continued decreases in total mean annual rainfall and increases in precipitation extremes in various tropical regions (e.g., Rauscher et al. 2010; Khalyani et al. 2015) and regions of Hawaii specifically (Lauer et al. 2013; Lehmann et al. 2015). We used a natural rainfall gradient on Hawaii Island that mimics these predicted changes (Fig. 1) to quantify the potential effects of climate change on tropical stream ecosystem function. We found that the nitrogen supplied by shrimp, caddisfly, and midge populations were nearly 10-fold lower at drier sites, suggesting a substantial decline in consumer-mediated recycling with climate change. Egestion rates showed similar patterns to excretion and declined by 10-fold with decreases in streamflow. These results provide important insights into the effects of climate change on ecosystem function in these vulnerable tropical island ecosystems.

We hypothesized that consumers would have lower mass-specific excretion rates at the drier end of the gradient, because consumers may need to compensate for lower resource quantity and quality. Previously we showed that resources shift from high quality macrophytes to low quality leaf litter with projected changes in rainfall (Frauendorf et al. 2019). Therefore, consumers might excrete less nitrogen to maintain a homeostatic balance. Contrary to our prediction mass-specific excretion rates of all three taxa showed weak relationships with streamflow. The lack of any pattern in the tissue C:N across streamflow indicates that these consumers were homeostatic (Sterner and Elser 2002). It is possible that these taxa deploy other physiological methods for maintaining homeostatic balance in response to changes in resources, such as increased consumption rate or increased assimilation efficiency (Sterner and Elser 2002).

As we predicted, population excretion across taxa was lower with projected changes in rainfall, even though mass-specific excretion did not vary. For all three taxa this decrease was more prominent for nitrogen population excretion rates compared to phosphorus. These exponential declines can likely be attributed to the steep drops (up to 200-fold) in invertebrate density with decreases in streamflow. However, in shrimp populations the average body size and per-capita excretion rates also declined at the drier end of the MAR gradient, indicating that size and per-capita excretion play a secondary role

in determining the changes in population excretion for some invertebrates. However, for the smaller invertebrate taxa (i.e., midge and caddisfly), body size and per-capita excretion did not contribute substantially to the declines in population excretion. This is because per-capita excretion of midges and caddisflies did not scale with body size. Consequently, the population size distribution was not incorporated when we scaled individual excretion rates to the population level. Meanwhile, per-capita excretion of caddisflies and midges varied considerably across the MAR gradient, but with no consistent pattern (Fig. 2). This contrast among taxa is not surprising as per-capita excretion can be very context specific to the individual and its environment (Atkinson et al. 2017), and we know that streamflow, resources, and consumers all change along this rainfall gradient (Strauch et al. 2015; Frauendorf et al. 2019). We encourage future studies to examine the drivers behind the variability in per-capita excretion rates of midges and caddisflies.

A 10-fold drop in the proportion of consumer-mediated nutrient supply along the gradient was mainly driven by changes in midge, and to some extent caddisfly, contributions. The differences in the relative contribution of each taxon along the MAR gradient can be attributed to the biomass changes of the three dominant taxa (Tingley III 2017; Frauendorf et al. 2019). As predicted, nutrient uptake varied consistently along the gradient, likely because decreases in primary producers were balanced by increases in fungal and bacterial decomposers. As a result, the relative amount of nutrients supplied by invertebrates declined 10-fold as well. However, our results suggest that projected climate change effects on stream flow will likely have little effect on invertebrate contributions to phosphate and nitrate budgets because invertebrate excretion contributed less than 5% to the phosphate and nitrate demand across streams. This contrasts to ammonium, where under current conditions invertebrates supply up to 70% of the ammonium demand within a stream.

A 10-fold decrease in consumer nitrogen supply can significantly impact in-stream productivity in the Tropics. Tropical streams are often nutrient poor and limited by nitrogen (Downing et al. 1999). The average nitrogen uptake rates in our streams are comparable to nutrient-limited temperate systems; however, our wetter rivers require three times as much nitrogen than reported in temperate zones (e.g., Griffiths and Hill 2014). In these high-flow streams consumers supplied up to 70% of the nitrogen demand, which is comparable to the contribution of consumers to nutrient cycling in temperate, low-nutrient streams (Grimm 1988; Atkinson et al. 2014; Griffiths and Hill 2014) and other tropical rivers (McIntyre et al. 2008). Therefore, based on our results, climate change can exacerbate the nitrogen limitations in these tropical streams by decreasing the consumer's contribution to the nitrogen cycle 10-fold. Since nutrients affect productivity at the base of a stream food web (i.e., microbes and plants), changes in nitrogen supply rates can potentially have direct

and indirect consequences for higher aquatic and terrestrial trophic levels.

When examining nutrient recycling, most studies focus on excretion but some have shown that egestion rates can be as high as excretion rates (Halvorson et al. 2015). Recent research has shown that egested material can become an important food resource for some aquatic organisms and generate sites of enhanced microbial activity (reviewed by Atkinson et al. 2017). The ingestion and mineralization of egested material in return increases the availability of egested nutrients (Joyce et al. 2007). While we could not determine the nutrient content of the egested matter based on the small amount of egested material available, we did determine the egestion rate. As with our excretion results, individual egestion rates did not vary with flow. However, when scaled to the population and community level, egestion rates declined by 10-fold in low-flow streams because of changes in density and size of the dominant taxa producing the egested material. We conclude that the availability of egested material will also decline with projected changes in rainfall. We recommend further analyses to examine the nutrient content of the egested material to determine the relative importance of lower egestion and excretion rates.

Island streams, like those in Hawaii, are relatively short and an alteration to upstream nutrient export can affect rates at which streams deliver nutrients to estuaries and coastal systems (Allan and Castillo 2007). Streams are continuous systems and changes in the amount of nutrients exported from the study reach can alter downstream labile nutrient availability. In the Tropics, near-shore habitat is often nitrogen limited and up to 80% of phytoplankton productivity can be attributed to stream nutrient supply (Ringuet and Mackenzie 2005; Hoover and Mackenzie 2009). Therefore, a 10-fold reduction in nitrogen supply can potentially have direct consequences for the structure and productivity of downstream ecosystems.

Interannual variation is often a concern for all space for time substitutions. Our data showed interannual variation in rainfall, especially during the extremely wet year in 2015 (Supporting Information, Fig. 1). Therefore, the slope of some relationships changed in response to differences in rainfall between the three sampling years. Yet, the trends of each relationship are consistent across years, despite the changes in hydrology. Therefore, our predictions about how ecosystem function will vary with climate change hold regardless of interannual variation, providing additional support for our conclusions.

Space-for-time substitutions are commonly used in terrestrial systems to estimate implications for ecosystem function. However, in freshwater systems there are few studies that have applied this tool in the context of climate change. These studies focus on implications of temperature changes for ecosystem structure (e.g., Woodward et al. 2010a; Stoks et al. 2014), while studies measuring effects of precipitation change, in particular on ecosystem function, are quite rare. We are aware of

only one other study that employed a large spatial gradient (i.e., ecoregions) to examine effects of various anthropogenic disturbances on excretion (Moore and Olden 2017). Therefore, our study is the first to use a space-for-time substitution to assess the effects of precipitation change on ecosystem function in freshwater systems. There are limitations to the space-for-time substitution approach. Natural systems often have restrictions in the number of comparable sites across a gradient of interest and we recognize that drawing trendlines with 7 or 8 data points has limitations. Therefore, we want to emphasize that when interpreting space-for-time substitution trends, it is important to sample across multiple years to verify the trends of the models. Other concerns in using space-for-time substitutions are underlying confounding gradients in physicochemistry, biogeography, or disturbance that can make it difficult to extrapolate the data (Johnson and Miyanishi 2008; Woodward et al. 2010b). Nevertheless, if these limitations are addressed, this tool can provide answers to important parts of the research question that cannot be addressed by experiments that often do not capture the complexity of the natural ecosystem. Our rainfall gradient has the advantage that many of these space-for-time substitution limitations are addressed (Frauendorf et al. 2019), and that several studies used this gradient, providing us with substantial background information to make strong predictions. This study shows that there is value and great promise in utilizing space-for-time substitutions as a tool to estimating anthropogenic impacts on freshwater ecosystem function.

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### Conflict of interest

The authors declare no conflict of interest.

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